

Control of Tundra Plant Allocation Patterns and Growth

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INTRODUCTION

There is no significant difference in photosynthetic potential among populations in the three major graminoid species in the coastal tundra at Barrow (Chapter 4), and all populations receive the same low solar irradiance. Nevertheless, there is as much as a ten-fold difference in standing crop among these same populations. Clearly, growth and primary production are limited by more than plant photosynthetic potential or energy available for photosynthesis. This chapter seeks to explain how tundra plants control allocation patterns and growth to successfully exploit the cold-dominated, nutrient-limited environment of Barrow.

Carbon and minerals may be allocated to: 1) leaf and stem growth, which exerts a direct positive feedback on canopy photosynthesis by augmenting the quantity of photosynthetic tissues; 2) root production, which increases the capacity of the plant to absorb water and nutrients; 3) rhizome production, which leads to vegetative reproduction and additional photosynthetic tissue and provides for carbon and nutrient storage; and 4) inflorescences, which can lead to the dispersal and establishment of genetically distinct individuals. The balance and timing of these alternative allocation pathways determine the pattern of plant growth and reproduction and the relative supply of carbon, water and nutrients that the plant acquires. We place special emphasis on *Dupontia fisheri*, which typifies the non-caespitose or single graminoid growth habit that constitutes the major part of the coastal tundra vegetation at Barrow (Chapter 3, Tieszen 1972b).

GROWTH PATTERNS OF TUNDRA GRAMINOIDS

Growth Form of *DuPontia fisheri*

DuPontia, like most grasses, consists of a prostrate, subterranean branched stem (rhizome), aerial shoots, and roots produced from below-ground nodes (Figure 5-1). Each new tiller is initiated from an axillary bud of a leafing node. As the bud develops and the rhizome elongates below ground, the tiller is termed a "V0," a tiller containing only rhizome phytomers. At Barrow a V0 tiller seldom reaches the stage of leaf exsertion in its first season of growth, whereas mid-latitude grasses generally exsert leaves in the same season that rhizome growth begins (e.g. Koller and Kigel 1972). During the second growing season, when the shoot appears above ground, the tiller is designated "V1," a tiller in its first season of shoot production. The tiller then produces three or four new leaves each year. Tillers in their second, third and fourth years of growth above ground are designated "V2," "V3," and "V4," respectively.

A second V0 and sometimes a third or fourth may be produced by any tiller in its first year of leaf production. These subsequently produced tillers are designated as "primes" (for example V0', V1') to indicate their age class and relationship to other members of that class. Sub-

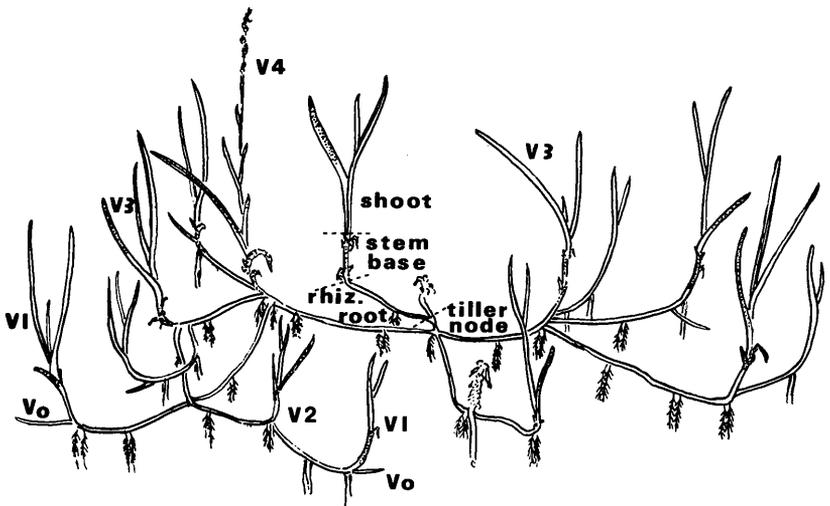


FIGURE 5-1. Typical tiller system of *DuPontia fisheri* showing age classes of component tillers. The letter V with associated number indicates the age class of the tiller (see text). (From Alessio and Tieszen 1975a.)

sequent development of "primes" may be slower, and they may take one year longer to complete their life cycles. Production of prime tillers is the means by which a tiller system branches, although prime tillers often do not produce daughter tillers and become "dead ends" or side branches of the main rhizome axis (Figure 5-1).

After production of approximately 18 nodes, the apical meristem typically differentiates into an inflorescence. The last four nodes and the inflorescence normally develop in the third (V3) or fourth (V4) season of aboveground growth, although induction and initiation occur at the end of the preceding season (Mattheis et al. 1976). The last growing unit develops into the flag leaf and the elongated lower internode of the culm. After flowering, the shoot dies. The tiller rhizome and roots continue to live for several years and may occasionally produce V0 tillers (Allessio and Tieszen 1975a, Shaver and Billings 1975).

The tiller system comprises all the vegetative offshoots of the original seedling or tiller, and in the tundra at Barrow consists of more than 20 to 30 tillers. Living tillers are often interconnected by dead rhizomes.

Seasonal Growth Patterns

Shoot Growth

The general pattern of leaf turnover in *Dupontia* is similar to that of temperate grasses (Evans et al. 1964, Langer 1966, Milthorpe and Moorby 1974) and does not represent any unique adaptation to arctic conditions. *Dupontia* produces leaves continuously through the growing season, although more rapidly early in the season (Figure 5-2) (Mattheis et al. 1976). Leaves that are not fully exerted by season's end lie quiescent until spring and then resume growth. Laboratory studies suggest that leaf growth is largely supported by reallocation of carbohydrate and nutrients from simultaneously senescing old leaves (McCown 1978), so that leaf production may represent a large sink for carbohydrates and nutrients only in the spring of the first year of aboveground growth. This hypothesis is supported by ¹⁴C labeling studies (Allessio and Tieszen 1975a, 1978) and computer simulations (Miller et al. 1978c) but lacks documentation of nutrient reallocation patterns.

Flowering tillers differ from vegetative tillers in their pattern of leaf turnover in that all leaves of flowering tillers senesce relatively early in the season. The accelerated senescence presumably represents a developmentally programmed redistribution of materials to reproductive structures, as in temperate graminoids (Williams 1955). Thus the pattern of shoot growth of *Dupontia* may maximize reutilization of nutrients from senescing leaves.

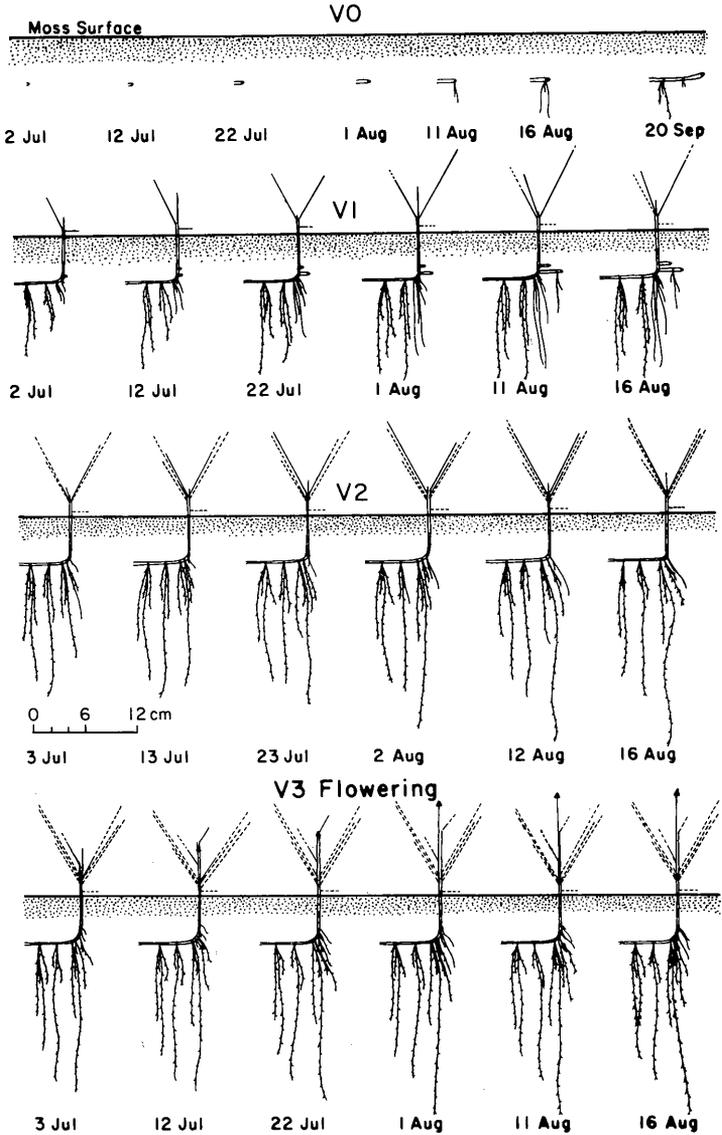


FIGURE 5-2. Seasonal growth patterns of *Dupontia* tillers of different age classes. Leaves are represented by lines inclined at 62° , the mean leaf inclination for *Dupontia*; the solid portion of the line represents green leaf length and the dashed portion represents senesced length. The most recently exerted leaf is inclined 90° until fully exerted. The inflorescence is represented with an arrow. [Drawn from data collected for shoots (Mattheis et al. 1976), roots (Alessio and Tieszen 1975a, Shaver and Billings 1975), and V0 tillers (Lawrence et al. 1978) in 1973.]

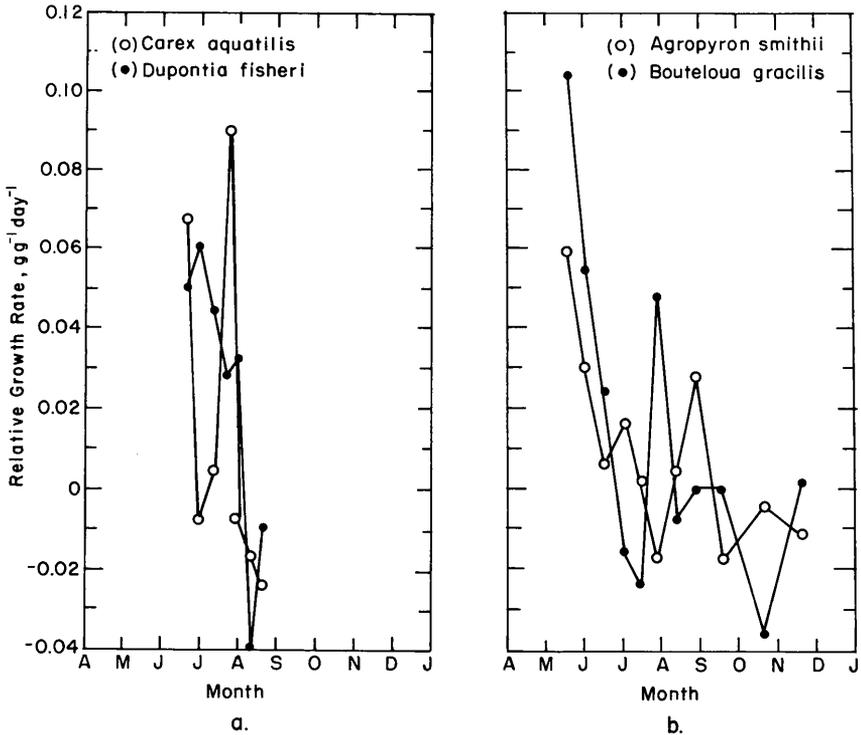


FIGURE 5-3. Mean relative growth rates of graminoids observed in situ in a) tundra (calculated from Tieszen 1972b), and b) temperate grassland at Cottonwood, S.D. (Lewis et al. 1971).

The most striking feature of plant growth at Barrow is the high production rate at low temperatures. Graminoids in the Biome research area have relative production rates ($g\ g^{-1}\ day^{-1}$) comparable to those of some dominant grasses of a mid-latitude grassland, in spite of a 15 to 20°C difference in average air temperature during the growing season (Figure 5-3). The principal difference in their patterns of production is not the rate of growth but the short period during which growth occurs in the tundra. The capability of tundra plants to grow effectively at low temperature is further seen in controlled environment experiments where graminoids from Barrow exhibit maximum rates of leaf initiation, elongation, and hence growth at 15°C (Tieszen, unpubl.). This is comparable to the optimum temperature for growth of some alpine grasses (Scott 1970), but some 10 to 15° cooler than the optimum growth temperature of temperate zone grasses (e.g. Evans et al. 1964, Warren Wilson 1966a). However, the 15°C temperature optimum for growth of tun-

dra graminoids is 5 to 10°C higher than average summer shoot temperature in the field. Transplant studies show that Barrow graminoids and other arctic species do grow faster in warmer climates (Warren Wilson 1966a, Chapin and Chapin, pers. comm.) than in their natural environment, indicating that arctic plant growth is limited in part by temperature despite adaptations that permit rapid growth at low temperature.

The similarity of relative production rates between tundra and mid-latitude grasses in the field suggests that the metabolic cost associated with this production (i.e. growth respiration) may also be similar, assuming comparable production efficiencies. This hypothesis is supported by laboratory studies showing that arctic plants have a higher respiratory rate than mid-latitude plants when measured at some standard temperature, but that the respiration rates of various populations at their respective habitat and growth temperatures may be comparable (Mooney and Billings 1961, Billings et al. 1971). High rates of mitochondrial oxidation are the cause of high respiration rates measured in intact plants (Klikoff 1966). Because respiration is temperature-dependent, a high respiratory capacity would be required for arctic plants to maintain their observed growth rates at low ambient temperature. The high respiratory capacity of arctic plants is determined both genetically and environmentally, although genetic factors appear more important than acclimation in explaining this temperature compensation (Klikoff 1966, Billings et al. 1971).

Many authors (e.g. Bliss 1962a, Billings and Mooney 1968) have commented upon rapid spring shoot growth of tundra species. However, Warren Wilson (1966a) found lower growth rates in the high Arctic than in England. Further critical studies of relative growth rates of arctic plants are needed.

Rhizome Growth

Simulations suggest that the rapid early-season leaf growth of *Dupontia* is correlated with a corresponding decrease in the biomass of the rhizome and to a lesser degree of the stem base (Figure 5-4). This has been corroborated in measurements of temperate and upland tundra sedges (Bernard 1974, Chapin et al. 1980). Later in the season there is substantial allocation of biomass to belowground organs and probably a retrieval of materials from senescing leaves to the rhizome and sheath/stem base in preparation for the following season. This agrees with conclusions of the carbon dioxide budgets (Chapter 12) and ¹⁴C and ³²P autoradiography (Allessio and Tieszen 1975a, Chapin and Bloom 1976). The main growth phase of new V0 tillers is from mid-July onward in contrast to the mid-June onset of leaf production. The delay of below-

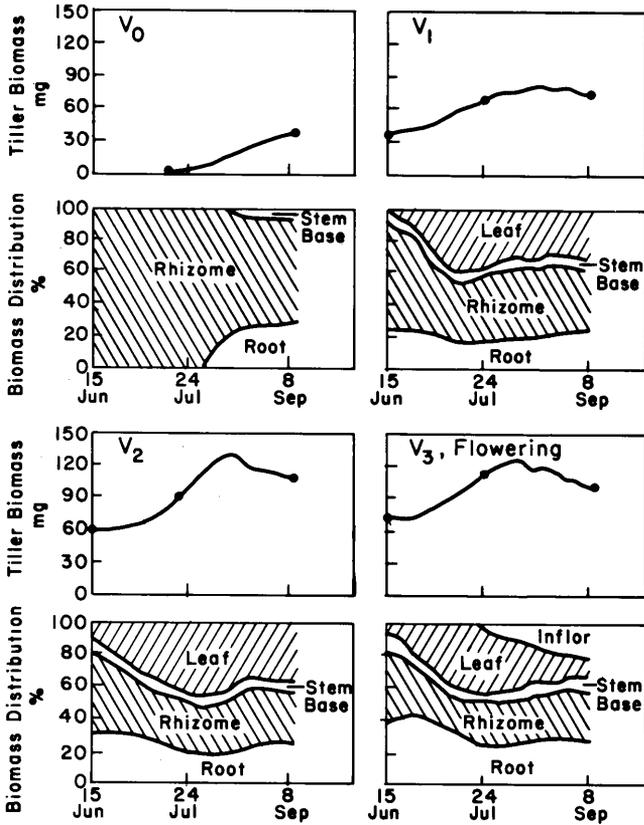


FIGURE 5-4. Simulated seasonal biomass pattern of different plant parts of *Dupontia fisheri* tillers of different ages. (After Stoner et al. 1978d, Lewis, unpubl.)

ground growth behind aboveground growth is common to temperate and other arctic graminoids and presumably is a consequence of programmed reallocation of resources from one plant part to another (Evans et al. 1964, Auclair et al. 1976, Callaghan 1976, Chapin et al. 1980). The soil reaches maximum temperature later in the season than does air, and this may have further selected for asynchrony of above- and belowground growth. Simulations suggest that rhizome weight in flowering tillers continues to decline through the entire season, coincidental with the growth of the culm and inflorescence. Although the overall seasonality of rhizome growth is probably genetically programmed, the absolute growth rate is subject to environmental modification. In contrast to the temperate graminoids investigated, *Dupontia* is capable of active rhizome growth at soil temperatures at least as low as 4°C (McCown 1978).

Root Growth

Primary root primordia begin accumulating new photosynthate in the spring while the soil is still frozen (Dadykin 1954, Allesio and Tieszen 1975a, 1978), but growth and elongation do not begin until after soil thaw. In *Dupontia* elongation of primary roots is complete by late July, whereas other major graminoids of the tundra continue primary root elongation throughout the growing season (Shaver and Billings 1975). *Dupontia* initiates two to four roots per rhizome node. Autoradiography shows that these roots remain functional throughout the life of the tiller, frequently remaining alive even after the shoot dies (Allesio and Tieszen 1975a). A few shorter, slender roots are initiated in later seasons from the nodes of older leafing phytomers and elongate upward between the dead sheaths; they may be important in retrieving leached nutrients from stem flow. Primary roots of *Dupontia* do not elongate after their first season (Shaver and Billings 1975). Toward the end of the first season lateral roots are initiated with a larger surface-to-volume ratio (Shaver and Billings 1975). As with primary roots, these roots actively accumulate new ^{14}C photosynthate much earlier in the season than they commence visible elongation (Allesio and Tieszen 1975a).

Root biomass in the tundra at Barrow shows more variation both among and within microtopographic units than between sample dates. Therefore the seasonality of root production is difficult to determine by the harvest method (Dennis and Johnson 1970, Dennis 1977, Dennis et al. 1978). ^{14}C translocation studies (Allesio and Tieszen 1975a) and direct observations of root elongation (Shaver and Billings 1975) suggest that much of the root production for the wet meadow tundra occurs in July and August, after the early flush of leaf production. It appears that early in the season new photosynthate is allocated primarily to new shoot growth, and that the root growth that does occur at this time proceeds largely at the expense of rhizome carbohydrate reserves acquired in previous seasons. In the community as a whole, approximately 25% of the root biomass (i.e. 100 g m^{-2}) may turn over each year (Shaver and Billings 1975). This percentage is considerably lower than that found in many temperate ecosystems such as the eastern deciduous forest (Harris et al. 1977), but is approximately the same as that reported for grassland communities (Dahlman and Kucera 1965). The seasonality of root loss through senescence is not known, but loss is assumed to occur largely during winter. Because of the large ratio of belowground to aboveground biomass, roots and rhizomes constitute a major carbon and nutrient input to the saprovores food chain and are probably a relatively more important carbon-nutrient source than in temperate ecosystems (Chapter 12).

Roots of tundra plants, of necessity, grow at temperatures below 5°C and can resume active elongation even after being temporarily frozen (Billings et al. 1977). Graminoids at Barrow have lower optimum temperatures for root initiation, elongation, and hence production than do comparable temperate species, when grown in the growth chamber (Chapin 1974a). In part due to low temperature sensitivity of root growth, root production in the field is not correlated with root temperature but appears to be controlled largely by photoperiod (Shaver and Billings 1977). For example, elongation of primary roots in *Dupontia* occurs during the first half of the growing season when root temperatures are lowest. Secondary root production predominates in August (Shaver and Billings 1975, 1977). In *Eriophorum angustifolium* most of the root tips are close to the retreating permafrost table, so the zone of most rapid elongation occurs in the coldest soil.

The primary roots of all graminoids at Barrow have large diameters and contain aerenchyma. These roots transport sufficient oxygen to produce an aerobic rhizosphere (Barsdate and Prentki, unpubl.) in a soil that is frequently oxygen-deficient. Because tundra plants are effective in transporting oxygen to roots, it is unlikely that metabolism of primary roots is ever limited by an inadequate oxygen supply. The root diameter probably results from a balance between selection for large diameter for adequate oxygen transport and selection for large surface-to-volume ratio for effective nutrient absorption (Chapin 1978). Both *Dupontia* and *Carex* produce secondary roots with small diameter, which are found primarily in the surface aerobic soil horizons and are important in nutrient absorption because of their large surface-to-volume ratio. These thin roots probably meet most of their oxygen requirement with soil oxygen rather than by diffusion through the primary roots. The small diameter rooting strategy allows continued exploitation of the surface soil horizon with a minimal carbon investment (Chapin 1978).

Graminoids at Barrow produce very few root hairs in the field, as is typical of aquatic and emergent plants (Sculthorpe 1967). Root hairs presumably require an external oxygen supply for proliferation and maintenance and for this reason are of minimal importance in Barrow tundra.

ALLOCATION OF CARBON COMPOUNDS

Seasonal Patterns

Growth and production depend in part upon availability of photosynthate in the form of total nonstructural carbohydrate (TNC), a pool that includes sugars and storage polymers. The TNC concentrations in leaves, stem bases and rhizomes of *Dupontia* are quite high, ranging

TABLE 5-1 *Biomass and Carbohydrate Composition of V2 tillers of Dupontia fisheri*

Plant part	Biomass (mg part ⁻¹)	TNC		Lipid		Other†† (mg part ⁻¹)
		(% dw)	(mg part ⁻¹)	(% dw)	(mg part ⁻¹)	
19-30 June						
Blade	5*	26*	1.3	16	0.8	2.9
Stem base	9*	24*	2.2	6	0.5	6.3
Rhizome	33*	36	11.9	6	2.0	19.1
Root	40†	8‡	3.2	10	4.0	32.8
Total (mg)	87		18.6		7.3	61.1
% of total plant pool			21.4		8.4	70.2
1-15 Aug						
Blade	35*	20	7.0	7	2.5	25.5
Stem base	10*	44*	4.4	4	0.4	5.2
Rhizome	20*	40*	8.0	5	1.0	11.0
Root	40†	2‡	0.8	4	1.6	37.6
Total (mg)	105		20.2		5.5	79.3
% of total plant pool			19.2		5.2	75.5
23 Aug-20 Sept						
Blade	5**	19*	1.0	5	0.3	3.7
Stem base	20*	40*	8.0	6	1.2	10.8
Rhizome	33*	42*	13.9	5	1.7	17.4
Root	40†	5‡	2.0	6	2.4	35.6
Total (mg)	98		24.9		5.6	67.5
% of total plant pool			25.4		5.7	68.9

* Lewis and Tieszen (unpubl.).

† Estimated as 30 to 40% of total biomass at peak season (from McCown 1978); seasonal changes assumed negligible with senescence equal to production.

‡ McCown (1978).

** Estimated as equal to early season.

†† By subtraction.

between 20 and 40% of the total dry weight (Shaver and Billings 1976, McCown 1978, McKendrick et al. 1978) (Table 5-1, Figure 5-5). High TNC levels are typical of arctic and alpine species (Russell 1940, Mooney and Billings 1960, Warren Wilson 1966a, Fonda and Bliss 1966, but see Payton and Brasch 1978). This raises the question of whether tundra plants have a carbon/energy surplus or whether there is strong selection to maintain high TNC levels in spite of high growth demands for TNC. Russell (1940), Warren Wilson (1966a) and Haag (1974) concluded that low temperature somehow prevented carbohydrate use in growth and respiration, resulting in large sugar accumulations. We suggest that inadequate nutrient supply is a major factor limiting use of carbohydrates in growth. Although there is considerable interhabitat variation in production along a gradient of nutrient availability at the Biome research

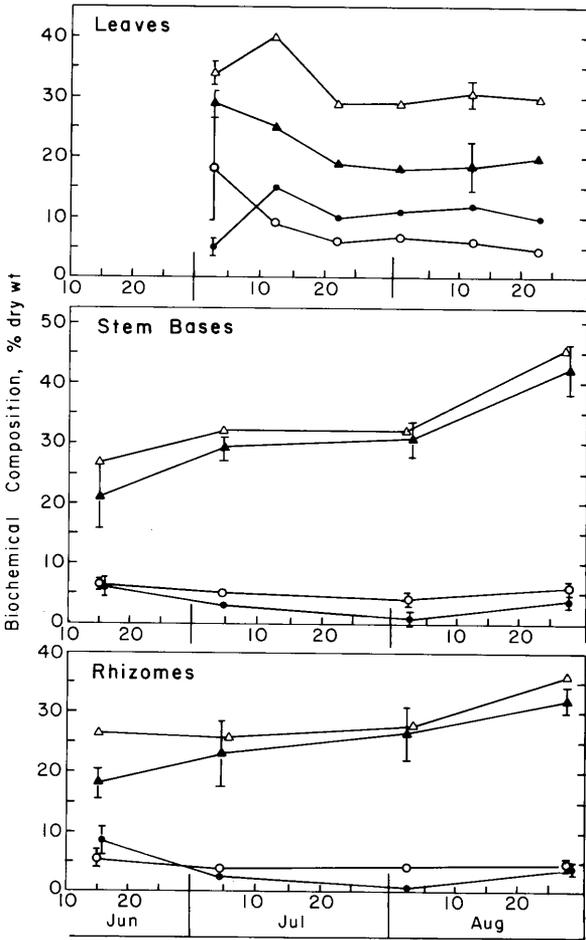


FIGURE 5-5. Seasonal changes in concentrations of total nonstructural carbohydrates (Δ), polysaccharides (\blacktriangle), lipids (\circ) and sugars (\bullet) in leaves of *Dupontia fisheri* and in stem bases and rhizomes of composite samples of all moist meadow graminoids. Vertical bars indicate standard error. (After McCown 1978.)

area (Tieszen, unpubl.), populations show markedly similar TNC concentrations (Table 5-2). Total nonstructural carbohydrate concentration tends to be higher in habitats with low tissue phosphorus and low production. These observations suggest that *Dupontia's* growth is limited more strongly by nutrients than by carbohydrate availability. Computer

TABLE 5-2 *Variability of Chemical Composition, Production, and Photosynthetic Potential in Leaves and Rhizomes of Dupontia fisheri Along a Moisture-Nutrient Gradient*

	Coefficient of variation (%)	
	Leaves	Rhizomes
Concentration		
Nitrogen	19.2	42.5
Phosphorus	37.0	64.9
Potassium	33.5	46.3
Calcium	33.1	51.0
Total nonstructural carbohydrate	16.4	3.6
Total community production	62.0	—
Photosynthetic potential	17.0	—

Source: Calculated from Tieszen (unpubl.).

simulations suggest a similar conclusion, i.e. that an increased photosynthetic rate, and hence increased TNC availability, would increase production at Barrow but that this TNC limitation of growth is less marked than is limitation by nutrients (Miller et al. 1976, 1979). It appears that although arctic tundra plants grow in a low radiation environment, carbohydrate availability does not unduly limit growth.

In mature shoots of *Dupontia* storage polysaccharides constitute the bulk of the TNC pool (Figure 5-5) (McCown 1978), in contrast to the predominance of sugars observed in other arctic and alpine species (Mooney and Billings 1960, Fonda and Bliss 1966, Warren Wilson 1966a). These reserves may be important for periods of intensive grazing. Although soluble carbohydrates are generally less than 15% of dry weight in Barrow graminoids, these levels are nonetheless high in comparison with temperate plants, and may contribute to the frost tolerance (Weiser 1970) that allows arctic plants to survive subzero temperatures at any time during the active growing season (Sørensen 1941). In *Dupontia* the rhizome is the largest compartment for TNC storage. From 40 to 65% of the total TNC is located in the rhizome throughout the year (Table 5-1). Fructosans rather than starch are the main storage polysaccharide in arctic (McCown 1978) and cool temperate (White 1973) grasses.

Tissue age strongly influences both the types and amount of carbohydrate present. In new roots and in the rhizomes and stem bases of young tillers, monosaccharides are the predominant carbohydrate, reaching concentrations as high as 40% dry weight (Shaver and Billings

1976). In these tissues carbohydrates play an active metabolic role, providing the energy necessary for rapid growth in a short growing season and protecting important tissues from freezing. It is mainly in the mature tillers that carbohydrate storage as polysaccharide becomes important. Hence, high TNC levels in plants at Barrow may reflect quite different processes, depending upon tissue age (Shaver and Billings 1976).

There is a gradual accumulation of carbohydrate reserves in rhizomes and shoots as the growing season progresses (Figure 5-5). Overwintering green leaf sections enclosed within the sheath bases may be important reservoirs for respiratory energy and precursor molecules utilized during the rapid production of photosynthetic tissue in spring (McCown 1978) and are an important energy source for grazers during the winter and spring months. In early spring sugar levels are high, presumably the result of hydrolysis of the polysaccharides built up the previous autumn (Shaver and Billings 1976, McCown 1978). After the period of rapid leaf production in June, sugar levels drop and do not rise again until autumn. The seasonal pattern of lipids is unclear. In 1970 early season levels of leaf lipids were unusually high (17%), but rapidly dropped to a constant level of 6% (McCown 1978). In other years lipid levels remained low throughout the growing season (Figure 5-5). High lipid levels in early spring could reflect energy storage (Bliss 1962b, Hadley and Bliss 1964) or could reflect small cell size and the abundant membrane lipid associated with meristematic tissue and high metabolic activity (Kedrowski and Chapin 1978). Early season lipids appear to have a lower melting point than those observed later and hence would function effectively in membranes at lower temperatures (McCown 1978).

The TNC concentration of *Dupontia* exhibits greater seasonal stability than that of temperate plants (McKendrick et al. 1975, McCown 1978), a feature of arctic plants also noted by Warren Wilson (1966a). The seasonal constancy of TNC pool size reflects a seasonal stability of allocation patterns as demonstrated by ¹⁴C translocation studies in *Dupontia*. From snowmelt until time of maximum aboveground biomass (which was the duration of the study) new photosynthate is largely retained in the shoot where it is synthesized, presumably to support the continuing production of new leaves through the season (Figure 5-6) (Alessio and Tieszen 1975b). Except in V1 tillers, which are in their first year of aboveground growth and which produce the majority of new roots and rhizomes, there is relatively little translocation of photosynthate to belowground structures during this first half of the season. Moreover, production of new leaves by a tiller is largely self-supported and is relatively independent of carbohydrate reserves stored below ground. Even reproductive tillers are largely self-sufficient and do not withdraw large quantities of photosynthate from their own or neighboring rhizomes (Alessio and Tieszen 1975a). These observations indicate a

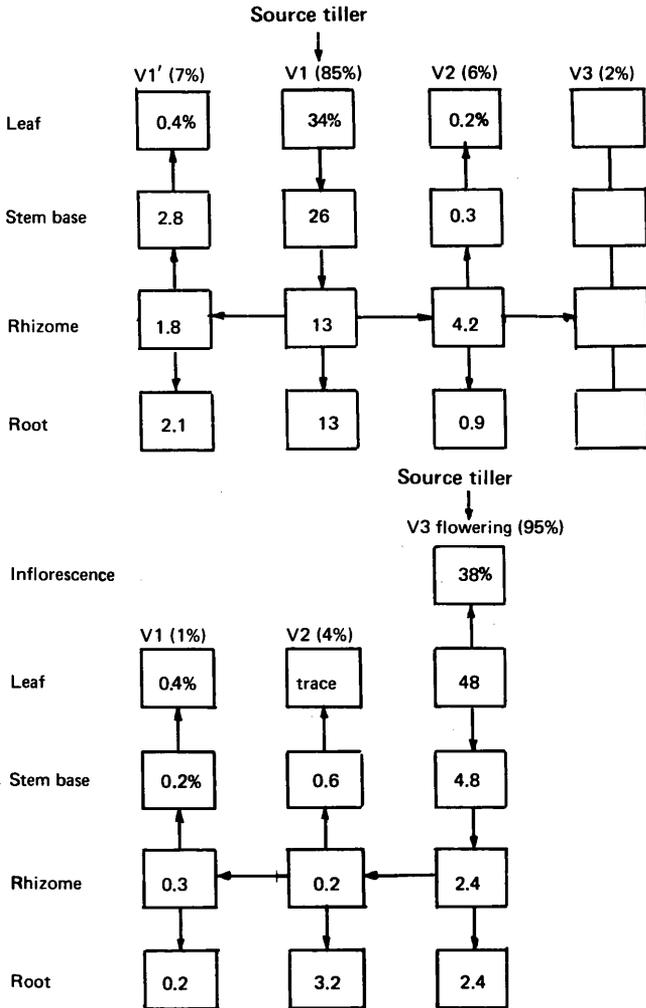


FIGURE 5-6. Distribution of ^{14}C in tillers and plant parts of a *Dupontia fisheri* tiller system after the source tiller (V1 or V3 flowering) was labeled. (After Alessio and Tieszen 1975a.)

substantial degree of tiller independence and suggest that the large belowground carbohydrate reserves may serve primarily to support late-season root growth and maintenance and as a reserve for rapid leaf growth in the event of grazing rather than to support the normal course of leaf growth as had been previously assumed (Mooney and Billings 1960, Fonda and Bliss 1966). However, leaf growth in the spring may be

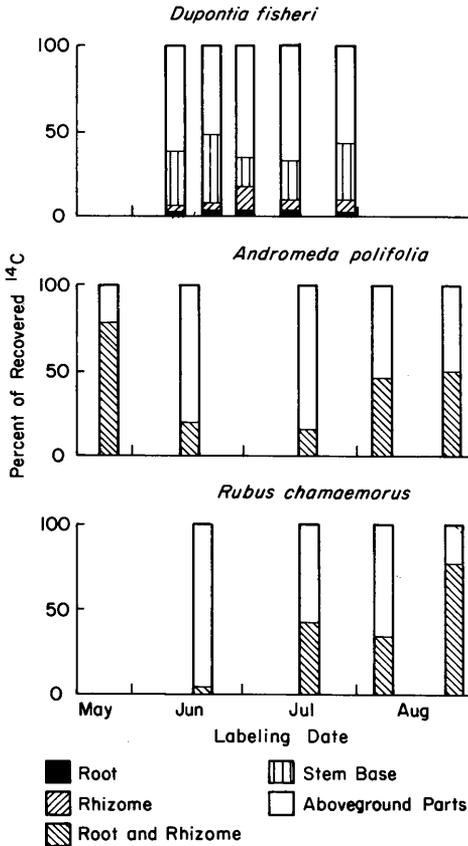


FIGURE 5-7. Distribution of recovered ^{14}C in different plant parts of *Dupontia fisheri* in mesic meadow tundra at Barrow (Alessio and Tieszen 1975a) and *Andromeda polifolia* and *Rubus chamaemorus* in an arctic mire at Stordalen, Sweden (Johansson 1974). *Dupontia* was harvested two days after labeling; the others were harvested three weeks after labeling.

highly dependent upon belowground mineral reserves.

Gas exchange and harvest measurements indicate that over the entire growing season only 34% of the annual carbon fixation is used in shoot growth and respiration. The remaining 66% is presumably translocated below ground, perhaps late in the season, to support growth and maintenance of roots and rhizomes. A downward translocation of this magnitude would be necessary to provide the energy source for the substantial root and rhizome respiration measured by Peterson and Billings (1975).

The retention of radiocarbon in shoots of labeled tillers and the seasonal stability of the allocation pattern in *Dupontia* differ strikingly from the allocation patterns of other growth forms (Figure 5-7) (Johansson 1974). In *Andromeda polifolia*, an evergreen shrub growing in Swedish tundra, 75% of the fixed carbon was translocated below ground early in the season. As leaf growth began, a larger proportion of the ^{14}C was retained in the shoot. Finally, at the end of the season, fixed carbon

was allocated above and below ground in approximately equal proportions (Figure 5-7). *Rubus chamaemorus* from Sweden had an allocation pattern consistent with its deciduous habitat. During the leaf production phase, virtually all the assimilated carbon was retained in the shoot, as in the actively growing *Dupontia* shoot. As the season progressed, an increasing proportion of the photosynthate was translocated below ground (Figure 5-7). Clearly, the allocation patterns of these three species are closely tied to their growth forms, phenological calendars, and locations of storage.

Environmental Influence upon Allocation Pattern

Environmental factors affect allocation pattern as well as the total quantity of production. High root-to-shoot ratios of plants observed in the field at the Biome research area (Dennis and Johnson 1970, Chapin 1974a, Dennis 1977, Dennis et al. 1978, Webber 1978) may indicate greater environmental limitation upon shoot than root growth (Dennis and Johnson 1970) or more likely reflects a genetically and environmentally controlled allocation of biomass to nutrient absorptive tissue (Chapin 1974a), as observed in laboratory studies (Brouwer 1965, Davidson 1969). Low root temperature may indirectly result in a high root-to-shoot ratio by decreasing rates of nutrient uptake, thus lowering the nutrient status of the plant, i.e. low root temperature and low nutrient status may influence allocation through similar mechanisms (Patterson et al. 1972, McCown 1975). Laboratory studies indicate that the increase in root-to-shoot ratio resulting from an impoverished nutrient status serves to increase nutrient supply and decrease nutrient demand, thus compensating for the nutrient deficiency (e.g. Leonard 1962, Brouwer 1965). Direct field evidence for this comes from long-term fertilization studies at Barrow, where after 10 years of fertilization, the root-to-shoot ratio was reduced from 7:1 to 3:1 (Dennis 1977). McCown (1978) observed that the root-to-shoot ratio of *Dupontia* was less affected by root temperature than was that of the temperate grass *Poa pratensis*. A relatively inflexible root-to-shoot ratio is typical of slowly growing species (Grime 1977).

When growth is strongly nutrient-limited, nonstructural carbohydrates accumulate to high levels (Leonard 1962) as observed in *Dupontia* at the Biome research area (Shaver and Billings 1976, McCown 1978). TNC levels are reduced, and shoot growth is enhanced by fertilization, a further indication of the importance of nutrients in limiting production in the tundra (McKendrick et al. 1978).

The number of daughter tillers (V_0 's) initiated is positively correlated

TABLE 5-3 *Correlation of Production Parameters with Nutrient Composition of the Plant Part in Tillers Sampled along a Moisture-Nutrient Gradient*

	Production parameter		
	No. leaves tiller ⁻¹	Leaf length	No. V0 (mature tiller) ⁻¹
<i>Carex aquatilis</i>			
Nitrogen	-0.21	-0.29	—
Phosphorus	0.49	0.52	—
<i>Dupontia fisheri</i>			
Nitrogen	0.10	-0.51	0.80*
Phosphorus	-0.12	0.37	-0.69†
<i>Eriophorum angustifolium</i>			
Nitrogen	0.47	-0.06	—
Phosphorus	0.45	0.59	—

Note: Numbers are correlation coefficients.

*Significant at the 0.05 level of probability.

†Significant at the 0.01 level of probability.

Source: Calculated from Tieszen (unpubl.).

with nitrogen concentration and negatively correlated with phosphorus concentration (Table 5-3), whereas leaf length shows the reverse correlation. No clear trend is evident with leaf number. This suggests that the intercalary and rhizome meristems respond quite differently and perhaps are limited by different nutrient balances. Apparently, leaf intercalary meristems are stimulated by favorable phosphorus status and/or a low nitrogen-to-phosphorus ratio. A high phosphorus content might be anticipated in meristematic cells because of the high requirement for membrane phospholipid and phosphorylated sugars. The high leaf meristematic activity under such nutritional circumstances would lead to strong apical dominance and could partially explain the concomitant low rates of rhizome growth and vegetative reproduction.

Translocation is inhibited by low temperature only temporarily, even in temperate plants (Swanson and Geiger 1967). Temperature does influence the rate of active loading and unloading of phloem cells, an effect that is indistinguishable from the temperature effect upon source and sink strength (Crafts and Crisp 1971). In contrast to temperate plants, *Dupontia* is capable of translocating ¹⁴C to root and rhizome primordia frozen in soil (Alessio and Tieszen 1975a), as discussed above. Similarly, low temperature inhibits translocation of sugars from leaves in C₄ grasses growing at their upper elevational limit but not in alpine gram-

TABLE 5-4 *Plant Responses in Warm (1972) and Cold (1973) Growing Seasons*

	Temperature (°C)		Biomass ⁴ (g m ⁻²)	Net annual photosynthesis ⁵ (g CO ₂ m ⁻² yr ⁻¹)	Phosphorus in <i>DuPontia</i> leaves ⁶		Phosphorus uptake ⁷ [μmoles hr ⁻¹ (g fresh wt root ⁻¹)]	
	Air ¹	Canopy ²			Soil ¹	(% dry wt)		(mg tiller ⁻¹)
1972	5.1	8.1	5.0	125 ± 19	620	0.163 ± 0.017	0.105	0.041
1973	4.0	5.5	3.1	93 ± 13	450	0.526 ± 0.068	0.105	0.039
Difference	1.1	2.6	1.9	32	170	0.363	0.0	0.002
% difference	-22	-32	-38	-25	-27	+223	0	-5

¹U.S. Department of Commerce, Barrow.

²Miller and Stoner (unpubl.), Miller et al. (1976).

³5-cm depth (MacLean 1975a).

⁴Average of 16 sites along a nutrient gradient (Tieszen, unpubl.).

⁵Miller et al. (1976).

⁶Average of 10 sites along a moisture-nutrient gradient (Tieszen, unpubl.).

⁷Uptake calculated for *DuPontia fisheri* in a solution of 1.0 μM inorganic phosphate (Chapin and Bloom 1976).

inoids in Wyoming (Wallace and Harrison 1978). Thus, it appears that the effects of low temperature upon allocation in tundra plants are involved more with growth processes than with inhibition of carbohydrate and nutrient transport. Data in support of this hypothesis are largely inferential, and direct experimental evidence is needed.

Roots are more strongly buffered against temperature variation from one growing season to another than is the plant canopy, and shoot growth increases more rapidly with increasing temperature than does nutrient uptake. For these two reasons, in a warm growing season production is greater and the demand for nutrients outstrips the slightly enhanced supply. The situation is aggravated by the asynchrony of shoot production and nutrient uptake, the bulk of the nutrient uptake occurring after shoot production is largely complete (Chapin and Bloom 1976). The asynchrony is demonstrated by a comparison of the 1972 and 1973 growing seasons (Table 5-4) and suggests the following hypotheses:

1. In tundra communities, warm years will result in greater nutrient deficiency than will cold years. Nutrient deficiency will be particularly severe with respect to phosphorus because phosphorus absorption is more strongly affected by temperature than is absorption of other nutrients (Nielsen and Humphries 1966). The effect upon nutrient content of yearly temperature differences will be particularly pronounced in tundra underlain by permafrost, where the temperature gradient is most pronounced from the canopy to the bottom of the rooting zone.

2. Changes as slight as 1 °C in air temperature above the plant canopy are sufficient to profoundly alter the nutritional status of plants. Data from the Biome research area indicate the sensitivity of allocation pattern to small changes in environmental parameters. Similar conclusions were independently reached by Wielgolaski et al. (1975) in studies of the Norwegian alpine.

In summary, studies of carbohydrate allocation suggest that plants of the coastal tundra at Barrow have compensated for the effects of low temperature by allocating a large proportion of their biomass to nutrient-absorptive and belowground storage tissues. The high TNC levels suggest that growth of ungrazed tundra plants is not unduly carbohydrate-limited.

CARBON COST OF PLANT GROWTH

Concepts

The carbon fixed through photosynthesis can be converted to new biomass, but there are certain energy costs of producing and maintaining an increment of biomass that must be considered in order to understand patterns of carbohydrate allocation. The rate of change in live biomass

of a plant compartment is the balance between the rates of photosynthesis, respiration, and death and the net translocation flux to that compartment. Growth also involves the accumulation and incorporation of nutrients. The rate of change in nutrient content of a plant compartment is the balance among the rate of uptake from soil, the net translocation flux, and losses from the living system due to leaching, exudation, grazing and death. There is inadequate information currently available to allow growth to be analyzed in terms of nutrient costs.

Respiration provides energy for a number of distinct metabolic processes and can be separated into at least three components: maintenance respiration, growth respiration and translocation respiration. Maintenance respiration provides the energy required to sustain the existing live biomass at its present level of metabolic activity. Maintenance respiration includes the energy requirement of basic metabolic processes and the replacement or turnover of structural and functional substances, particularly of proteins, and is assumed to be proportional to protein content and turnover (Penning de Vries 1975). The proportionality constants of maintenance respiration have been calculated (Miller 1979) for various plant parts according to the relationship derived for crop plants (McCree 1974, Penning de Vries 1975) and corrected for values measured in plants from the Biome research area (Chapin et al. 1975, Billings et al. 1978). The relatively high protein content of graminoids in the tundra at Barrow (Chapin et al. 1975) suggests a high maintenance respiration and is in agreement with the high shoot respiration rates measured (Tieszen 1975). Leaves have a higher proportionality constant of maintenance respiration (0.012) than do roots or rhizomes (0.006) because of higher protein content, which is consistent with the higher respiration rate measured in leaves than in roots.

Growth respiration provides the energy required to synthesize various components of new tissues from glucose (Penning de Vries 1972b; Table 5-5). Although plants contain a variety of sugars that function as metabolic intermediates, these will be viewed as glucose equivalents for the sake of simplicity. The investment in new tissue is equal to the quantity of glucose equivalents contained in the added biomass plus that glucose respired in the synthetic process, the growth respiration (Figure 5-8). The total growth respiration for production of new biomass is calculated from the increase in biomass and a constant c that apportions the cost of synthesis among the biochemical constituents of the new tissue (Table 5-5):

$$c = 1.15(\% \text{ lignin}) + 0.17(\% \text{ cellulose}) + 2.03(\% \text{ lipids}) + \\ + 0.59(\% \text{ protein}) + 0.17(\% \text{ polysaccharide}) + 0.09(\% \text{ sucrose}).$$

TABLE 5-5 *Costs of Synthesis and Breakdown, and Biochemical Composition, of Different Plant Parts of Dupontia fisheri*

Biochemical constituent	Investment in synthesis* (g glucose g ⁻¹ product)	Maximum glucose regained during senescence* (% of original)	Minimum loss in senesced tissue† (% of original)	Biochemical composition** (% of nonmineral dry wt)		
				Leaf	Rhizome	Root
Sucrose	1.09	98	2	13	3	2
Storage polysaccharide	1.17	95	5	7	37	0
Protein	1.59	56	44	18	7	6
Lipid	3.03	46	54	7	5	4
Cellulose	1.17	0	100	51	42	80
Lignin	2.15	0	100	5	6	8
Total cost (g glucose) of synthesizing 1 g of tissue:				1.28	1.30	1.30
Maximum glucose potentially regained during senescence‡:				0.40	0.55	0.11

*Based on Penning de Vries (1972b, 1974) and Penning de Vries et al. (1974).

†Assumes no leaching and total breakdown of all compounds except cellulose and lignin.

**Sucrose (McCown 1978); polysaccharides (TNC-sugars) (McCown 1978); protein estimated from nitrogen (Chapin et al. 1975); lignin (Penning de Vries 1972b, White et al. 1975); cellulose estimated as remainder.

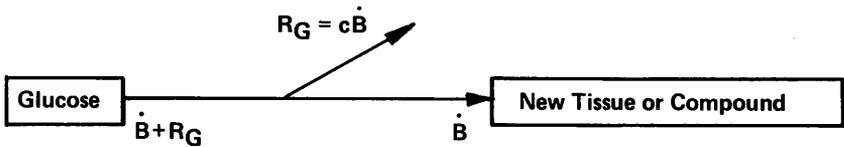


FIGURE 5-8. Processes of growth and growth respiration. When new tissue is created, glucose is metabolized, some glucose appearing in the form of the new biochemical compounds (\dot{B}), and some being lost (R_G) as it supplies energy for the synthesis of these compounds. For example, to produce 1 g of lignin (B), 2.15 g of glucose is used ($\dot{B} + R_G$) and R_G involves 1.15 g of glucose. Other compounds use varying amounts of glucose per gram, as listed in Table 5-5. R_G is calculated for each compound by subtracting the gram of product from the total gram of glucose used. The total R_G for creating new tissue is found by summing the R_G 's for synthesizing each compound, weighting each by the percentage composition.

Tundra graminoids have a relatively low lignin content and a relatively high polysaccharide and sugar content and hence may be able to produce more biomass per unit carbon fixed than can temperate counterparts. More complete data on chemical composition of tundra graminoids are needed to verify this hypothesis.

Translocation is a vital process requiring energy, particularly for the loading and unloading of phloem elements, and energy cost is proportional to the translocation rate; available estimates (Penning de Vries et al. 1974) suggest a value of 0.05 for the proportionality constant. Because both loading and unloading costs are involved, 1 g of glucose will be required to translocate 10 g from source to sink. Because of the high belowground-to-aboveground biomass ratio of tundra graminoids, more of the maintenance and growth respiration occurs in nonphotosynthetic tissues than would be the case in their temperate counterparts. Hence, translocation respiration may be relatively more important in tundra than in temperate graminoids.

The carbon cost involved in growth is partially regained during senescence when some of the biomass components are broken down and retranslocated to storage areas to support future growth. Remobilization is not complete, and different classes of compounds are remobilized to different extents (Table 5-5).

Sucrose and the various storage polysaccharides require a minimal energy investment for synthesis and subsequent breakdown. In contrast, lipid requires a major energy investment, half of which is lost during reconversion to glucose. Although complete conversion of lipid to glucose is unlikely in any system, it is clear that lipid is a costly compound to synthesize and would be utilized as an energy source primarily where space or weight is limited, as in a seed. Plants growing in permafrost soils have larger amounts of membrane lipid but smaller amounts of storage

lipids than do plants in warm soil (Kedrowski and Chapin 1978). The high lipid content reported for arctic and alpine plants (Bliss 1962b) is probably associated with membrane lipid for metabolism or for anti-herbivore defense, such as resins, and not with an energy storage function, as previously assumed.

Lignin and cellulose, two important structural compounds, also differ strikingly in their carbon cost of synthesis. Neither is significantly broken down for retranslocation during senescence. Lignin should be an important component of a tissue only where strong support is essential or where selection has led to strategies to discourage herbivory. Neither selective force appears to have led to a high lignin content in tundra graminoids.

The implications of biosynthetic cost for successful adaptation to the tundra environment are discussed in Chapter 6.

It is of interest, especially when considering the relatively anaerobic soil conditions of the coastal tundra, that biosynthetic processes under anaerobic conditions are 18-fold less efficient because of the incomplete oxidations that can be performed. In addition, toxic end products must be excreted, requiring additional energy expenditures. Although the native graminoids appear to have efficient oxygen transport systems and thus circumvent such problems, introduced plants and some dicotyledons may be severely stressed by the saturated soils and anaerobic conditions characteristic of many arctic soils.

Biomass Flux Analyses for *Dupontia*

A detailed picture of the fluxes involved in growth and allocation of carbohydrates and nutrients through the season can be built from simulations of the seasonal courses of dry matter accumulation, percentage composition, and metabolic cost estimates in *Dupontia* (Figure 5-9). Estimates of photosynthesis and respiration derived from the flux analysis can be compared with direct measurements of net photosynthesis and respiration. Analyses of this type are essential to a thorough understanding of the way the plant uses available resources to grow and produce offspring in a particular environment. Biomass changes provide an indication of biosynthetic activity but the costs of biosynthesis, translocation, uptake, and maintenance must be known to truly understand the allocation pattern and overall physiological balance. The following description is based upon simulations of translocation, respiration and growth.

In a newly initiated tiller (V0), simulated rates of translocation and growth generally increase steadily through the season until about 20 August. Subsequently, the rate of growth falls as maintenance respiration

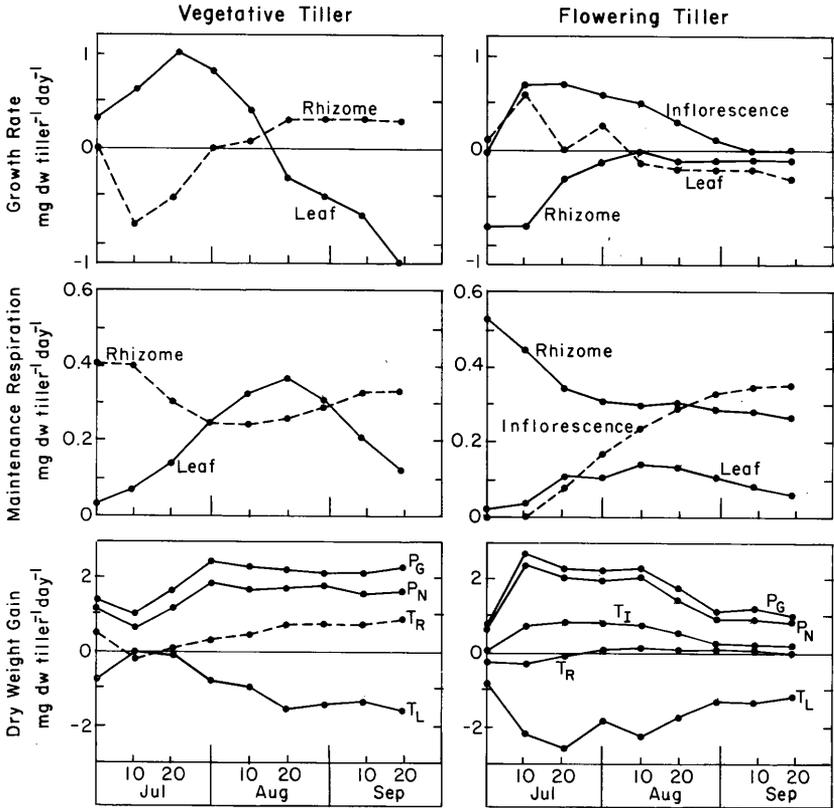


FIGURE 5-9. Simulated seasonal changes in rates of growth and maintenance respiration, and in dry weight gain by gross (P_G) and net (P_N) photosynthesis, and translocation to rhizomes (T_R), leaves (T_L) and inflorescences (T_I) for vegetative (V2) and flowering tillers of *Dupontia* during 1973. (Calculated from Lawrence et al. 1978.)

increases in parallel with biomass. The translocation rate represents a net import from other members of the system, because there are no leaves and hence no photosynthesis in a V0.

Simulations suggest that the rhizome of a vegetative tiller (Figure 5-9) has a significantly negative growth rate, i.e. decreases in weight, through July and recovers through August and early in September. The simulated seasonal course of growth in blade tissue is negatively correlated with growth of the belowground organs, changing from positive values early in the season to negative ones in late August. Calculations predict accurately the observed seasonal changes in biomass. The simulated seasonal changes in maintenance respiration reflect changes in size

of the live compartments. Most of the photosynthate produced in the blade is retained within this compartment. Both the stem base and rhizome export carbohydrate in early July but become net importers as the season progresses. The calculated rate of net photosynthesis increases gradually through the season even though the blade biomass decreases from early August onward. Net photosynthesis rates calculated from the flux analyses are consistently lower than measured rates until the end of August but then persist at unexpectedly elevated levels until freeze-up. No convincing explanation can now be offered for these discrepancies.

The simulated patterns of growth and allocation in flowering tillers (Figure 5-9) contrast strikingly with those in vegetative tillers. In flowering tillers the growth rate of the rhizome is strongly negative at the beginning of the season, and the rhizome continues to lose weight throughout the season, although it never assumes the role of a major exporter of photosynthate. The stem base grows rapidly and blades develop their exporting capacity early in the season. The phase of positive leaf growth is truncated compared with vegetative tillers and never attains the same maximum rate. The second, smaller peak in leaf growth may be associated with the production of the flag leaf. The inflorescence exhibits the highest growth rate, particularly through midseason, and represents the largest sink for photosynthate. In contrast to vegetative tillers, there is no late-season recovery of stem base and rhizome because the photosynthetic rate decreases and inflorescence maintenance respiration increases throughout the season.

Implications of Biomass Flux Analysis

Simulations suggest that although the rhizome rapidly decreases in weight early in the season, there is relatively little upward translocation of reserves at this time. Maintenance respiration accounts for the major change in rhizome weight. In general, these simulations suggest that the rapid early-season development of leaves is self-sustaining and that remobilization of reserve carbohydrates is of minor importance. This conclusion is supported by evidence from radiocarbon and carbohydrate analyses and contrasts strongly with earlier conclusions concerning arctic and alpine forbs. Russell (1940), Mooney and Billings (1960) and Fonda and Bliss (1966) concluded on the basis of correlations between growth and changes in carbohydrate levels that rhizome reserves were utilized to support rapid spring shoot growth. Further research is necessary to determine whether the difference in conclusions results from differences in methods and interpretation or from differences between graminoid and forb growth patterns and phenology.

Simulations, seasonal measurements of TNC, and autoradiography

all suggest that the large pools of nonstructural carbohydrate contained in belowground structures of *DuPontia* are not redistributed to any great extent through the growing season and mainly provide substrate for maintenance respiration and, except in the reproductive tillers, are replenished during August and September in readiness for metabolism the following season. Simulations support ^{14}C translocation studies (Allessio and Tieszen 1975b) showing that inflorescence development is self-sustaining and not dependent on reserve utilization, even though the rhizome rapidly loses weight early in the season. Later development of the inflorescence may well depend on photosynthesis produced by its own chlorophyllous tissue.

NUTRIENT ABSORPTION

Seasonal Patterns

The high levels and relatively stable pool size of nonstructural carbohydrate strongly suggest that nutrient availability, absorption rates and/or translocation rates are among the important factors limiting plant growth at Barrow. The nitrogen and phosphorus status of the soils is quite low (Chapter 7). More than 99% of the nitrogen and phosphorus present in the rooting zone is organically bound and available to plants only after being released by decomposition, a process that occurs slowly at low temperatures and low oxygen levels. Nitrogen is frequently cited as a key limiting nutrient at the Biome research area and in other tundra systems (Russell et al. 1940, Warren Wilson 1957, Bliss 1966, McKendrick et al. 1978). Exchangeable ammonium, the principal ionic form of nitrogen, remains seasonally constant in the rooting zone but increases through the growing season in lower soil horizons (Flint and Gersper 1974), suggesting that nutrient absorption by plants has a significant impact upon soil nutrient dynamics. In contrast to nitrogen, available soil phosphorus and potassium decrease in concentration through the growing season (Barèl and Barsdate 1978), suggesting that phosphorus and potassium will be absorbed by plants earlier in the season than will nitrogen.

An important asynchrony is apparent in environmental favorability for aboveground and belowground plant processes. Light and air temperature regimes are most favorable for photosynthesis immediately following snowmelt, whereas soil temperatures and thaw depth increase until late July or early August. Seasonal changes in depth of thaw, soil temperature, and the quantity and activity of root biomass influence the seasonal pattern of nutrient absorption. However, simulations suggest that these parameters are less important than seasonal changes in soluble

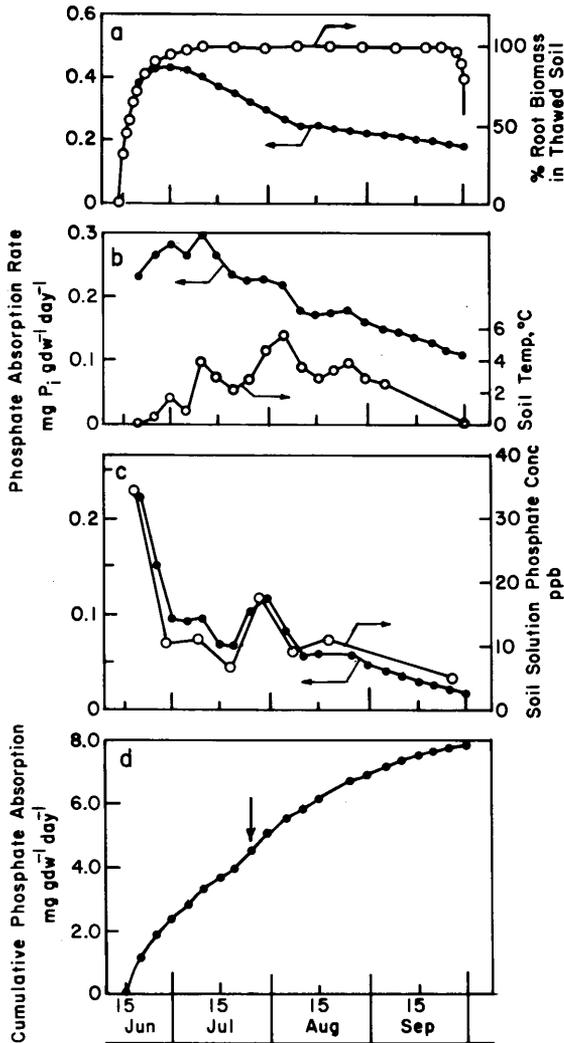


FIGURE 5-10. Predicted rate of phosphate absorption per gram of *Dupontia fisheri* root during the 1973 growing season. a) Measured phosphate absorption capacity of roots corrected for percentage of root biomass present in thawed soil (calculated from Dennis 1977). b) Absorption rate in a corrected for soil temperature (MacLean 1973). c) Absorption rate in b corrected for soil solution phosphate concentration (Barèl and Barsdate 1978). d) Predicted cumulative phosphate absorption per gram of root during the growing season. Vertical arrow indicates date when net downward translocation of phosphorus from shoots to below-ground storage organs begins. (After Chapin and Bloom 1976.)

soil phosphorus in determining the seasonal pattern of phosphorus uptake (Chapin and Bloom 1976). The seasonal pattern of phosphorus release from decomposers is probably the single most important factor governing phosphorus availability and therefore phosphate uptake by vascular plants (Chapin et al. 1978). Absorption of phosphate continues actively until late September when the soil begins freezing from the surface downward (Figure 5-10). More than 40% of the total phosphorus absorbed by a given root biomass is acquired after 25 July, the date when shoots begin a net downward translocation of phosphorus for below-ground winter storage. Clearly, aboveground phenological patterns are an inaccurate gauge for determining periods of plant activity. Because total root biomass increases through the growing season, end-of-season nutrient absorption is probably even more important than the above discussion would indicate.

Physiological Basis

Tundra graminoids differ from their temperate counterparts in having higher phosphate absorption rates under standard measurement conditions (Figure 5-11). Furthermore, tundra plants maintain substantial rates of phosphate absorption at temperatures that would inhibit active uptake by most temperate plants (Sutton 1969, Chapin 1974a, Carey and Berry 1978). For example, *Dupontia* grown in the field still maintains 35% of its 20 °C phosphate absorption rate at 1 °C (Chapin and Bloom 1976), which suggests that tundra plants actively absorb phosphate from cold soils and do not depend upon daily or seasonal warming of the soil to fulfill their phosphate requirements. Phosphate absorption by tundra plants is relatively insensitive to temperature changes and has an optimum temperature of at least 40 °C. It would appear that the phosphate absorption process in graminoids has adapted to low temperature by a decrease in temperature sensitivity below optimum temperature, by an increased affinity of roots for phosphate at low temperatures (Chapin 1977), and by an increase in uptake rate at all temperatures, but not by any change in temperature optimum. Similar conclusions were reached for the photosynthetic process (Chapter 4). The ability to acclimate in compensation for temperature changes is not well developed in plants at Barrow, as might be anticipated in a thermally stable environment such as the tundra soil (Chapin 1974b). The overall effects of temperature upon rate of phosphate absorption by *Dupontia* are such that the rate at the bottom of the soil profile (0.2 °C) is approximately 75% of the rate at the top of the profile (5.0 °C) (calculated from Chapin and Bloom 1976).

A plant's capacity to absorb nutrients depends upon its nutrient status and allocation pattern. Plants with low concentration of an essen-

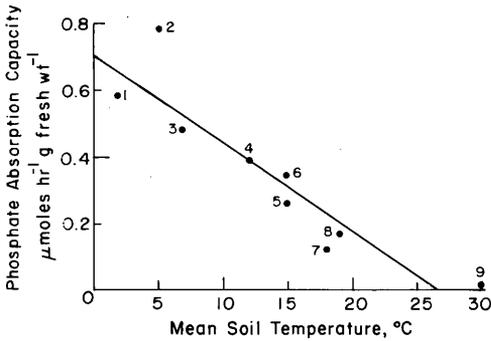


FIGURE 5-11. *Phosphate absorption capacity (N_{max}) of roots grown and measured at 5°C in relation to the July mean soil temperatures of the site. 1) Eriophorum angustifolium, Barrow, Alaska; 2) Dupontia fisheri, Barrow, Alaska; 3) Carex aquatilis, Barrow, Alaska; 4) Eriophorum scheuchzeri, Fairbanks, Alaska; 5) Scirpus microcarpus, Los Gatos, California; 6) Eleocharis palustris, Fairbanks, Alaska; 7) Carex aquatilis, Circle Hot Springs, Alaska; 8) Eleocharis palustris, Corvallis, Oregon; 9) Scirpus olneyi, Thousand Palms, California. (After Chapin 1974b.)*

tial nutrient develop a high capacity to absorb that nutrient (Hoagland and Broyer 1936, Cole et al. 1963). For example, individuals of *Carex* with a high phosphate status had lower capacities for phosphate absorption (Chapin and Bloom 1976).

Soil oxygen, which appears to be a major determinant of plant distribution at Barrow, has a direct impact upon absorption of both essential and toxic nutrients. Graminoids have well-developed aerenchyma that transports sufficient oxygen to the rooting zone to create an aerobic zone around each root (Barsdate and Prentki, unpubl.). Many dicotyledons lack aerenchyma and are excluded from the wetter habitats. The oxygen in the aerobic soil zone around a root decreases the solubility of toxic heavy materials. In spite of this relatively aerobic rhizosphere, graminoids absorb sufficient iron and manganese to reach levels that would approach toxicity in crop plants (Ulrich and Gersper 1978). Nothing is known about the influence of these minerals on tundra plant growth.

The uniform distribution of nutrient absorptive capacity along

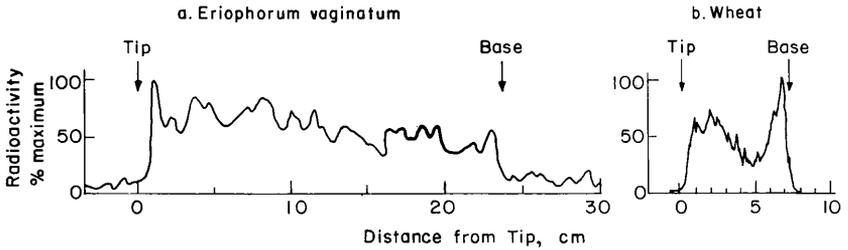


FIGURE 5-12. *Distribution of phosphate uptake rate along roots of Eriophorum vaginatum (Chapin 1974a) and wheat (Bowen and Rovira 1967).*

graminoid roots (Chapin 1974a) reflects the lack of a well-defined root hair zone (Chapin 1978), a consequence of the anaerobic soil conditions. The maintenance of absorptive capacity along the entire length of *Eriophorum vaginatum* roots is a striking difference from temperate grasses (Figure 5-12) and may be selected for by the moist soil environment, where suberization to prevent water loss and consequent loss of absorptive capability is disadvantageous.

NUTRIENT ALLOCATION

Seasonal Patterns

Since nutrients are among the prime factors affecting carbohydrate allocation, it is important to know how nutrients are allocated within the plant and the factors that control this allocation. Graminoids at Barrow begin the growing season with a small amount of overwintering green material. Translocation of nutrients to these shoots presumably begins at or before snowmelt, coincident with the initial carbohydrate translocation to shoots. Early in the season the nitrogen and phosphorus concentrations of aboveground tissues are quite high (Figure 5-13) and the nitrogen-to-phosphorus ratio is relatively low. This suggests that a large proportion of the tissue is actively growing and metabolizing and hence has a high phosphorus requirement for membrane phospholipid and phosphorylated intermediates. As leaves approach maturity, they develop more structural material, as indicated by the seasonal increase in percentage calcium (Chapin et al. 1975). The increase in structural material causes percent nitrogen to decline (Figure 5-13a), though the total aboveground standing crops of nitrogen and phosphorus are increasing (Figure 5-13b). Phosphorus follows the same pattern as nitrogen. The net transfer of nitrogen and phosphorus to shoots continues until 25 July, ten

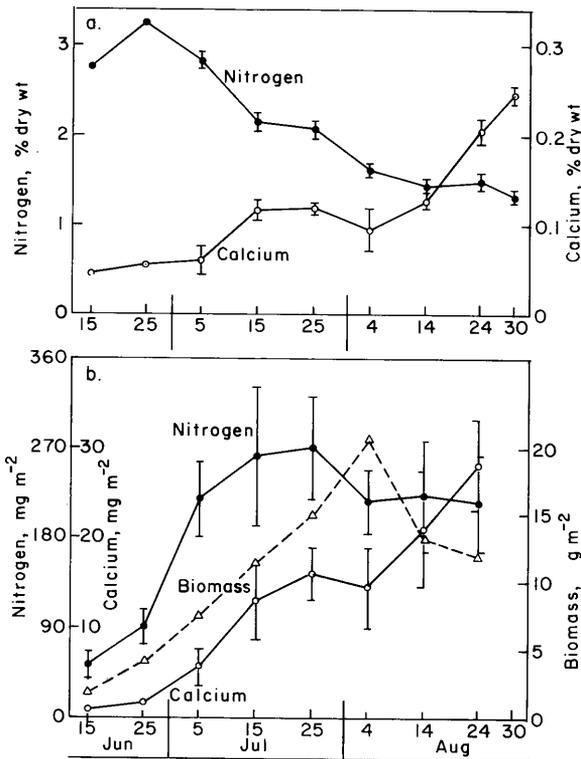


FIGURE 5-13. Seasonal course of (a) percentage nitrogen and calcium and (b) standing crop of nitrogen, calcium, and biomass in *Dupontia* sampled from moist meadow tundra. (After Chapin et al. 1975, Chapin 1978.)

days before the maximum standing crop of biomass is achieved. The most rapid transfer of nitrogen to the shoots occurs during the first three weeks of the growing season (Figure 5-13), at which time the activity of old roots would be minimized by poor aeration and low temperatures. It is probable that most of the early-season aboveground nitrogen and phosphorus comes from stored reserves rather than from current-season absorption by roots as demonstrated for upland tundra (Chapin et al. 1980). The bulk of all plant nutrients are located below ground (Table 12-3), such that seasonal changes in aboveground standing crop involve at most 20% of the total plant nutrient content.

Precipitation and dew drip continually leach nutrients (particularly potassium) from shoots at a rate that depends upon local weather conditions and the solubility of the different elements. Nitrogen and phos-

TABLE 5-6 *Estimated Nutrient and Standing Crop Removed from Shoots by Retranslocation Below Ground*

	Percentage of maximum standing crop removed				
	Biomass*	Nitrogen	Phosphorus	Potassium	Calcium
<i>Carex aquatilis</i>	43	21	44	25	0
<i>Dupontia fisheri</i>	38	53	55	64	0
<i>Eriophorum angustifolium</i>	34	43	61	48	0
Graminoid	35	48	45	42	0
Dicotyledon	33	65	78	76	0
Community average	34	40	49	44	0

Note: Assumes that all nutrient disappearance from time of maximum standing stock of nutrients until 24 August results from retranslocation.

*Calculated from Tieszen (1972b).

Source: Chapin et al. (1975).

phorus are probably leached slowly (Tukey 1970, Morton 1977) so that the decrease in aboveground concentration of nitrogen and phosphorus after 25 July must be due primarily to downward translocation.

Because of downward translocation, shoots begin acting as a nutrient source rather than a nutrient sink even before peak standing crop is achieved (Figure 5-13). Graminoids retranslocate more than 40% of their maximum aboveground standing crop of nutrients below ground before the end of August (Table 5-6), a quantity comparable to that observed in other communities (Goodman and Perkins 1959, Morton 1977, Chapin et al. 1980). Autoradiography indicates that phosphorus, which is absorbed in late season (September), is stored in the rhizome/stem base rather than being translocated to other plant parts (Chapin and Bloom 1976). Clearly, nutrient storage plays an essential role in the strategy of tundra graminoids.

Effect on Shoot Growth and Photosynthesis

The pronounced increase in aboveground plant production when nutrients are added to the tundra system indicates that growth is strongly limited by nutrients under natural conditions (Russell et al. 1940, Schultz 1964, Bliss 1966, Haag 1974, Chapin et al. 1975). Nitrogen and phosphorus have been specifically identified by field fertilization studies as two of the most important limiting nutrients in the tundra at Barrow (McKendrick et al. 1978). Yet the precise nature of the effect of these two nutrients upon production remains unclear. Phosphorus and nitrogen concentrations in young leaves of *Dupontia* collected in the field were

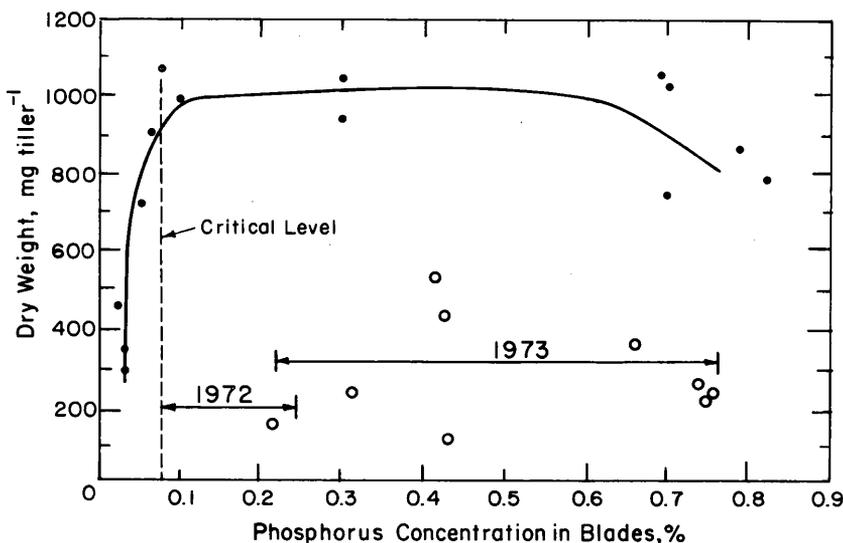


FIGURE 5-14. *Tiller weight of aboveground material of Dupontia fisheri in relation to the phosphorus concentration of the leaf blades (after Ulrich and Gersper 1978) and the range of concentration measured in the field in 1972 and 1973 (Chapin et al. 1975, Tieszen, unpubl. data). In the laboratory, experimental plants (●) were grown in solution culture with different phosphorus concentrations and the total leaf phosphate was estimated from measurements of acid-soluble phosphate. Field measurements of biomass and nutrient concentration (○) were made in the moisture-nutrient gradient.*

always higher than the critical level necessary for maximum growth in the laboratory (Figure 5-14). Moreover, weights of field plants were consistently below those of laboratory plants when either nitrogen or phosphorus was tested in the laboratory as the only factor limiting growth (Ulrich and Gersper 1978). Laboratory studies on plant critical levels suggest two hypotheses: 1) nitrogen and phosphorus never act as the sole limiting factor in the field but are both among a complex of limiting factors, and 2) tundra graminoids never produce nutrient-deficient tissues, but rather limit growth rate. Graminoids at Barrow produce new tissue only if an adequate quantity of nitrogen and phosphorus is available for maximal development and presumably for optimal function. Environmental factors such as nutrients restrict growth rather than compromise the effectiveness of new tissues that are produced. Agricultural crops and species from fertile habitats differ substantially in this regard, responding to nutrient stress with deficiency symptoms and reduced respiration and photosynthesis (Chapin 1980a).

In spite of a 15-fold variation in soil solution phosphate concentration and a 6-fold variation in leaf phosphorus between microtopographic units, leaf phosphorus concentration shows no correlation with photosynthetic rate (Chapter 4), suggesting that the photosynthetic apparatus of a graminoid is relatively insensitive to changes in phosphate concentration. In contrast, shoot production is positively correlated with 1) availability of soil phosphorus, 2) capacity of the plant to absorb available phosphorus (Chapin 1978), and consequently 3) concentration of phosphorus in leaves (Table 5-3). The correlations suggest an intimate association between the phosphorus nutrition of the plant and growth under natural conditions in the field. However, the nature of the relationship between phosphorus nutrition and growth requires further study.

The maximum nitrogen and phosphorus contents of graminoids at Barrow are as high as or higher than those of native temperate zone graminoids (Chapin et al. 1975). This might be anticipated because of a low percentage of structural material. Nitrogen requirements may be high in tundra plants because of high enzyme complements, as discussed previously. A high phosphorus complement may result from 1) a high incidence of polyploidy (Johnson and Packer 1965) and consequently high DNA content, and 2) high concentrations of membrane phospholipid to support metabolism and convey cold tolerance (de la Roche et al. 1972, Thomson and Zalik 1973, Kedrowski and Chapin 1978). *Dupontia* probably has a higher proportion of its phosphorus tied up in structural material, DNA and phospholipid than do temperate plants (Figure 5-15). The total phosphorus complement of leaves varies considerably through the season and between habitats of different phosphorus status. Plants with low phosphorus content may have as much as 85% of their phosphorus complement structurally bound and have essentially the same phosphorus composition as standing dead material (Figure 5-15).

Along a nutrient gradient nitrogen concentration of mature leaves is not correlated with photosynthetic potential. The percentage change in carboxylation activity from early season to mid-season and then from mid-season to end-of-season is greater than the corresponding change in nitrogen content, indicating that early and late in the season a higher proportion of shoot nitrogen is bound as structural protein and as nonphotosynthetic enzymes than at mid-season (Figure 5-16). This may partially explain the low photosynthetic rates early in the growing season (Chapter 4). The parallel decrease in carboxylation activity and total nitrogen content in the latter half of the growing season suggests that ribulose diphosphate carboxylase is broken down more rapidly than it is synthesized after mid- to late July and that the nitrogenous breakdown products are translocated out of the shoot at this time. The decrease in total carboxylation activity and shoot nitrogen after mid- to late July indicates a strong selection for early senescence and downward translocation of

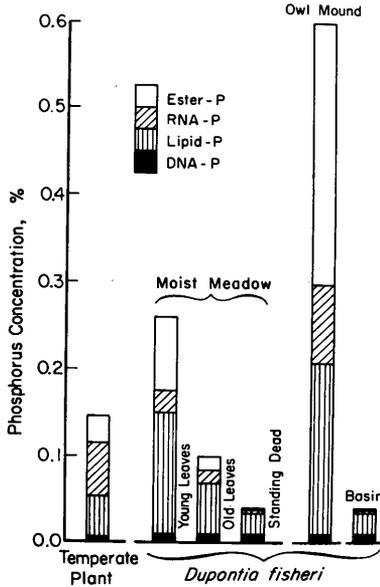


FIGURE 5-15. Estimated compartmentalization of phosphorus into various classes of compounds in shoots of a temperate plant (Bielecki 1973) and *Dupontia fisheri* from three microsites. Ester-P includes inorganic-P and was determined by a weak acid extraction (Ulrich and Gersper 1978). Lipid was measured (McCown 1978) and assumed to contain the same proportion of phospholipid as cold-acclimated winter wheat seedlings (de la Roche et al. 1972). Phosphorus in DNA is assumed to be constant in *Dupontia* and 40% greater than that observed in temperate grasses (Bielecki 1973). The phosphate contained in RNA was determined by subtraction.

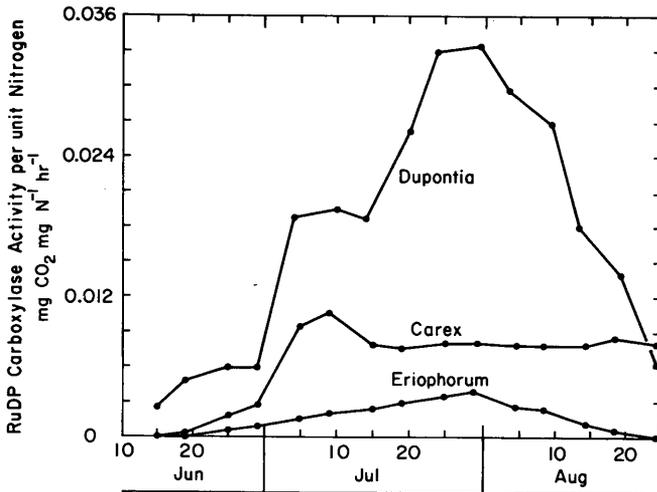


FIGURE 5-16. Seasonal course of ribulose diphosphate carboxylase activity per unit nitrogen in leaves of *Dupontia fisheri*, *Carex aquatilis* and *Eriophorum angustifolium*. (Calculated from Tieszen 1975, Chapin et al. 1975.)

nitrogen, despite the importance of length of photosynthetic season in limiting total carbon gain (Chapter 4, Miller et al. 1976). At Barrow, the probability of a killing frost increases after early August and may select for downward nutrient translocation at this time to minimize the probability of large nutrient losses. Moreover, root and rhizome growth is quite active in late July, and the belowground demand for nitrogen may be met in part by nitrogen translocated from leaves (Chapin et al. 1980).

REPRODUCTIVE ALLOCATION AND POPULATION STRUCTURE

Tiller Interaction

Growth and allocation patterns have been discussed in terms of a single tiller unit. However, the tiller system is the genetic unit in *Dupontia*, and it responds to selection and interacts to maximize short-term carbon and nutrient gain and long-term reproductive success for the entire tiller system.

^{14}C and ^{32}P translocation studies (Allessio and Tieszen 1975b, Chapin and Bloom 1976) indicate that although mature tillers act largely as independent physiological units, there is still considerable translocation from old V2 and V3 tillers to young V0 and V1 tillers that have little or no photosynthetic tissue. Experiments in which individual tillers are severed from the tiller system corroborate these conclusions (Mattheis et al. 1976). Only tillers in their first season of leaf production were highly dependent upon other members of the tiller system for normal seasonal growth. Mature tillers initiated and supported more daughter tillers when their reserves were not tapped by the tiller system (Mattheis et al. 1976). Tiller interdependence may be particularly important during regrowth following grazing. Similar intertiller relationships have been observed in temperate grasses (Evans et al. 1964, Marshall and Sagar 1968).

Neighboring tillers compete for available resources. Nutrients are probably more critical than carbohydrates in governing dry weight increases of tillers. Even young tillers have high available carbohydrate concentrations. The number and the length of new V0 rhizomes are strongly correlated with rhizome nutrient concentration (Table 5-3). Clearly, the nutritional status of the plant governs the balance between growth of an individual shoot and vegetative propagation and hence has profound effects upon population structure.

Population Dynamics

New shoot production and the interaction between members of a single tiller system are important primarily because of implications for population structure. Each tiller may draw upon the resources of older tillers to colonize, grow and reproduce, particularly during its first two years, thus minimizing carbon costs of growth and respiration and the risks of mortality during the early stages of growth. Unlike *Carex bigelowii* (Callaghan 1976) *Dupontia* tillers show minimal mortality until after flowering occurs in V3 or V4 tillers. Consequently, V0, V1, V2 and V3 tillers have similar frequencies, whereas V4 tillers are relatively uncommon (Figure 5-17). Tiller interdependence averages out the growth and reproductive performance over an environment that is variable in both time and space. The vegetative reproduction characteristics of *Dupontia* and other graminoids are not an alternative to sexual reproduction but rather a strategy of expanding the number of loci at which flowering may eventually occur (Lawrence et al. 1978). Vegetative reproduction is important under situations where 1) a given tiller has a low probability of survival, e.g. due to grazing, 2) the probability of successful seed set in any given year is low, or 3) the probability of seedling establishment from the seed crop produced in a given year is low. All of these conditions characterize the coastal tundra at Barrow and may be important in selecting for extensive vegetative reproduction. The selected strategy, of allocating most resources to competition and to growth rather than to extensive short-term reproductive output, typifies tundra

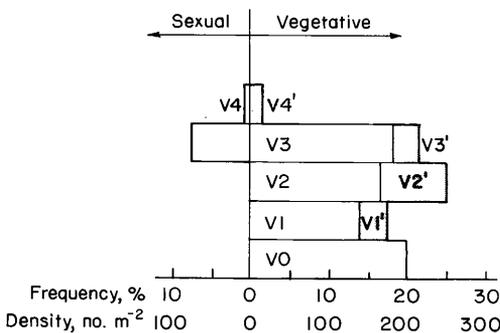


FIGURE 5-17. Relative frequency and density of *Dupontia fisheri* tillers in various age classes and sexual conditions in moist meadow tundra in August 1973. (Lewis and Tieszen, unpubl.)

species (Bliss 1971). Rough calculations based on carbon cost of inflorescence production, percentage seed set, percentage seedling survival, etc., suggest that the carbon cost of producing a new tiller in coastal tundra by sexual reproduction is 10,000 times greater than the cost of tiller production through vegetative reproduction. The fact that sexual reproduction receives substantial carbohydrate allocation in spite of the low frequency of seedling establishment points out the necessity of a long-term evolutionary framework within which to view growth and allocation processes. On successional and evolutionary time scales there must be substantial selection for sexual reproduction to maintain genetic variability and flexibility and to permit dispersal to new areas. The selective advantage of dispersal capability results from the heterogeneous nature of the microtopography that limits the expansion of clones, and the occasional creation of new unvegetated areas such as frost scars and drained lake basins that are not effectively colonized by clonal expansion. Population processes and evolutionary strategies deserve attention in future tundra studies.

EFFECT OF GRAZING ON ALLOCATION AND POPULATION STRUCTURE

Lemmings periodically graze wet meadow communities to such an extent that maximum aboveground biomass may be decreased from 100 g m⁻² to as little as 5 g m⁻² (Dennis 1968, Tieszen 1972b, Chapter 8). Simulations suggest that the long-term effect of lemming grazing is to reduce total foliage by an average of 33% (Lawrence et al. 1978). Grazing alters graminoid allocation patterns in the tundra at Barrow and affects plant survival and community structure. Certain gross morphological features of *Dupontia* and other graminoids appear to be adaptive under a grazing regime. The shoot meristem and virtually all the storage and perennial tissues are located below ground, protected from grazing. Tissues that are available to grazers are only weakly lignified and are potentially replaceable at a minimal biochemical cost. Grazing may be a critical factor leading to the dominance of the graminoid growth form at Barrow.

Clipping experiments on *Dupontia* indicate that the movement of carbohydrate from one tiller to another is important in allowing *Dupontia* to survive intensive grazing. *Dupontia* leaves regrow rapidly following grazing because of the abundance of belowground carbohydrate reserves (Mattheis et al. 1976). Light clipping to simulate grazing can even result in a slight increase in the available carbohydrate pool of the rhizome, provided the clipped tiller remains attached to the tiller system (Mattheis et al. 1976), perhaps due to decreased shading and increased photosynthesis. After six consecutive clippings in a single season, to simulate the

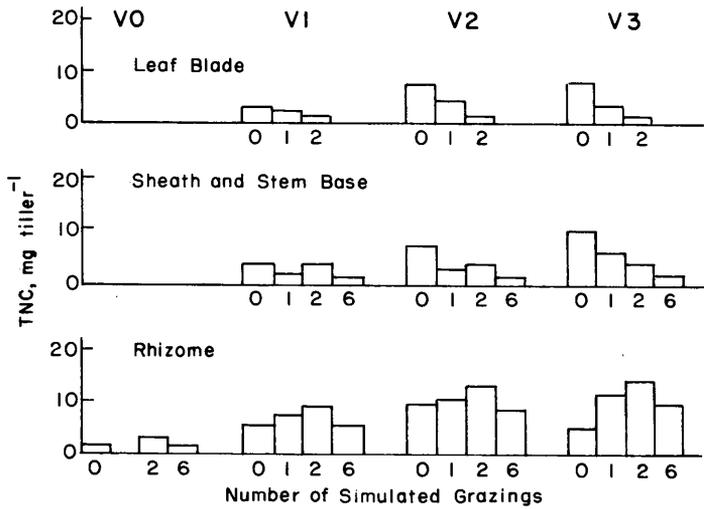


FIGURE 5-18. Total nonstructural carbohydrate (TNC) content in various plant compartments and tiller age classes of *DuPontia fisheri* following clipping at various intensities. Plants were clipped at weekly intervals to simulate grazing and were sampled on 20 August in moist meadow tundra. (After Mattheis et al. 1976.)

maximum grazing intensity that might be sustained in a lemming high, total nonstructural carbohydrate concentrations still remained high in rhizomes (Figure 5-18), and shoot weight was not affected. However, when a tiller no longer had access to the reserves of the entire tiller system, clipping decreased shoot weight substantially (Table 5-7), as has also been noted by Babb and Bliss (1974).

Results of clipping experiments suggest that even chronic grazing would have little effect upon survivorship of vegetative tillers, because the tiller meristem is normally not damaged. However, at times of high lemming densities and inadequate food supply, lemmings may grub in the moss layer and remove the shoot meristem, killing the shoot. The impact of grazing upon reproduction is most pronounced 1) through the grazing of flowering shoots, since the inflorescence is lost, and 2) through the general lowering of the reserve status of the entire tiller system so that the chances of successful seed set are diminished.

The number of new rhizomes produced is curtailed by grazing much less than is shoot production (Table 5-7). Grazing causes not only a decrease in reserves but also a shift in the allocation pattern from shoot production toward greater rhizome production and vegetative reproduction. Grazing causes a change in age class structure only because above-

TABLE 5-7 *Effect of Simulated Grazing upon Dry Weight of Shoot Regrowth and Number of Newly Initiated (V0) Rhizomes of Dupontia fisheri Growing in Moist Meadow Tundra*

Tiller age	Treatment				
	Control	One clipping		Two clippings	
		Clipped only	Ringed and clipped	Clipped only	Ringed and clipped
Dry weight above ground (mg)					
First year tiller (V1)	7.7 ± 3.4	8.8 ± 2.4	2.5 ± 0.7	5.8 ± 1.8	0.3 ± 0.1
Established tiller (V2 or V3)	6.8 ± 2.8	11.4 ± 2.1	4.0 ± 3.0	0.0	2.0 ± 0.6
Number daughter tillers (no. V0s tiller⁻¹)					
First year tiller (V1)	0.8	1.1	0.7	0.6	0.4
Established tiller (V2 or V3)	0.2	0.7	0.2	0.0	0.3

Note: Treatments involved clipping all leaves of the tiller at the moss surface (clipping) and/or severing all rhizome connections between the treated tiller and the rest of the tiller system (ringing). Tillers were clipped or ringed and clipped on 25 July, leaves were reclipped on 4 August, and shoots and rhizomes were harvested on 16 August 1973 ($n = 10$).

Source: Mattheis et al. (1976).

average numbers of newly initiated (V0) tillers are recruited into the population in the year of a lemming high. Computer simulations suggest that the differential mortality and reduced competition due to grazing are not responsible for change in age structure (Lawrence et al. 1978). Hence, grazing by moderate lemming populations influences population structure more by increasing recruitment of new tillers than by increasing mortality.

The maximum stress that lemmings are likely to exert upon the nutrient reserves of the wet meadow vegetation is simulated and shown in Figure 5-19. Simulations suggest that grazing depletes nitrogen and phosphorus reserves more rapidly than carbohydrate reserves which, in turn, are depleted more rapidly than are calcium reserves. The strain on below-ground nitrogen or phosphorus reserves may not differ significantly in grazed or ungrazed situations until after four or five defoliations, because the early part of the growing season is characterized by rapid upward nutrient translocation regardless of whether grazing occurs or not. Grazing would, however, prevent downward translocation of nutrients lost to herbivores and would likely affect growth primarily in subsequent years. In fact, detailed studies (Tieszen and Archer 1979) of various growth forms at Atkasook, Alaska, have not only shown that seasonal carbon balance is seriously affected (Chapter 3) but also that a single grazing event can reduce reserves in a manner which influences growth

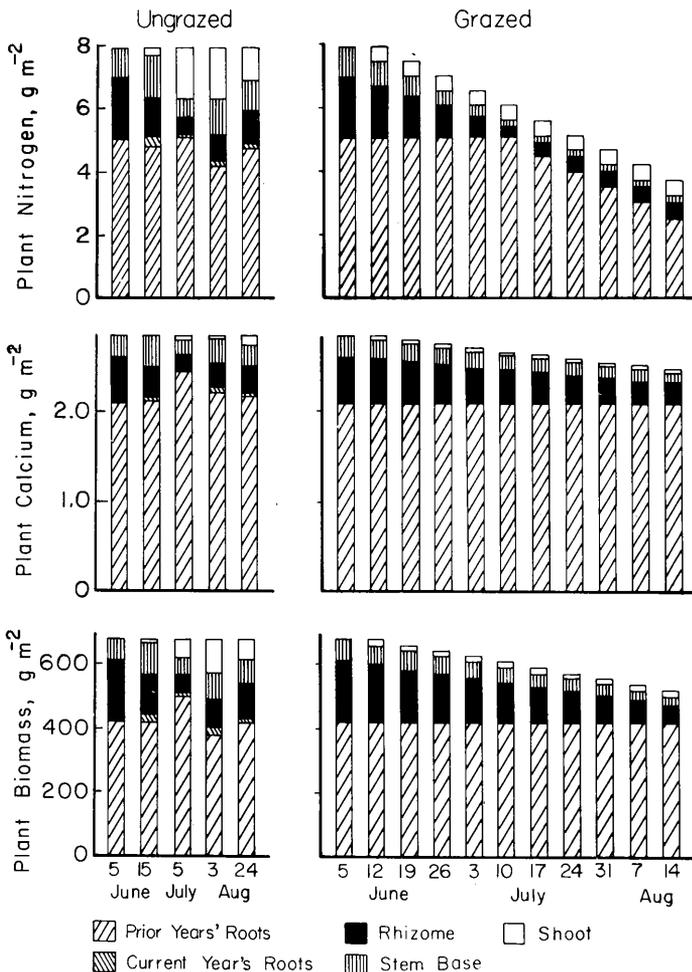


FIGURE 5-19. Standing crops of plant nitrogen, calcium and biomass in moist meadow tundra with and without maximum lemming grazing, calculated assuming: 1) the total plant nutrient and biomass contents were altered through the season only by grazing (i.e. that no nutrient gain or loss occurred through uptake, senescence, or leaching, and that maintenance and growth respiration equaled photosynthesis); 2) translocation to aboveground parts after grazing occurred at the maximum rate observed during the 1970 growing season; 3) grazing occurred weekly and totally removed the aboveground compartment; 4) roots did not normally serve a storage function (nutrients and carbohydrates contained in roots were translocated upward only after all other reserves were exhausted); and 5) no new roots were produced when plants were intensively grazed. (After Chapin 1975.)

and production the next year. Since this longer-term effect is most harmful to evergreen shrubs and then deciduous shrubs, and least harmful to graminoids, it is clear that vegetation units will change under different kinds of grazing regimes.

VARIABILITY IN GROWTH AND ALLOCATION PATTERNS

Substantial interspecific differences in the growth and allocation patterns of three dominant graminoids (*Dupontia fisheri*, *Eriophorum angustifolium* and *Carex aquatilis*) have resulted in niche differentiation. *Carex* is generally dominant in phosphorus-poor sites such as pond margins and basins and rims of low-centered polygons, which receive low grazing pressure. In contrast, *Dupontia* predominates on phosphorus-rich sites such as polygon troughs. *Eriophorum* also tends to occur in more phosphorus-rich sites, particularly where vegetative cover has been broken by frost or human disturbance.

Differences in allocation pattern between the three principal graminoids partially explain distribution patterns (Table 5-8). Leaf production and elongation occur earlier in the growing season and are more syn-

TABLE 5-8 *Characteristics of the Growth and Allocation Patterns of Dupontia fisheri, Carex aquatilis and Eriophorum angustifolium*

	<i>Dupontia fisheri</i>	<i>Carex aquatilis</i>	<i>Eriophorum angustifolium</i>
Leaf production*	Asynchronous	Somewhat synchronous	Somewhat synchronous
Shoot longevity*	3 to 4 (5) yr	4 to 7 yr	5 to 7 (8) yr
Root longevity†	4 to 6 yr	5 to 8 (10) yr	1 yr
Root elongation ability†	1 yr	2 to 3 yr	1 yr
Seasonality of root elongation†	Mid-late season	Continuous	Continuous
Lateral root production†	90% 1st yr	2nd to 4th yr	None
Seasonality of lateral production†	Mid-late season	Continuous	—
Root origins†	Predominantly rhizome nodes	Stem base	Stem base

*Shaver (1976).

†Shaver and Billings (1975).

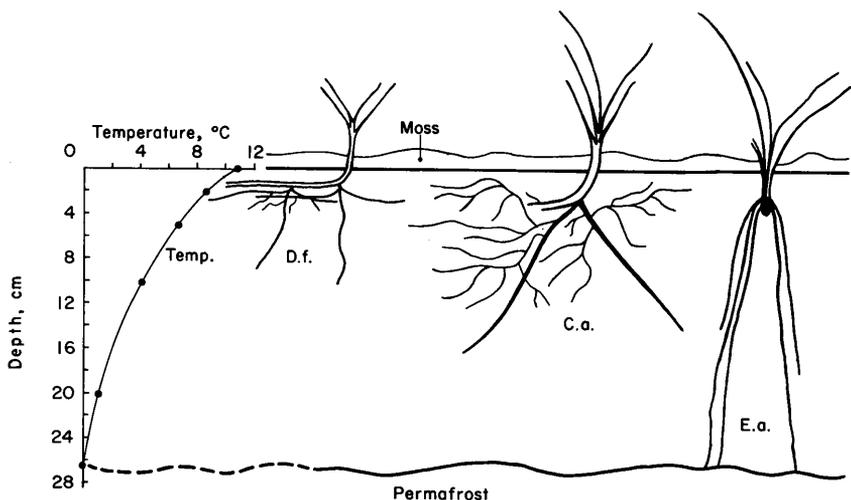


FIGURE 5-20. Patterns of root distribution of *Dupontia fisheri* (*D.f.*), *Carex aquatilis* (*C.a.*) and *Eriophorum angustifolium* (*E.a.*) at peak season.

chronous in *Carex* and *Eriophorum* than in *Dupontia* (Mattheis et al. 1976), suggesting that shoots of *Dupontia* might be able to regrow more rapidly following grazing than would shoots of the other two graminoids. However, in the ungrazed situation earlier canopy development by *Carex* and *Eriophorum* may give these two species a more favorable carbon balance that in turn allows them to invest in new structures, particularly roots and rhizomes, to a greater extent than can *Dupontia*.

The interspecific differences in growth and allocation patterns for the three species are more pronounced below ground than above ground (Shaver and Billings 1975), suggesting that at the Biome research area competition is more intense and niche differentiation more clearly delineated in soil than in air. Nutrient and oxygen concentrations, pH and temperature all vary substantially with depth. The three principal graminoid species have strikingly different rooting patterns and exploit different depths (Figure 5-20).

Roots of *Dupontia* are concentrated in the top 5 cm of the soil where phosphate and potassium are most abundant and where temperature and aerobic conditions are most favorable for absorption (Shaver and Billings 1975). *Eriophorum* has thin annual roots that grow vertically downward following the seasonal thaw (Bliss 1956, Shaver and Billings 1975). At the freeze/thaw interface, phosphorus may be highly available (Saebø 1969). The disadvantages of the deep-rooting habit are that soils are colder and less aerobic and that deep roots are locked in frozen soil

the following season, which is perhaps why the entire root system of *Eriophorum* is replaced annually. Annual replacement avoids the cost of maintenance respiration during the second year when the roots may be less functional (Shaver and Billings 1975). *Carex* produces long-lived, thick primary roots that exploit intermediate soil horizons and thin secondary roots that are quite abundant in surface horizons. *Carex* invests proportionately more tissue in roots than do the other two species and is most successful in nutrient-poor situations.

Interspecific differences in growth and allocation, tiller interdependence, and age class distribution lead to distinct population structures in the three graminoid species. *Dupontia* from the nutrient-rich habitat shows considerable tiller interdependence, low tiller mortality, and a uniform age class structure (Shaver and Billings 1975, Allesio and Tieszen 1975a, Lawrence et al. 1978). Tiller interdependence may be important in allowing *Dupontia* to survive acute and chronic grazing.

In contrast, the longer-lived *Eriophorum* tillers lose rhizome connections and become physiologically independent within two or three years (Shaver 1976). Heavily grazed *Eriophorum* tillers cannot rely upon the reserves of an interconnected tiller system and tend to occur less frequently in heavily grazed polygon troughs. Lack of tiller interdependence may be important in explaining *Eriophorum*'s apparent success in sexual reproduction, since its reserves may accumulate to support the inflorescence rather than being continuously siphoned away into the rest of the tiller system. Allocation to sexual reproduction and the windblown seed dispersal pattern in *Eriophorum* are in part responsible for its abundance in disturbed habitats. An annual rooting pattern is adaptive in disturbed sites, where roots are subject to breaking by frost heaving. Little is currently known about mortality of *Eriophorum* tillers, but the greater tiller independence in *Eriophorum* than in *Dupontia* may well lead to greater variability in recruitment and death in the former and hence more variation in age class structure.

Carex has a dual tillering pattern. Some tillers (clumping tillers) have very short rhizome internodes so that new shoots are produced adjacent to the parent tiller (Shaver and Billings 1975). Other (spreading) tillers have elongated rhizome internodes so that daughter tillers occupy space quite far from the parent tiller. The spreading pattern is most common in phosphorus-deficient sites like polygon basins. The low phosphorus-to-nitrogen ratio may stimulate rhizome elongation, minimizing competition between parent and daughter tillers. Such an effect has been proposed in temperate grasses (Evans et al. 1964, Langer 1966).

These consistent differences in allocation patterns among the various graminoids are consistent and appear to explain their distribution patterns. Differences in life forms are more pronounced and are discussed in Chapter 6.

SUMMARY

The component processes of growth and allocation in graminoids of the coastal tundra at Barrow have compensated for low temperature to such an extent that these processes occur at nearly the same rates in situ as those observed in temperate grasslands. Temperature compensation may be achieved at substantial carbon and protein cost and thus be accompanied by lowered reproductive output. Latitudinal temperature compensation has been demonstrated for shoot growth, photosynthesis, respiration and phosphorus uptake, but requires documentation for growth of belowground organs. Because the air warms faster than the soil, shoot growth and photosynthesis predominate early in the season, whereas root growth and uptake continue well after shoot senescence. Nutrients absorbed in one year have their most pronounced effect upon growth and reproduction in subsequent years.

The lower levels of annual plant production in tundra than in comparable temperate communities are more a consequence of shortness of the growing season than of the difference in ambient summer temperature. This hypothesis is supported by computer simulations but has not been tested by field experiments or long-term observations.

Allocation patterns are altered genetically and environmentally in a way that minimizes limitation to growth by any one environmental resource but maximizes long-term survival through vegetative and sexual reproduction. Growth is limited simultaneously by several factors. Experimental manipulations under field conditions indicate that phosphorus and nitrogen strongly limit plant growth. Simulations predict that light, carbon dioxide concentration, and water availability also limit growth to a lesser extent. Low temperature limits production in a complex fashion involving all of the above environmental variables. The high root-to-shoot ratio of the graminoids compensates for low nutrient availability. The environmental and genetic determinants of typical allocation patterns remain to be determined.

Plant growth at Barrow is generally more strongly limited by an inadequate supply of certain nutrients, especially nitrogen and phosphorus, than by inadequate carbohydrate. Available carbohydrate levels are high in the graminoids, particularly in habitats of low nitrogen and phosphorus availability. Carbohydrate levels are reduced by fertilization. We suggest that the low radiation environment of the Arctic limits plant growth more strongly by the indirect effects of low temperature upon nutrient availability than by a direct effect upon photosynthesis. Shoots also become photosynthetically self-sufficient quite early in the season and depend upon rhizome reserves for nutrients more than for carbohydrate. The decrease in rhizome weight that coincides with early season

shoot growth is primarily a consequence of high rates of maintenance respiration and translocation to roots.

The evolutionary response of plants to the nutrient-limited environment is to limit production to the formation of a small amount of tissue that is well supplied with nutrients and highly effective metabolically. This would explain the apparent paradox of relatively high nitrogen and phosphorus concentrations in leaves of plants that respond dramatically to nitrogen and phosphorus fertilizers, in contrast to graminoid crop plants where nutrient deficiency is evident in foliar nutrient analysis.

Rapid upward translocation early in the season supports rapid shoot growth when radiation is most favorable for photosynthesis. Net downward translocation begins six weeks after growth commences, a full month before onset of obvious leaf senescence. The belowground carbohydrate and nutrient reserves appear to exceed levels required for growth in any given season and may allow the graminoids to successfully survive intensive lemming grazing and to regrow even after successive clippings.