

# ADAPTATIONS OF ARCTIC AND ALPINE PLANTS TO ENVIRONMENTAL CONDITIONS\*

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## Introduction

**W**HEN one considers extreme environments and plant adaptations that have evolved from the selection of species populations by various environmental factors, desert and tundra vegetation are frequently the first to receive attention.

Tundra, as used here, refers to the treeless expanses beyond climatic timberline both in the north (arctic tundra) and on high mountains (alpine tundra). As delimited by Polunin (1951), arctic regions lie north of whichever of the following is situated farthest north: (1) a line 50 miles north of coniferous forest or taiga; (2) north of the present day northern limit of microphanerophytic growth (i.e., trees 2 to 8 m. in height, but excluding bushes in unusually favourable sites); or (3) north of the northern Nordenskjöld line using the formula  $V = 9 - 0.1K$ , where  $V$  is the mean of the warmest month and  $K$  is the mean of the coldest month in degrees Centigrade. Absolute boundaries based upon these or any other criteria are far from perfect, though they serve as a useful guide for delimitation.

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## Floristics

One of the characteristic features of the tundras is the relatively small flora that has been selected out by the severe environments. In his "Circumpolar Arctic Flora" Polunin (1959) recognizes 66 families, 230 genera, and 892 species of the division Tracheophyta. According to Löve (1959), probably two-thirds of the arctic species are endemic. Löve further

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stated that of this flora of 600 species only about 200 are roughly circumpolar with a number of species extending to mid-latitudes in the alpine tundra.

There is a striking reduction in number of species with increasing latitude that results from an increasing severity of the environment and a reduction of land area and available soil. There are 604 species in the arctic parts of Alaska and Yukon (Porsild 1951). The Greenland flora includes 590 species, about 490 of which are indigenous (Böcher *et al.* 1957). In Iceland, 540 species are known with 387 of them indigenous (Löve and Löve 1956). According to Porsild (1957), 340 species are found in the Canadian Arctic Archipelago; 143 species occur in Spitsbergen (Höeg 1956), 97 in Peary Land, North Greenland (Holmen 1957), 65 in northern Ellesmere Island (Bruggemann and Calder 1953) and 49 species on Ellef Ringnes Island with probably fewer species on other islands of the Northwestern Queen Elizabeth Islands (Savile 1961). Woody plants decrease rapidly going northward in the Canadian Arctic Archipelago (Porsild 1951).

Fewer figures are available for alpine floras, though the following give some suggestion of the numbers. Hedberg (1957) listed 377 species representing 44 vascular plant families for the East African alpine flora. Rydberg (1914) reported approximately 250 species for the Colorado alpine flora, and Holm (1927) stated that about 37 per cent of the Colorado alpine species were found in the Arctic. These are conservative figures, for the work of Weber and others in the past 10 years has provided numerous new alpine records (Weber 1955, 1961a, 1961b). Some of these new records are of species quite common in the Arctic. In a personal communication Weber reported that over 65 of the alpine species in Colorado seem to be desert derived. Annuals are present, but represent only a very small percentage of the alpine flora (Holm 1927, Little 1941, Daubenmire 1943). This is also true for the Arctic (Sørensen 1941, Porsild 1951, Bliss 1956). Went (1948, 1953) reported that 75 per cent of the numerous alpine annuals in the Sierra Nevada have close relatives in the deserts below. He felt that the desert and alpine climates have in common: a short growing season, high insolation rates, limited moisture supply, and extremes in daily temperature.

In the Presidential Range in New Hampshire there are approximately 70 alpine species, nearly all of which also occur in the Arctic. Thus, although the flora is small, it is decidedly more arctic floristically than the alpine flora of the western mountains. This is also true for the cryptogams. Measurements of environmental factors by the author show that the alpine environment is more like that found in Labrador and Alaska than that in the western alpine areas.

Vascular plants seem to reach their maximum altitudes in the Himalayas, where *Stellaria decumbens* occurs at 20,130 ft. (Swan 1961). Other high altitude records are given by Webster (1961). Although the tundra floras are small when compared with those of temperate and tropical regions, the data presented do show that vascular plants are adapted to survive in very extreme environments at high latitudes and high altitudes.

Another feature of the tundra is the low degree of endemism. When restricted geographic areas are considered the number of endemics in arctic and alpine tundras is quite low (usually less than 5 per cent of the flora). Whereas the number of endemics in the continental Northwest Territories and in Ungava, as well as in Greenland is low, a higher percentage of endemism is found in the Canadian Arctic Archipelago (Porsild 1951). This may be interpreted as an indication of a greater age of the flora in the last named region, which agrees with Hultén's (1937) refugium ideas for the Arctic Archipelago during the Pleistocene, a theory also supported by Löve (1959). The importance of autecological and cytogenetical studies in establishing areas of periglacial survival, subsequent migration, and present distribution patterns were discussed by Böcher (1951).

### Community dynamics in relation to environment

Intense frost action processes or congeliturbation have a profound effect on soil and vegetation of arctic regions. The same processes operate to a smaller extent in many alpine environments, but are seldom if ever encountered in temperate and tropical environments. This has led some investigators to state that new interpretations regarding succession and climax need to be developed in the Arctic with the elimination of regional climatic climax concepts as used by Clements (1916) and land surface and soil stability concepts as used by Cowles (1911) in temperate regions (Hopkins and Sigafos 1950, Sigafos 1951, Raup 1951). Certainly intense frost action creates instability in both the vegetation and soils and the communities may remain in a state of considerable fluctuation (Sigafos 1951). In many areas where the processes are less intensive, it seems unrealistic to separate frost action phenomena from the other environmental factors acting and interacting upon species populations, the end products of which are relatively stable communities, which form a part of the mosaic vegetation pattern.

Climax and successional concepts as applied to tundra vegetation have been reviewed by Churchill and Hanson (1958). They concluded that steady-state community patterns that correspond to relatively long enduring patterns of environmental gradients represent climax types. Phasic cycles that occur in these communities resulting from frost action are considered by them to be within the framework of this broad concept of climax as long as the cycles are not directional as they are in succession. The writer follows these concepts of directional change in succession leading to a steady-state or climax in which phasic cycles may occur. The problems are in differentiating directional from non-directional cycles as influenced in part by the intensity of congeliturbation. The populations of species seem rather well adapted to the varying degrees of frost action, which allows the eventual development of rather stable communities. The necessity to evaluate the role of frost action phenomena in relation to succession and steady-state communities in the tundra is not met with in temperate regions.

Tedrow and Cantlon (1958) have shown that there are fairly good relationships between plant communities and soils on well-drained sites and on areas of shallow soils. Correlations between soils and vegetation on Tundra and Bog soils present greater problems. They reported that minor regional differences in climate have a less profound effect on soil pattern and vegetation than the local micro-variation in drainage. This can be well illustrated in the mosaic pattern of vegetation in relation to micro-variation in drainage as controlled by microtopography (Figs. 1 and 2).



**Fig. 1.** Slightly raised ground supporting a community of *Betula nana* ssp. *exilis* and dwarf heath shrubs with cottongrass tussocks, *Eriophorum vaginatum* ssp. *spissum* on the lower ground. Photograph taken on river terrace near Umiat, Alaska.

In alpine tundras, where frost action is less evident, a greater stability of soils and vegetation can be recognized. The interrelationship between soil development and plant succession was described by Braun-Blanquet and Jenny (1926) for the central Alps. A pioneer community of *Carex firma* and *Dryas octopetala* on disintegrating limestone is replaced by a transition community of *Kobresia myosuroides* developed on soils classed as rendzina. The climax vegetation dominated by *Carex curvula* occurs on climax soil characterized by being acid, highly leached, and containing much organic matter. A similar pattern of soil and vegetation development in the alpine zone of other mountains was reported by Braun-Blanquet (1932).

Another feature of community dynamics in tundras is that in some places there is a shift in the relative importance (dominance) of the species comprising the existing flora in the stages of succession, rather than a

change in floristic composition of the vegetation in the seral stages leading to a stable community (Oosting 1948, Muller 1952). In the High Arctic, physical environmental factors exceed biological competition, the end product of which may be the random occurrence of plants with few distinct associations (Savile 1960).

Two recent papers in English review much of the Russian literature on tundra ecology (Aleksandrova 1960a, Tikhomirov 1960). The former paper deals mainly with the vegetation of Novaya Zemlya, whereas the latter includes all aspects of Russian tundra ecology.



Fig. 2. Raised rim of a depressed-centre polygon supporting *Salix richardsonii* with *Carex aquatilis* in the centre of the polygon. Coastal plain of northern Alaska approximately 500 ft. east of the Colville River and 15 miles from the coast.

## Environmental factors

### Soils

In the vast area extending from scattered "islands" of alpine tundra at high elevations in low mid-latitudes to broad expanses of arctic tundra in the north, there is a considerable range of environmental factors, including soils.

Tundra soils have received considerable attention in Eurasia, especially by the Russian pedologists. However, on our continent little work on tundra soils has been done until the excellent studies of Tedrow and associates in

arctic Alaska. The arctic representative of mature or zonal soils, the Arctic Brown soil (Tedrow and Hill 1955), is very restricted in areal extent, occurring only under conditions of adequate drainage. A similar soil type called sod-bare rock soil was described by Karavaeva (1958) for the alpine region of eastern Sayan, USSR. The Tundra soils and Bog soils are northern extensions of humic glei and bog soils respectively (Tedrow and Cantlon 1958, Tedrow and Harries 1960). Both soil groups are azonal. The dominant process operating in the Tundra soils is a type of gleization at low temperatures; a process found also in forests to the south (Tedrow and Harries 1960). In both arctic and alpine tundras, soil formation results from pedologic as well as cryopedologic processes (frost-phenomena).

If the concept climax vegetation is restricted to communities developed under mesic, stable soil conditions, upland meadow and heath communities associated with Arctic Brown soils only could be designated climax (Tedrow and Harries 1960). This concept of climax vegetation is too narrow as discussed in the community dynamics section.

Organic matter decomposition rates have been investigated in northern Alaska by Douglas and Tedrow (1959). They reported that soil temperature is more important than soil moisture in regulating organic matter decomposition, and found that annual rates of decomposition are of the same order of magnitude as rates of organic matter production per year.

Alpine soils in the Rocky Mountains have been grouped into 3 broad classes (alpine turf, alpine meadow, alpine bog soils) by Retzer (1956). He stated that the presence of kaolinite in the soils indicates a rather advanced stage of weathering. A brief description of alpine soils in the Andes of Colombia was presented by Jenny (1948). He divided the soils into cold humus and podzol types. Soil profile development is greater in most alpine tundra regions due to better internal drainage that results in part from the minor role of permafrost and less intensive frost action.

Patterned ground is a conspicuous feature of both arctic and alpine environments. The extensive literature regarding the origin of patterned ground was reviewed by Washburn (1956). Troll (1944) described earth patterns, stone nets, and stone stripes as ranging from small regular forms in the alpine zone of tropical mountains where nightly freezing occurs to the much larger forms typical of the Arctic where development is controlled by the seasonal course of freezing and thawing.

Low levels of plant growth in the Arctic have been attributed to low levels of soil nitrogen (Russell 1940a, Sørensen 1941, Warren Wilson 1954, 1957a). Russell (1940a) stated that nitrogen deficiency results from low bacterial activity due both to low temperature and low nutrient supply. Certainly plant growth is more luxuriant around old settlements and where manured by animals. Dadykin (1954) has carried on extensive physiological studies on roots in cold soils in arctic Russia. He reported that nitrogen levels of plants grown in cold soils were equal to or greater than nitrogen levels of control plants grown in warmer soils. However, the low temperatures reduce the assimilation of nitrogen into organic compounds, probably

nucleo-proteins and their derivatives. This was true regardless of the form of nitrogen supplied (nitrate, ammonium nitrate, or organic nitrogen). He further stated that boron and certain other elements augment the yield of plants grown in cold soils. Whereas nitrogen appears to be a limiting factor in tundra plant growth, certain other soil nutrients seem to be present in fairly adequate amounts in some arctic and alpine soils (Feustel *et al.* 1939, Böcher 1949, Retzer 1956, Warren Wilson 1957a).

### Light intensity, duration, and quality

Whereas relatively few records of solar radiation have been obtained in the tundras, solar radiation is exceedingly important, because it not only affects soil and air temperatures, humidity, and soil moisture, but also the energy flow within the ecosystem. The data available show that, at least for short periods of time, solar energy in the Arctic may be equal to or exceed that received in mid-latitudes on a 24-hour basis. Isolated figures are rather meaningless, but they do give some general indication of environmental conditions. Data from various sources (Sørensen 1941, Bliss 1956, Warren Wilson 1960) show that in mid-summer in the Arctic on level land, solar radiation ranges from 318 to 510 langleys/24 hr. (1 Langley = 1 gr.-cal./cm.<sup>2</sup>). Solar radiation data on Mt. Washington give a summer average of 436 langleys/24 hr. from June to August (Haurwitz 1937). Values obtained by the writer for 1959 range from less than 100 in heavy fog to over 800 langleys/24 hr. on clear days in July. The higher values are seldom attained for this nearly constantly fog-bound mountain.

In mid-summer light intensity at noon is usually greater in the alpine than in the arctic tundra due to the thinner alpine atmosphere. In general, on a 24-hour basis, it appears that solar radiation values in the arctic tundra are rather less than in the alpine, though many more data are needed.

Furthermore, the length of day during the growing season is of great importance. In the alpine tundras of the United States photoperiod does not exceed 15 to 16 hours in summer, but in the Arctic at least 2 months of continuous light prevail. From the work of Mooney and Billings (1961) and others it is becoming apparent that many populations of arctic species are physiologically adapted to a 24-hour photoperiod whereas their alpine counterparts are adapted to a shorter daylength.

The greater intensity of ultraviolet light in the alpine environment has led some investigators to state that this is the cause of the low growth form of alpine plants. There are few, if any, experimental data to support this hypothesis.

### Temperature

Of the various environmental factors temperature is the most important limiting factor with regard to plant growth and development in the tundra.

The physiological explanation for the critical temperature effect is two-fold according to Warren Wilson (1957b). With mean summer air temperatures frequently just above 0°C., the temperatures are near the lower cardinal point for many metabolic processes, and secondly, acceleration of physiological processes by a temperature increase is greater at low temperatures.

A considerable amount of information on temperatures in tundra micro-environments is contained in papers by Sørensen (1941), Cook (1955), Bliss (1956), Warren Wilson (1957b), Billings and Bliss (1959), Aleksandrova (1960b), Conover (1960), and Marr (1961). Whereas temperatures are relatively low in the Arctic, they nevertheless show normal day-time temperature gradients in the microenvironment with temperature inversions typical at "night". In these severe environments, where day-time temperatures at 0.7m. seldom exceed 13° to 18°C. and more frequently are 5° to 8°C., it is of considerable interest to note that soil surface temperatures in excess of 38°C. have been recorded by the writer in arctic Alaska as well as in the alpine tundras of Wyoming and Mt. Washington. Night-time soil-surface temperatures for the same dates were 4° to 7°C. Diurnal temperature extremes are thus considerable, usually being greater in the alpine tundra on account of the longer night period. Temperature regimes in the micro-environment on north- and south-facing slopes are quite different, which helps to explain the diversity of plant communities encountered.

Most of the tundra plants are greatly reduced in size, frequently forming a mat not higher than 6 to 8 cm. Thus the above-ground parts are in the lower part of the microenvironment where considerably higher temperatures prevail, which permits metabolic processes to proceed more rapidly than would otherwise be possible. Tundra plants are adapted by their caespitose or low growth form to take advantage of the more favourable temperatures that prevail near the ground. Frequently these temperature conditions are not apparent when temperature data of weather stations in the area are used. Warren Wilson (1957b) recorded leaf and air temperature 1 cm. above the ground with a thermocouple. Temperature differences were less during periods of mist or cloud but still measurable. In early September with short periods of darkness leaf temperatures fell 1°C below air temperatures (Warren Wilson 1957b).

A striking example of temperature stratification within a small clump of *Saxifraga oppositifolia* is cited by Warren Wilson (1957b). On June 23 at 1430 hrs. the air temperature at 2 m. was 0.5°C., at 1 cm. above the clump it was 3.5°C. and the temperature inside two flower buds was 6°C. Even greater extremes were recorded by Wulff (cited in Porsild 1951) in northern Greenland (82°N.). With the air temperature at -12°C., a reading of 3.5°C. was recorded among dead leaves in a tuft of saxifrage and 10°C. in a dark clump of mosses. These microenvironmental temperatures are not as extreme as in temperate regions, but in the tundra relatively small temperature increases become highly significant with regard to plant metabolic processes.



The diurnal rhythms of flowering and pollinating agents of tundra plants have been studied by Shamurin (1958) at 71° N. near Ashkutz, USSR. He found that temperature is the most important factor controlling flowering. Data presented show that flowers of many species open at minimal air temperatures of 3° to 8°C. with mass opening of flowers at 5° to 12°C.

The most intensive study of arctic plant temperatures known to the writer is that of Tikhomirov *et al.* (1960). They gathered data on 40 species of flowering plants at Tiksi, Yakutsk, USSR (71°35'N.). On sunny days they found that the temperature of plant parts exceeded the air temperature by 2° to 5°C. whereas on cloudy days plant temperatures may fall below that of the air. They reported that temperatures inside white flowers were 0.7° to 2.0°C. higher than adjacent air, and blue- and lilac-coloured flowers were 3.4° to 4.2°C. warmer than the adjacent air. Many temperatures are presented for various parts of a *Sieversia glacialis* plant including root temperatures.

Tundra plants are not only adapted to take advantage of the favourable temperature balance in the microenvironment, but they can also withstand sudden drops in temperature to levels below freezing, often with little or no ill effect. Porsild (1951) found masses of *Epilobium latifolium* in full bloom, frozen stiff with the air temperature at -3.5°C. The following day, after thawing, no evidence of frost damage could be found. On Mt. Washington the writer has seen plants in flower covered with rime ice at temperatures of -3° to -1.5°C. When the ice melted there was no evidence of damage. In June 1959, *Diapensia lapponica* and *Rhododendron lapponicum* were in bloom on Mt. Washington when a sudden snow storm occurred. A continuous temperature record at the height of the plants showed temperatures ranging from -5° to -0.5°C. (-0.5° predominated) during 5 days, yet the flowers continued blooming and set seed following snow melt. If arctic and alpine species had not acquired this physiological adaptation to withstand severe temperature conditions associated with sudden and violent storms, they would have been eliminated from the flora long ago, for severe storms are characteristic rather than exceptional in the tundra.

The most remarkable tolerance to low temperatures of any plant in various stages of development seems to be that of *Braya humilis*. Sørensen (1941, p. 109) states that "*Braya humilis* occupies a unique position among all the seminiferous species of the area in that inflorescences or infructescences at any stage of development may survive the winter and continue their development in the succeeding growing season". Sørensen like others, however, discounted the reports of a similar capacity for winter survival of flowers and fruiting shoots of *Cochlearia officinalis*. Apparently the bulbils produced by some species also can tolerate low winter temperatures.

Sørensen's (1941) excellent paper on temperature relations and phenology in Greenland plants includes much information on the developmental stage of overwintering buds. He stated that Greenland species with a more northern distribution frequently possess flower buds that overwinter in a very advanced stage of development. Floral organs in many of these

species take 2 years to develop, with floral initiation in the 1st year and floral expansion within the buds in the second summer. These species are thus adapted to burst into flower and vegetative growth as soon as spring temperatures permit. This rapid flower expansion with the arrival of favourable temperatures is a good adaptation to the all-too-short growing season. Sørensen further stated that formation of floral organs in the Arctic may be induced by low temperature-thermoperiodical adaptation.

Root stratification in cold tundra soils has been reported by Porsild (1951) and Bliss (1956). Roots are typically confined to the warmer and slightly better drained soil layers above the permafrost. In contrast, alpine plants possess roots that penetrate more deeply into the soil (Daubenmire 1941, Holch *et al.* 1941, Bliss 1956) for drainage is generally much better and permafrost, if present, is quite deep during the growing season (Retzer 1956).

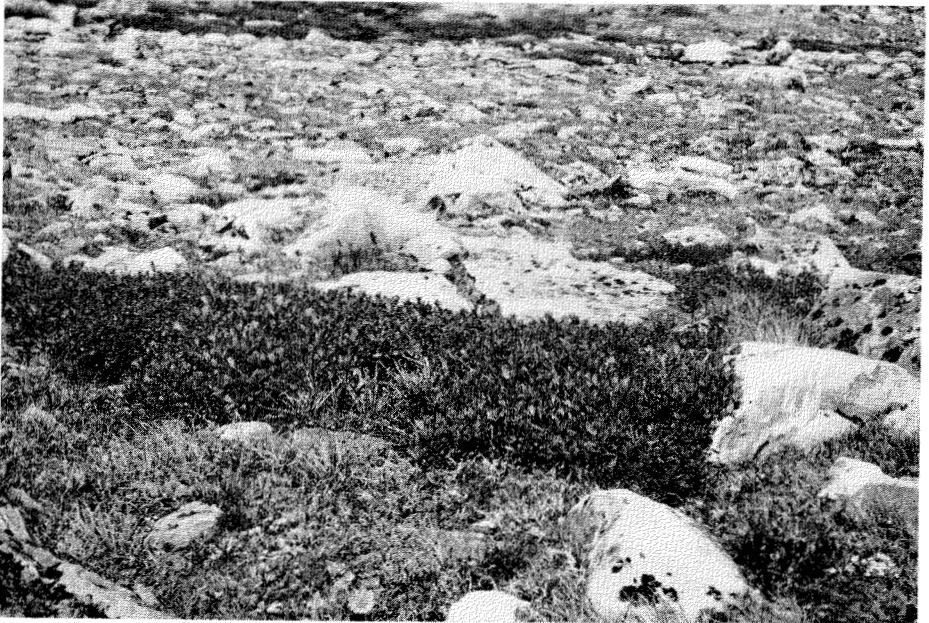


Fig. 3. Wind-pruned *Salix brachycarpa* growing on the leeward side of a rock. Alpine fellfield in the Medicine Bow Mountains, Wyoming, at an altitude of 11,000 ft.

During much of the summer in northern Alaska the root tips of *Arctagrostis latifolia* and *Eriophorum vaginatum* ssp. *spissum* followed within 0.5 to 1.5 cm. of the retreating frost level in a saturated soil whose temperatures were between 0° and 1°C (Bliss 1956). Dadykin (1954) reported that young roots of *Calamagrostis langsдорffii* and *Rosa acicularis* were found near the surface of the frozen layer in soil with a temperature of 0°C. He further stated (after Grigorieva) that roots of *Rubus chamaemorus*, *Carex globularis*, and *Equisetum silvaticum* were removed from the frozen soil, immediately fixed, and that these roots were accumulating starch grains

and that meristematic cells were found in metaphase and anaphase stages of nuclear division. Dadykin has demonstrated water absorption by roots in frozen ground where part of the water remained in the liquid state because of high osmotic concentration in the soil as well as in the root.

Relatively high osmotic values have been reported for both arctic and alpine plants as compared with temperate-region species. Wager and Wager (1938) reported that osmotic values for East Greenland plants are higher in winter than in summer, and that the spring drop in values is associated with temperature rise and the utilization of food reserves. They further stated that plants covered by winter snow have slightly lower osmotic values than plants growing in exposed situations. Heilborn (1925) related the higher osmotic values of plants in the Equadorian paramo to stronger winds and lower atmospheric pressure when compared with plants at lower altitudes. According to him, these factors control the water economy of the plants, which is reflected in the higher values for exposed shrubs (25 to 29 atm.) than for rosettes with thick tap roots (12-17 atm.). Other investigators have related the higher osmotic values of alpine plants to low temperatures (Meier 1916).

Mooney and Billings (1961) concluded that the primary restrictive factor limiting the distribution of arctic and alpine populations of *Oxyria digyna* appears to be relatively high summer temperature. Under these conditions, carbohydrate reserves are depleted owing to low photosynthetic economy at high temperatures. This hypothesis is supported by the findings of Dahl (1951) for alpine plants in Fennoscandia and Müller (1928) on arctic plants in west Greenland.

As a last point to be made on temperature, rates of plant growth in northern Alaska were correlated with temperature, and in those species in which growth was relatively large, statistically significant correlations were found (Bliss 1956).

## Wind

Wind is an ever-present environmental factor in both arctic and alpine tundras with wind-pruned vegetation a common sight, especially on exposed ridges and slopes in the Alpine and in the High Arctic (Fig. 3). Although wind speed is greatly reduced near the ground, the low stature and sparse cover of the vegetation enable the wind to be more effective than with taller and more stratified vegetation. Wind-erosion of vegetation mats and cushions has been discussed by Whitehead (1954) and Billings and Mooney (1959) for alpine vegetation and by Hopkins and Sigafos (1950) in Alaska. Billings and Mooney (1959) postulated a natural cycle involving wind-erosion and frost heaving in the degradation of peat hummocks through frost scars to sorted polygons on which, after flooding, peat accumulation is again initiated. Thus any community that might be called "climax" is of short duration. The importance of wind in the formation and degradation of hummocks in the alpine zone of the Old Man Range in New Zealand was discussed by Billings and Mark (1961). Whitehead (1954) stated that

caespitose growth forms have a definite adaptative significance in the Italian Alps. He also indicated that wind may affect growth rates through temperature changes.

Wind is effective in reducing leaf temperatures as well as air temperature, thus upsetting the more favourable temperature microclimate of low arctic and alpine vegetation according to Warren Wilson (1959). He concluded that the potent effect of wind on tundra vegetation is a result of the sensitivity of plant growth to wind, and that the sensitivity is due less to excessive transpiration and more to temperature conditions as they affect net assimilation and shoot growth rates. Although wind speeds are greatly reduced within clumps of tundra plants in the summer (Warren Wilson 1959), the abundance of winter-killed branches, especially in the alpine tundra, testifies to the lack of snow cover and strong winds in winter (Bliss 1956).

Bliss (1960) reported that transpiration rates for tundra shrubs are low, and directly related to air temperature, vapor pressure deficit, and wind speeds below 6 m.p.h., but inversely proportional to wind speeds above 6 to 8 m.p.h. and cloud cover. Relatively low transpiration rates for tundra plants have been reported by other workers (Wulff 1902, Stocker 1931, Cartellieri 1940, Hygen 1953, Dadykin 1954). Transpiration differences in 3 species of *Vaccinium* were related to morphological structure and leaf anatomy according to Hygen (1953). He further reported that cuticular transpiration losses were quite low in the xerophytic *Vaccinium vitis-idaea*, but quite high in wet-site species such as *Pinguicula vulgaris*.

It has been stated that, in general, tundra plants appear to be able to absorb water in adequate amounts to meet the demands of transpiration (Dadykin 1954, Warren Wilson 1959), though drought has been reported in some studies (Michelmore 1934, Böcher 1949, Whitehead 1951), and Webster (1961) concluded that water supply may be the most important limiting factor in the upper altitudinal limits of flowering plants in high alpine regions.

The importance of wind in seed dissemination has been discussed by Porsild (1951), Tikhomirov (1951), and Gavriliuk (1961).

### **Snow cover**

Snowbank or snowflush vegetation is commonly found in the tundra of mountainous areas where winter snow accumulation in large drifts is favoured by strong winds and heavy snowfall. In most low-arctic and alpine tundras there is a rather specialized flora associated with snowbanks (Polunin 1948, Gjaerevoll 1956, and others). The microzonation of species and vegetation is largely the result of adaptations to depth and duration of snow cover (Billings and Bliss 1959). These plants must be able to complete at least a vegetative life cycle in a few weeks and even that cannot occur every year. Some species begin growth under as much as 50 to 100 cm. of snow (Billings and Bliss 1959, Mooney and Billings 1960) whereas other species await the melting of the snow before starting to grow. Kovakina

(1958) reported development of new shoots including an accumulation of nitrogen under less than 110 cm. of snow starting in January. This work was done on the Kola Peninsula, USSR. In some instances, species may remain under snow for 2 or more years, unable to carry on many physiological processes. It is under such conditions that relatively large carbohydrate reserves in roots and rhizomes may permit survival that otherwise could not occur.

Plants buried under winter snow do have protection during critical periods of high wind and low temperature. In summer the meltwater prevents their being subjected to soil drought (Billings and Bliss 1959). In general, tundra shrubs are found only where winter snow cover prevails. Thus, shrub height is quite well correlated with mean winter snow depth. Accumulation of dirt on snowbanks in the Arctic and its role in building a fine organic soil as well as the possible increase in soil nitrogen has been presented by Warren Wilson (1958). In the Alps there are no annuals in the *schneetälchen* flora and vegetative reproduction is very important since seed production does not occur every year (Braun-Blanquet and Jenny 1926).

### Aspects of adaptation

#### Pollination

The relation of air temperature to the diurnal pattern of flowering and pollination by bumble-bees and flies was studied by Shamurin (1958) near Ashkutz, USSR. The fertilization of 20 species of flowering plants in southeastern Chukotk, USSR is reported to depend entirely upon 2 species of bumble-bees (Gavriliuk 1961), though in general there are indications that wind and insect pollination are less important than in other environments (Löve 1959). Self pollination thus seems to be most important. Whereas self pollination may be an important mechanism in severe environments where little time can be lost to chance pollination, cross pollination helps to insure greater genetic diversity within the populations.

#### Seed production

Although viable seeds are produced by many tundra species, seeds of other tundra species fail to germinate (Nichols 1934, Söyrinki 1938-9, Sørensen 1941, Bliss 1958). Holch *et al.* (1941) reported that rhizomes provide the best means of propagation of alpine plants in Colorado. Seed germination under severe conditions was studied by Sørensen (1941), who found that germination occurred even though the seeds remained frozen for half of each 24-hour period. Environmental conditions in the alpine and arctic tundras, as in the desert, seem to be adequate for seed production and germination only in some years. There appears to be a considerable production of seedlings in some years followed by several years in which few if any seedlings become established. This differential survival of seedlings can have a profound effect on vegetation patterns. Studies in Colorado alpine

areas indicate that soil drought and needle ice activity are the most important environmental controls (Osburn 1961).

Germination studies by Bliss (1958) showed that seeds of *Salix planifolia* var. *monica* ripen in July and germinate immediately; the seed seldom remaining viable over winter. The seed of *Salix brachycarpa* ripens in late August and probably does not germinate until the following spring, for the seeds remain viable over winter. The former species grows in sites that are moist throughout the summer, whereas the latter species grows in sites that are frequently quite dry by August. The overwintering of viable *Salix brachycarpa* seed with germination occurring in moist soil the following spring may be of importance for survival. This pattern is of interest, for species of *Salix* in general produce seed of short viability. Fruits of some arctic species do not mature and dehisce until after snow covers the ground (Porsild 1951). This is an important mechanism for seed dispersal and subsequent establishment because snowbank communities are enriched by wind transported soil and seeds that accumulate in the snow during winter (Porsild 1951).

Observations by the author (Bliss 1956) in arctic and alpine tundras indicate that flowering intensity and seed production decrease with an increase in the severity of environments caused by local microenvironmental conditions. Thus, local variation in flowering and fruiting as a result of topographic differences (exposed ridges, sheltered slopes, snowbank vegetation) may be as great as over large geographic areas such as the reduction in fruiting of some species from the Low Arctic to the High Arctic.

The frequency of apomicts is also quite high in the tundra (Löve 1959). Certainly, this mechanism of asexual seed production enables the survival of new vigorous and well-adapted biotypes that because of sexual sterility could not otherwise survive. This permits a rapid build up of a population of genetically similar individuals, which, if adapted to the prevailing environmental conditions, could permit colonization of newly available habitats such as in the Arctic following ice retreat (Stebbins 1950). Vivipary (germination of a propagule while attached to the parent plant) as in *Polygonum viviparum*, *Saxifraga cernua*, and *Poa alpina* var. *vivipara* is a means of reproduction that equips the progeny for establishment during the same growing season.

### **Polyploidy**

Although the number of species in the flora decreases from middle to high latitudes, there is an increase in the frequency of polyploidy from about 30 to 35 per cent in warm temperate regions to over 60 per cent in the Subarctic and Arctic and 70 to 80 per cent in the arctic islands (Löve and Löve 1957). A high incidence of polyploidy has also been reported for the Mexican alpine flora (Beaman *et al.* 1962). Stebbins (1950) reviewed the literature on polyploidy in the Arctic and concluded that it is due to a combination of causes including: (1) a high percentage of perennial herbs

in which polyploidy is somewhat higher; (2) many grasses and sedges in which polyploidy is frequent; and (3) wider tolerance limits of polyploids for occupying new habitats. However, some of the plants found under the most adverse conditions are diploids (e.g., *Silene acaulis*, *Oxyria digyna*, *Saxifraga oppositifolia*, *Vaccinium uliginosum*, and others), which shows that genes for hardiness are present in the diploid as well as in the polyploid condition (Löve and Löve 1949, 1957; Hagerup 1933). Gustafsson (1948) has viewed the increase of polyploids in the Arctic as a result of the breakdown of the diploid sexual mechanism leading to vegetative reproduction rather than an increase in polyploids due to severe climatic conditions as stipulated by Hagerup (1932).

Following an extensive review of the literature, Löve and Löve (1949) favoured the hypothesis that the increased frequency of polyploids in the Arctic is due to the increased genetical superiority of polyploids. This hypothesis is based on data from numerous papers, which show that the increased tolerance of plants toward extreme conditions, as in the Arctic, results from the greater physiological and morphological adaptability of polyploids. Related to this is the work of Sokolovskaya and Strelkova (1960). They reported, based upon 168 species, that the majority of the diploid species belong to the ancient arcto-alpine flora whereas the polyploid species represent that part of the arctic flora that has spread over the Eurasiatic Arctic during post-glacial time.

In evaluating the importance of polyploidy in any environment one must keep in mind the relative proportion of genera and families known to have a high incidence of polyploids as the Cyperaceae, Gramineae, and Rosaceae.

### Phenology

Plant phenology can be a useful tool in helping to describe microenvironmental differences between various habitats. Bliss (1956) reported that many species living in a given habitat break dormancy, flower, and fruit together, whereas the same species exhibit different cycles of development in different habitats. This shows the control of local microenvironmental factors on the rate of plant development. Data on phenology of arctic plants are also contained in the papers by Söyrinki (1938-9), Sørensen (1941), McClure (1943), and Aleksandrova (1960c). Limited data by Bruggemann and Calder (1953) and Savile (1959) indicate that the growing season comes earlier in the High Arctic (Alert 82°30'N.) of the Canadian Arctic Archipelago than in the Low Arctic (Chesterfield Inlet 63°21'N. and Coral Harbour 64°09' N.). This is in part due to the extent of snow cover, angle of incidence and daylength. The establishment of phenological seasons for various locations in the tundra would be a very useful tool in delimiting macro- and microenvironments, but it must await the gathering of more detailed data on phenology for important species that occur in the arctic and alpine tundras.

### Gross morphology

The literature on tundra plant morphology is rather extensive. Worthy of special mention are papers on structure and biology of arctic flowering plants by Warming and others that appeared in *Meddelelser om Grønland* from 1908 to 1921, and the section on biological morphology of the East Greenland plants by Sørensen (1941).

In general, many arctic plants possess buds that over-winter in a very advanced stage of development so that with the advent of favourable temperatures, shoot growth and flowering occur rapidly. A conspicuous feature of tundra plants is the relatively large size of flowers in proportion to the vegetative shoots (Sørensen 1941, Daubenmire 1943). In alpine tundras the caespitose growth form is very important (Daubenmire 1943) as it is in the High Arctic. Some species in both tundras have fleshy leaves, though this is probably more characteristic of alpine species. Evergreen leaves are rather common in arctic plants. Thick cuticle and an abundance of epidermal hairs are considered by some to be adaptations of alpine plants. According to Holch *et al.* (1941), epidermal hairs of alpine plants absorb large quantities of light thus reducing the amount of light reaching the chlorophyll. However, the hairs may reflect visible light as reported for subalpine species by Billings and Morris (1951). Krog (1955) has reported higher temperatures in willow catkins with hairs than in catkins painted black. He felt that long-wave radiation from the catkins is trapped by the hairs in addition to their functioning as a black body. Thus species with hairs or dark scales could flower earlier, when temperatures are still near freezing, than species lacking these characteristics. This may be an important factor in both arctic and alpine plants possessing hairs and dark scales, for many of these species do flower early (Bliss 1956). The importance of hairs in bud development and the ripening of seeds in pubescent racemes was discussed by Tikhomirov *et al.* (1960).

The work of Zhuikova (1959) on the Kola Peninsula, USSR, has shown that in several species of *Vaccinium* there are different forms of shrub growth in different habitats. Zhuikova worked on the branching development of individuals from seedling to mature size and found that in general plants of *Vaccinium uliginosum*, *V. myrtillus*, and *V. vitis-idaea* do not flower until they are 14 to 20 years old.

### Life-form

The life-form spectrum of a flora can be used as a rough measure of the prevailing climate and the selective action of the climate on those plant forms best adapted for survival. Raunkiaer (1934) reported a chamaephyte climate for the tundras in which chamaephytes constitute at least 20 per cent of the spectrum. Phanerophytes, plants with perennating buds more than 30 cm. above the ground, and therophytes or annuals are either lacking or are at least quite minor in the tundra. The most important groups are



the chamaephytes and hemicryptophytes. As a generalization, the percentage of chamaephytes gradually increases as the climate becomes more severe with increase in latitude — arctic, and an increase in altitude — alpine (Raunkiaer 1934). Certainly the cushion growth-form of many chamaephytes is a form well adapted to take advantage of the higher surface temperatures, reduced wind speeds as well as being adapted to greater survival in areas of little snow cover in winter. This growth-form has evolved in unrelated plant families in the tundra and is a good example of parallel evolution of a form well adapted for survival in the severe tundra environments (Bliss 1956).

### Photosynthesis and respiration

The characteristically dwarf nature of tundra plants and their slow growth rates have been variously interpreted. Wager (1938) stated that low temperatures and low carbohydrate synthesis were more limiting than the small supply of nitrogen, soil nutrients, and water. In contrast, Sørensen (1941) believed competition for soil moisture and nutrients, especially nitrogen and the inherent developmental morphology of the species were causal. Though low levels of plant growth have been related to low levels of nitrogen (Russell 1940a, Warren Wilson 1954, 1957a), Dadykin (1954) has shown that nitrogen may be adequate but that low levels of protein synthesis may be the limiting factor. Polunin (1955) also discussed slowness of protein synthesis combined with reduced cell elongation at low temperatures. He further stated that there is no evidence for carbohydrate shortage in arctic plants. This has been clearly shown for arctic species (Russell 1940b, Warren Wilson 1954, 1960), and for alpine species (Russell 1948, Mooney and Billings 1960). High levels of soluble carbohydrates may help to account for rapid spring growth and flowering (Wager 1941, Russell 1948, Midorikawa 1959) as well as an increase in cold resistance of underground parts during the winter (Russell 1948).

The concentration of total carbohydrate in the leaves of *Oxyria digyna* on Jan Mayen Island showed a diurnal rhythm during continuous daylight (Warren Wilson 1954). Total carbohydrate averaged 33 to 45 per cent of the dry weight during a 3-day period. These values were considerably higher than those obtained for *Oxyria* leaves in England. A diurnal rhythm in the opening of stomata was also found under continuous light. Kislyakova (1960) has shown that *Vaccinium uliginosum*, potato, and beans assimilate continuously in midsummer on the Kilskkii Peninsula, USSR (67°30' N.). Under clear skies at "night" assimilation rates are about 1 mg. CO<sub>2</sub>/dm.<sup>2</sup>/hr. but under cloudy weather "night" assimilation is absent or nearly so. By 4 a.m., rates increase to a level of 3 to 15 mg. CO<sub>2</sub>/dm.<sup>2</sup>/hr. Similar findings have been reported by other Russian botanists (Dadykin and Grigorieva, Kostichev *et al.*, cited in Kislyakova 1960).

The annual carbohydrate cycle and its relation to growth has recently been described for 3 alpine species in Wyoming (Mooney and Billings 1960).

It was found that the carbohydrate content of underground storage organs was highest in the fall. At the start of growth in the next spring, the carbohydrate level is somewhat reduced, which indicates that development must occur under the snow in the underground organs at temperatures around 0°C. When the snow melts there is a burst of growth at the expense of carbohydrate reserves (Billings and Bliss 1959). Mooney and Billings (1960) reported a 50-per-cent drop in rhizome carbohydrate reserves in a 1-week period during leaf expansion and the appearance of flower buds for *Polygonum bistortoides*. These reserves that were laid down in the previous year thus permit the rapid rate of growth and flowering during a 1- to 4-week period. As in the Arctic, these alpine plants no doubt have buds that overwinter in an advanced stage of development. Replacement of rhizome reserves occurred from flowering until fall dormancy in all 3 species.

Although field data on photosynthesis and respiration rates from tundra plants are quite limited, the data summarized in Table 1 and those presented by Pisek (1960) indicate that net assimilation and respiration rates are quite similar for plants growing in different tundras. However, the physiological activity of deciduous and evergreen leaves appears to be quite different (Pisek and Knapp 1959, Pisek 1960). The latter paper cited data from the Kola Peninsula, USSR (Danilov and Mirimanjan 1948), which showed that net assimilation rates were higher in arctic herbs and deciduous shrubs than in evergreen shrubs. Respiration rates were also higher in deciduous than in evergreen plants according to Pisek and Knapp (1959). Their data included several alpine shrubs. Pisek and Knapp reported that measurable rates of respiration occur in evergreen leaves of *Rhododendron ferrugineum* at 0°C. in winter, and the summer rates were higher in leaves of the present year when compared with rates from older leaves. Wager (1941) concluded that at the same temperature, arctic leaves have on the average a higher rate of respiration than leaves of temperate plants. This is supported by the findings of Stocker (1935) and to a less degree by Scholander and Kanwisher (1959). The latter authors concluded that respiratory temperature compensation may be a minor factor in arctic plants, though 2 of the 9 species examined showed significantly higher respiration rates for arctic than for temperate region-species when measured at the same temperature.

Bukharin (1961) reported that plants from several ecological habitats were transplanted at various altitudes (340 to 1000 m.) in the Murmansk region. All species were reduced in growth and rate of development with increase in altitude; reductions that were correlated with lower levels of carotene at higher altitudes. Native species in contrast frequently had higher carotene levels at higher altitudes and definite correlations were found between carotene level and developmental stage. It is known that carotene plays an important role in photosynthesis, oxidation-reduction reactions, and growth. If tundra plants possess higher carotene levels especially in more severe environments, this may help to explain distribution patterns. This is certainly worth further investigation.

Working with the limited arctic data, Warren Wilson (1960) concluded that net assimilation rates of tundra plants are about one-half the values reported for temperate region plants, and that respiration is about 20 to 25 per cent of the net assimilated rate. He further stated that low temperatures are basically responsible for depression of net assimilation in arctic environments rather than the levels of light intensity.

**Table 1.** Net assimilation and respiration rates for detached leaves of arctic and alpine plants.

Net assimilation		
Locality	Species	Carbohydrate increase gr./dm. <sup>2</sup> /week
Jan Mayen Island (71°N.)*	<i>Oxyria digyna</i>	0.30
Jan Mayen Island**	<i>Oxyria digyna</i> (windy hilltop)	0.34
	<i>O. digyna</i> (sheltered hillside)	0.46
	<i>O. digyna</i>	0.54
	<i>Salix herbacea</i>	0.53
	<i>Sibbaldia procumbens</i>	0.50
Cornwallis Island (75°N.)**	<i>Salix arctica</i>	0.73
East Greenland (69°N.)†	<i>Oxyria digyna</i>	0.68
Alaskan Arctic group††	<i>Oxyria digyna</i>	0.53
Western American alpine group††	<i>Oxyria digyna</i>	0.31
Respiration		
East Greenland (69°N.)†	<i>Oxyria digyna</i>	0.06-0.19
Jan Mayen Island (71°N.)**	<i>Oxyria digyna</i>	0.11
Alaskan Arctic group††	<i>Oxyria digyna</i>	0.16
Western American alpine group††	<i>Oxyria digyna</i>	0.15

\* Russell 1940.

\*\* Warren Wilson 1960.

† Data of Wager (1941), adjusted by Warren Wilson (1960).

†† Mooney and Billings 1961. Control-chamber-grown whole plants were measured with an infrared gas analyser. Data calculated from rates of photosynthesis and respiration given in Fig. 15 of Mooney and Billings.

Müller (1928) and Wager (1941) reported that light saturation for several species in Greenland occurred between 500 and 2,000 ft. candles. Müller (1928) concluded that at low light intensities (150 to 650 ft. candles) assimilation rates for *Epilobium latifolium* and *Salix glauca* decreased with a temperature increase from 10° to 20°C. but at 1,900 f. candles, assimilation increased with temperature rise. Data presented by Cartellieri (1940) showed that net assimilation rates were higher for *Ranunculus glacialis* under cool, cloudy skies than on clear, warm days, and that assimilation

fluctuations followed light intensity as long as the intensity did not exceed 2,800 to 3,700 ft. candles.

The data of Mooney and Billings (1961) indicate that variation in photosynthetic and respiration rates for *Oxyria digyna* are quite well correlated with ecotypic variation within this wide-ranging species. Of the many data presented, two examples will illustrate the point. The upper temperature compensation point for alpine populations from the central Rocky Mountains was 35°C., whereas temperature compensation occurred at 26°C. in the arctic populations. Light saturation was not complete at 5,200 ft. candles in the Loveland Pass Colorado alpine plants whereas the plants from Donjek Mountains, Yukon Territory were light saturated at approximately 2,000 ft. candles. A further study on physiological variation in arctic-alpine populations of *Oxyria digyna* shows that races from mid-latitude alpine environments are photosynthetically more efficient at lower concentrations of CO<sub>2</sub> than populations of the same species from near sea-level at high latitudes (Billings *et al.* 1961). Certainly more comparative physiological studies on populations of wide-ranging arctic-alpine species will shed a great deal of light on the genetically controlled physiological mechanisms that enable the plants to survive in these severe and diverse tundra environments.

**Table 2.** Net primary production rates for Russian arctic tundra plant communities based on air-dry weights.

Locality	Vegetation type	Cover per cent	gr./m. <sup>2</sup>	gr./m. <sup>2</sup> /day*
Liakhovskii Island† (New Siberian Islands)	Shrubby-mossy tundra shoots roots	60.0	185.0	0.51
			511.0	1.40
	Polygonal ground mossy tundra shoots roots	35.0	119.0	0.33
			260.0	0.71
European Russia††	Shrubby-mossy tundra shoots	—	120.0	0.33

\* Based on entire year.

† Aleksandrova 1958.

†† Lavrenko *et al.* 1955.

### Productivity and efficiency

Although a considerable amount of information is available on plant growth and the various environmental factors affecting growth, relatively little is known about plant growth per unit area or primary production and efficiency of the producers. Estimates of gross and net primary production give a rather good measure of the effect of the complex of environmental factors on the species comprising a given plant community.

The limited data available indicate that the values for the standing crop at the end of the growing season for the Arctic range from 0.01 gr./m.<sup>2</sup>/day on Cornwallis Island for a *Salix arctica* barren to 0.66 gr./m.<sup>2</sup>/day for *Carex rostrata* meadow at Abisko, Sweden. The general range of net production in the Arctic is from 0.20 to 0.60 gr./m.<sup>2</sup>/day based upon the entire year (see Bliss 1962a).

Table 2 gives production rates based on roots and shoots of arctic plants. The above ground rates of production are quite comparable to those from other arctic communities. The interesting and most important point is the tremendous biomass of living roots. From the methods given, great care was employed in washing out the roots from the soil to a depth of 25 to 36 cm. (Aleksandrova 1958). It must, however, be kept in mind that these data for root biomass represent the production of many years.

The data for alpine ecosystems are quite similar to those for the Arctic with a general range of production from 0.20 to 0.60 gr./m.<sup>2</sup>/day based on the entire year. The values range from 0.06 gr./m.<sup>2</sup>/day near the centre of a late-melting snowbank in Wyoming to 0.57 gr./m.<sup>2</sup>/day in a Mt. Washington carex meadow (see Bliss 1962a). When production rates are calculated on the length of the growing season (50 to 70 days), the values for both tundras range from 1 to 3 gr./m.<sup>2</sup>/day.

There is some indication in these limited data that net production of shoots is slightly greater in the Arctic, at least in the Low Arctic of Alaska, in comparison to the various alpine ecosystems. This may result from the longer arctic photoperiod with its resultant greater number of hours available for photosynthesis during a considerable part of the short growing season. The frequently observed greater height of the same species in the Arctic as compared with their alpine counterparts may be related to this suggested difference in diurnal assimilation rates in addition to the somewhat more severe alpine environment, at least when compared with that of northern Alaska (Bliss 1956).

Efficiency of the alpine plant communities on Mt. Washington was calculated by converting the dry weight of the vegetation per metre<sup>2</sup> to gram-calories per metre<sup>2</sup> using the caloric value of the respective communities as determined with an oxygen bomb calorimeter. The caloric value per metre<sup>2</sup> was then divided by one-half of the solar radiation available during the growing season ( $200.6 \times 10^6$  calories per metre<sup>2</sup>), a 3-year average for the summit of Mt. Washington (Haurwitz 1937). One-half of the total solar radiation values are used in the calculations for only this amount of energy is in the range of visible light absorbed by chlorophyll (Daubenmire 1959). Solar energy of the growing season is used, for it is the only part of the year during which plants can carry on assimilation. Thus, efficiency percentage for the *Juncus*-dwarf shrub heath meadow in 1959 would be  $81 \times 4,743$  divided by  $200.6 \times 10^6$ , or 0.19 per cent after multiplication by 100 (Table 3).

The Mt. Washington efficiency percentages presented in Table 4 show relatively little fluctuation from year to year in the same community. The

efficiency rates of these alpine communities are comparable to those of several temperate region communities, though much more work is necessary before primary production efficiency data for various communities in different environments can be properly evaluated.

This seemingly comparable efficiency of certain alpine communities with temperate communities results in part from a more complete utilization of the growing season for growth. Most temperate communities produce larger standing crops, but this is achieved over a greater portion of the year. Limited data available indicate that these alpine plant communities have higher caloric values than temperate and tropical plant communities, increases that are statistically significant (Golley 1961).

**Table 3.** Calculation of percentage efficiency of net production in the Mt. Washington alpine tundra.

Annual total solar radiation (3-year average)		$1,077.3 \times 10^6$	gr.-cal./m. <sup>2</sup>	
Annual solar radiation available for photosynthesis		$538.6 \times 10^6$	gr.-cal./m. <sup>2</sup>	
Total solar radiation during growing season (June-Aug.)		$401.2 \times 10^6$	gr.-cal./m. <sup>2</sup>	
Solar radiation available for photosynthesis during growing season		$200.6 \times 10^6$	gr.-cal./m. <sup>2</sup>	
percentage of efficiency =	$\frac{\text{caloric values of plant material per metre}^2}{\text{solar radiation in cal. per metre}^2}$			
			<i>Efficiency in per cent*</i>	
<i>Vegetation 1959</i>	<i>gr./m.<sup>2</sup></i>	<i>cal./gr.</i>	<i>Entire year</i>	<i>Growing season</i>
<i>Juncus-dwarf shrub heath meadow</i>	81	4,743	0.07	0.19
<i>Carex meadow</i>	203	4,802	0.18	0.48

\* Based on one-half of the total solar energy value.

From a recent analysis of 40 species (entire plant samples) of vascular plants and 15 species of cryptogams from Mt. Washington it is apparent that the caloric and lipid (ether extract) values are high, especially in evergreen shrubs, (Bliss 1962b). Caloric values for evergreen shrubs averaged  $5078 \pm 69$ , deciduous shrubs  $4915 \pm 52$ , herbs  $4567 \pm 32$ , mosses  $4410 \pm 70$ , and lichens  $4324 \pm 59$  cal./gr. oven dry wt. It seems that these high caloric values can be accounted for in part by the relatively high lipid percentages, which range from  $3.72 \pm 0.5$  in the evergreen shrubs to  $1.41 \pm 0.1$  in the herbs. It is postulated that these high percentages of lipids, assuming that some are in the form of food reserves as well as structural materials, may account for the rather high rates of respiration of tundra plants referred to earlier and the rapid rates of growth and development when temperatures become favourable in the spring; an important adaptation mechanism if substantiated by further work.

In conclusion, though the tundra is characterized by having a very short growing season with low air and soil temperatures, and though wind as it affects the air and plant temperatures is important together with the low utilization level of nitrogen, tundra plants seem amazingly efficient with regard to energy conversion. This is in part due to the utilization of a large

portion of the growing season for growth and development, the use of considerable carbohydrate reserves of the previous year, and the higher caloric values of the species. The biomass production of shoots ranging from 1 to 3 gr./m.<sup>2</sup>/day during the growing season is comparable to the values found in numerous communities of temperate regions. These points and those mentioned earlier in the paper, show that tundra plants are quite well adapted to the environments in which they grow and reproduce.

**Table 4.** Efficiency of net primary production for various ecosystems based on usable solar radiation during growing season.

Community	Plant material		Usable solar radiation gr.-cal./m. <sup>2</sup>	Efficiency per cent
	gr./m. <sup>2</sup>	cal./gr.		
<i>Typha</i> marsh—Minnesota*	1680 (shoots)	4,000	337 × 10 <sup>6</sup>	1.99
<i>Zizania aquatica</i> marsh—Minn.*	580 (shoots)	4,000	337 × 10 <sup>6</sup>	0.68
<i>Sorghastrum nutens</i> old field—Minn.*	160 (shoots)	4,000	337 × 10 <sup>6</sup>	0.19
<i>Poa compressa</i> old field—Michigan†	385 (shoots)	4,080	471 × 10 <sup>6</sup>	0.33
<i>Poa compressa</i> old field—Michigan†	385 (shoots)	4,080		
	1023 (roots)	3,300	471 × 10 <sup>6</sup>	1.06
<b>Mt. Washington</b>				
<b>1958</b>				
<i>Juncus</i> -dwarf shrub heath fellfield	80 (shoots)	4,640	200.6 × 10 <sup>6</sup>	0.18
<i>Juncus</i> -dwarf shrub heath meadow	109 (shoots)	4,689	200.6 × 10 <sup>6</sup>	0.25
<i>Carex</i> meadow	208 (shoots)	4,745	200.6 × 10 <sup>6</sup>	0.49
<b>1959</b>				
<i>Juncus</i> -dwarf shrub heath fellfield	80 (shoots)	4,764	200.6 × 10 <sup>6</sup>	0.19
<i>Juncus</i> -dwarf shrub heath meadow	81 (shoots)	4,743	200.6 × 10 <sup>6</sup>	0.19
<i>Carex</i> meadow	203 (shoots)	4,802	200.6 × 10 <sup>6</sup>	0.48

\* From Bray et al. 1959.

† From Golley 1960.

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