

4

Photosynthesis

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INTRODUCTION

The interception of solar radiation and the conversion of that energy by photosynthesis into stable organic forms is essential for the maintenance and growth of plants as well as for their vegetative or sexual reproduction. Accumulating information on photosynthesis of tundra plants suggests that this process is highly adapted to the extreme conditions of the tundra. This chapter describes photosynthesis in the coastal tundra at Barrow and the sensitivity of carbon dioxide assimilation to abiotic and biotic factors. Response patterns and internal and external controls over photosynthesis in vascular plants and mosses are described in an attempt to quantify those factors that govern rates of carbon dioxide uptake. The objectives of Chapter 4 are to understand the controls over photosynthesis, analyze the sensitivity of the system, and estimate community productivity as reviewed in Chapter 3.

Photosynthesis is a photochemical, diffusion, and enzymatic process with a rate controlled by intrinsic and extrinsic factors. The process is basically similar in all vascular plants and mosses, although variations in component dark reactions have evolved and are most notable in the distinctions between C_3 and C_4 plants (Hatch et al. 1971). Tundra vegetation consists mainly of C_3 plants (Tieszen and Sigurdson 1973), and no significant differences would be expected in the basic mechanisms between C_3 plants in the Arctic and C_3 plants in more temperate climates. However, component reactions, e.g. at the enzyme level, have probably evolved and could be manifest as quantitatively different response patterns.

The amount of carbon dioxide assimilated is a function of the maximum capacity (rate) for carbon dioxide uptake, which may be related to intrinsic factors such as component enzyme levels (Treharne 1972), the concentrations of ribulose-1,5-diphosphate, nutrient status, innate leaf growth, or development patterns. The extent to which this maximum

capacity is realized is a function of the microenvironment within the canopy (see Chapter 3.). At the cell and leaf level, responses to light, temperature and water are most crucial in determining the rate of photosynthesis. Nutrients can limit leaf carbon dioxide uptake at the cell level by affecting the internal capacity and at the plant and canopy level by affecting the allocation for the production of more photosynthetic tissues. Similarly, grazing will alter this pattern directly by removing established tissues at various developmental stages. Most of these interactions are discussed in this chapter and have been incorporated into a canopy photosynthesis model (Miller et al. 1976).

INTRINSIC FACTORS AFFECTING CARBON DIOXIDE EXCHANGE

Maximum Rates and Growth Forms

The maximum photosynthetic rates for expanded blades range between 7 and 31 mg CO₂ dm⁻² hr⁻¹ (Table 4-1) or nearly as widely as those of vascular plants in other Biomes (Tieszen and Wieland 1975). Within the tundra, however, similar species, e.g. *Carex* spp. at Barrow and Devon Island, Canada (Mayo et al. 1977), show very comparable rates. Furthermore, photosynthetic rates show a distinct relationship to growth forms. The rates are highest in graminoid types and forbs (~30 mg CO₂ dm⁻² hr⁻¹), slightly lower in some of the deciduous dwarf shrubs (~20 mg CO₂ dm⁻² hr⁻¹), except for *Salix* species which tend to be higher, and still lower among the evergreen dwarf shrubs (7 mg CO₂ dm⁻² hr⁻¹) such as *Cassiope tetragona*, *Ledum decumbens*, and *Vaccinium vitis-idaea* (Johnson and Tieszen 1976). Photosynthesis rates in vascular plants are equivalent to rates of similar growth forms in more temperate zones (Table 4-2), suggesting that these species are adapted genetically or physiologically to the low ambient temperatures. As expected, photosynthetic rates are much lower in mosses than in vascular plants (Table 4-2), ranging between 1.0 and 4.4 mg CO₂ gdw⁻¹ hr⁻¹ (Oechel 1976, Oechel and Collins 1976, Oechel and Sveinbjörnsson 1978). Although the rates of different moss species vary widely, they are similar to those of temperate,

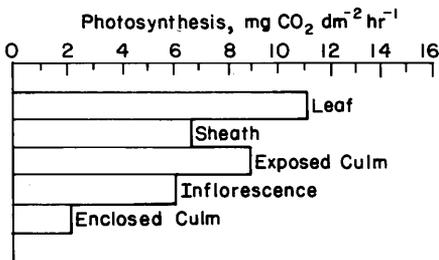


FIGURE 4-1. Photosynthetic rates of various plant parts of *Dupontia fisheri* near mid-season. The rates were determined with the ¹⁴C system. N = 8. (After Tieszen and Johnson 1975.)

TABLE 4-1 *Maximum Photosynthetic Rates of Field-grown Tundra Plants at the Tundra Biome Research Area under Ambient Light and Temperature Regimes*

Species	Leaf area basis (mg CO ₂ dm ⁻² hr ⁻¹)	Dry weight basis (mg CO ₂ gdw ⁻¹ hr ⁻¹)
Barrow		
Graminoids ¹		
<i>Alopecurus alpinus</i>	16	35
<i>Arctagrostis latifolia</i>	14.7	37
<i>Arctophila fulva</i>	19.6	34
<i>Calamagrostis holmii</i>	12.6	33
<i>Carex aquatilis</i>	18.5	24
<i>Dupontia fisheri</i>	17.1	25
<i>Eriophorum angustifolium</i>	20.9	
<i>Elymus arenarius</i>	30.8	33
<i>Hierochloe alpina</i>	7	12
<i>Poa arctica</i>	11.5	14
<i>Poa malacantha</i>	10.1	
Forbs ¹		
<i>Petasites frigidus</i>	13.4	17
<i>Ranunculus nivalis</i>	18	21
Deciduous dwarf shrubs ¹		
<i>Salix pulchra</i>	28	
Mosses ²		
<i>Pogonatum alpinum</i>		4.4
<i>Calliergon sarmentosum</i>		2.7
<i>Polytrichum commune</i>		2.9
<i>Dicranum angustum</i>		1.0
<i>Dicranum elongatum</i>		1.3
Niwot Ridge		
Graminoid ³		
<i>Deschampsia caespitosa</i>	21.3	
Forbs ³		
<i>Geum rossii</i>	26.7	
<i>Kobresia myosuroides</i>	21.3	

¹Tieszen (1973, 1975, unpubl.) and Tieszen and Johnson (1975).

²Oechel (1976), Oechel and Collins (1976), and Oechel and Sveinbjörnsson (1978).

³Johnson and Caldwell (1974).

TABLE 4-2 *Maximum Photosynthetic Rates of the Major Plant Growth Forms Among all Biomes*

Species	Leaf area basis (mg CO ₂ dm ⁻² hr ⁻¹)	Dry weight basis (mg CO ₂ gdw ⁻¹ hr ⁻¹)
Herbaceous plants		
Cultivated with C ₃ pathway ¹	20-35	30-60
Herbs from sunny habitats ¹	15-60	30-90
Herbs from shaded habitats ¹	4-16	20
Tundra graminoids ²	7-31	18
Tundra forbs ²	13-18	15
C ₄ plants ¹	30-70	40-120
Succulents ¹	4-12	8
Submerged macrophytes ¹	4-6	
Woody plants		
Deciduous broad-leaved trees ¹		
Sun leaves	10-25	15-30
Shade leaves	6-15	
Tundra deciduous dwarf shrubs, average ²	13	15
Tundra evergreen dwarf shrubs, average ²	7	5
Evergreen broad-leaved trees ¹		
Sun leaves	10-16	6-10
Shade leaves	3-8	
Semi-arid sclerophyllous shrubs ¹	4-12	4-6
Evergreen conifers ¹	4-12	3-15
Mosses		
Tundra mosses ^{3,4}		0.1-4.4
Temperate mosses ⁴		1.1-3.5
Temperate epiphytic mosses ⁴		0.6-1.5
Lichens ⁴		0.3-3.9

¹Sesták et al. (1971).²Tieszen et al. (1981).³Kallio and Heinonen (1973), Oechel (1976), Oechel and Collins (1976), Oechel and Sveinbjörnsson (1978).⁴Kallio and Kärenlampi (1975).

subarctic and antarctic mosses (Stålfelt 1937, Hosokawa et al. 1964, Rastorfer 1972, Kallio and Kärenlampi 1975).

The proportion of shrubs decreases and that of graminoids increases with increasing latitude in tundras. This may reflect the higher ratio of potentially productive to supporting tissue (e.g. stems) in the graminoid growth form. In *Dupontia* the leaf is obviously the most important photosynthetic component; however, other components (Figure 4-1) are photosynthetically active and contribute to the total amount of carbon

dioxide incorporated. Mosses and lichens represent an extreme development of this trend since nearly all tissues are photosynthetic. Thus at high latitudes plants are selected which either have little nonphotosynthetic tissue or are highly opportunistic in their CO₂ uptake.

Enzyme Levels and Component Resistances

The maximum rates of carbon dioxide uptake among all vascular species are highly correlated with specific leaf density or thickness ($r = +0.83$) and with carboxylation activity ($r = +0.76$, $N = 54$) (Tieszen 1973). Chabot et al. (1972) noted an acclimation response of *Oxyria digyna* that resulted in higher carboxylation levels at low temperatures, and Treharne (1972) suggested a causal relationship between carboxylation activity and photosynthesis. Their data suggest that the range in carbon dioxide uptake potential is determined by differences in carboxylation activity. Further support is provided by data from the Biome research area, which showed high correlations between photosynthesis near light saturation and carboxylation activity among all leaves throughout the season (*Dupontia*, $r = +0.74$, $p > 0.97$; *Carex*, $r = +0.81$, $p > 0.99$; *Eriophorum*, $r = +0.75$, $p > 0.99$). Therefore, species differences and seasonal patterns are directly related to carboxylation activity. Since ribulose-1,5-diphosphate carboxylase is a substantial portion of total cell protein (Huffaker and Peterson 1974), this enzyme also accounts for the major changes of nitrogen content through the season.

The high correlation of maximum photosynthesis with carboxylation activity further suggests that differences in photosynthetic rates are related more to differences in some component of the mesophyll resistance than to leaf resistance. In the field, minimum leaf resistances for *Dupontia* are generally less than 2 to 3 s cm⁻¹, whereas minimum mesophyll resistances are rarely below 7 s cm⁻¹ and are often well above 12 s cm⁻¹. Similar values for *Carex*, *Eriophorum angustifolium*, *Salix pulchra* and *Petasites frigidus* support this contention. This trend is even more pronounced in mosses, where leaf resistances are generally less than 1 s cm⁻¹ but mesophyll resistances are large (Oechel and Sveinbjörnsson 1978).

Growth Rate and Developmental Stage

Photosynthetic competence is a function of leaf development, increasing as the leaf elongates or expands until a mature stage is attained. The leaf usually remains at full competence until senescence occurs and carbon dioxide uptake ability decreases as proteins and other materials

are hydrolyzed and mobilized. Obviously, the dynamics of leaf photosynthesis will vary with plant growth forms as patterns of leaf development and retention vary. In *Dupontia* exsertion is followed by an elongation period of 20 to 22 days, followed by a shorter period of 8 to 10 days during which the growth rate is near zero. At the end of this period, the leaf initiates senescence and in about 25 to 30 days it is dead. Thus, in comparison with other growth forms where the mature phase may last more than one growing season, *Dupontia* has a short period of maximal photosynthesis (Johnson and Tieszen 1976). *Carex* and *Eriophorum angustifolium* have somewhat longer mature periods than *Dupontia*, while moss tissue may remain photosynthetically active for at least 3 years (Collins and Oechel 1974).

Photosynthetic activity of vascular plants does not occur beneath the winter snow even though substantial carboxylation activity is present (Tieszen 1974). Thus photosynthesis begins concurrently with growth, which is initiated within one day of snowmelt. This has now been confirmed in the Arctic not only for graminoids but also for *Dryas* (Mayo et al. 1977), which remains inactive until snowmelt. This is not unexpected since the plant temperatures beneath late-winter snow may approximate the permafrost temperature, thereby presenting a distinct contrast with conditions that may occur in mid-latitude alpine areas. As meltwater percolates through the snowpack, however, temperatures abruptly approach 0°C (Tieszen 1974).

Following snowmelt, leaf expansion and growth of *Dupontia* occur rapidly and are accompanied by the development of photosynthetic competence. The first leaf elongates and exserts some chlorophyllous tissue produced the previous season. This tissue never becomes very active although it does make a positive contribution to the carbon balance. By about 19 June, however, the second and third leaves have elongated and they are soon active (see Chapter 5). Although the sequential pattern of photosynthesis is somewhat obscured by the short growing season, successive leaves become more active as the season progresses. This general ontogenetic leaf pattern is similar to that of other graminoids, and results in a sequence of developing photosynthetic competence as leaves elongate or enlarge, a period of maximal photosynthetic competence associated with maturation, and a subsequent decline in photosynthetic competence as senescence develops (Johnson and Caldwell 1974, Johnson and Tieszen 1976, Tieszen 1978b).

In a short growing season a sequential leaf pattern seems costly since it requires a large investment in synthetic and growth processes (see Chapter 5). Although it does replace leaves at successively higher positions in the canopy in more favorable radiant flux (but less favorable thermal) environments, this pattern must have other selective value, e.g. as a mechanism for withstanding acute or chronic grazing pressures.

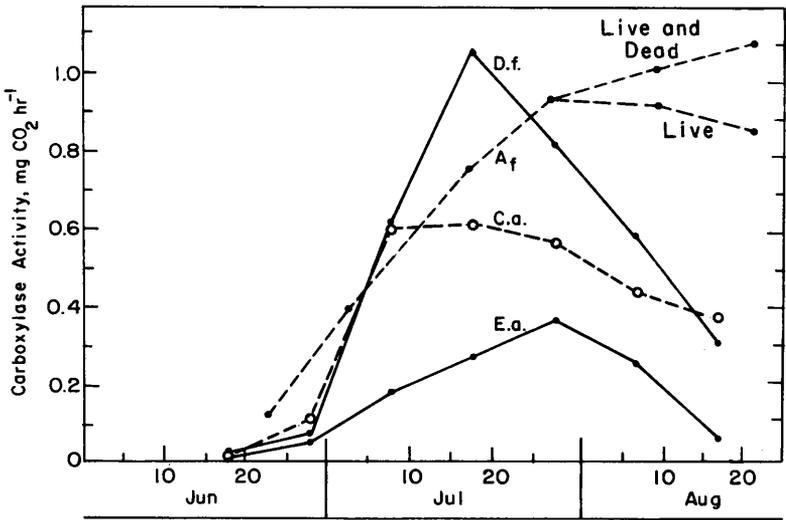


FIGURE 4-2. Seasonal progression of the carboxylation activity for entire tillers (summation of leaf activity times leaf area) in 1971 of: *Dupontia fisheri* (*D.f.*), *Carex aquatilis* (*C.a.*), *Eriophorum angustifolium* (*E.a.*), and the total foliage area index (A_f) of the community. The foliage area indices of the species are given in Figure 3-3. Absolute rates not directly comparable among species. (After Tieszen 1978b.)

On both a daily and seasonal basis, leaf photosynthetic rates are highly correlated with carboxylation activity (Tieszen 1978b). The integration of carboxylase activity among all leaves suggests that on a tiller basis the greatest potential for photosynthesis occurs well before the time of maximum standing crop or leaf area index (Figure 4-2). Although the greatest conversion efficiency on a green leaf area basis should occur on 20 July, the increased canopy or tiller density later in the season results in a greater efficiency on a land basis. Mosses begin each season with a high proportion of chlorophyllous tissue which may equal 50% of the maximum for the season. This tissue is photosynthetically competent under the snow, with potential in situ photosynthesis rates of about 25% of the normal seasonal maximum (Tieszen 1974, Oechel and Sveinbjörnsson 1978). In contrast to vascular plants, the photosynthetic moss tissue does not decrease in activity during the growing season (Oechel 1976), but net photosynthesis is reduced as the tissue ages. Early in the season photosynthesis is carried out by tissue from the previous 1 or 2 years. This pattern permits early season photosynthesis but at rates for 2- and 1-year-old tissue of only 40% to 75% of new tissue, respectively (Collins and

Oechel 1974). As the season progresses, new tissue is produced with high photosynthetic capacities. The moss growth pattern has the potential for significant late season photosynthesis since no end-of-season senescence is observed. However, mortality of older age classes is high, and the amount of older tissue decreases markedly at ages greater than 1 year (Collins and Oechel 1974).

Nutrients

Nutrients can limit photosynthesis at the leaf and plant level if the allocation for photosynthetic structures exceeds the support capabilities of available nutrients. Under field conditions *Dupontia* appears to control allocation to produce a complement of photosynthetic structures operating at near optimal capacities. The main response to chronic and intense fertilization (Schultz 1964) was an increase in productivity due to the stimulation of greater plant density (Dennis et al. 1978) and a two times greater leaf area index. Although fertilizer stimulated a slight increase in leaf width in *Dupontia*, there was no significant difference in carboxylation activity and presumably no difference in leaf photosynthesis. The short-term responses at site 2 were similar (Dennis et al. 1978) and resulted in statistically significant, but small, increases in plant phosphorus and potassium, but not nitrogen (Chapin et al. 1975).

In an attempt to document the spatial variability of photosynthesis and to determine the extent to which large changes in production were associated with changes in photosynthetic rates, a study was made along a productivity and growth form gradient (Tieszen, unpubl.). Although aboveground production ranged from 21 g m⁻² in the basins of low-centered polygons to 215 g m⁻² in a disturbed vehicle track, there were no significant ($p = 0.95$) correlations among photosynthesis and soil or leaf potassium, nitrogen and phosphorus (Tieszen 1978b) (Table 4-3). This

TABLE 4-3 *Range of Nutrient Concentrations in Leaves (%) in which Photosynthesis was Independent of Leaf Nutrient Concentration (P = 0.95)*

	<i>Dupontia fisheri</i>	<i>Carex aquatilis</i>	<i>Eriophorum angustifolium</i>
Nitrogen	1.83-3.28	2.74-3.28	1.50-3.21
Phosphorus	0.07-0.24	0.07-0.40	0.15-0.31
Potassium	0.64-1.59	0.55-1.55	0.45-1.14

independence of photosynthesis and potassium, nitrogen and phosphorus over a large range of field concentrations provides strong evidence for precise control of allocation in response to available nutrients. Plants of the coastal tundra at Barrow do not appear to produce additional leaf area unless they can operate at near maximal capacity. Thus, under field conditions, plants seem to avoid nutrient limitations of photosynthesis by limiting the amount of photosynthetic tissue within the support capabilities of the available nutrients (see also Chapter 5). Ulrich and Gersper (1978), however, show that these plants are always on the borderline of being nutrient-limited; and the addition of phosphorus and nitrogen clearly stimulates production (Chapin et al. 1975, Dennis et al. 1978).

EXTRINSIC FACTORS AND THE RATE OF PHOTOSYNTHESIS

Light

Arctic tundras have often been described as light-limited ecological systems. Daily totals of irradiance can be high at Barrow, but instantaneous irradiances are generally low because of the low sun angle and frequent cloudiness. Light response curves for vascular plant species are

TABLE 4-4 *Irradiance (300 to 3000 nm) Required for Photosynthesis to Equal Respiration as Determined from Field Measurements at Temperatures near 0°C*

Species	Irradiance (J m ⁻² s ⁻¹)
Vascular plants	
<i>Dupontia fisheri</i>	16.7 ± 2.1
<i>Carex aquatilis</i>	9.1 ± 0.7
<i>Eriophorum angustifolium</i>	9.1 ± 0.7
<i>Salix pulchra</i>	14.0 ± 2.1
Vascular plant mean	12.6 ± 3.5
Mosses	
<i>Pogonatum alpinum</i>	9.1 ± 2.1
<i>Calliergon sarmentosum</i>	10.5 ± 3.5
<i>Dicranum angustum</i>	5.6 ± 2.8
<i>Dicranum elongatum</i>	10.5 ± 4.2
<i>Polytrichum commune</i>	11.2 ± 1.4
Moss mean	9.1 ± 2.1

similar (Tieszen 1973) and tend to approach saturation at 280 to 350 $\text{J m}^{-2} \text{s}^{-1}$ (400 to 700 nm). These saturation requirements are sufficiently high that leaves are rarely light-saturated in situ, which suggests that the entire canopy might be responsive to increased irradiance.

Individual leaves of tundra plants require very low light for carbon dioxide compensation, 5.6 to 7 $\text{J m}^{-2} \text{s}^{-1}$ (400 to 700 nm) (Tieszen 1973, Mayo et al. 1977). Under field conditions, whole shoots possessed similarly low compensation requirements (Table 4-4), especially at low temperatures. Although the respiratory capacities of these tundra plants are high, the combination of efficient photosynthesis and low daily temperatures often resulted in the maintenance of a positive carbon budget for 24 hours (Tieszen 1975). The close coupling of the daily course of carbon dioxide uptake to irradiance implies a direct dependence even during mid-day hours. This is further documented by the significant positive regression between daily carbon dioxide uptake and daily irradiance which is discussed later.

This light dependence may be mainly a vascular plant phenomenon

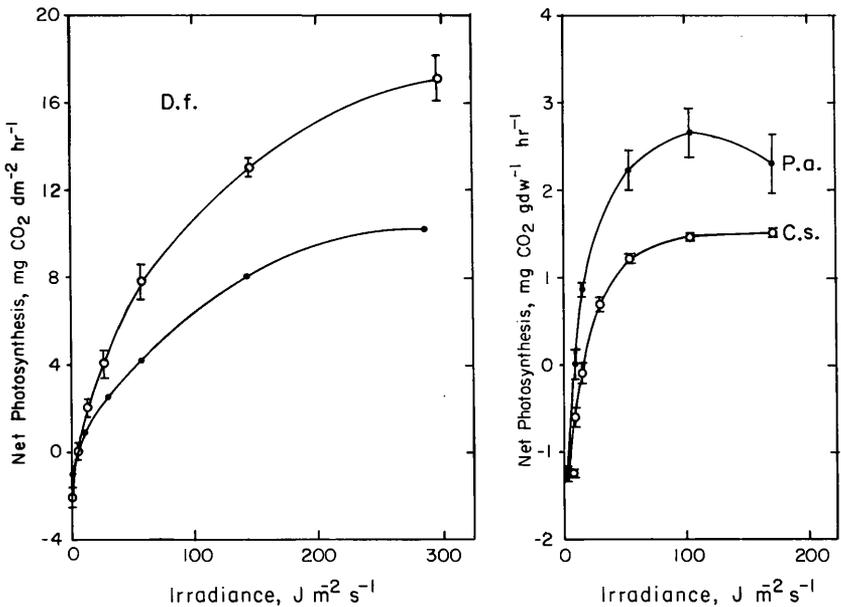


FIGURE 4-3. The response of photosynthesis to irradiance (400-700 nm) in *Dupontia fisheri* (*D.f.*), *Pogonatum alpinum* (*P.a.*), and *Calliergon sarmentosum* (*C.s.*). The curves for *D. fisheri* are from the field (\circ) and from plants grown in the laboratory at 5°C (\bullet). The curves for the mosses are from field-collected samples measured in the laboratory. Note the different vertical scales. Standard errors are shown by the vertical bars. (After Tieszen 1974, 1975, Oechel and Collins 1976.)

since arctic mosses tend to reach light saturation at lower radiant fluxes than vascular plants— $98 \text{ J m}^{-2} \text{ s}^{-1}$ (400 to 700 nm) (Figure 4-3). Mosses are generally light-saturated for most of the midday periods. The tendency for light intensities above saturation to reduce the rate of photosynthesis in *Pogonatum alpinum* may be a result of photo-inhibition or photo-oxidation of the photosynthetic apparatus (Oechel and Collins 1976). This pattern is in contrast to graminoids, which increase photosynthesis to radiation levels approaching full sunlight, and represents a major response difference between *Pogonatum alpinum*, especially populations from low light environments, and the graminoids. The different light saturation requirements result in different daily responses between mosses and vascular plants. During the season, mosses show only a slight daily dependence of photosynthesis on total daily irradiance (Oechel and Sveinbjörnsson 1978), in marked contrast to vascular plants (Tieszen 1975).

Temperature

An effective photosynthetic system at low ambient temperatures is essential for maintaining a positive carbon balance. Although mean ambient air temperatures during the growing season are less than 4°C and graminoid leaf temperatures are closely coupled to air temperatures, detailed studies at Barrow (Tieszen 1973, 1978b) and in other areas (Mayo et al. 1977) have shown a temperature optimum for leaf photosynthesis between 10 and 15°C and significant carbon dioxide uptake at 0°C . Photosynthesis in *Dupontia* is generally active until the leaf freezes, which may not occur until -4 to -7°C . However, the destruction of enlarging cells was observed at a temperature of -4°C , which usually represents the lower limit of photosynthesis. Very low temperatures are infrequent in July and do not appear to affect carbon dioxide uptake as significantly as other growth processes.

The underlying physiological and biochemical bases for the temperature response curve are not clear. All resistances in the graminoids, including leaf resistance, remained low down to 5°C (Figure 4-4). Leaf resistance did not increase at 0°C . At higher temperatures there was a slight increase in leaf resistance but the mesophyll components of resistance became significantly more important, indicating an internal diffusion or carboxylation limitation to photosynthesis. A substantial increase in light respiration may account for the net photosynthesis decrease at temperatures greater than 15°C .

Mosses also have relatively high photosynthetic rates at low temperatures (Figure 4-5). Temperature responses are similar to those observed in vascular plants with temperature optima between 10 and 19°C (Oechel

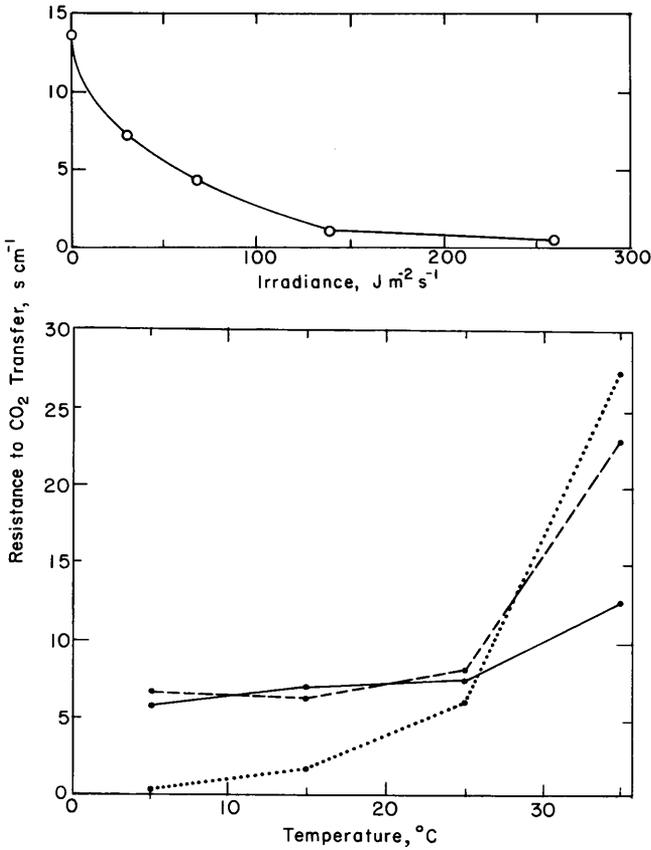


FIGURE 4-4. Relationships of the resistance to CO₂ transfer to irradiance and temperature. The resistances include leaf (stomatal and cuticular) (—), cell wall (---) and carboxylation (...). The plants were grown in growth chambers at 5°C. (Tieszen, unpubl.)

1976, Oechel and Collins 1976). Rates are only slightly decreased at 5°C. *Pogonatum* photosynthesizes at 55% of the maximum rate at 0°C. The high rates of photosynthesis at low temperatures are of obvious adaptive significance, since tissue temperatures frequently drop to between 5 and 0°C during the growing season. Continuous sunlight results in positive net photosynthesis during these periods.

Temperature optima from 10 to 19°C seem high; however, during periods of high irradiance, moss tissue temperatures exceed air temperature. In 1973, midday tissue temperatures were above 5°C 87% of the time and above 10°C 44% of the time. In 1972, which was warmer and

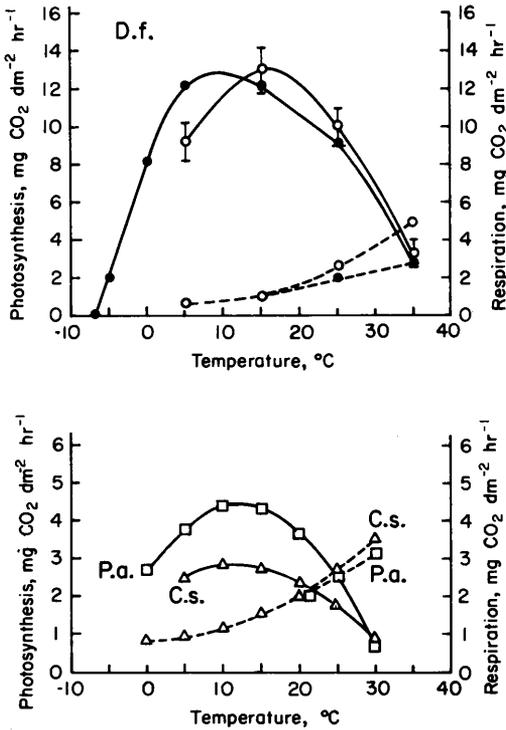


FIGURE 4-5. The response of photosynthesis (—) and dark respiration (- - -) to temperature in *Dupontia fisheri* (*D.f.*), *Pogonatum alpinum* (*P.a.*) and *Calliergon sarmentosum*. (*C.s.*). The curves for *D. fisheri* are from the field (○) and laboratory (●). The curves for *P. alpinum* and *C. sarmentosum* are for field-grown samples measured in a field laboratory. (After Tieszen 1973; unpubl.; Oechel and Collins 1976.)

drier, temperatures were above 10°C at midday 73% of the time and reached as high as 30 to 35°C. However, in 1974 tissue temperatures above 20°C were seldom measured (Oechel 1976, Oechel and Collins 1976). The broad temperature responses of arctic bryophytes make them well adapted to the wide range of tissue temperatures encountered in the Arctic. However, at least in the case of *Dicranum*, simulation modeling indicates that the relatively high values for temperature optima for photosynthesis result in a seasonal depression of photosynthesis of about 25% (Oechel et al. 1975).

Photosynthesis in vascular and nonvascular plants appears well adapted to the low temperatures, although the mechanism for this is not known. Low temperatures, therefore, must exert relatively greater effects on growth and developmental processes, possibly including respiration. At low temperatures all processes function in an integrated manner, suggesting a general adaptation to low temperatures rather than specific changes at the enzyme level.

Water

The water relations of the wet meadow are particularly conducive to bryophyte growth. Low temperatures, low radiation, and precipitation greater than evapotranspiration maintain hydrated tissues, resulting in high photosynthetic rates and avoiding tissue damage due to desiccation. The photosynthetic responses of mosses to water content reflect the water relations of the microtopographic units (Figure 4-6). *Pogonatum alpinum*, which occurs in drier areas and is a more drought-resistant species than *Calliergon sarmentosum*, reached photosynthetic compensation at 60% water content, and optimal rates were observed at 200% to 350% water content. *Calliergon*, which occurs in wetter areas including polygon troughs and the wet meadows, appears to require higher moisture contents to reach compensation (about 75% w.c.) and maximum photosynthesis (about 400 to 500% w.c.) than does *Pogonatum*. Both species generally remain hydrated, allowing photosynthesis to proceed to near maximal rates. Polygon troughs that have drained free of standing water

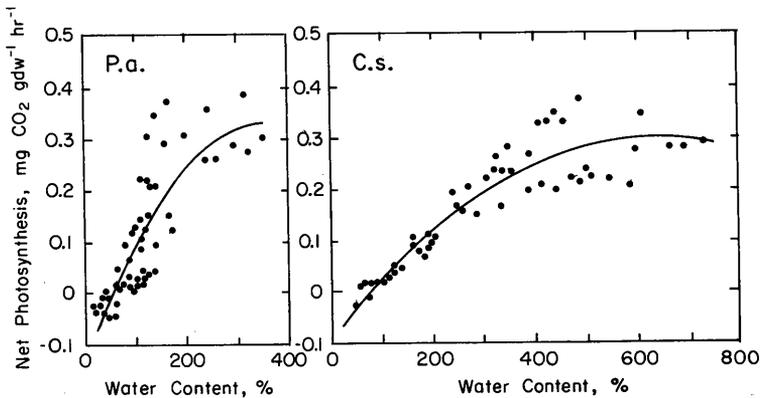


FIGURE 4-6. Response of photosynthesis to water content (percentage of dry weight) in *Pogonatum alpinum* (P.a.) and *Calliergon sarmentosum* (C.s.). (After Oechel and Collins 1976.)

and occasional summers with warm, dry periods (e.g. 1972) can result in the desiccation of mosses. However, these conditions are relatively uncommon. As indicated in the previous chapter, the vascular plants maintain low leaf resistances and generally high water potentials. Although occasional midday stomatal closure is seen, water is generally not limiting to carbon dioxide uptake in these *Carex-Oncophorus* meadow forms.

Diurnal and Seasonal Patterns of Carbon Dioxide Exchange

The daily and seasonal trends of photosynthesis integrate the response patterns of the plant to environmental variables with the plant's seasonal ontogenetic pattern. The early season pattern is characterized by positive rates of photosynthesis throughout the day in both vascular plants and mosses. (Oechel and Collins 1973, Tieszen 1975, Oechel and Sveinbjörnsson 1978). However, at the time of snowmelt the foliage area index is near zero for vascular plants. Immediately after snowmelt vascular tissues develop photosynthetic competency, elongate, and begin to produce an intercepting canopy (Tieszen 1975, Dennis et al. 1978, Tieszen 1978b). Mosses, on the other hand, have tissues that may overwinter 1 or 2 times (Collins and Oechel 1974) and can continue photosynthesizing as soon as they become snow-free, although at reduced rates. The relatively large moss biomass at the beginning of the season can result in high rates at a time when the vascular canopy is just developing (Miller et al. 1976, Oechel and Sveinbjörnsson 1978).

In all vascular species the highest values for carbon dioxide uptake on a leaf basis occur early in the season. As the season progresses (Figure 4-7), maximum values become lower, and towards the end of August they are near $5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ for all species. Earlier in the season periods with similar radiation and temperature produce substantially higher rates of photosynthesis. The response patterns for mosses (Figure 4-8) show some interesting differences from the patterns displayed by vascular plants, including more negative "night" values and depressed early-season rates in some species.

Integrating hourly values for a 24-hour period provides an estimate of daily net carbon dioxide uptake by plants. Daily totals are generally high for all vascular species, even early in the summer. Absolute amounts vary somewhat, depending upon specific light and temperature combinations, and are greatest on days of high solar irradiance. Carbon dioxide incorporation correlates more highly with daily totals of radiation than with temperature. Photosynthetic efficiencies for the entire season are about 1% for the graminoids and 1.7% for *Salix* (Table 4-5). An extrap-

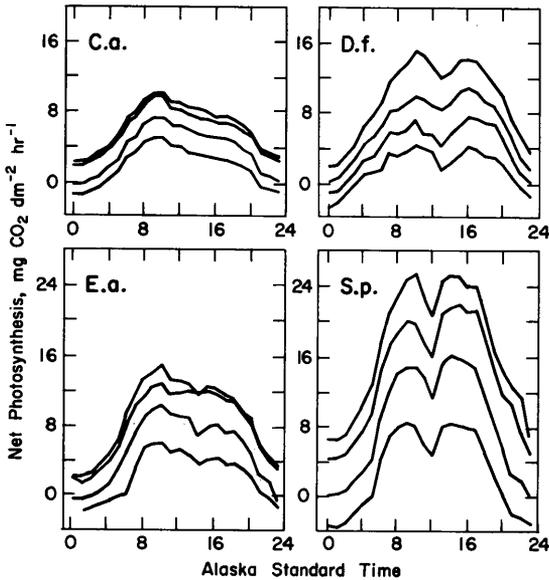


FIGURE 4-7. Seasonal progression of the daily course of net photosynthesis in 1972. The upper curve represents the period 25 June to 4 July and lower curves are at successive 10-day intervals predicted by regression equations for *Dupontia fisheri* (*D.f.*), *C. aquatilis* (*C.a.*), *E. angustifolium* (*E.a.*) and *S. pulchra* (*S.p.*). (After Tieszen 1975.)

TABLE 4-5 Mean Daily Totals of Net CO₂ Uptake by Leaves (in mg CO₂ dm⁻² day⁻¹) by Important Vascular Species Through Summer 1972 (from regression estimates of Tieszen 1975) and Efficiencies of Conversion (in parentheses, in percent)

Period	<i>Dupontia fisheri</i>	<i>Carex aquatilis</i>	<i>Eriophorum angustifolium</i>	<i>Salix pulchra</i>
25 June-4 July	235 (0.94)	149 (0.90)	215 (0.86)	401 (1.60)
5 July-14 July	190 (1.09)	142 (0.81)	186 (1.07)	361 (2.07)
15 July-24 July	163 (0.90)	149 (0.83)	196 (1.10)	318 (1.78)
25 July-3 Aug	105 (1.03)	116 (1.14)	143 (1.41)	234 (2.31)
4 Aug-13 Aug	113 (0.85)	89 (0.67)	125 (0.94)	204 (1.53)
14 Aug-23 Aug	80 (0.74)	73 (0.68)	103 (0.95)	146 (1.34)
24 Aug-3 Sept	41 (0.64)	43 (0.69)	62 (0.96)	72 (1.11)

Efficiency is the ratio of the energy fixed per unit leaf area to the intercepted irradiance per unit leaf area.

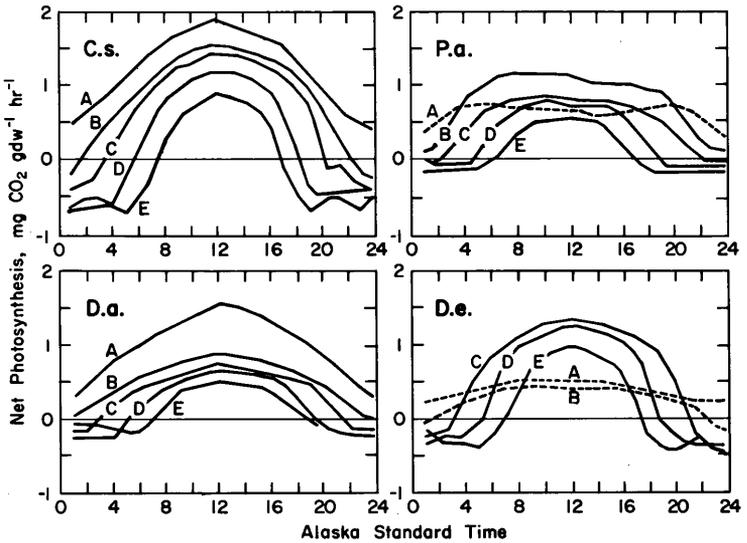


FIGURE 4-8. Diurnal patterns of CO_2 flux for alternate 10-day periods through the 1973 growing season simulated for *Pogonatum alpinum* (P.a.), *Calliergon sarmentosum* (C.s.), *Dicranum elongatum* (D.e.), and *Dicranum angustum* (D.a.). The environmental input was the 10-day average for the hour simulated. Periods began on 24 June (A), 14 July (B), 3 Aug (C), 23 Aug (D), and 12 Sept (E). (After Miller et al. 1978a.)

olation of the linear equation relating daily totals of carbon dioxide uptake to radiation suggests that for the three graminoids slightly less than $4.2 \text{ MJ m}^{-2} \text{ day}^{-1}$ is required to compensate for daily aboveground respiratory carbon dioxide losses. The value is somewhat greater than the compensation points actually measured during night runs, and may suggest a higher respiration rate during daytime than at night.

Late in the season the combination of shorter photoperiods, reduced irradiances, a developing senescence, and self shading results in a decrease in the daily incorporation of carbon dioxide. Thus, by 25 August, daily photosynthetic totals for some graminoids are well below $50 \text{ mg CO}_2 \text{ dm}^{-2} \text{ day}^{-1}$.

A multiple linear regression analysis (Tieszen 1975) suggests that in all species there is a highly significant change in photosynthesis which is independent of the seasonal changes in radiation for the entire plant, which could be caused by an increase in the proportion of supporting or other non-chlorophyllous tissues, developing senescence, or other phenomena. The overall seasonal trend of photosynthesis is one of decreasing

diurnal amplitude and of decreasing photosynthetic input. However, photosynthetic efficiency computed on a land area basis remains high and attains its maximum between the middle of July and the first week in August, which agrees with tiller carboxylation data (Figures 4-2 and 5-16). Maximum efficiencies are above 1% for the graminoids and attain 2.3% for *Salix pulchra*.

Early in the season, while light intensity is high and often above saturation, mosses under simulated canopies show rates of carbon dioxide incorporation similar to those of mosses growing in open areas. During this period, protection from photoinhibition and higher rates at midday under reduced sunlight offset the effects of reduced levels of carbon dioxide incorporation during the evening. However, as the light intensity decreases, especially during the period around solar midnight, and as dark respiration increases, relative rates of carbon dioxide incorporation by mosses under the canopy decrease. When midday radiation values are high, advantage is conferred through shading, but if midday radiation values are below saturation, there is a lowering of photosynthetic rates at midday in response to shading. During evening hours photosynthesis is also lowered by shading, often below the compensation point, and the period of dark respiration is increased as a result.

The mosses differ from vascular plants in their levels of energy capture. The mosses are much lower in overall efficiencies than are vascular plants, except under periods of low radiation when the percentage of energy capture increases. They also differ from vascular plants in that mosses show no decreasing efficiencies at the end of the season resulting from senescence. Moss photosynthesis shows less seasonal variation than does vascular plant photosynthesis, but both have equally marked diurnal changes. Light intensity as well as water status are important controlling factors in moss photosynthesis.

Other Factors

Other factors could potentially influence photosynthesis and alter the daily and seasonal courses just described. Plant pathogens, for example, commonly inhibit photosynthesis by damaging chloroplasts and/or by destroying proteins. Pathogens are not obvious on plant species of the tundra at Barrow. One of the most striking impressions given by the vegetation is the absence of leaf lesions. Root nematodes are present and fungi become active after the leaf senesces, but neither of these relationships affects photosynthesis directly. Grazing may also influence the photosynthetic response patterns, but mainly by altering the relative number of young, mature and senescent leaves. These phenomena and the role of acclimation are discussed in the following sections.

SIMULATION ANALYSIS OF PHOTOSYNTHESIS AND VASCULAR CANOPY INTERACTIONS

Models

Vascular Plant

Previous discussions of photosynthesis have considered the physiological responses of single leaves, tillers or moss mats to independent biotic and abiotic factors. In plant communities these factors do not operate independently. They result from complex feedbacks involving regional climate, canopy structure, and the process of carbon dioxide uptake. In an attempt to quantify these relationships and to determine their relative and absolute importance, they have been incorporated into an interactive model called Stand-Photosynthesis which is basically an outgrowth of models discussed earlier (Miller and Tieszen 1972, Miller et al. 1976, Stoner et al. 1978b).

The stand photosynthesis model is based on the fluxes of carbon dioxide, water, and heat for a single leaf located in the canopy in profiles of direct and diffuse solar and infrared radiation, wind, air temperature, and vapor density. The canopy consists of horizontal strata of live and dead leaves, stems, and reproductive structures. The vegetative canopy produces profiles of solar and infrared radiation, by intercepting, absorbing, and emitting radiation, which are calculated for each stratum. Similarly, the canopy effects on wind, air temperature, and humidity are

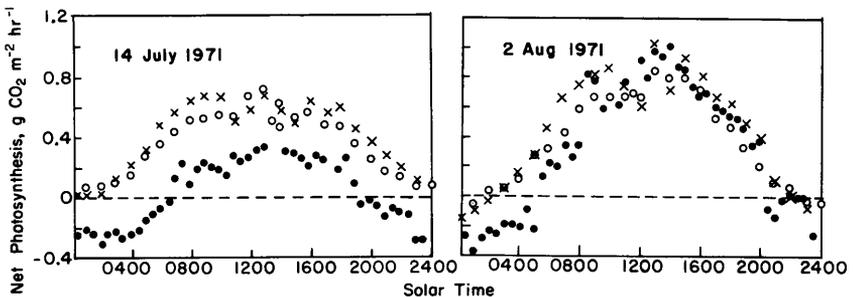


FIGURE 4-9. Comparison of net CO_2 exchange from field cuvette (\circ), simulation (\times), and aerodynamic estimates (\bullet). The aerodynamic data represent flux from the atmosphere only. The cuvette measurements and simulations are for vascular plants. Cuvette data from Tieszen (1975), aerodynamic data from Coyne and Kelley (1975), simulations from Miller et al. (1976).

calculated as described previously. The energy budget is solved for each stratum, and the partitioning of energy exchange by convection and transpiration is determined for stems and leaves. Transpiration is the resultant relative saturation deficit which affects leaf water potential and thereby leaf resistance and the carbon dioxide diffusion pathway. Photosynthesis on a leaf area basis is calculated for sunlit and shaded leaves and stems in each stratum. In this model the internal resistances depend on solar radiation and temperature.

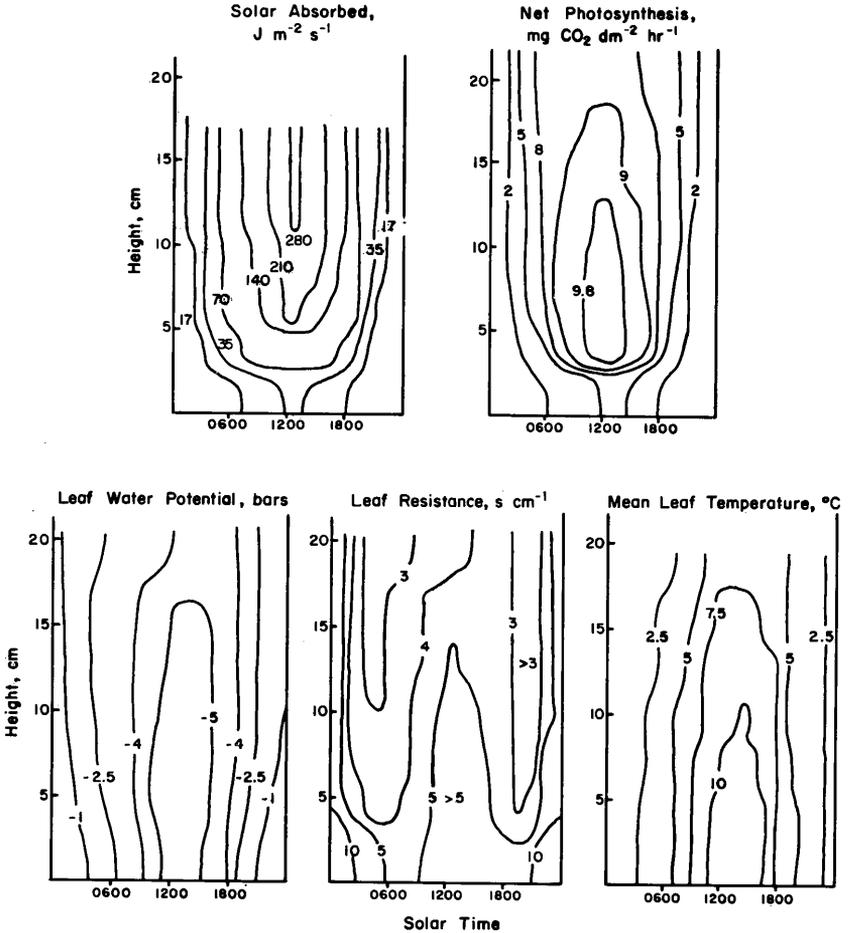


FIGURE 4-10. *Isopleths showing the simulated daily course of various plant responses to environmental conditions through the canopy for a 5-day period beginning 15 July 1971. (After Miller et al. 1976.)*

The output for the canopy model was validated with production data (Miller and Tieszen 1972) and more recently with photosynthesis data from both field cuvette experiments and an assessment of community carbon dioxide exchange (Miller et al. 1976). Daily courses were generally similar (Figure 4-9) as were the estimates of seasonal incorporation. Production data were simulated for various periods throughout a growing season and, in some cases, for a variety of seasons. Sensitivity analyses of several environmental parameters were made with a standard day (Figure 4-10) that represents the mean input data for the 5-day period beginning 15 July 1971. The standard day represents midseason conditions in 1971; mean temperatures and solar radiation used in the model are near the means for the four years of the field program.

Moss

The moss simulation model is similar in concept to the vascular plant model (see Miller et al. 1978b). Photosynthesis and transpiration follow from the solution of the energy budget equation, with the inclusion of appropriate physiological relations. The input climatic data consist of solar and infrared irradiance, air temperature, air humidity and wind speed. The vascular canopy is composed of leaves, stems and standing dead material of different species, each defined by inclination and by vertical profiles of area per unit area of ground. Solar and infrared radiation from the sun and sky are intercepted by the canopy and produce profiles of direct, diffuse reflected solar, and reflected infrared radiation within the canopy. The air temperature and humidity above the canopy at the moss surface interact with the canopy structure, wind profile, and radiation profiles to produce profiles of air temperature, humidity and leaf temperature.

At the moss surface the receipt of net radiation is balanced by heat exchanges due to convection, evaporation and conduction. The convective heat exchange occurs by turbulent exchange of air from the surface across a surface boundary layer and across a bulk canopy air layer to a reference height in the canopy. Surface evaporation is related to the turbulent exchange of water vapor across the surface boundary layer and bulk canopy air layer.

Moss photosynthesis is related to solar irradiance, tissue temperature and water status. Solar and infrared irradiance, air temperature, humidity, and wind velocity affect the plant water status through their effect on leaf temperature and transpiration. The plant water status influences the rates of transpiration and photosynthesis through their common resistance to water and carbon dioxide diffusion. Water, in the form of precipitation and dew, that is not intercepted by the vascular

canopy is added to the moss surface water film. Water flows between the green moss surface and the non-green moss and peat layers below. Surface water can be evaporated directly or absorbed into the moss tissue, to be lost by transpiration later.

The seasonal progression of microclimate and production was simulated using a standard set of climatic conditions and deviations from the standard. The standard input climate is based on climatic and microclimatic data collected at the Biome research area during summer of 1973. Climate data were adjusted using long-term records to produce two other sets of conditions which were each 3 standard deviations above or below the standard temperature conditions. The two contrived climates are hereafter referred to as hot and cold. The microclimatic data from 1973 have been used in other studies (Ng and Miller 1975, Stoner and Miller 1975, Miller et al. 1976, Ng and Miller 1977, Stoner et al. 1978b) and were used here as the standard case to aid in interpreting the results.

Simulation Results

Temperature Relationships

Analyses suggest that the vascular plant photosynthetic system has adapted to function at near maximal capacities under existing temperatures of the coastal tundra at Barrow while maintaining a leaf temperature optimum above mean ambient temperatures (Figure 4-11). Large amounts of leaf area occur in positions of the canopy where temperatures are ameliorated at times of the day when irradiances are high enough for carbon dioxide uptake to respond to temperature. Furthermore, since within-season temperature changes are small, the results suggested that seasonal acclimation responses, i.e. compensatory shifts in the response curve, are not necessary to maintain high daily photosynthesis rates. Strong acclimation responses have not been seen in the Barrow tundra plants (Oechel and Sveinbjörnsson 1978, Tieszen 1978b).

As the temperature optimum for photosynthesis increases, the stratum which supports the highest photosynthetic rates on a leaf area basis shifts to lower levels in the canopy (Figure 4-12). However, the total daily photosynthesis rate of each stratum remains similar, because strata with high irradiance and potentially high photosynthetic rates have less leaf area than do strata at the base of the canopy. The model simulations suggest that dwarf shrubs and cushion plants should be characterized by higher optimum temperatures for photosynthesis than the graminoids, which are more closely coupled to ambient air temperatures.

In part, plants are capable of effective photosynthesis because the response curves are broad enough that with an optimum of 15°C rates

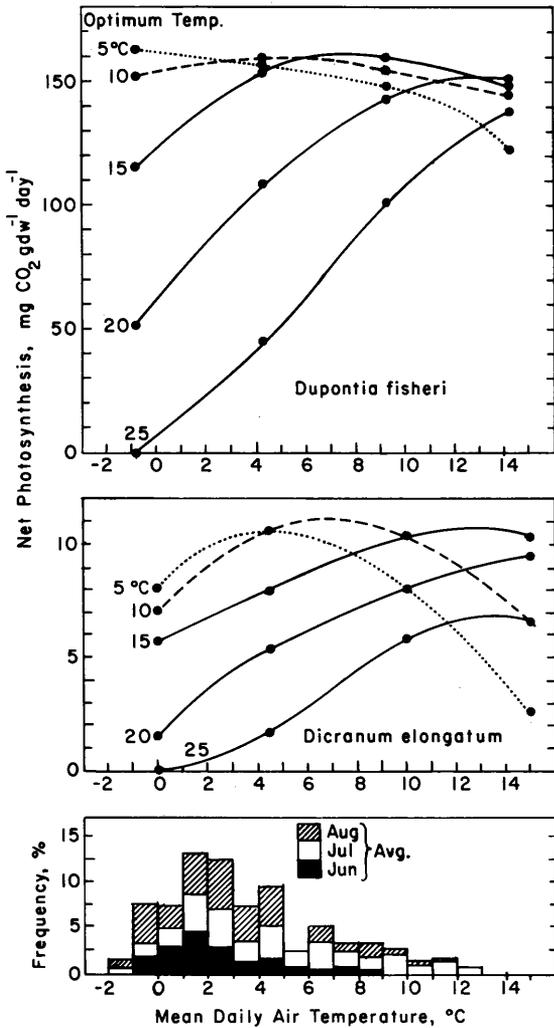


FIGURE 4-11. The simulated effect of various temperature optima for photosynthesis on daily net photosynthesis of *Dupontia fisheri* and *Dicranum elongatum* at varying mean daily air temperatures. Also presented is the frequency of days with the indicated mean temperatures during 15–30 June, July and August, 1970–73. (After Oechel et al. 1975 and Miller et al. 1976.)

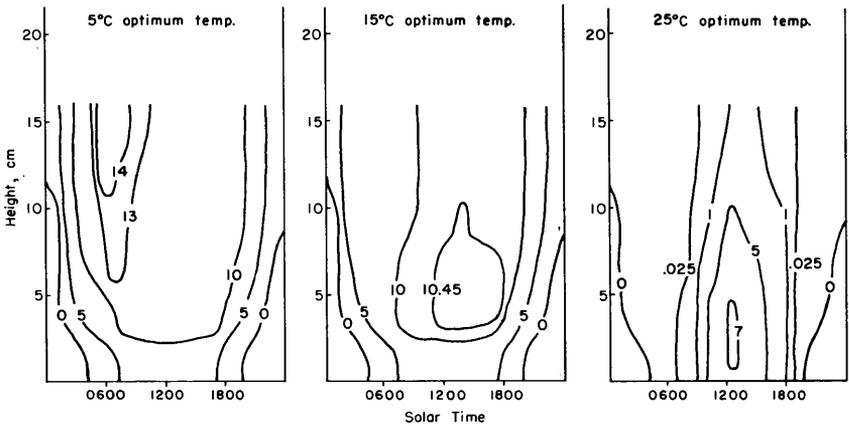


FIGURE 4-12. *Isopleths of simulated net photosynthesis (mg CO₂ dm⁻² hr⁻¹) through the day at different levels in the canopy, using the stand photosynthesis model with different temperature optima. (After Miller et al. 1976.)*

are still positive at 0°C. The significance of the breadth and shape of the response curve is illustrated by simulations in which the curve was enhanced or depressed at 0°C. When the response at low temperatures was increased so rates at 0°C were increased 100%, the daily increase was only 7%. When the rates were decreased by 50% at 0°C, daily photosynthesis was reduced only 3%. If, however, the curve was depressed so carbon dioxide uptake at 0°C was zero, daily uptake was reduced 27%. Thus a photosynthetic capability at 0°C is very important, and it appears that the *Dupontia* response curve is well-adapted to prevailing temperatures.

Carbon dioxide uptake is much more temperature-sensitive in mosses than in graminoids. In simulations where the temperature optimum for photosynthesis is varied and the shape of the response surface held constant, a temperature optimum of 5°C yields the highest uptake rates for the most frequently observed temperatures 1–3°C (Figure 4-10). Uptake is suppressed only slightly at a temperature optimum of 10°C under these conditions. However, temperature optima of 15°C and higher result in large depressions in carbon uptake at ambient temperatures below 10°C. The high temperature optima typical of the mosses result in significant losses of carbon. For example, the observed temperature optima of 11 to 19°C in *Dicranum* result in a seasonal carbon uptake 25% lower than that possible with lower optimum temperatures (Figure 4-13) (Oechel et al. 1975). Other moss species at the Biome research area show similar patterns (Oechel 1976, Oechel and Sveinbjörnsson 1978). The temperature optimum in *Dicranum elongatum* does not acclimate season-

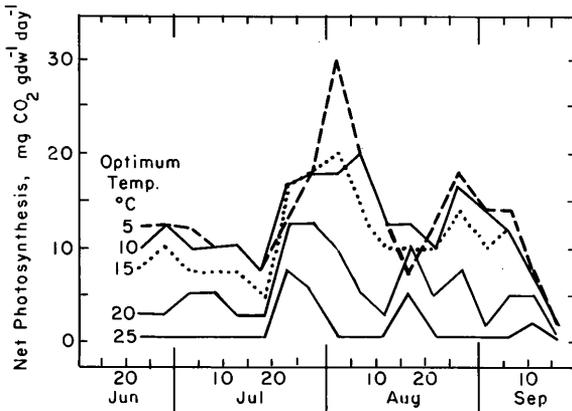


FIGURE 4-13. The simulated effect of different temperature optima on the seasonal course of net photosynthesis in *Dicranum elongatum*. The environmental input data are from 1973. (After Oechel et al. 1975.)

ally in a manner that would maximize carbon uptake, despite the fact that the low temperature optima necessary to maximize carbon uptake in *Dicranum* have been observed in *Dicranum fuscescens* in the Subarctic (Hicklenton and Oechel 1976). The controls on low temperature acclimation are not understood. The carbon uptake benefits of such acclimation or genetic adaptation are known, but the costs are not.

Because of the temperature sensitivity in mosses, they should be affected more by climatic temperature changes than are the vascular plants. Compared to the standard climate, photosynthesis in the simulated cold climate described above decreased from 22% in *Dicranum* to 72% in *Calliergon*. Under the hot climate photosynthesis increased slightly in *Dicranum*, relative to the standard year. Photosynthesis decreased in *Calliergon*, because of water stress induced by the higher temperatures. Although mosses are more temperature-limited than are vascular plants, increased temperatures may reduce the success of certain species of moss by creating an unfavorable moisture balance (Stoner et al. 1978b).

Maximum Rates and Competency

Simulations show that *Dupontia* is very sensitive to the light-saturated rate of photosynthesis (Figure 4-14). Doubling the rate of light-saturated photosynthesis results in a 58% increase in daily uptake of carbon, whereas a reduction of the saturated rate to 25% results in a reduc-

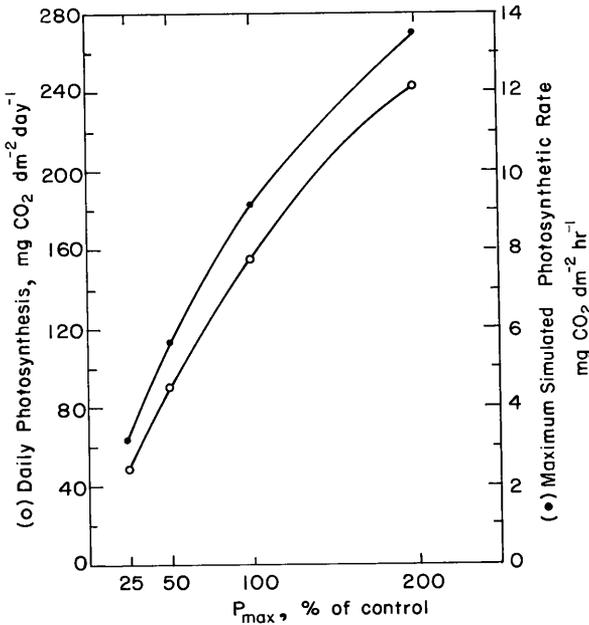


FIGURE 4-14. Simulations of the effect of the light-saturated rate of photosynthesis (P_{max}) on daily photosynthesis and maximum simulated rates using conditions for the standard day.

tion to 32% of the control rate. As was indicated earlier, one of the compensatory adjustments of these vascular plants is the maintenance of photosynthetic rates comparable to temperate region plants. The model assumes maximum competency in all photosynthetic leaves, an assumption which leads to at least a slight overestimate of uptake. The justification for this assumption was that developing leaves with incomplete competency are located near the base of the canopy where irradiance is reduced; the error resulting from light-saturated responses is therefore minimized.

Irradiance

The sensitivity of daily photosynthesis to daily irradiance (Figure 4-15) illustrates that the mean daily photosynthetic rate approaches saturation near 25 MJ m⁻² day⁻¹. *Dupontia*, therefore, approaches maximum daily photosynthesis rates at the upper range of daily intensities received. For major portions of the season the leaves are light-limited and would

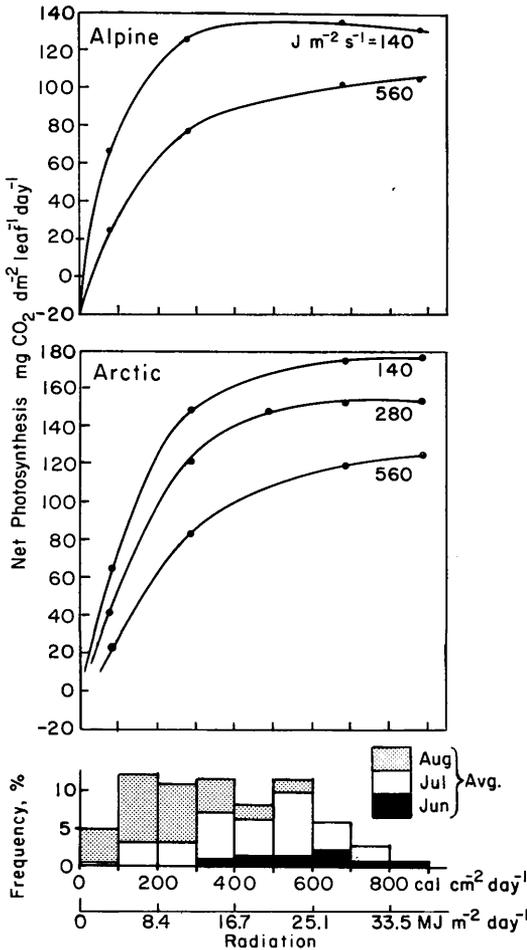


FIGURE 4-15. *The simulated response of daily total net photosynthesis to daily irradiance and saturation irradiance (indicated below curve). Also indicated is the frequency of daily irradiances for 15-30 June, July and August 1970-73. (Other input = standard day.) Simulations of the effects of varying requirements for saturation are also shown. (After Miller et al. 1976.)*

remain so even if they saturated at 140 J m⁻² s⁻¹. In the alpine similar response curves and equivalent daily total irradiance result in less carbon dioxide uptake because at solar noon, when the irradiances are substantially greater, plants become saturated, and water stress often develops.

Vapor Density, Soil Water Potential, and Root Resistance

Cuvette data and the simulations indicate that water stress develops to a sufficient extent to cause some stomatal closure and therefore occasional reductions in the photosynthesis of vascular plants. However, the

field data and vascular plant simulations suggest that such water stress occurs infrequently and only when leaf temperatures and/or irradiances are significantly higher than the mean. *Dupontia* may have allocated sufficient resources to root absorptive tissue to meet the demands of the evaporative leaf surfaces.

The water vapor density gradient is one of the factors determining the rate of water loss. The gradient is normally small because the air is nearly saturated and the leaves are close to air temperature. Simulations, in which air water vapor density was varied from -40% to +30% of ambient, indicate a slight sensitivity of -9% to +9% change in photosynthesis to changes in the water vapor density gradient. This effect was related to lower leaf water potentials and higher leaf resistances as the water vapor density gradient increased. Transpiration losses also increased as the gradient increased, to the maximum simulated, resulting in an increase in water loss of 42% in the upper part of the canopy, 26% in the center, and 21% at the bottom. The greater increase at the top of the canopy was because the gradient of water vapor density from the air to the leaf became more important than the higher leaf temperatures at the bottom of the canopy.

The slight increase in leaf resistance and the associated slight decrease in photosynthesis when transpiration changes are large suggests that root resistance in *Dupontia* is small relative to the water requirements. Increasing root resistance by 50% results in less than a 6% reduction in daily photosynthesis. The reduction is caused by a midday decrease of -2.6 to -3.8 bars in leaf water potential at the top of the canopy and a decrease of -3.7 to -4.9 bars at the canopy bottom. However, leaf water potentials increase to standard day values near solar midnight as the plant regains its water deficit. These simulations strongly suggest that *Dupontia* is sensitive to periods of high water demand but that it can normally supply the amount of water required to keep stomates open. Although this is in agreement with data for *Carex* from both Barrow and Devon Island, it contrasts sharply with *Dryas* (Mayo et al. 1977), which shows decreased rates of uptake, associated with low water potentials, at high temperatures.

Calliergon is more sensitive to a decrease in soil moisture levels than are the other moss species analyzed. For *Dicranum elongatum*, *Dicranum angustum* and *Pogonatum alpinum*, simulations indicate a 25% decrease in photosynthesis associated with a 10-bar decrease in soil water potential (from 0 to -10 bars). Under the same conditions, *Calliergon* undergoes an 80% decrease in photosynthesis. *Calliergon* appears to be much more dependent than the other species on a liquid water film and on standing water to maintain a beneficial moisture status (Figure 4-16).

Calliergon takes up water poorly from depth and displays low resistances to water loss when compared to the other species. In the *Dicranum*

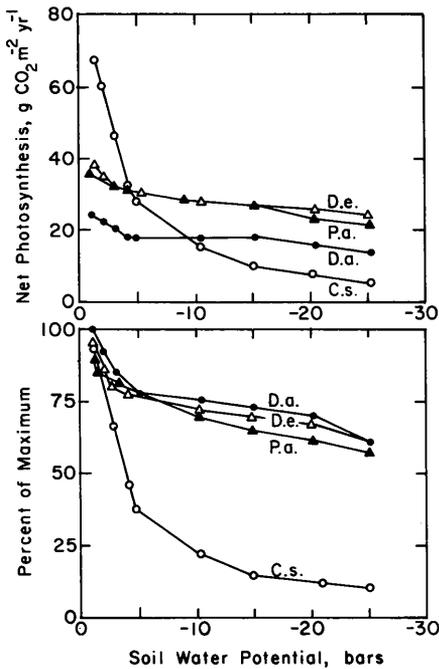


FIGURE 4-16. Simulated annual net photosynthesis at different soil water potentials expressed in absolute terms and as a percentage of maximum for four arctic moss species: *Pogonatum alpinum* (P.a), *Calliergon sarmenosum* (C.s.), *Dicranum elongatum* (D.e.), and *Dicranum angustum* (D.a.). (After Miller et al. 1978a.)

species examined, the mat growth form plays an important role in water retention by increasing the apparent air resistance to water loss and in aiding water uptake by maintaining a nearly saturated environment at the base of the photosynthetically active zone. In *Pogonatum*, xeromorphic adaptations of tissues that are deeply rooted in the substrate and are efficient in translocating moisture are important in maintaining advantageous moisture balances under xeric conditions (Miller et al. 1978a).

Calliergon's susceptibility to xeric conditions is shown by the effect of a hot season. At soil water potentials of -5 bars and less, *Calliergon* shows net carbon dioxide loss in the hot climate. By comparison, *Dicranum* and two vascular plant species show little suppression by photosyn-

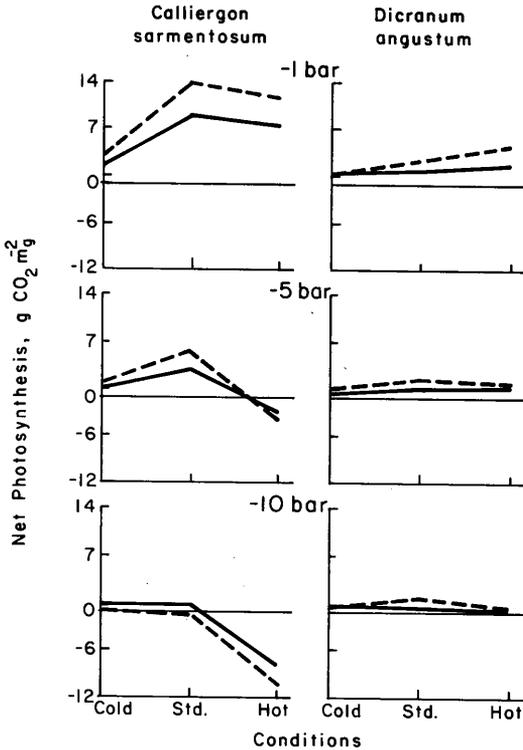


FIGURE 4-17. Annual net photosynthesis for *Calliergon sarmentosum* and *Dicranum angustum* at different substrate water potentials for three simulated seasons and conditions ("cold," standard, "hot") for moss in full sun (—) and under the canopy (---). (After Stoner et al. 1978b.)

thesis in the hot climate as compared with the standard climate (Figure 4-17).

Canopy Architecture Effects

Previous simulations and field data have shown the importance of physiological parameters and the dependence of photosynthesis on certain environmental variables. Since these variables are influenced by structural features of the plants as well as by physical features of the canopy, their potential influence on photosynthesis needs to be understood.

The graminoid leaf, especially in the single-shooted growth form, is closely coupled to air temperature. The temperature correspondence is mainly a result of the low boundary layer resistances associated with narrow leaves and the generally turbulent wind conditions of the Biome research area. As leaf width increases, leaf temperatures should increase and more closely approach the temperature optimum for photosynthesis. However, at the same time, the water vapor density gradient between the air and the leaf, and the transpiration rate, increase, resulting in a potentially large water deficit and in a decrease in leaf water potential. Altering leaf width from 4 to 15 mm under standard conditions has no effect on carbon dioxide uptake. The radiation load is low; therefore the leaf temperature remains close to the air temperature.

The rate of photosynthesis for any given leaf will also vary as a function of its position in the canopy, since irradiance and leaf temperatures are markedly influenced by the canopy. Leaves at the top of the canopy protrude above the standing dead material and are occasionally light-saturated although they are usually at low temperatures. The trends are reversed for the leaves positioned at the bottom of the canopy. Because of the effect of canopy density on thermal and radiance properties, the foliage area index will determine the range of photosynthesis rates by all leaves. Increasing live foliage area will reduce available light, since the absorptivity of visible wavelengths by live leaves is high. Mean photosynthetic rates should decrease, although stand photosynthesis should increase up to a maximal foliage area index. Beyond this point self-shading should result in a decrease in carbon dioxide uptake. Mean leaf photosynthetic rates decrease as the live foliage area index exceeds 0.74 (Figure 4-18). With a live foliage index of 1.0, a common upper value, mean leaf rates are decreased to 14% of the open canopy, a decrease which results principally from the absorption of radiation by the live leaves, resulting in high light extinction in the canopy. Thus, with a foliage area index of 1.0 or higher, relatively few leaves in the 10 to 15 cm stratum are saturated and then for only 1 hour around solar noon. Although mean photosynthetic rates on a foliage area basis continue to decrease, community uptake increases up to a foliage area index of from 3 to 6. With a foliage area index of 6 as much as $34 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ is assimilated. In terms of carbon dioxide exchange, a foliage area index as high as 8, which has been measured (Dennis et al. 1978), can be supported by the graminoid vegetation. With such a high foliage area index the lower leaves are in a negative carbon balance. Canopy architecture becomes increasingly important in affecting photosynthesis at high foliage areas. In the standard canopy with a dead area index of 1.24, photosynthesis increases at all times of the day as leaf inclination increases.

One of the characteristic features of graminoid canopies, especially in the absence of lemmings, is the accumulation of standing dead mate-

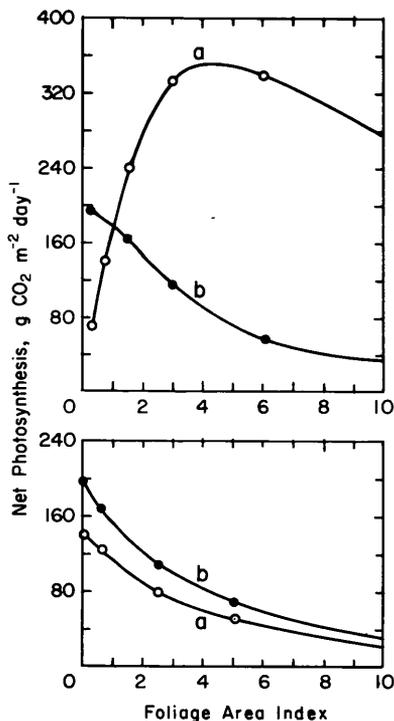


FIGURE 4-18. A simulation illustrating the effect of increasing live (upper graph) and dead (lower graph) foliage area index on photosynthetic rates per unit ground area (a) and per unit leaf area (b). Other input is for the standard day. In the upper graph, ground area rates are the sum of all vascular plants. In the lower graph ground rates are for *Dupontia* only with a foliage area index of 0.125 in the presence of a total live foliage area index = 0.744 plus a dead foliage area index given. (After Miller et al. 1976.)

rial (Tieszen 1972b). As an intercepting and emitting component in the canopy, the effect of the accumulation of standing dead material on photosynthesis and soil thaw could be quite significant. But because of the decreased absorptivity of the dead material its effects on photosynthesis are less than that of live material (Figure 4-18). In the simulations a dead foliage area index of 5.0, 2 to 3 times that usually measured in the field, results in a 64% reduction of photosynthesis. Accumulation of dead material has a depressing effect on photosynthesis, which is minimized as long as winter snows and some decomposition reposition this potentially intercepting material at the bottom of the canopy. At the bottom of the canopy, however, the effects of dead material will be greater in *Dupontia* than most other species, since *Dupontia* has more leaf area near the base of the canopy.

Canopy relationships also have profound effects on mosses. A vascular plant canopy under moist conditions reduces the carbon dioxide uptake by mosses from the levels simulated in the open. The canopy reduces radiation and temperature at the moss surface, which would tend to decrease photosynthesis, especially during periods of low radiation. The canopy also reduces turbulence and results in a lowered vapor density gradient between the moss and the air. Therefore the reduction in car-

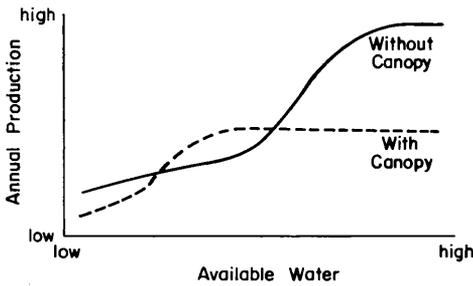


FIGURE 4-19. A diagrammatic summary of the effect on moss production of the vascular canopy along a moisture gradient. (After Stoner et al. 1978b.)

bon dioxide uptake due to the lowered irradiance and temperature may be more than compensated for by the increased photosynthesis because of the improved tissue moisture status.

The result of an interplay between the environment in the vascular canopy and the moss-water relation is a changing relationship of moss production and canopy cover along a moisture gradient (Figure 4-19). The simulations indicate that at high levels of available moisture, there is no water limitation, and mosses are most productive in the absence of a vascular plant canopy under full ambient radiation. Production is limited by light, and plant resistances to gas exchange are important. At moderate moisture availability, a vascular plant canopy increases moss production by decreasing evaporation by more than the amount lost through interception. At low levels of available moisture, mosses are most productive in the absence of a canopy. In this situation, a canopy intercepts much of the precipitation available and mosses are seldom hydrated. Under these conditions, brief periods of light precipitation are not effective in penetrating the canopy to hydrate the moss tissue (Stoner et al. 1978b). These results should be viewed as speculative because of uncertainties in the interception model and in the water uptake relationships in mosses. The water relationships of mosses are poorly understood compared with the level of understanding of moss photosynthesis.

Grazing

Grazing is an important biotic interaction that affects the photosynthetic rates and patterns described above. In the absence of a peak in the lemming population, the grazing pattern in the coastal tundra at Barrow results in the removal of some vegetation, usually as tiller units or shoots, near the moss surface. Thus, photosynthetic tissues at various stages of photosynthetic competency are removed and consequently seasonal production is reduced. Heavy grazing, especially in late winter or early spring, removes the canopy, including standing dead and live material. Thus, the microenvironment surrounding the photosynthetic leaves

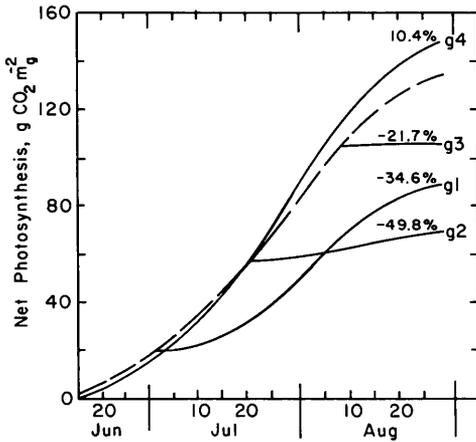


FIGURE 4-20. Simulated responses of a *Dupontia fisheri* tiller to grazing. Leaf photosynthetic rates were estimated for 1971 environmental data and 1972 leaf growth data. Grazing was simulated by the complete removal of photosynthetic tissue. The numbers represent the percent change in seasonal CO₂ uptake resulting from four grazing events.

is altered dramatically. Leaves near the moss surface are exposed to more intense radiation and have lower temperatures, since convectational losses are greater (Figure 4-20).

Early season grazing by lemmings has little effect on photosynthesis in *Dupontia* because photosynthetically competent tissues are not available to be harvested and because mean photosynthetic rates of new tissues increase in a more open canopy. Midseason grazing, however, is very detrimental to seasonal carbon dioxide uptake. In plants grazed in midseason, carbon dioxide uptake was 42% less than in ungrazed plants. This results mainly because photosynthesis is limited by the available leaf area, and grazing at midseason removes photosynthetic tissue at a time when its contribution is greatest. In addition to the major effect on ecosystem carbon balance, grazing reduces storage reserves (Tieszen and Archer 1979), which will affect plant performance for one or more growing seasons. We have not assessed the occasional severe grazing pressure which can result in rhizome and stem base destruction. This may have dramatic effects on population structure.

Seasonal Course of Carbon Dioxide Uptake

Primary production varies both spatially and from season to season. Since the rate of net photosynthesis is not strongly depressed because of the low temperatures, other factors must account for major portions of the variation. The primary factors limiting primary production or canopy development appear to be: 1) the length of the growing season (see Figures 3-1, 3-2), which is dictated by the duration of snow cover and related to topography and seasonal radiation patterns, and 2) the alloca-

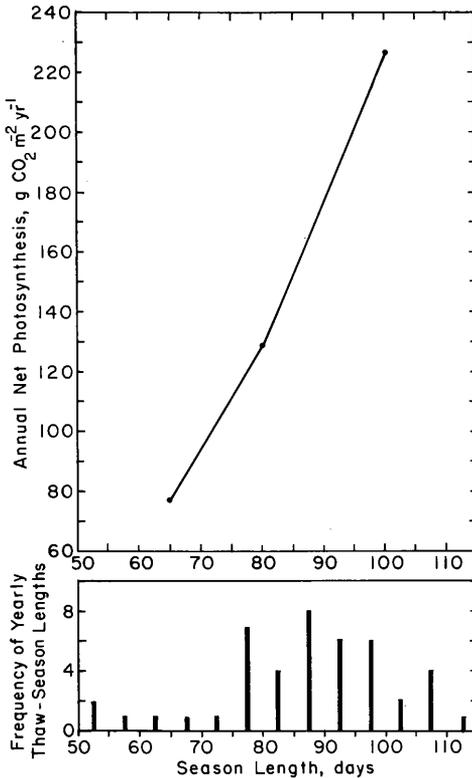


FIGURE 4-21. The simulated effect of season length on annual net photosynthesis for *Dupontia fisheri* in the canopy of the *Carex-Oncochlopus meadow*. The frequencies of yearly thaw season lengths of periods with above 0°C mean daily temperatures for the years 1922 to 1973 are given also. Other input is for the standard season. (After Miller et al. 1976.)

tion of carbohydrates for leaf production which, in the coastal tundra at Barrow, is controlled to a large extent by the availability of soil nutrients, principally nitrogen and phosphorus. The spatial pattern of above-ground primary production reflects these topographic and nutrient relationships; and the magnitude of production depends upon climatic factors. Simulating the seasonal courses of carbon dioxide uptake for *Dupontia fisheri* can be used to assess the response of the graminoids to some of these variables.

Season length was simulated by initiating the season earlier or later than the 15 June date used for 1971. Environmental factors and rate of canopy development were assumed to be the same as in the 1971 simulation. Under these conditions, there is a marked effect of season length on total carbon uptake (Figure 4-21), primarily because plants can more fully utilize the high levels of radiant energy at the time of the solstice. During the simulated long season, *Dupontia* attained a foliage area index of 0.22 on 4 August, nearly 30% greater than the standard season. Conversely the foliage area was reduced by 30% during the short season. Unfortunately, long-term field observations covering this range of season lengths are not available for comparison with productivity estimates. Production and carbon dioxide uptake are increased in the short season

if the canopy delays senescence and continues to develop until a standard canopy is attained. The simulations and an analysis of the seasonal course of CO₂ uptake (Figures 3-1, 3-2) suggest that production is very sensitive to the rate of allocation to leaves. We have estimated (Tieszen 1978b) that a 25% increase in leaf production results in a 45% increase in CO₂ uptake. Thus, it appears that both the date of initiation and the pattern of canopy development are among the most important factors controlling CO₂ uptake and primary production.

Variations in the amount of radiant energy received during a season of constant length affect seasonal uptake and production. An increase in incoming solar radiation equivalent to one standard deviation results in a 13% increase in uptake.

The overall sensitivity of the carbon dioxide uptake system to temperature variations is much less significant. Decreasing temperatures by one standard deviation results in a mean temperature of +3.0°C, or 2.3°C lower than the long-term mean, but reduces carbon dioxide uptake by only 1.4%. Early in the season, low temperatures inhibit carbon dioxide uptake on a leaf basis. However, the small foliage area at this time makes its effect on the total season budget nearly negligible. Increasing temperatures by one standard deviation increases carbon dioxide uptake by only 0.4% (Tieszen 1978b).

In order to determine the effect of several factors interacting simultaneously, two seasons were simulated, one warmer and brighter than the mean and one colder and with less irradiance than the mean. The warmer season with higher irradiance resulted in an 11% increase in carbon dioxide uptake whereas the colder season with less irradiance reduced carbon dioxide uptake by 17%. If these patterns are associated with changes in rates of allocation, the effect is great. When the warmer, brighter season was combined with a 20% increase in live foliage area index, net photosynthesis increased 53%. When the colder, darker season was combined with a similar decrease in the foliage area, net photosynthesis decreased by 41%. The carbon dioxide uptake system, however, appears relatively insensitive to temperature, is quite dependent on radiant energy, and is very dependent on allocation to photosynthetic tissue. The sensitivity of allocation to various environmental factors must now be understood because photosynthesis, per se, functions quite well at the prevailing ambient temperatures.

SUMMARY

The photosynthetic rates of plants of the coastal tundra at Barrow show consistent patterns among growth forms that are comparable to similar plant types in more temperate zones. Maximal rates of carbon

dioxide uptake are greatest in leaves of short duration, for example grasses and forbs, and are lowest in the evergreen dwarf shrubs, mosses and lichens. The dominant graminoids attain rates around 17 to 21 mg CO₂ dm⁻² hr⁻¹ and the mosses 1 to 5 mg CO₂ gdw⁻¹ hr⁻¹.

Leaves rapidly develop photosynthetic competency following snow-melt, and maximal rates are highly correlated with carboxylation activity. The continuous irradiance and a relatively open canopy result in high daily rates of carbon dioxide uptake. Net rates for whole plants are highest in early July, 200 to 400 mg CO₂ dm⁻² hr⁻¹, and decrease progressively until early September as senescence progresses, self-shading increases, and the irradiance decreases following the summer solstice. Efficiencies of energy conversion are above 1% for the graminoids and are as high as 2.3% for *Salix pulchra*. The net seasonal incorporation is 602 g m⁻², a field value corroborated by the aerodynamic assessment of carbon dioxide exchange and the simulation model. Approximately two-thirds of the seasonal incorporation occurs after the canopy has developed and has replenished belowground reserves.

Plants are well adapted to prevailing tundra environments. The vascular plants and mosses have similar, low light compensation requirements (5.6 to 15.8 J m⁻² s⁻¹, 400 to 700 nm), but differ with respect to light saturation. Grasses saturate around 279 J m⁻² s⁻¹ and mosses saturate around 98 J m⁻² s⁻¹. On a daily basis vascular leaves are rarely light-saturated, but mosses may be inhibited by high irradiances, especially in open canopies.

Temperature optima for leaf carbon dioxide uptake are commonly around 15 °C or well above mean ambient temperatures. The high uptake efficiencies on a daily and seasonal basis suggest that this optimum allows plants to function effectively under climatic conditions of the coastal tundra at Barrow. Simulations confirm that a temperature optimum of 15 °C allows vascular plants to take up carbon dioxide efficiently across the range of temperatures experienced. This occurs in part because the leaf area is concentrated at the base of the canopy where leaf temperatures are higher and because the leaves often function on the light-dependent portion of the light response curve. Seasonal temperature acclimation is not apparent. Mosses, however, show a greater sensitivity to temperature changes and a greater vulnerability to water loss. Thus, they show more frequent water stress than the vascular plants, which are rarely water-stressed even though leaf resistances are low. This results from a low evaporative demand and a high soil water potential.

Annual carbon dioxide uptake and net primary production are mainly limited by the availability of photosynthetic leaf area. In a typical season, photosynthesis on a land area basis is strongly limited because the canopy is not well developed until late July when solar irradiance is already decreasing. Season length, or more precisely, the date of snow-

melt, is an important factor dictating the extent of canopy development and therefore the uptake of carbon dioxide.

Spatially, the uptake of carbon dioxide is under a similar control. The productivities of the vegetation types are largely a function of the plant densities or foliage area indices, which are determined by the moisture and nutrient (mainly phosphorus) gradients. Wetter and more fertile areas are more productive because the plants composing the vegetation types in these areas allocate more carbon for photosynthetic tissues. The photosynthetic rates on a leaf basis of a given growth form remain comparable across a wide range of microtopographic units.