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- - -

PHYSIOLOGICAL ECOLOGY OF ALPINE PLANTS

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George G. Spomer

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GEORGE G. SPOMER

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Committee on Graduate Work

Frank B. Salisbury Richard T. Ward Cleon W. Ross

Major Professor

C. Vernon Cole

Head of Department

Examination Satisfactory

Committee on Final Examination

Frank B. Salisbury Cleon W. Ross

Wm E. Marlatt

Richard T. Ward C. Vernon Cole

Chairman

Permission to publish this dissertation or any part of it must be obtained from the Dean of the Graduate School.

COLORADO STATE UNIVERSITY

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Chapter I

THE SCIENCE OF PHYSIOLOGICAL ECOLOGY AND THE ALPINE HABITAT

The fundamental question in plant ecology is why do plants grow where they do? That is, what conditions and interactions permit a particular plant species to occupy the particular habitat or habitats that it does? It is the purpose of this dissertation to contribute to the solution of this problem.

The general approach

Theory.--Whether or not a plant can survive and reproduce in a given habit depends largely upon the interaction between the particular environment and the genetic potential of the plant itself. The existence, direction and rate of physiological processes in the plant are the manifestations of this interaction and should collectively determine the success of the plant in the habitat. Investigation into the "interaction between environment and function" (148) should therefore yield valuable clues and possible explanations as to the nature of plant adaptation and distribution. This approach has been designated as "physiological ecology" (10, 11, 148).

The origin of the concept of the physiological ecology approach stems largely from the early work of Sachs (145) and Schimper (151) but little progress was made in this field until fairly recently when

the development of technical skills and equipment and the development of plant ecology and physiology, have advanced to a high enough level to make the physiological approach to ecology more fruitful.

Definition.--Physiological ecology is often said to be synonymous with autecology. This is an erroneous concept, since the physiological approach can be used in synecological problems as well. Physiological ecology has been defined as "the study of plant processes under natural or simulated environmental conditions" (10) and as "the science which attempts to gain answers to the problems of plant ecology through understanding of plant function...", with the "interaction between environment and function constituting the principle area of research" (148). In this study physiological ecology was taken in the latter sense.

The subject of physiological ecology has been reviewed by Billings (11) and to a certain extent by Mason and Stout (115).

Procedure.--The nature of the physiological ecology approach implies certain steps which are essential to this type of investigation (148). First, it is necessary to become acquainted, through field measurement and analysis, with the environmental factors which characterize the habitat. Coincidental with these measurements are preliminary and superficial observations on the nature of the vegetation and selected individual plants, intended to suggest possible mechanisms and correlations operating between the plants and their environment.

Secondly, it is necessary to test and analyze the functions of the plants as affected by the individual environmental factors and by combinations of various factors. This phase of the study is largely carried out in the laboratory and controlled environment facilities;

however, in the third phase, or earlier in the study if circumstances dictate, this type of investigation may also be conducted in the field. The approach is somewhat circular in this sense, as the problem in the early stages is described and analyzed in the field and is then broken down into its various components in controlled situations and finally resynthesized in progressive steps until we essentially carry the problem back to the field.

Limitations.--There are limitations in the physiological approach to plant ecology that should be mentioned. This approach will not yield the basic and essential data of descriptive ecology. The method is also limited somewhat by the advance of technology, particularly in the area of environmental measurement and control, and the advance of basic knowledge emanating from the disciplines of plant physiology and plant ecology and related fields. The small numbers and varieties of plants that can be investigated at any one time may be the most severe present limitation.

The chance factor in plant distribution seems to be outside the realm of physiological ecology. It is usually assumed that disseminules of the organism have arrived at the habitat. The physics and, to some degree, the morphology involved in distribution may also be beyond the scope of this approach.

Value.--The value of the physiological ecology approach lies primarily in its inquiry into the basic mechanisms involved in inherent plant adaptation. It thereby contributes to solution of the problems of plant distribution. Study of the physiological mechanisms involved should reciprocally contribute basic knowledge to the field of plant

physiology. The determination of these mechanisms might conceivably also allow the plant ecologist to better predict to some degree the type of plants that would exist in a given habitat, as well as explaining the particular distribution of plants as it is already known. Knowledge of the mechanisms could also be used to regulate and alter plant growth to suit a certain situation and thus have applications in agriculture and even space biology. The greatest value, and one which relates to those above, is that this approach can give us a better insight into the nature of life itself.

The meaning of "Alpine"

Definition.--The original Latin meaning of the term "alpine" (alpinus) was used to refer specifically to the Alps; however, it soon came to pertain to any lofty mountain (126). In particular, alpine is used to define the "tundra" region which occurs beyond the upper limits of normal tree growth. Therefore, in defining alpine we are actually interested in, and are referring to, the alpine zone.

A difficulty arises in this definition of the alpine in determining the essence of the term "tundra". For instance are we to consider "treeless balds" (16) which occur above "timberline" in the Appalachians? How should we treat the Andean "páramo" which occurs above timberline but below the "alpine" (133)? It would be tempting to refer to the tundra as that type of vegetation which occurs beyond the northern limit of tree growth in the arctic, and indeed, some early authors considered the alpine tundra to be no more than a southern extension of this arctic vegetation (76). This, however, is quite misleading since it has been recognized by many workers that the two zones (alpine and arctic) differ

to a considerable extent in climate (20, 21, 76, 122) and may also contain a high percentage of different plant species. Daubenmire (52), for example, estimated that only 37 per cent of the Colorado alpine species occur in the arctic. Thus it appears, like most other major vegetational formations, that there is no really sharp definition for the term "alpine tundra".

Since Colorado does not contain conflicting formations above timberline, the "alpine" will refer to the tundra region above timberline. "Timberline", as the lower limit of the alpine in Colorado, will refer to the upper edge of "normal", upright tree growth--perhaps a midway point in the subalpine forest-alpine tundra transition.

Characteristics.--It is important in understanding the physiological ecology of the alpine to consider some of the unique factors and combinations which characterize this region. Altitude is a major influence in the determination of the alpine--especially farther south. The lower limit or timberline varies with latitude from approximately 1500 feet at 70° north to as high as 12,000 feet at 30° north, whereas in the southern hemisphere it apparently reaches only about 11,500 feet and then drops off much more rapidly towards the antarctic (51). In Colorado, timberline varies from 11,500 feet in the north to about 12,000 feet in the south with local differences due to topography (51, 79).

The alpine in Colorado extends to the top of the highest peaks--over 14,000 feet; however, in other alpines the upper limit for higher plants may be as high as 20,130 feet (169) (or 22,000 feet for lower plants). This limit is apparently a function of the upper altitudinal

limits of the plants themselves, but it may be set by the presence of "permanent" snow (199) which may fluctuate from year to year.

The topography of the alpine is often very rugged, with the common occurrence of boulder fields, scree slopes, steep rocky ridges and sharp peaks. However, large, relatively gentle rolling and stable alpine plains frequently occur. It is the topography and its "youthfulness" along with the altitude which determines much of the nature of the rest of the alpine environment--particularly the climatic and edaphic features.

The climate of the alpine will be discussed in more detail in Chapter II. Here it may be said that it is probably one of the most harsh climates to which vascular plants are exposed on this planet, considering all of the factors involved. The edaphic features will also be described in Chapter II.

Since the alpine is characterized and defined largely on the basis of its vegetation, it is important to summarize the general morphological plant types and some of the most commonly recognized associations. The emphasis in this discussion will be placed mainly upon the North American alpine, especially in Colorado.

Harrington (79) lists approximately 270 species in the Colorado alpine constituting 104 genera and 30 families of flowering plants. Similar to plants in other areas of the North American alpine, these seem to fall mainly into five morphological categories--uprights, rosettes, mats, sedge-grass, and woody (trees and shrubs). The woody types include the willows, which cover extensive areas of the alpine, and the so-called Krummholz which consists of dwarfed and usually wind pruned tree species

that are generally associated with the upper limits of subalpine forests. The rosettes are typified by plants such as Geum turbinatum,[1/] Claytonia megarrhiza, etc. Few upright plants occur in the alpine, and these are usually dwarfed and found in somewhat sheltered locations. This morphological type is exemplified by Cirsium scopulorum, Penstemon spp., Aquilegia spp., Gentiana spp., etc. The sedges and grasses make up a very large portion of the alpine vegetation. Certain forbs, such as Arenaria fendleri are morphologically similar, and with the sedges and grasses constitute a morphological type. The mat or cushion plants, although not unique to the alpine, are found more abundantly here than in any other vegetation type. These plants grow on the more exposed, wind-blown sites and generally form round, low mounds of vegetation of from four to 12 inches or more in diameter. Silene acaulis and Trifolium nanum are good examples of cushion plants.

Generally speaking, all of the alpine plants seem to share the dwarf growth habit which becomes more severe with increasing altitude. Many also possess a very well developed root system, which is relatively large compared to the aerial portions of the plant. Alpine plants typically have smaller, fleshier leaves than do many of the subalpine plants, (45, 91). The value of such morphological features to plant adaption may become evident as more physiological ecology studies are made.

The vast majority of alpine plants fall into the categories of chamaephyte and hemicryptophyte, with a few phanerophytes and cryptophytes (33). Koenigia islandica is considered as the only true alpine therophyte (annual) in Colorado (198).

1/ Nomenclature will follow Harrington (79) except where specified.

Common vegetational associations.--The delimitations of discrete plant groupings presupposes either of two conditions; 1) that there is some sort of direct or indirect interaction and species interdependency between the plant species constituting the group, or 2) that the plant species characterizing the groups have similar environmental requirements and tolerances which are different from the environmental amplitudes of species of other groups. There is little evidence to support either contention, but it is often useful in describing the alpine as well as other vegetational formations to utilize type habitats or arbitrary "stands" as a basis of organization. Many such divisions pertaining to the alpine have appeared in the literature as "real" or arbitrary associations (41, 44, 45, 76, 82, 97, 112, 113, 130, 189, 209). Some of these divisions are wet bog, wet meadow, willow bog, alpine turf, fell-field and boulder field. Each of these represents a type of habitat (which, of course, may blend into another) that is characteristic of most alpines.

The alpine as an area of investigation

This dissertation will be concerned with the use and results of the physiological ecology approach as applied to the alpine region. The general aspects and advantages of the alpine as an area of study are discussed below.

Advantages.--The alpine lends itself particularly well to a physiological ecology study for many reasons. A major advantage is found in the small size of alpine plants which makes the use of controlled environments more economical. Also, the relative endemic nature of much of the alpine vegetation suggests that the plants may have narrow and

somewhat unique tolerance ranges, and the gradients of the physiographic and edaphic as well as the climatic features of the alpine environment are quite variable so that the limits of these tolerances may be approached within a relatively short distance.

The circumpolar nature of the alpine region also has advantages in allowing studies to be made on a wide geographic scale--particularly since the environment and species composition to some extent are much the same (51, 76, 80, 107, 133, 168, 212, 218). The relative simplicity and stability of this formation facilitates long-range studies, and major alteration of the environment through vegetational development and succession is relatively slight.

Specific problems and general organization

The inability for a single investigator to approach all of the problems connected with all of the alpine areas of the world or even of a small area makes it necessary to limit the problems under investigation in this paper.

Study area.--The field study area chosen for investigation lies along and just within the northern border of Rocky Mountain National Park in section 36, range 74 west, township 7 north. This area, known as False Mummy Pass, was selected for its proximity to the Colorado State University Forestry Camp at Pingree Park and its relative freedom from grazing and other human disturbances. As in most alpine regions, this area also has the advantage of containing a wide variety of habitats from wet bog to fell-field within a relatively short distance from one another. The topography and general nature of the study area has been described extensively by Holway (92, 93) and Spomer (161), and Wegemann's description

of the geology of Rocky Mountain National Park presents a general picture of the region (200). The vegetation of the area has been sampled and discussed by Ward (189) and Holway (92, 93) so that descriptions of vegetation will be limited to specific locations of particular interest to this study.

Some field observations and measurements were also carried out on the summit of Mt. Evans, near the top of Trail Ridge Road, and in the alpine of the Iron Mountain region of Larimer County near Cameron Pass. The field phase of investigation was largely limited to the measurement of environmental factors during the growing seasons of 1960 and 1961.

Laboratory studies were made during 1960, 1961, and 1962 using the facilities of the Colorado State University Botany Department (Chapter II).

Problems.--Specific physiological ecology problems in these regions were singled out partly for their relevency to the question of alpine plant adaptation and partly out of interest on the part of the investigator. The major problem under investigation was the endemic nature of Geum turbinatum, which may be stated as: What physiological features of G. turbinatum allow this plant to survive and reproduce in nearly every alpine habitat while excluding it from the subalpine regions.

Preliminary studies on the nature of the cusion growth habit, cold-hardiness in Ranunculus adoneus, and the temperature of plants in the alpine in relation to the ambient conditions and radiation environment will also be reported and discussed.

Organization.--Since the environment is an essential component in any physiological ecology study, a chapter will be devoted to the nature of the alpine environment (supplemented by observations made in our study areas), to the known effects of different environmental factors on plants as they might pertain to this study, and to the theory and design of controlled environment facilities for use in physiological ecology studies.

The temperatures of alpine plants in conjunction with the factors which affect them will be discussed. The growth, flowering, and dormancy processes of alpine plants will also be considered.

Chapter II

THE ENVIRONMENT

A study of the environment, as pointed out in Chapter I, is an integral part of any physiological ecology investigation. Based upon knowledge of environment in general, the nature of the particular environment must be analyzed. This information along with a knowledge of the known responses to environmental factors by plants can be used to formulate hypotheses which, in turn, can be tested through control of the plant environment. Thus, it will be the object of this chapter to discuss the concept of environment, describe the alpine environment, summarize some of the known effects of different environmental factors as they might pertain to alpine plants, and finally to discuss the theory behind environmental control with a description of the facilities used in this study.

Environment

Definition.--Environment is defined in this paper as: The sum of all phenomena to which the organism or its constituent parts are exposed at any given time. This definition follows the ideas of several workers (1, 81, 185) and includes the original meaning of the word...i.e. that which surrounds (126). Many definitions which tend to be more idealistic have also appeared in the literature and generally fall into two groups: (a) those which define environment on the basis of an interaction between phenomena and the organism...i.e., the phenomena

which affect the organism (50, 114, 116, 126), and (b) those which define environment and the phenomena which may affect the organism (78, 123). These two groups of definitions really represent the goal of a physiological ecology study and are therefore not practical approaches to the initial analysis of the environment. In a physiological ecology study, then, we are attempting to sort out those factors which constitute the "operational environment" of Mason and Langenheim (114). But, we must measure as much of the environment as possible in order to increase our chances of including the total operational environment.

Subdivisions of the environment.--The environment is an integration of many phenomena, and any divisions of environmental factors or phenomena is purely arbitrary and for convenience only. Thus it is convenient to distinguish between factors external to the organism and those which are internal conditions, the latter constituting the environment of the individual constituents of the organism rather than the whole organism.

The internal conditions are probably the more difficult to evaluate since it must be done largely through physiological and cytological techniques. Plant temperatures, water stress, pH, plant pigmentation, and chemical concentrations are examples of the phenomena which may be placed in this category. It is the phenomena internal to the organism which ultimately interact with the genes and other cellular components to produce the physiological responses which in turn determine the future course of the plant (164). To discover and relate the internal conditions and function to the problems of ecology is the real essence of physiological ecology.

Due to the inherent difficulties in attempting to study the internal conditions of alpine plants, few investigations of this division were made in this study. Some evaluation of plant temperature, however, was made and will be discussed in the following chapter.

The internal conditions are largely a function of the environment of the whole organism. A knowledge of the nature of this environment should then indicate what the plant is experiencing internally. The factors constituting the environment are numerous. Therefore, Billings' (12) subdivision or classification of these factors will be largely followed in this paper. The groups, factors and subfactors considered in this study are listed below.

Climatic group -

Radiation factor -

Infrared radiation
Visible radiation
UV radiation

Temperature factor -

Air temperature
Soil temperature

Moisture factor -

Precipitation
Humidity (and transpiration)
Soil moisture
Melt water

Atmospheric gases -

Wind
Gas composition

Edaphic group -

Structure factor
pH factor

Geologic group -

Topography and drainage

Biotic group

Micro- vs. macroenvironment.--Given a defined geographic region it is theoretically possible to describe the general environment extending over this region. Subregions could then be defined within the given region and the environments associated with these subregions could also be analyzed apart from the general environment of the given region. The term "macroenvironment" will be used to represent the first condition... e.g. the general environment, and "microenvironment" will refer to the subdivision of the general environment. Thus, according to this concept, both terms are relative and neither can really be defined without at least implying the other.

The importance in considering the microenvironments or certain microenvironmental groups...e.g. microclimates, has been demonstrated by many workers (8, 13, 21, 34, 38, 43, 86, 120, 153, 154, 215). Most of these investigations show that although the microenvironments of a region have some fundamental relationships with each other through the macroenvironment, the vegetational patterns are more closely related to the differences between microenvironments.

Principles of environmental measurement.--Measurement of the entire plant environment may be theoretically limited by imperfect instrumentation and is often practically limited by economics. It is therefore necessary to decide which environmental factors appear to be most important to a particular region, and the precision to be attained in their measurement. The decisions will probably result in the

selection of factors known to influence plant response, some of which may be unique to each microsite and which fluctuate significantly over a period of time.

How often a factor is to be measured must also be considered. Some factors which fluctuate only over a wide period of time, such as deep soil temperatures, need usually be recorded no more than once or twice each week, while other factors such as radiation may require continuous measurement.

Placement of the environmental sensors is another important consideration. In general the instrument should be placed as close to the organisms or its parts as possible. In the alpine, then, the sensors usually need not be placed over 30 cm above or below the soil surface.

The basic assumption underlying all environmental measurement in relation to an organism is that the instrumentation is exposed to essentially the same phenomena as the organism, and the response of the organism and the sensors are related to each factor in a similar fashion. This means that the larger the geographic area is to which we apply a measurement, the more we must assume. To get around this assumption, some workers have attempted to use the plants themselves as environmental indicators (39, 40, 209). Their use, however, is strictly comparative and cannot indicate absolute environmental conditions due to genetic differences and plasticity.

The Alpine Environment

The data presented in this section are largely the results of studies made at two microsites in the False Mummy Pass area, stations 4 and 12 (161), and to a lesser extent studies made on Trail Ridge Road and Mt. Evans during the seasons of 1960 and 1961. Reports from the literature will be used to supplement these data.

It should be recognized that there are seldom sharp breaks between most microenvironment factors, but rather a gradual transition is found in both environment and vegetation type. It should also be re-emphasized that the factors interact to a high degree so that variation in one factor may result in or from changes of many other factors.

The climactic environmental group

That group of environmental phenomena which shows variation such as seasonal or diurnal changes, will be defined as climactic factors.

Radiation.--The term radiation will apply in this paper to the form of energy transferred by photons and making up the electomagnetic spectrum. Cosmic radiation consisting of high energy particles exhibiting properties of extremely short waves is also included.

Measurement of the quality, quantity and duration of a radiation subfactor is usually accomplished in one of two basic ways: (a) measurement of the change in kinetic energy of molecules as they absorb or emit radiant energy... i.e. heat measurement; or (b) measurement of the changes in the energy states of electrons of molecules and atoms due to the absorption of radiant energy as indicated by chemical reactions or flow of electrical current.

In this study fluctuations in the total radiation were recorded near station 12 in 1960 and at station 4 in 1961 by a Belfour Pyrheliograph, while a Goodell Pin-ball totalizing net radiometer (75) and a Stoll-Hardy radiometer were used on Trail Ridge Road and Mt. Evans to measure the net radiation flux and temperatures of the radiation environment or radiating surfaces. Attempts to evaluate the relative intensities of visible were made using a Weston photometer with suitable neutral density filters. A General Electric exposure meter with a booster attachment was used to measure low light intensities on Mt. Evans. No critical studies were made of the qualitative aspects of the solar spectrum in the alpine, nor were the factors of cosmic and terrestrial radiations measured, due to the lack of suitable equipment.

According to the literature (68, 101) the quality of the alpine solar radiation is only slightly different from the radiation reaching other parts of the earth. If anything, one might expect to find a slight shift towards the blue, but due to the sharp cut-off below 2920 Å by the ozone layer at 25 km, this shift is merely one of intensity. Thus no new shorter waves should appear in the alpine spectrum.

Photometric light intensity readings lasting seconds to minutes were generally quite high in the alpine compared to lower elevations. Light intensities of up to 16,000 ft-c were measured on Mt. Evans and Trail Ridge Road. Maximum light intensity readings (meter pointed towards the sun) made over a nine hour period on June 21 at 14,100 ft elevation near the summit of Mt. Evans increased rapidly during the early part of the morning to a maximum of about 13,000 ft-c (Fig. 1). Little variation was experienced during the day with the exception of that due

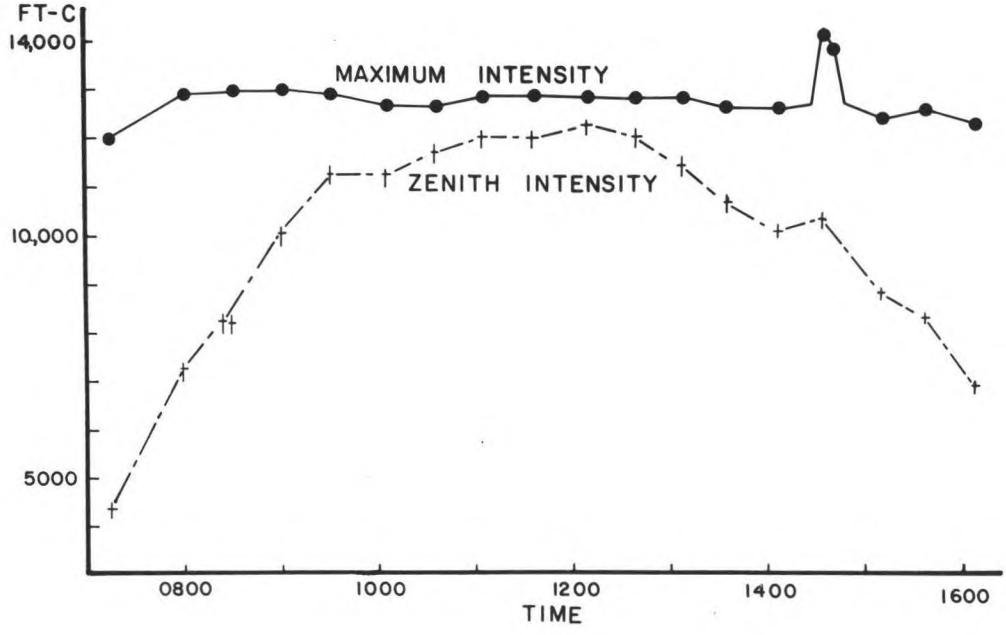
to a few clouds. In the evening the values dropped rapidly as the sun began to set. Zenith readings during this same period showed a general rise to a peak of 13,000 ft-c about midday, after which they began to fall off.

The intensity of the total incoming radiation as measured by the pyrheliograph was also exceedingly high and under the proper cloud conditions (168)...i.e. the thin edge of a cloud, even surpassed the solar constant of 2.00 langleys*(ln) (96). The highest peak recorded during the 1960 season was 2.20 ln on July 13, while in 1961 a maximum of 2.17 ln was recorded on June 6. There were nine days with maximum intensities of 2.00 ln or over between July 4 and October 19, 1960 and ten days with maxima above the solar constant during the 1961 season of from May 22 to October 8. The peak intensities on cloudless or nearly cloudless days, however, were generally lower with maximums of around 1.9 ln on or about June 21, while in October they had fallen off to about 1.1 ln. The mean weekly maxima during the season actually reach a plateau of about 1.9 ln in May. These lasted through the middle of July, after which there was a gradual decline to the neighborhood of 1.4 ln (Fig. 2).

The daily incoming solar radiation, similar to maximum intensity, is also relatively high in the alpine, but there is much more variation. Values obtained by integrating the area beneath the pyrheliograph curves frequently exceeded 800 cal per cm^2 per day and it is estimated that they might reach 1000 around June 21. Clouds, although they may increase intensities for short periods, usually decrease the total radiation received as compared to cloudless or nearly cloudless days. Total radiation values during relatively clear days actually tend to form

*A langley = 1 cal per cm^2 per min.

Fig. 1.--Light intensities measured near the summit of Mt. Evans on June 21, 1961.


FT-C
14,000
10,000
5000
MAXIMUM INTENSITY
ZENITH INTENSITY
0800
1000
1200
1400
1600
TIME

the upper limit for daily radiation readings during the season, with peak values occuring about June 21 (Fig. 4). The weekly and monthly average cal per cm^2 per day also followed this pattern (Fig. 3).

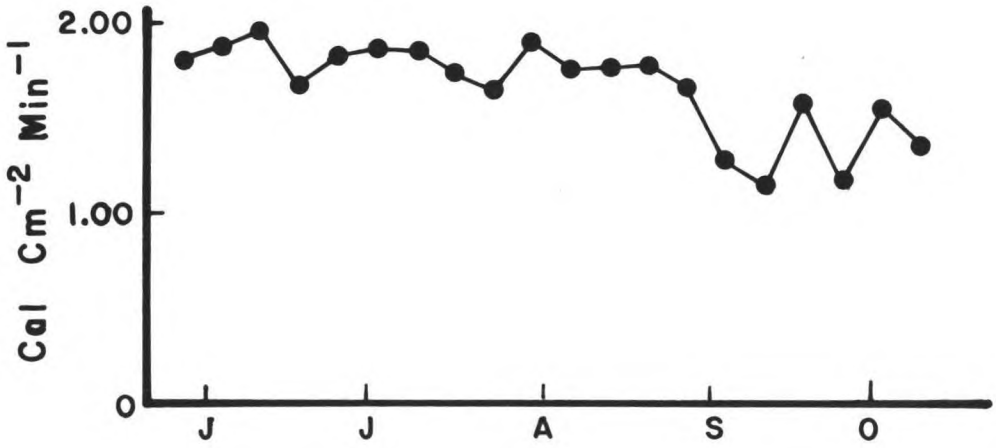
The total radiation recorded for the 140 day season in 1961 was approximately 77,000 cal per cm^2. This is enough energy, if all of the radiation received is absorbed and converted to kinetic energy, to evaporate a layer of water from the area at 0 C and 525 mm pressure to a depth of 1.3 meter. The range of daily values during 1961 ran from 0 ln per day to 860 ln per day and from 5 ln per day to 875 ln per day in 1960.

Objects radiate energy according to the Stefan-Boltzmann equation, $E = \sigma T^4$ (49), where T is the absolute temperature of the object and σ is a constant. Thus while organisms and objects in the alpine are receiving radiation, they are also emitting radiant energy. It is, therefore, important to consider the net radiation flux. Unfortunately no measurements of net radiation were made in the False Mummy Pass area to compare with the total energy received, yet the readings from Trail Ridge and Mt. Evans should give some indication of what is happening in the alpine (during the day at least).

The average net radiation over 30 minute periods on Mt. Evans during a 21 hour period on July 14 and 15, 1961 reached a maximum of 1.35 ln about noon on July 14, while a minimum of -0.14 ln was recorded several times during the night (Fig. 20). Positive values indicate a net influx of radiation, while negative values imply anoutward net flow of energy. The minimum figure is probably too high, since a snow storm during the evening had covered the ground beneath the radiometer unit and acted as

Fig. 2.--Weekly average maximum radiation intensities recorded from May to October, 1961.

Fig. 3.--Weekly and monthly average radiation received each day during the 1961 season.


2.00
1.00
0
Cal Cm^{-2} Min^{-1}
J
J
A
S
O

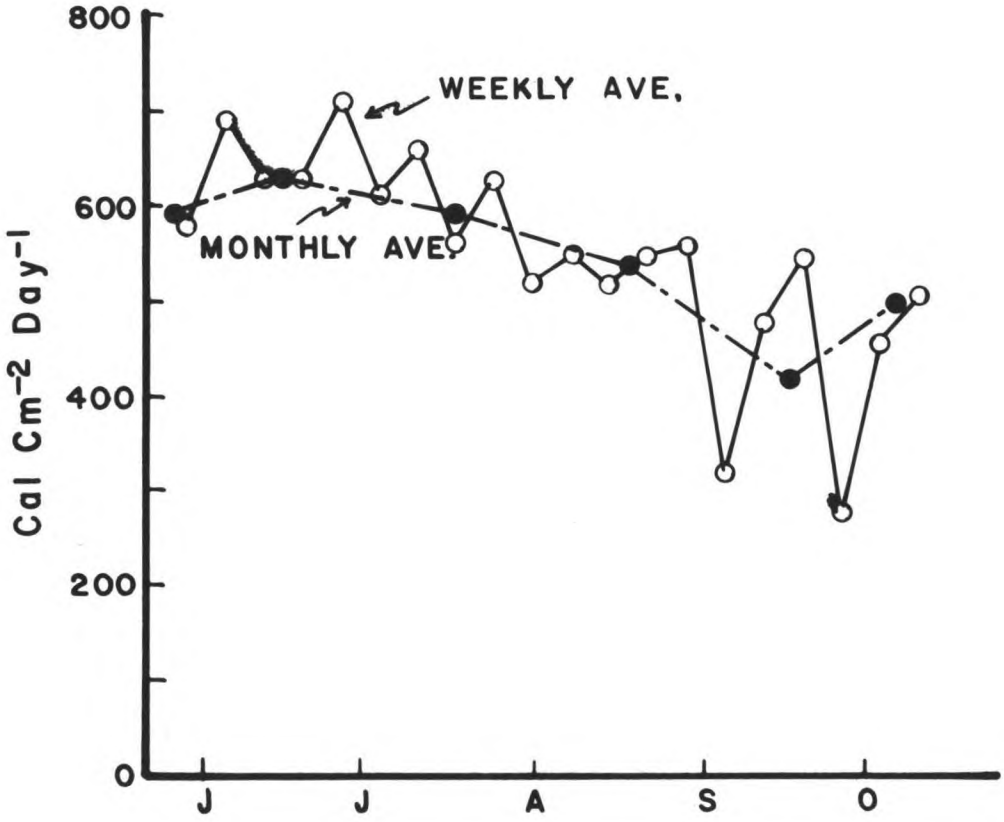
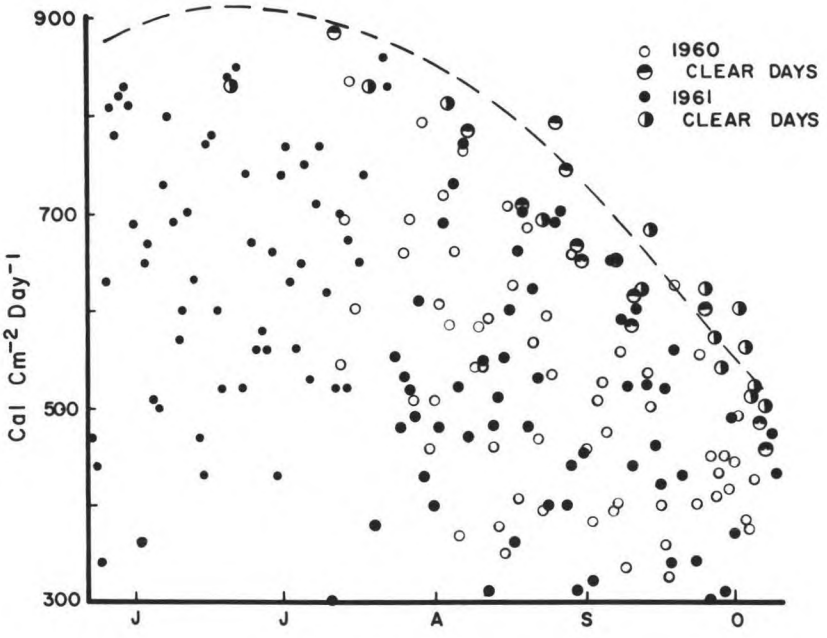

800
600
400
200
0
Cal Cm^{-2} Day^{-1}
WEEKLY AVE.
MONTHLY AVE.
J
J
A
S
O

Fig. 4.--Daily radiation values recorded by a pyrheliograph on False Mummy Pass from May through September, 1960 and 1961. (Values below 300cal per cm^2 per day are not shown).


900
700
500
300
Cal Cm⁻² Day⁻¹
J
J
A
S
O
1960
CLEAR DAYS
1961
CLEAR DAYS

an insulator against radiation from the soil. Values ranging from 0.34 to 1.19 ln were recorded on Trail Ridge during 1961.

The net radiation is really a function of the temperatures of a point and the radiation sphere about that point. For this reason an attempt was made to evaluate the temperatures of the radiation sphere to which the alpine plants are exposed using the Stoll-Hardy radiometer. Since the radiation sphere is an integration of many points the values recorded are merely indications of the sources and sinks from which and to which radiant energy is flowing. For example, apparent temperatures of clear sky of less than -30 C were measured on Mt. Evans during the evening of July 14, while temperatures of less than -20 C were not uncommon during the day on Trail Ridge or Mt. Evans. Cloud cover, on the other hand, was usually a point of higher temperatures with readings frequently approaching 30 C.

Temperature.--Temperature is here considered to be the measure of the relative kinetic energy state of the atomic or molecular sized particles in the systems surrounding the plant or any of its component parts or the relative kinetic energy state of the plant and its component parts. Since the rate, existence and direction of plant function (assuming it is the result of physio-chemical phenomena) should obey the laws of thermodynamics, it would be best to use a temperature scale which can readily be related to the energy of a system. For this reason the centigrade scale (C) is used in this paper (i.e., deg C + 273.16 = deg K).

Temperature measurement is accomplished in several basic ways which include changes in the volume and pressure of liquids and gases,

the relative lengths of solids, the resistance of a conductor or semi-conductor, or electromotive force produced between two junctions of two metals. The emitted radiation may also be used according to the Stefan-Boltzmann law to indicate temperature (with an emissivity factor). In this study, temperatures were measured above the soil with Bendix hygro-thermographs, mercury thermometers, thermistors, thermocouples and a Stoll-Hardy radiometer. Air temperatures in the two microsites of the False Mummy Pass area were recorded by hygrothermographs shielded from insulation by specially designed shelters (162). These shelters were constructed to place the sensors of the instruments about 6 cm above the soil surface and to record the temperatures at approximately the mean plant level.

Soil temperatures were measured by thermistors contained in the Colman soil-moisture units (42). These units were placed at 3 cm, 15 cm and 30 cm depths in the soil. Some indication of surface temperatures were given by thermometers placed in the surface of the soil during a 48 hour period in 1960 (161). Although soil temperatures were recorded at some 12 locations in the False Mummy Pass area, only those from station 4 and 12 will be reported here. The results from the other stations have been analyzed by Spomer (161) and by Holway (92).

The results from the two False Mummy Pass microsites show that the air temperatures during the 1960 season were higher during the day than in 1961, particularly at station 12 (Figs. 5 and 6). The range of maximum temperatures at station 4 was from 1.5 to 22.5 C in 1960 while in 1961 maximum temperatures of from -0.5 to 22.0 C were recorded.

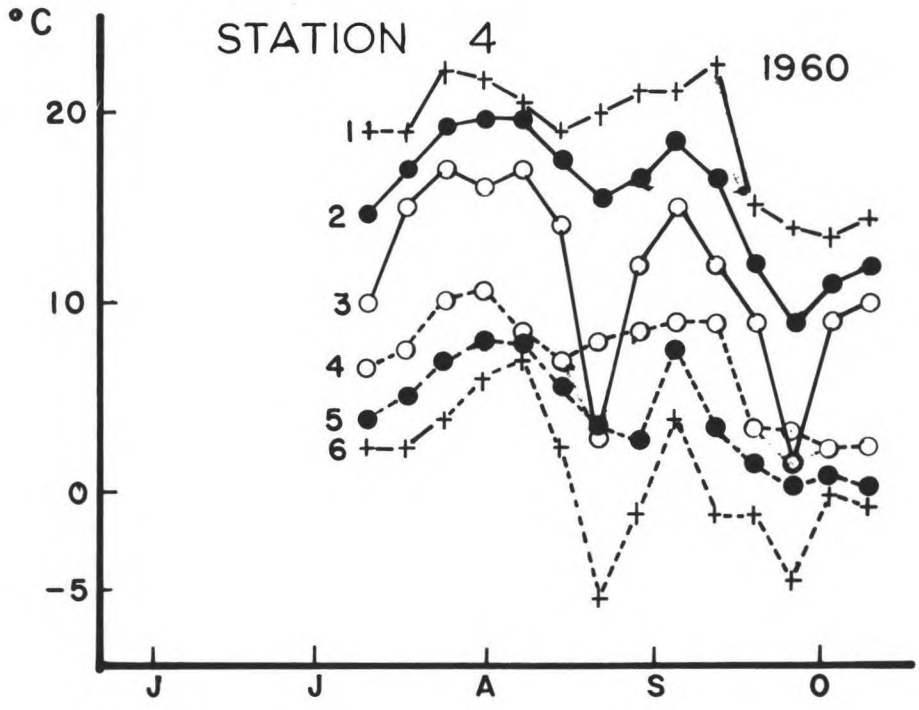
At station 12, on the other hand, maxima of from 1.0 to 24.0 C and 0.0 to 22.0 C were recorded during these two seasons. Generally the maximum temperatures at station 12 were the same or slightly higher than those at station 4. The absolute maxima at both stations showed relatively small amounts of variation when compared to the mean or minimum daily maxima. The patterns, however, show that the maximum temperatures increased gradually in the early part of the growing season until about mid-July after which they leveled off. The winter season, on the other hand, was heralded by sharply decreasing maxima with considerable day to day variation.

The minimum daily temperatures in contrast to the maxima differed fairly consistently between the two stations, with station 12 generally being cooler than station 4 (Figs. 5 and 6). This is probably related to differences in exposure and elevation although exact relationships are not obvious.

The range of daily minimum temperatures at station 4 was -5.5 to 10.5 C in 1960 and -6.5 to 10.0 C in 1961. At station 12 the minimum daily temperatures ranged from -6.0 to 8 C in 1960 compared to -5.0 to 8.0 C in 1961. The patterns of minimum temperatures in all cases seemed to be less variant over the long seasonal trends. It should be noted that frost may occur any time during theyear in the alpine (113, 161).

The rate of chemical reactions is, within certain limits, dependent (directly or inversely) upon the kinetic energy state of the component atoms and molecules of the reactants and products. Thus, the rate will be related to the average energy state of the system over a

Fig. 5.--Air temperatures at stations 4 and 12 during the 1960 season. (1 - absolute weekly maximum, 2 - mean weekly maximum, 3 - minimum weekly maximum, 4 - maximum weekly minimum, 5 - mean weekly minimum, 6 - absolute weekly minimum).


°C
STATION 4
1960
20
10
0
-5
1
2
3
4
5
6
J
J
A
S
O

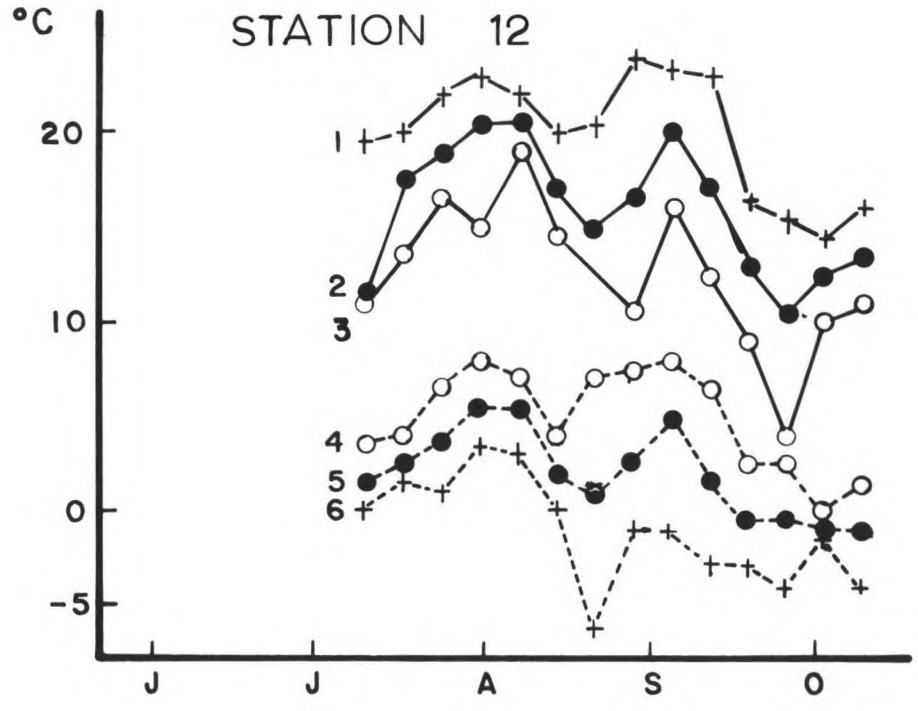
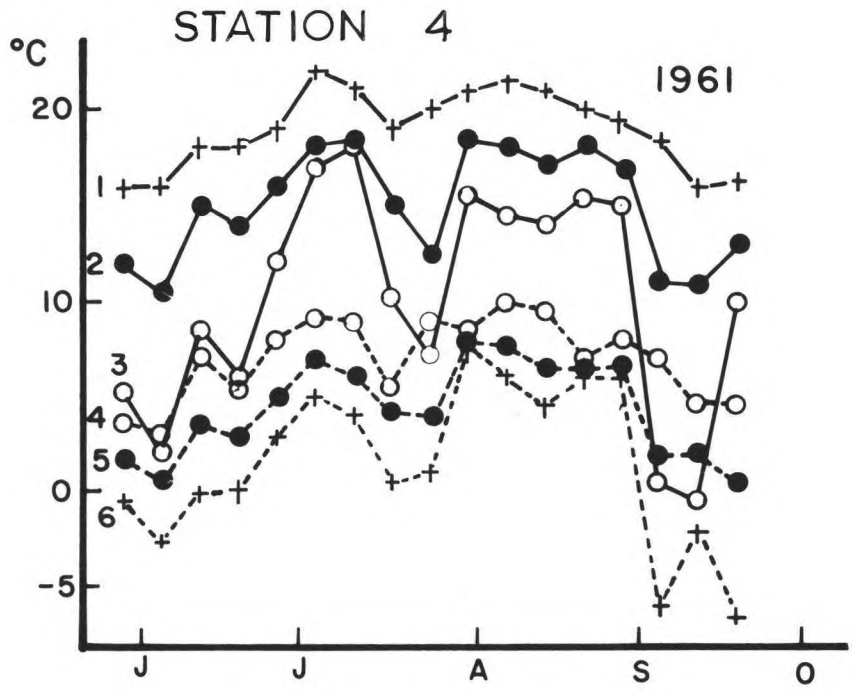
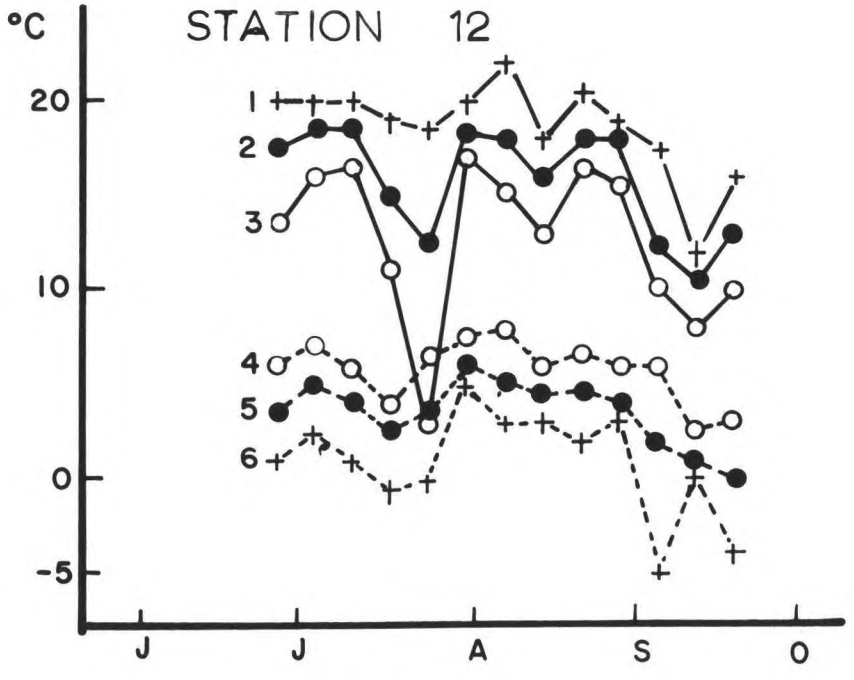

°C
STATION 12
20
10
0
-5
1
2
3
4
5
6
J
J
A
S
O

Fig. 6.--Air temperatures at stations 4 and 12 during the 1961 season. (1 - absolute weekly maximum, 2 - mean weekly maximum, 3 - minimum weekly maximum, 4 - maximum weekly minimum, 5 - mean weekly minimum, 6 - absolute weekly minimum).


STATION 4
1961
°C
20
10
0
-5
1
2
3
4
5
6
J
J
A
S
O

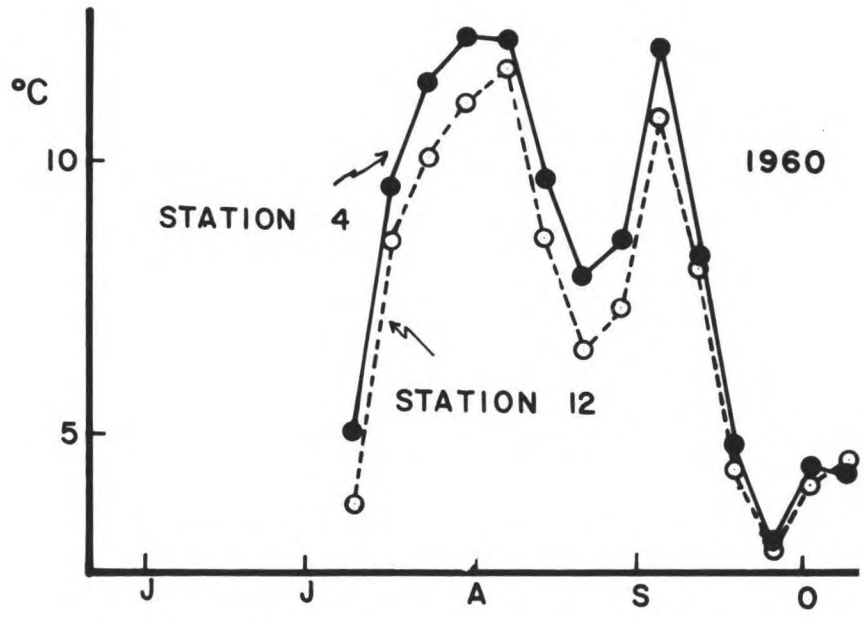

STATION 12
°C
20
10
0
-5
1
2
3
4
5
6
J
J
A
S
O

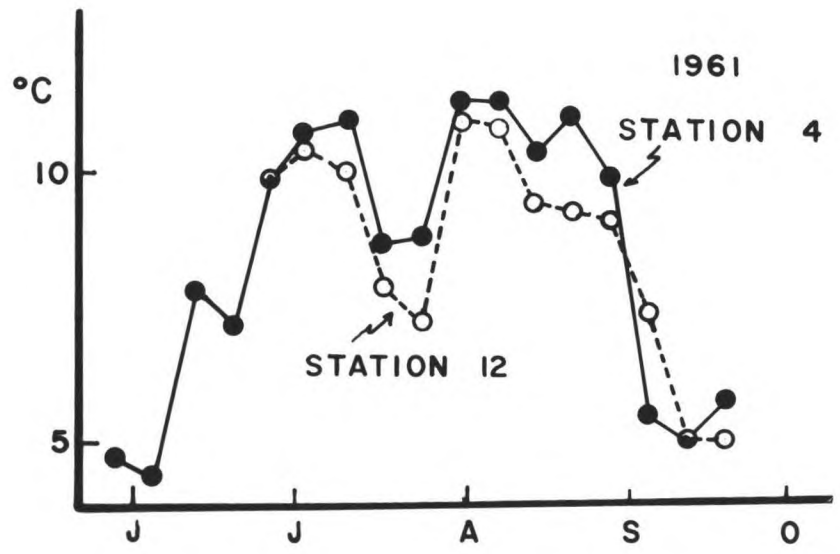
period of time. Using the air temperatures as a possible indication of plant temperatures, an attempt was made to evaluate the average daily kinetic energy state of the plant systems by integrating the temperature curves from the hygrothermograph records over 24 hour periods. The values so obtained have the units of deg min, which can be converted to average daily temperatures by dividing by 1440 minutes per day. It should be emphasized that this is not a measure of the quantity of heat received by an organism, but merely an indication of the relative daily energy level of the organism.

The season curves for the average air temperatures obtained in the above manner for areas 4 and 12 show more variation than those of the maximum or minimum temperatures (Fig. 7). From a comparison of patterns, the 1960 season appears to have been warmer, but there was more variation in the daily average temperatures than in 1961. In both years station 12 was consistently lower than station 4 until the last of each season when they were approximately the same. The ranges in average daily temperatures recorded during the 1960 and 1961 seasons at station 4 were -4 to 14 C and -6 to 13 C, while at station 12 these ranges were -4.5 to 13 C and -1 to 13 C respectively. The minimum value at station 12 during the 1961 season is probably too high since there was no record of temperatures at this station on the day that the minimum was recorded at station 4.

Soil temperatures at these stations were measured only once or twice each week during the two seasons, yet there is reason to believe that the temperatures at the 15 cm and 30 cm levels can be validly compared for the two stations throughout the seasons due to their

Fig. 7.--Average weekly air temperatures at stations 4 and 12 during the 1960 and 1961 seasons.


°C
10
5
STATION 4
STATION 12
1960
J
J
A
S
O


°C
10
5
1961
STATION 4
STATION 12
J
J
A
S
O

relative stability over long periods (161). In general the soil temperature patterns were the same over the two seasons with the exception that the season of 1961 was somewhat shorter, as indicated by the relatively earlier sharp drop in temperatures near the end of the season (Fig. 8). Also, the fluctuation was greater in 1960 with the exception of the 15 cm level at station 12 which shows more variation early in the 1961 season. It is interesting to note that the rate of increase in the 30 cm temperatures at station 12 during the first part of the season was very similar in both years with approximately the same lag relative to station 4. This is probably the result of the flow of melt water from the snow field above 12, and indeed, soil temperatures in general seem to decrease with an increase in ground water. Table 1 summarizes the ranges of temperatures at the different depths and stations over the two seasons.

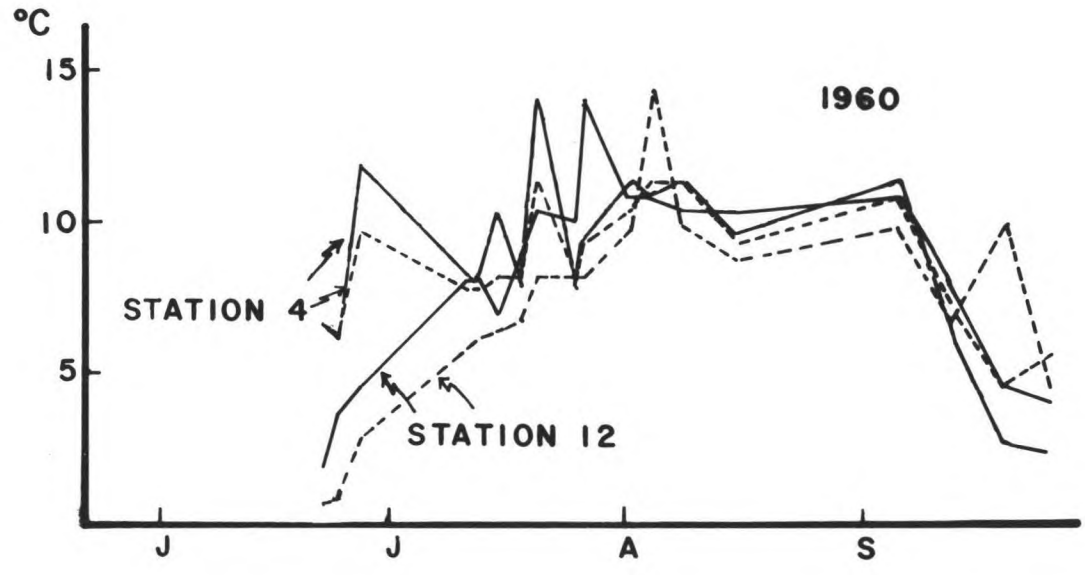
Table 1.--RANGES OF SOIL TEMPERATURES FROM DIFFERENT DEPTHS AT TWO MICROSITES IN THE FALSE MUMMY PASS AREA IN 1960 AND 1961.

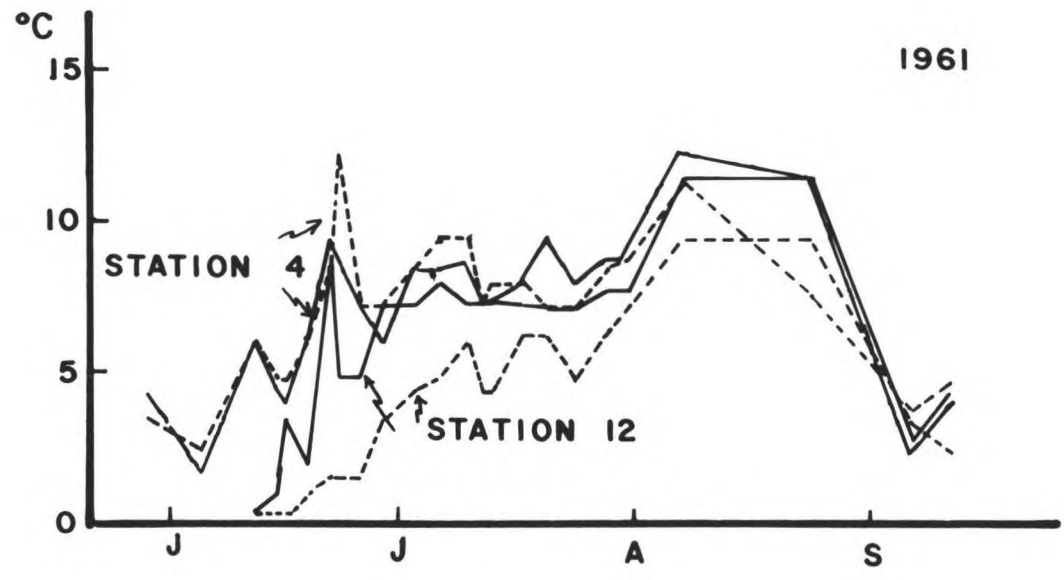
Depth	1960		1961	
	4	12	4	12
15 cm	2.5-14.2 C	1.9-13.9 C	1.7-12.3 C	0.3-11.5 C
30 cm	3.6-11.4	0.6-14.2	2.5-12.3	0.3- 9.5

During snow free periods, the soil probably also acts much like a net radiometer, and thus soil temperatures indicate to some degree the trends in the integrated radiation flux which is occuring in the areas.

Moisture.--Moisture will be taken as that part of the phenomena to which a plant is exposed which deals with water in the solid, liquid or gaseous state or in the bound state where it does not lose its molecular identity.

Fig. 8.--Soil temperatures at stations 4 and 12 during the 1960 and 1961 seasons. (Solid lines indicate the 15 cm depth while broken lines indicate temperatures at the 30 cm depth).


°C
15
10
5
1960
STATION 4
STATION 12
J
J
A
S


°C
15
10
5
0
1961
STATION 4
STATION 12
J
J
A
S

Measurement of moisture in the form of precipitation is usually accomplished by collecting the moisture and weighing it or determining its volume. Moisture in the atmosphere (humidity) can be sampled through the use of resistance readings in a hygroscopic crystal, by the expansion or contraction of a hair as water is adsorbed on its protein fibers and equilibrates with atmospheric moisture, by the enthalpy of evaporation, by the temperature of condensation, or by infrared absorption. Soil moisture may be measured by the changes in electrical resistance of structures or materials as they gain or lose water, by the weight difference between wet and oven dried soil, by the capacitance of a soil, by manometric measurements of the tensions developed in removing the water from a soil, or by neutron absorption and scattering.

Moisture in the form of precipitation was measured in this study by standard 12 inch Forest Service rain gauges, while hygrothermographs and sling psychrometers were used to indicate the relative humidity. Soil moisture was calculated from the Colman soil-moisture unit resistance readings (temperature corrected).

Precipitation in the alpine may occur in virtually any form (show, sleet, hail, graupel or rain) throughout the growing season. Normally rain is the predominant type of precipitation, but it is generally preceeded and followed by some graupel. The absolute amount and distribution may vary from year to year as indicated in this study (Figs. 9 and 10). In 1960 much of the precipitation either fell early in the season or late in the season leaving a relatively dry period during July and August. In contrast, the precipitation in 1961 was fairly evenly distributed over the entire season with no really dry

periods occuring. The 1961 season was recorded as an unusually wet year at other official weather stations near the Front Range.

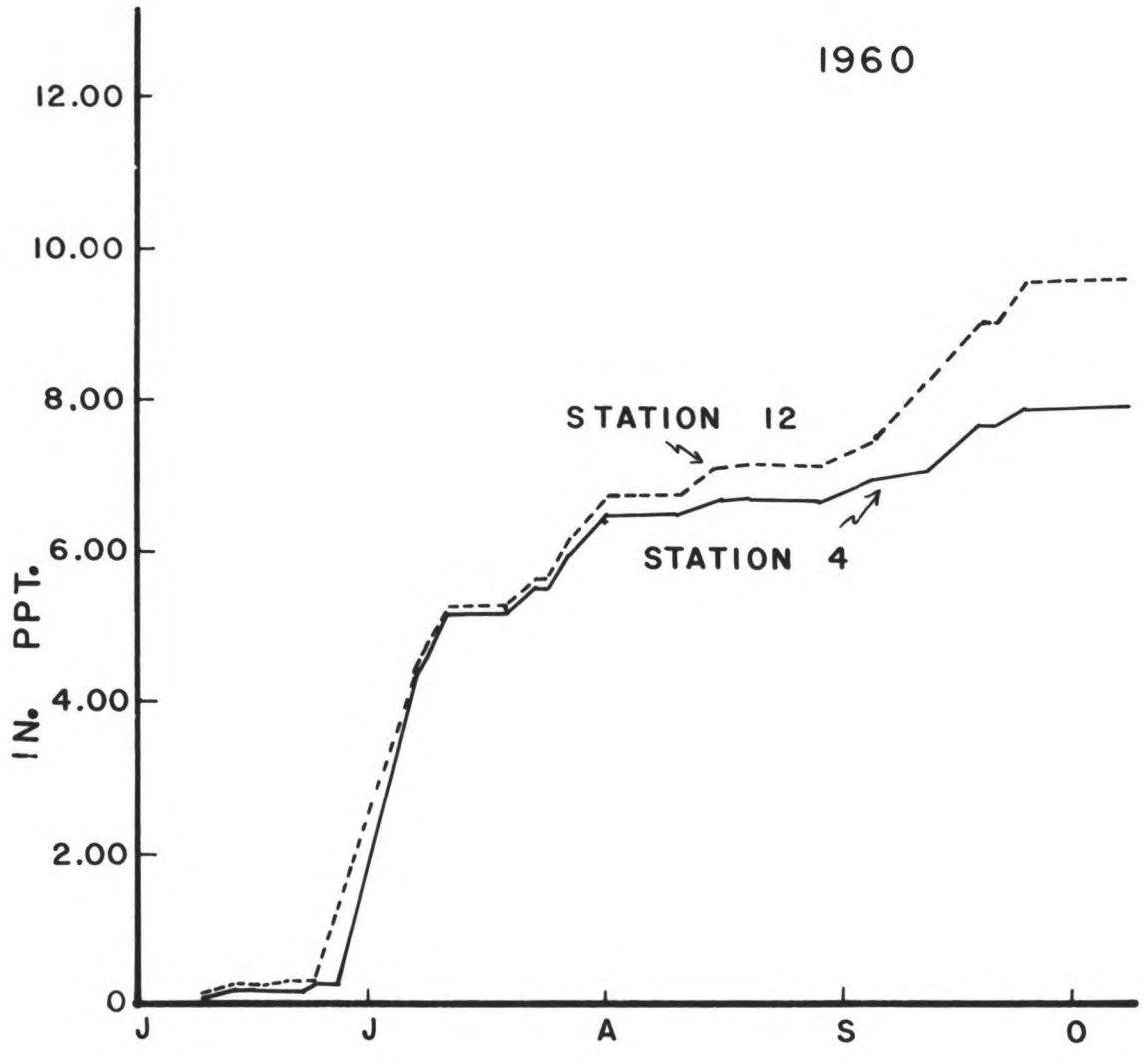
The lateral distribution of precipitation over a small area in the alpine seems to depend to a considerable extent upon wind exposure and the form of the precipitation. The final winter accumulation of snow, for example, may be exceedingly deep in protected areas in contrast to the bare, wind blown ridges. Rain distribution in the False Mummy Pass area also seems to be correlated somewhat with the wind distribution, particularly during seasons with relatively high winds (161). The difference between the relative amount collected at stations 12 and 4 during 1960 may be an illustration of this wind effect, while during 1961 which seemed less windy no difference in precipitation was noted until the occurrence of an early snow storm and the subsequent wind shifting of the snow to protected areas. The wind effects measured in this study may also be discrepancies in measurement techniques (83). There was essentially no difference in the times of precipitation at the two stations both years.

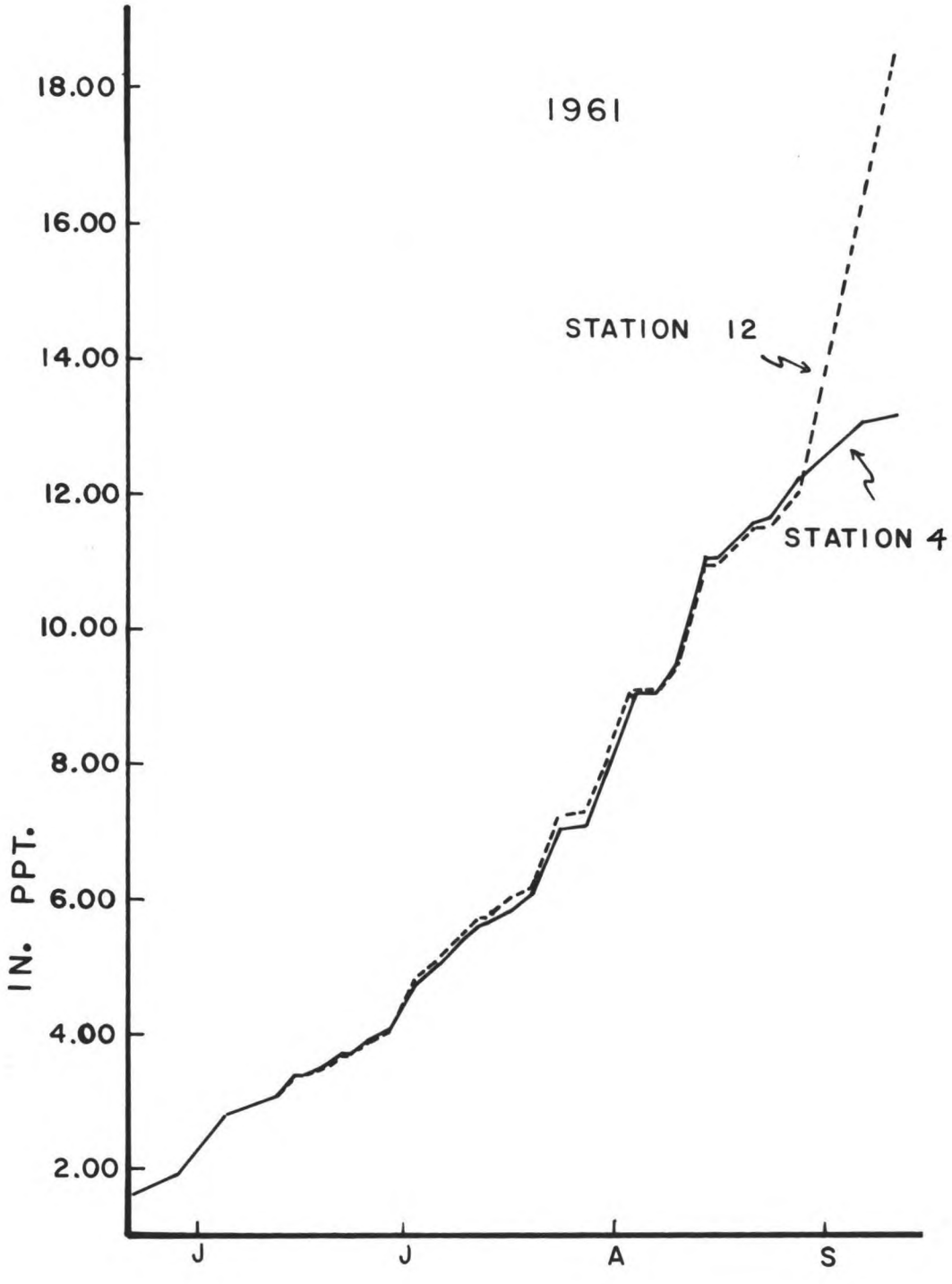
Humidity refers to the amount of water vapor in the atmosphere. What influence the amount of water vapor in the air has on the evaporation from plants (transpiration) has been debated by many authors (86, 107, 176), but as yet no completely satisfactory answers have been given. Much of the argument has centered around the manner of expressing the humidity of the air so as to give the best indication of the evaporative power of the air in relation to the plant... i.e. relative humidity (RH), vapor pressure deficit (VPD), or vapor pressure gradient (VPG).

Fig. 9.--Relative accumulative precipitation at stations 4 and 12 during the 1960 season.

Fig. 10.--Relative accumulative precipitation at stations 4 and 12 during the 1961 season.

Department of Botany and Plant Pathology
COLORADO STATE UNIVERSITY
Ft. Collins, Colorado


1960
12.00
10.00
8.00
6.00
4.00
2.00
0
IN. PPT.
STATION 12
STATION 4
J
J
A
S
O


1961
STATION 12
STATION 4
IN. PPT.
18.00
16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
J
J
A
S

Relative humidity is the moisture in the air expressed as the per cent of the total amount of water which the atmosphere will hold at a given temperature. The fallacy of using RH as an indication of the evaporative power is that the actual amount of water that may enter the unsaturated atmosphere increases as temperature increases. Thus the amount of water which can evaporate into the atmosphere will be less at a lower temperature than at a higher temperature even though the RH value is the same in both cases.

Proponents of the use of VPD point out that the difference in the vapor pressure of the saturated air versus that of the actual reading is directly related to the amount of absolute moisture which the air will hold regardless of the temperature, thus overcoming the shortcomings of RH. Thornthwaite (176), however, points out that regardless of the difference in the vapor pressure between the saturated condition and the measured state, evaporation from a water surface will depend upon the vapor pressure gradient between the water and the atmosphere. Thus if the temperature of the water is such that the vapor pressure of the water is lower than that of the air, condensation will occur on the water surface even though there is a large vapor pressure deficit in the atmosphere. The VPG as normally used, however, has disadvantages in that it is difficult to determine in the case of plants. One usually assumes evaporation from water surface instead of cell surfaces.

Aside from evaporation, absolute humidity also influences the amount and quality of transmitted radiation and may add to the heat capacity of the air. Thus convection or conductive heat removal or addition will be somewhat faster with high absolute humidities. In the

alpine, periods of higher humidity acting in this way may tend to reduce the amount of fluctuations in the net radiation and temperatures of the air and probably the plant.

As was indicated earlier in this paper, the activity of soil moisture was inferred through the use of Colman soil-moisture units which actually measure the amount of electricity which can flow through a fiberglas-monel screen wafer (42, 127). The resistance, or amount of current flowing between two potential points in the wafer is a function of the amount of water adsorbed on the fiberglas. The affinity of the fiberglas for water at a given temperature should be constant, but the amount of water it can adsorb will depend upon the free energy of the water, hence how tightly the water is adsorbed on the soil particles. The ability of the soil particles to hold different amounts of water against the attraction of the fiberglas will be a function of the type and number of each particle present, i.e., the type of soil. Thus in order to determine the absolute amount of water in a soil, it is necessary to calibrate the units for each type of soil and location, and this is time consuming and extremely difficult (35, 85, 134).

The absolute amount of water, however, does not necessarily indicate to what degree soil moisture is available to the plants, which is the important consideration in a physiological ecology study. Water availability depends upon the tenacity with which the soil holds the water in relation to the plant's own attraction for water molecules. Therefore, the situation existing between the plant and the soil is closely analogous to that of the Colman unit and the soil, and one might expect that these units are actually measuring moisture availability.

A further bit of evidence in favor of this idea, is that the calibration curves of resistance plotted against per cent moisture (42) are very similar to curves of moisture tension and per cent moisture (31).

To calibrate the Colman units, some units were placed in small cans of soil which could be sealed (Fig. 11). Moisture was then added to the soil and readings were made as the moisture was allowed to evaporate. Cans were sealed and laid on their sides for at least 24 hours after an evaporation period to allow distribution equilibration of the moisture before reading resistance of the Colman unit and weighing the can plus soil. Soil temperatures were also measured by each unit and resistances could then be corrected to a 60 Farenheit standard line. Calibration of the soil (Fort Collins acid) had previously been worked out in terms of per cent moisture and pf (the log of the height of a column of water in centimeters which corresponds to the moisture tension in the soil), so that per cent moisture could be converted directly to tension values (31).

A plot of the log of the corrected resistance (pR) versus the pf revealed a linear relationship between the unit readings and the moisture tension for tensions above one-third atm (field capacity). Below this point pR was almost completely independent of pf, which would be expected on the basis of there being essentially no resistance to the adsorption of water onto the fiberglas (Fig. 12), which is apparently saturated. This type of relation was similar in nearly all of the units tested (slopes equal), there is some indication, however, that some units may have to be calibrated separately to find the y-intercept in the linear region of the curve.

Fig. 11.--Diagram showing the method of calibrating the Colman soil-moisture units.

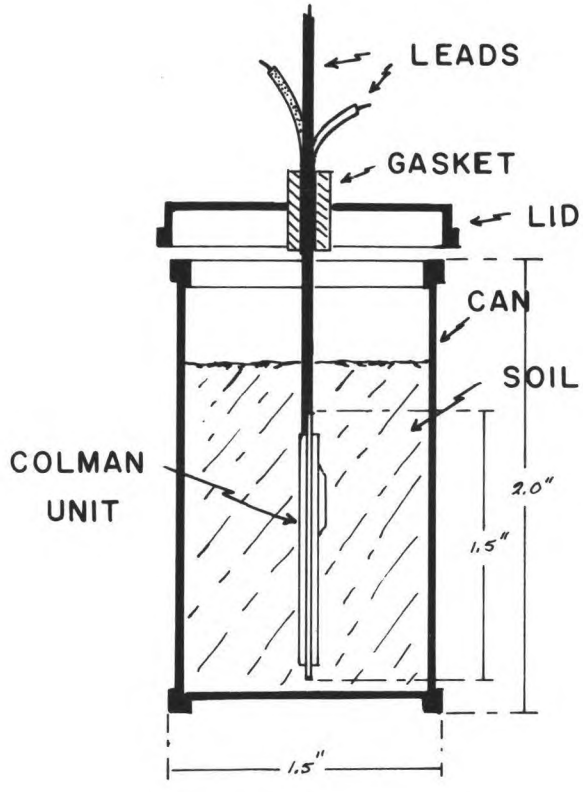
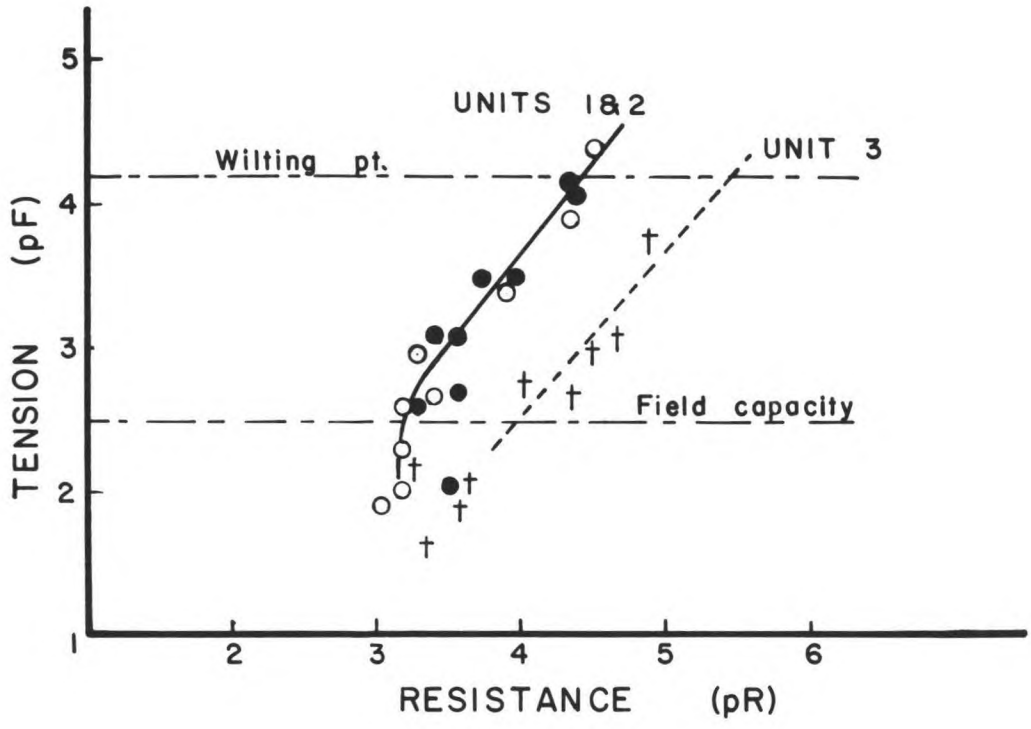

LEADS
GASKET
LID
CAN
SOIL
COLMAN
UNIT
2.0"
1.5"
1.5"

Fig. 12.--Calibration curves obtained from three Colman units in preliminary studies.


UNITS 1&2
UNIT 3
Wilting pt.
Field capacity
TENSION (pF)
RESISTANCE (pR)
5
4
3
2
1
2
3
4
5
6

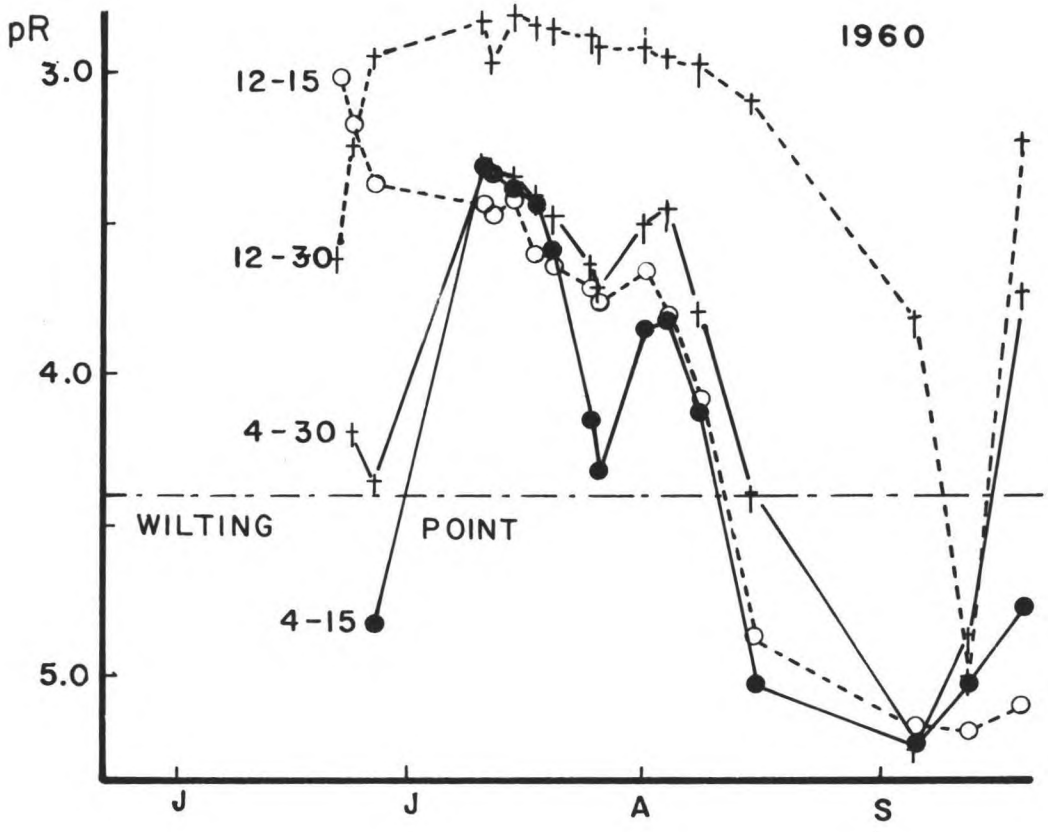
If we assume that this relation is true generally for all soils having relatively low salt contents, pR values of about 4.4 correspond to the permanent wilting point of a soil (15 atm). Values of about 3.2 indicate field capacity, although this figure is not as reliable as the wilting point figure.

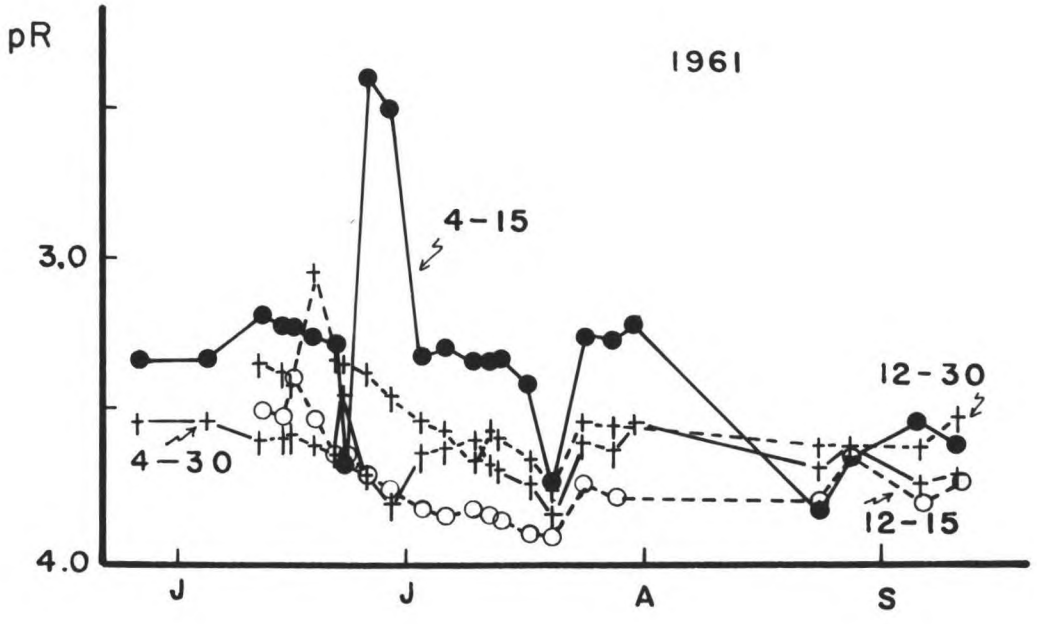
Based on Daubenmire's work (53) the 15 cm and 30 cm depths approximately include the region of active root absorption so that plots of the pR values at these depths at stations 4 and 12 during the 1960 and 1961 seasons should indicate the moisture availability levels to which the alpine plants are subjected. These curves show that water was available to the plants at both stations for the entire 1961 season, but in 1960 moisture was available only at the 30 cm depth at station 12 during a period from the middle of August until the middle of September (Fig. 13). Water during the 1960 season was generally less available throughout the entire season compared to 1961, yet during the early part of 1960 there was a greater amount of water available at 30 cm at station 12 than in 1961.

The soil moisture in conjunction with the freezing temperatures, which frequently occur, may act to produce large amounts of frost heaving and other frost actions. No prominant evidences of active frost action were noted in the False Mummy Pass area, although many workers have indicated its importance in other alpine areas (15, 17, 97).

Atmospheric gases.--Atmospheric gases constitute those environmental phenomena pertaining to matter in the gaseous state, with the exception of water.

Fig. 13.--Moisture avilability patterns at the 15 and 30 cm depths at stations 4 and 12 during the 1960 and 1961 seasons.


pR
1960
3.0
4.0
5.0
12-15
12-30
4-30
4-15
WILTING
POINT
J
J
A
S


pR
1961
3.0
4.0
4-15
12-30
4-30
12-15
J
J
A
S

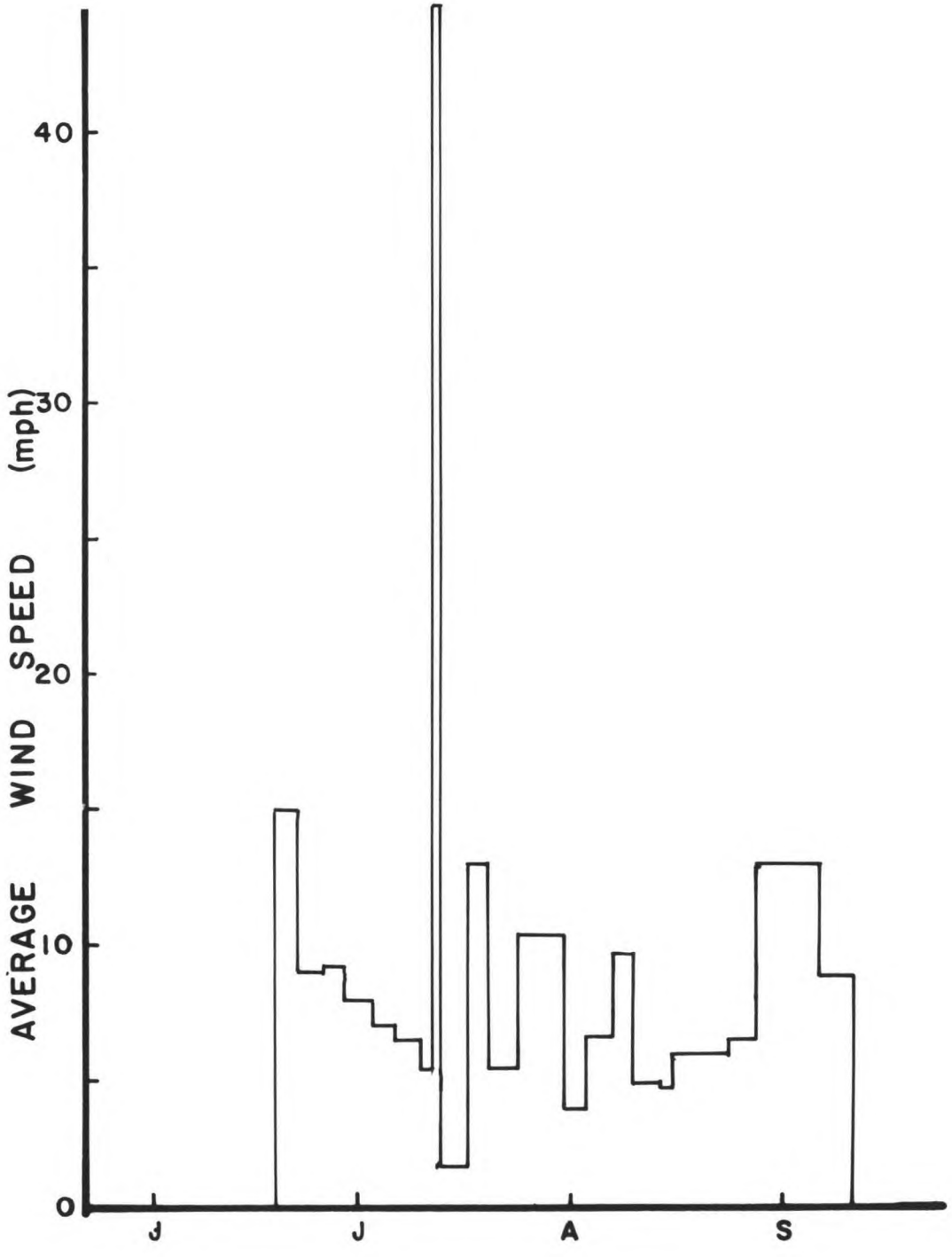
Wind can be measured through its pressure on rotating cups, pith balls, and rotating tubes, by the cooling action of the wind on hot wires, or by sonic devices. In this study wind was recorded by a totalizing conical cup anemometer, by spot readings from a Dwyer wind meter, and by a hot wire anemometer. No attempts were made to study gas compositions or barometric pressure.

Results from the two seasons show that the winds during the 1960 season were more frequent, and speeds were relatively higher. Wind speed ranges during 1960 frequently exceeded 30 mph while in 1961 no wind was recorded above 22 mph. These differences in absolute values are complicated, however, by the fact that wind speeds were measured at different heights each season. Station 4 was usually exposed to the most air movement both years. Winds over the two seasons ranged from essentially zero to over 70 mph.

During the 1961 season the totalizing cup anemometer was installed at station 5' between stations 4 and 5 (161). Dial readings were taken on the average of twice per week, and the average wind speed was determined over the period. The total wind mileage between June 19 and September 11, 1961, was 16,814.9 miles or an average of 8.34 mph over this period. The average wind speeds ranged from 1.75 mph over a four day period to 44.5 mph over a 24 hour period (Fig. 14).

The average wind speed values, however, are not completely representative of the actual wind conditions since alpine winds are typically gusty. As an example, readings were made from the totalizing anemometer simultaneously with those from a Dwyer wind gauge. The readings during short intervals (1 minute periods) on the Dwyer ranged

Fig. 14.--Average wind speeds computed from the totalizing anemometer at station 5′ during the 1961 season.


AVERAGE WIND SPEED (mph)
40
30
20
10
0
J
J
A
S

from 2-8 mph while the anemometer averaged 6 mps. Thus the winds may be extremely high or low over short periods without being indicated on the anemometer dial unless readings are made regularly at very short intervals.

The partial pressures in the alpine, though not evaluated in this study, could possibly be a very important factor, since many of the other environmental factors, especially radiation may be influenced to a considerable extent by the amount of atmosphere present. If we consider relative gas composition to be essentially the same in the alpine compared to sea level, we still find that the actual amounts or partial pressures of gases are only about two-thirds those at sea level based upon the lowering of the atmospheric pressure due to altitude. The amount of gases in the soil and plant tissues must also be reduced. Partial pressures might therefore influence the functioning of the plants and should be investigated in future studies.

Additional environmental groups and factors

The edaphic, geographic and biotic environmental groups have not been evaluated in our alpine study, yet certain features of these groups are important and warrant discussion. The information included in this discussion has largely been derived from the literature.

Edaphic factors.--The edaphic environmental factors will be defined as those phenomena which pertain to the physical and chemical nature of the soil and its constituents, with the exception of gases and the amount of water. There have been relatively few studies dealing with alpine soils (47, 130, 142, 163, 171) and much more work is needed

in this area. Most of these studies indicate that alpine soils tend to be acidic with pH's generally near 4.5 to 5.0, although the pH readings of from 4.2 to 8.4 have been obtained (142, 163). Organic content and mineral content also vary considerably in alpine soils. Retzer (142) has divided alpine soils into three types as controlled primarily by drainage. These types include: the Alpine Turf, which may contain up to 20 per cent organic carbon but usually contains only about five per cent and usually has well developed horizons and is well drained; the Alpine Meadow which has much more organic matter but is not peaty and has less well developed horizons and imperfect to poor internal drainage; and the Alpine Bog which occurs in bogs and other wet places and is quite peaty with poorly developed horizons and a mottled C-horizon. According to this classification, station 4 has an Alpine Turf soil while that of station 12 is more nearly an Alpine Meadow.

Geologic factors.--Those factors which deal with the shape or changes in the earth's mantle or are concerned with its relative astronomical position and movement or the relative position on the earth are included in the geologic environmental group.

Topography is the factor of interest since it may affect exposure to radiation, drainage, relative stability of the surface, and wind. The topographic effects on stations 4 and 12 have been described in the section on temperature, but it should be mentioned that the drainage from 4, which is located more on a ridge, is much better than the drainage from station 12, and this must account for the difference in the types of soils occuring at these stations. There is relatively little unstable area

in the False Mummy Pass study area, but rock slides, scree slopes and soil fluction areas can occur in the alpine.

Geographic position as pointed out by Daubenmire (51) has considerable bearing upon the lower limit of the alpine zone, but it should be recognized that this is due to the variation with latitude in climatic and other environmental factors. The differences in the geographic positions of the areas in this study are negligible.

Biotic factors.--The final group of factors, biotic, includes any phenomena to which a plant is exposed that is the result of life. This group of factors is large and complex, including the actions of and interactions with animals and other plants. Man himself becomes an important entity in many environments, even in the alpine (211). No attempt was made in this study to investigate biotic phenomena, but it is important to note that biotic factors can and probably do influence the other environmental factors. In the alpine the effect is much less than in the subalpine regions, which is a major reason for choosing this zone for study.

Effects of Environment

The environmental factors of the alpine discussed in the previous section can be important to a physiological ecology study in so far as they directly or indirectly affect an alpine plant. It would, therefore, be advantageous to review some reported effects of environmental factors with quality and quantity similar to those in the alpine. These effects are summarized in Table 2 and some of the more interesting aspects are discussed.

Discussion.--High light intensity is one of the most interesting and unique features of the Colorado alpines. This aspect of the alpine environment could either be excluding many lowland species or lower intensities may be limiting the downward extension of many of the alpine plant species through its possible affects on germination, seedling establishment, photosynthesis, or growth in general. It is interesting to note that McLeod (117) has found a slight shift towards the blue in the action spectrum of saturated photosynthesis, especially since the solar spectrum in the alpine probably also shifts in this direction. Heat and drought resistance in some cases has also been shown to be increased by high light intensities (50, 155). This may be operating as a survival factor during the long dry spells and intense solar radiation which occur frequently in the alpine.

The high light intensities coupled with the photoperiod may also be important in limiting the normal phenological processes of alpine plants at lower elevations, since it is feasible that the photoperiod being measured must exceed a high threshold intensity to operate. This is a feature which should be looked into further.

In considering the intensity of radiation reaching the plants, it is important to note that the orientation of the leaf influences the amount of light reaching its surface according to the cosine law. Many of the plants located in our study area which do not change their leaf orientation are associated with shaded areas ... e.g. Oxyria digyna and Bessya alpina.

Ultraviolet light in the alpine, as pointed out earlier, may be only slightly higher in intensity than it is at lower elevations.

Also the period during the day when damaging intensities are reached conceivably occur only during a short interval when the sun is at or near the zenith. This should leave plenty of time for photoreactivation to occur (6, 173). Nonetheless, the characteristic dwarfing of the alpine plants has been attributed to ultraviolet radiation by some workers (50). It is also possible that germination or other phenological events in alpine plants may require or be promoted by the higher amounts of ultraviolet radiation.

The relatively low temperatures found in the alpine would probably inhibit growth of many subalpine plants. Seedling establishment for alpine plants may be very difficult in exposed areas due to frost heaving according to W. Osborn (personal communication). Germination, longevity of the seeds and generally better overall growth at lower temperatures could operate as adaptive features in alpine plant species.

Studies by Went (204) and by Bliss (21) have indicated that soil temperatures may in certain cases be more closely associated with plant growth and function than are air temperatures. This might well be explained on the basis that the soil temperatures are better indicators of the net radiation flux.

The dwarf nature of alpine plants has been attributed to many things. In the light of Highkin's work (80) with peas, where it was found that suboptimal environments produced stunting responses which were cumulative over many generations, alpine dwarfness might be partially explained in this way rather than as a nonflexible genetic character or the result of contemporary conditions. At first glance the low alpine temperatures could also be considered as detrimental to the photosynthetic

rates of the plants, since it is well known that the saturation point is reached at lower intensities when the temperatures are low. Due to the high amount of incoming radiation in the form of heat, however, the alpine plants themselves might be quite warm (see Chapter III). Thus the saturation intensities for alpine plants may be much higher than would be suspected.

Photoperiodism in certain instances operates only within a certain temperature range (72, 73, 146). It is conceivable that this range is much lower for alpine plants than in lowland plants, thus limiting their photoperiodic responses to alpine conditions, while the lowland species may have much higher ranges than are found in the alpine. A good deal of work is needed in this area.

Moisture is generally considered to be a critical factor in the alpine, particularly during the last of the growing season. This, coupled with the large amounts of incoming radiation, could produce high water tensions in the plants, which in turn can influence absorption of nutrients and alter the internal distribution of these nutrients. The high tensions, however, might also result in greater frost-hardiness. It is also interesting to note that contrary to the environmental data which would indicate a high transpiration rate in the alpine, Whitfield (209), using phytometers in the Pikes Peak area, found that the relative transpiration rates of alpine plants and sunflower plants grown in the alpine to be lower than those growing at lower elevation. No critical studies of this phenomenon seem to have appeared in the literature since Whitfield's work, and there is a definite need for such work.

The lower partial pressures of O_2 and CO_2 both in the air and in the soil may be another limiting factor in the invasion of the alpine by lowland species. The O_2 concentrations could be particularly critical in the process of active uptake and translocation of nutrients, germination and general root growth. The CO_2 levels, of course, are very important in relation to photosynthetic process under the high alpine light intensities. Still, it has been shown by Billings, et al. (14) that alpine races of Oxyria digyna are able to photosynthesize at a higher rate at low carbon dioxide concentrations than are the arctic or sea level races of this species. The whole area of plant response to atmospheric composition and pressure needs intensive study.

The relatively high wind speeds characterizing the alpine are probably most important due to the mechanical injury of plants caused by wind born particles. Winds may also be important in their effect on plant establishment, overall growth rate, and plant temperature. It should be pointed out, however, that the wind speeds at the level of the plants in the alpine are considerably reduced compared to the air movement a few centimeters above the plants (71). Trees and shrubs, on the other hand, are exposed to the higher winds and as a result are wind pruned and trained by mechanical injury and desiccation of the exposed parts.

In conclusion, it can be seen that the effects of the alpine and alpine-like environmental factors are many and varied, and the responses of separate species to a given factor may vary with individuals of that species, depending upon the other factors present. Many factors

could also be operating to determine the relative position of timberline. These factors probably fluctuate within the timberline transition zone and as a result sometimes favor alpine growth and sometimes favor subalpine growth. Beyond the transition zone, however, these same factors probably are consistent in that they do not overlap into the range which is conducive to alpine growth in the subalpine or subalpine vegetation in the alpine. Thus the two zones are created.

Simulation of the Alpine by Controlling Environment

Theory

Since in a given field situation there may be many environmental factors present in different amounts and of different qualities, and since any one of a number of factors may affect a certain plant response, it is difficult to discover which factor or group of factors is the cause of the response. For this reason it is desirable to control as many of the environmental factors as is possible so that only one or two factors are being varied while the others are held constant. This, then, is a means for testing response-factor correlations found in field studies.

Controlled environments may be divided into three types depending upon the degree of control. The first type includes field plots and outdoor gardens where such factors as moisture, sun, or wind may be altered within the limits of "natural" variation. The second type includes greenhouse facilities where temperature and soil moisture can be held within a certain desired by very broad range. Greenhouses, however, are still subject to variations in the light intensity, and

Table 2.--A SUMMARY OF THE EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON PLANTS.

Factor	Aspect	Effects	Relation to increases	References
Light	Intensity	Morphological:		
		Stem elongation	Inverse	157,57,102,50
		Production of xylem and mechanical tissue	Direct	155,102,50, 157,57
		Germination	Varies	184,46,11,50, 122,84
		Xeric features of leaf anatomy	Direct	157,102,50
		Leaf lobing	Direct	157,172
		Field orientation	Varies	175,50
		Stomatal opening	Inverse at high intensity	102
		Dry weight	Direct	102,50
		Root/shoot ratio	Direct	102
		Seedling establishment	Varies	102
		Growth and vigor	Varies	157
		Branching	Direct	50

Table 2.--A SUMMARY OF THE EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON PLANTS.--Continued

Factor	Aspect	Effects	Relation to increases	References
Light	Intensity	Physiological:		
		Photosynthesis	Direct to saturation and inverse at very high intensity	184,160,102, 50,117,175
		Anthocyanin production	Varies	184,167,50,4
		Chlorophyll production	Direct at low intensity, inverse at high	184,102,2
		Size of plastids	Direct	102
		Number of plastids	Inverse	102
		Chlorophyll destruction	Direct	184,102,2
		Heat, and drought resistance	Direct	50,155
		Respiration	Complex	188,110,77
		Cell division	Varies	174
	Photoperiod	Morphological:		
		Development of food storage organs	Varies	184
		Elongation	Varies	184,102
		Leaf growth	Varies	184
		Vegetative reproduction	Varies	184

Table 2.--A SUMMARY OF THE EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON PLANTS.--Continued

Factor	Aspect	Effects	Relation to increases	References
Light	Photoperiod	Morphological:		
		Leaf abscission	Short days promote	192,102
		Diameter growth	Varies	102
		Physiological:		
		Dormancy	Short day	184,55,192,102
		Anthocyanin formation	Varies	184
		Flowering	Varies	184,192,84,147
		Endogenous rhythms	Varies	30
		Overcomes adverse temperatures	Varies	99
		Frost resistance	Short day	102
		Cell sap osmotic pressure	Varies	131
	U-V	Morphological:		
		Death of epidermis	Direct	28,184,156, 173,6
		Germination	Not well known	139
		Dwarfing	Direct (?)	50

Table 2.--A SUMMARY OF THE EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON PLANTS.--Continued

Factor	Aspect	Effects	Relation to increases	References
Light	U-V	Physiological:		
		Cellular rhythmicity	Shifts it	59
		Anthocyanin prod.	Direct	139
		Respiration	Temporary acceleration	110
		Cell division	Inverse	174
Radiation	Cosmic	Genetic changes	Direct	103,168
		Germination	None (?)	7
		Seedling development	None (?)	7
Temperature	Freezing	Physical:		
		Frost action	Direct	102,50
	Quality and quantity	Morphological:		
		"Highkin" affect	Inverse	88,202,165
		Cell elongation	Varies	204,102,21
		Germination	Varies	204,181,11,50, 122
		Flower color	Varies	204
		Longevity of seeds	Inverse	204
		Rate of development and general growth	Varies	102,50,195, 158,157,204,203, 122,145,54

Table 2.--A SUMMARY OF THE EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON PLANTS.--Continued

Factor	Aspect	Effects	Relation to increases	References
Temperature	Quality and quantity	Leaf lobing	Varies with night temperature	157
		Petiol length	Varies	122
		Leaf number	Varies	122
		Physiological:		
		Low temperature damage	Varies	21,50
		Heat damage and its translocation	Varies	107,50,140, 219
		Vernalization	Inverse	100,50
		Enzyme activity	Cardinal*	102
		Respiration	Direct	204,56,152, 50,122
		Sugar content	Inverse	204
		Flowering in bulbous plants	Inverse	204
		Dormancy of seeds and plants	Varies	204,55,50
		Translocation	Cardinal	60
		Breaking of dormancy	Inverse, but varies	50,55,122
		Protoplasmic streaming	Direct to denaturation	204

*Implies that the response increases as temperature increases from some minimum temperature to some optimum temperature after which the response decreases until at some maximum there is no response.

Table 2.--A SUMMARY OF THE EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON PLANTS.--Continued

Factor	Aspect	Effects	Relation to increases	References
Temperature	Quality and quantity	Absorption	Direct	213
		Endogenous rhythms	Varies (cardinal ?)	30
		Cell division		102,174
		Chlorophyll synthesis	Complex	102,95
		Thermoperiodic responses	Varies	50,102
	With light	Photosynthesis	Varies with intensity Cardinal at saturation	193,160,56, 102,50,135,204, 175,117
		Germination	Varies	180,182,46,181
		Photoperiodism	Cardinal	100,192,73, 72,64
	With water	Seed stratification	Inverse	132,46,50,131
		Transpiration	Complex	20,102,50
Moisture	Soil and internal	Morphological:		
		Growth	Direct or cardinal	13,124,94,187
		Xeric structure	Inverse	157,50
		Stomatal opening	Complex	94
		Physiological:		
		Protoplasmic hydration	Threshold	183
		Cellulose production	Direct	183,124

Table 2.--SUMMARY OF THE EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON PLANTS.--Continued

Factor	Aspect	Effects	Relation to increases	References
Moisture	Soil and internal	Photosynthesis	Complex	183,175,102, 187
		Starch conversion sugars	Inverse	183
		Flowering	Direct	183,131
		Frost-hardiness	Inverse, but complex	105,106,186
		Translocation of phosphorous	Inverse	214
		Accumulation of phosphorous at growing points	Inverse	214
	Humidity	Flowering	Little	73
		Transpiration	Inverse, but complex	20,94,187
		Stratification	Direct	46,132
		Breaking of seed dormancy	Specific amounts	205
Atmosphere	Gas Composition in air	Photosynthesis and CO_2 conc	Direct	14,117,56,175
		Active uptake of ions, etc and O_2 conc	Direct	70
		Active uptake and CO_2 conc	Inverse	70
		Translocation and O_2 conc	Direct	60
		Germination and O_2 conc	Direct (?)	46,181

Table 2.--SUMMARY OF THE EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON PLANTS.--Continued

Factor	Aspect	Effects	Relation to increases	References
Atmosphere	Gas composition in air	Respiration and O_2 conc.	Direct (?)	74
	Soil	Root growth and O_2 conc	Direct	102
		Toxicity and CO_2 conc	Direct	50
	Wind	Mechanical injury	Direct	194,208
		Growth rate	Inverse	194,50,206,207
		Root/shoot ratio	Direct	207,206
		Deformation	Direct	50
		Plant establishment	Varies	13
		Production of mechanical tissue	Direct	206,157
	Wind and moisture	Transpiration	Very complex	194,217,118
		Winter desiccation	Direct (and inverse with respect to moisture)	50,21
	Wind and temperature	Leaf temperature	Complex	194,195,118, 216
		Net assimilation	Optimum	193
Soil	pH	Photosynthesis	Varies	175
		Respiration	Varies	175,47
		Root growth	Varies	32

temperature control is seldom accurate. The third and last type of controlled environment includes chambers, rooms and climatrons which have environments that are essentially independent, with the possible exception of gas composition, magnetism, cosmic rays, and the like, of most external environment. The important advantage to the latter type of control facility is in the reproducibility of conditions. This may be the case even when a factor cannot be varied at will, since in most instances it still may be held at a relatively constant level.

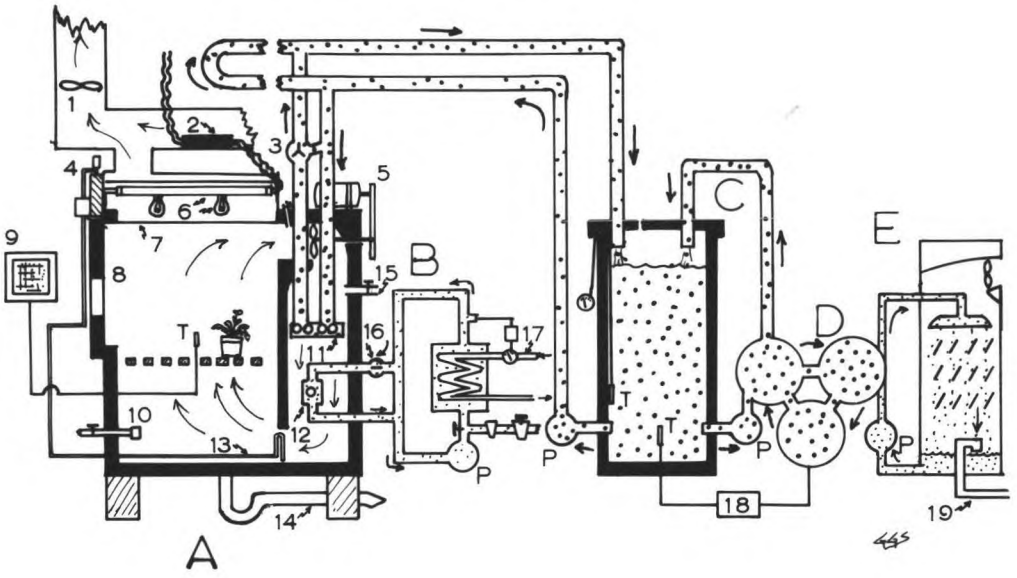
Description of the controlled environments of this study

All three types of controlled environments were used in this study. Environments were altered in the field in various manners, and some alpine plants were transplanted to an outdoor garden in Englewood, Colorado. The greenhouse facilities used were primarily the new botany department greenhouses. Temperatures were controlled largely through hot water heating and evaporative (wet pad) cooling. The day and night temperatures, which were generally different, were changed manually. The range of temperatures in the greenhouse was well above that in the alpine. Few critical studies were carried out in these facilities.

Growth chambers.--Although some early work was carried out in chambers designed and built by Mellor (119), most of the investigations in this paper were carried out in six new chambers designed and engineered by Professor F. B. Salisbury of the Colorado State University Botany staff. The diagram in Fig. 15 shows the fundamental design and mode of operation. Each chamber has an inside vertical dimension of six feet and offers approximately 4 x 4 ft of horizontal area. The plants stand on a wooden grid which can be raised or lowered with a pulley system.

Fig. 15.--Diagram showing the general operation and parts of the growth chambers.

A	Side view of the chamber
B	Hot water system
C	Brine system
D	Compressor system
E	Cooling tower
P	Pump
T	Thermocouple
1	Roof exhaust for wiring and lighting ventilation
2	Ballast for flourescent lamps
3	Three-way modulating valve
4	Pneumatic controls and solenoid switch
5	Chamber fan and motor
6	Flourescent and incandescent lamps
7	Plexiglas filter
8	Chamber door with a window
9	Bristol 12 point recorder
10	Water tap for irrigating plants
11	Brine coils
12	Hot water coils
13	Liquid filled capillary
14	Drain
15	Gas exchange valve
16	Two-way modulating valve
17	Steam pipes and coils
18	Thermostat
19	Overflow


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Light is provided by 13 pairs of 48 inch Sylvania cool white VHO flourescent lamps in combination with nine 100 watt incandescent lamps. Each pair of flourescent lamps is operated from a ballast which is connected to a clock system through a separate mogel switch, a 3 amp fuse, and a magnetic starter switch. Four of the incandescent lamps are connected through one mogel switch and five through another to the magnetic starter and the clock system. The lights in each chamber are separated from the plants by a partition of one-eighth inch clear Plexiglas which is removable and can be replaced by other filters. The wiring is ducted and connected so that air is pulled over the wires from the outside at the rate of 20 to 30 feet per second. The ballasts are also ventilated. Operating at maximum efficiency with new bulbs the light intensity at the plant level of 1.5 to 2.0 feet is about 5000 ft-c, however, within a week after the installation of new bulbs, the intensity at this level drops to approximately 2000 ft-c where it essentially remains for the life of the bulbs.

Temperatures are controlled by a pneumatic system operating through modulating valves which control the flow of cold brine and hot water through two different sets of coils. About 20 psi are maintained in the overall system by a small compressor. A pneumatic thermostat system regulates, by lever action, the amount of pressure in the line to the controlling valves. At approximately 12 psi the cold brine valve is wide open. As the pressure is reduced by the thermostat in response to lowering chamber temperatures as sensed by a liquid filled capillary, the cold brine valve is gradually closed until at approximately 7 psi

(depending upon the chamber), the cold valve is completely closed. At approximately 6 psi the hot water valve begins to open until at 2 or 3 psi it is wide open.

The air, in the mean time, is being circulated in the chamber at the rate of two to three feet per second by a one-fourth hp squirrel cage fan. With this type of system it is possible to regulate the temperature from 0 C to 40 C or higher with a minimum of fluctuation. The air temperatures are recorded every 1.5 minute by a 12 point Bristol recorder from amplified responses of shielded thermocouples placed in each chamber. Manually operated valves in the back and on top of each chamber allow some gas exchange with the outside air.

The cold brine, which consists of a 1:3 mixture by volume of ethylene glycol and water, is cooled by two ten horse power compressors and a cooling tower all located in a small room adjacent to the growth chamber room. The cooled brine is then stored in an insulated reservoir until it is needed in the system. The brine temperature may be controlled within certain limits, but is usually below freezing, which causes frost instead of dripping on exposed pipes. For low temperature experiments it is usually regulated just below the lowest temperature required. This reduces the amount of frosting on the coils. The hot water temperature is also regulated at about 80 C.

Day and night temperatures are controlled separately in each chamber and are changed from one to the other by time switches. Four chambers have separate temperature clocks, but these along with the remaining two chambers may be controlled by the same clocks which turn the lights on and off.

Each chamber is also provided with a short length of hose and a spray nozzle for watering plants. Drainage is provided in the floor of each chamber to a gutter in back of the chambers. No provisions are made in these chambers for controlling humidity, as a result it is usually quite high when the chambers are filled with plants.

Simulation of the alpine environment

In order to test the ability of the growth chambers to simulate alpine conditions, as far as temperatures and photoperiod are concerned at least, plants were collected in the dormant state from Loveland Pass on February 25, 1961, and placed in a chamber. Some were also placed in the greenhouse for comparison. Temperatures were then gradually increased from 0 C nights and 5 C days to about 6 C nights and 20 C days and then lowered again (Fig. 16). Photoperiods over this period of 80 days were varied from 11 hours to 16 hours. Colored photographs were taken each day of the whole chamber and of the plants near the center of the chamber. Table 3 summarized the results of this experiment.

In general most of the species grown in this chamber seemed to respond similar to the way in which they respond in the field. It is noteworthy that Geum turbinatum not only bloomed prolifically but also produced some seed. Some of the species present, however, did not respond to the simulated environment in the same manner that they do to field conditions. For example, Polemoneum viscosum did not flower in the chamber, while in the field it flowers readily. Some of the mat plants such as Trifolium nanum and Paronychia pulvinata began to lose their mat appearance but not to the degree that they did under greenhouse conditions.

Fig. 16.--Temperature and photoperiod conditions for the simulated alpine season. (Period of high temperature was the same as the photoperiod).

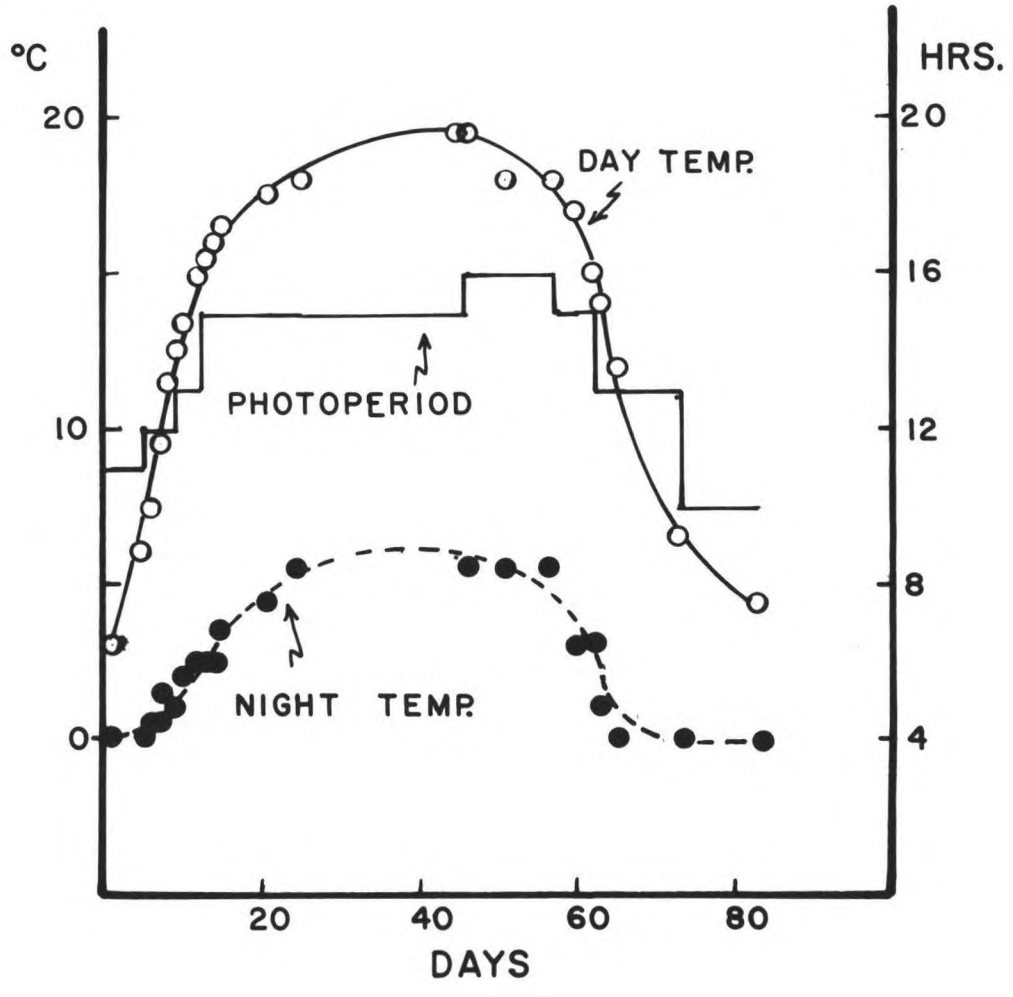

°C
20
10
0
HRS.
20
16
12
8
4
DAY TEMP.
PHOTOPERIOD
NIGHT TEMP.
20
40
60
80
DAYS

Table 3.--SUMMARY OF THE EVENTS OF ALPINE PLANTS IN A SIMULATED ALPINE SEASON.

Day of experiment	Phenological and other events
10	Some Geum turbinatum beginning to grow.
12	More G. turbinatum growing. G. turbinatum in greenhouse blooming.
13	Trifolium nanum developing.
14	Arenaria obtusiloba mat greening up.
19	G. turbinatum buds prominient.
20	Geum turbinatum blooming, Paronychia pulvinata mat greening up, Polemonium viscosum plants growing and T. nanum mat blooming.
22	Many Geum turbinatums blooming with field-like appearance.
26	Paronychia pulvinata beginning to bloom.
32	P. pulvinata in full bloom, Artimesia spp. elongating and Castilleja occidentalis budding.
35	Castilleja occidentalis beginning to bloom.
36	Draba spp. beginning to bloom and elongate.
37	Artemisia blooming
40	Artemisia in full bloom.
41	Arenaria obtusiloba with a flower.
47	Castilleja occidentalis in full bloom
56	Leaves of Potentilla spp. turning red.
58	Geum turbinatum showing some red.
62	Many of the plants are taking on a fall-like appearance.
63	Geum turbinatums definitely going dormant.
67	A Geum turbinatum plant is completely dormant.
70	Many of the plants are going dormant.
74	Much of the Geum turbinatum is dormant.

In this growth chamber experiment there were indications that the breaking of dormancy might depend upon temperatures and possibly photoperiods to some extent. As evidence, it was noted that Geum turbinatum placed in the greenhouse for comparison began developing and were in bloom less than 12 days after being brought in from the field, whereas those in the chambers under shorter daylengths and cooler temperatures did not bloom for 20 days, or some eight days after they bloomed in the warmer conditions in the greenhouse.

It was concluded from this experiment that the temperatures and photoperiodic requirements for some of the species and some of the responses could be met by the chambers, yet the quality and intensity of the light may not have met the light requirements of many of the species. Wind conditions in the alpine were obviously not simulated in these chambers and could well have been a factor in the "unnatural" growth response of the mat plants. Further studies on the growth, flowering, and dormancy of alpine plants were made in these facilities and will be described and discussed in the following chapters.

Chapter III

ALPINE PLANT TEMPERATURE

In many botanical studies it has been tacitly assumed that plant temperatures correspond to the ambient temperatures. However, since both plant and ambient temperatures in the field are both largely a function of the amount of radiation absorbed, and since the radiation absorbed is determined by the physical properties of a system, which are surely different for plant tissue and air, this assumption is not valid in a dynamic situation.

Many workers since Curtis' classic experiment (48) also arrived at this conclusion, and it has been shown in several studies that plant temperatures do differ significantly and fluctuate independently from ambient temperatures (3, 9, 18, 66, 67, 68, 69, 118, 216). Little work, however, has been done under alpine conditions (68) where large deviations in plant temperatures from ambient temperatures might be expected on the basis of the relative rarity of the atmosphere and the resultant high radiation intensities. Continuous measurement of plant temperatures, however, is at present much more difficult in the field than the continuous recording of climatic factors. For this reason a study was made during 1961 to determine the influence of various environmental factors on plant temperatures so that these temperatures could be estimated from the measurement of other environmental factors.

The investigations were made primarily in the Trail Ridge Road area of Rocky Mountain National Park at 12,500 ft elevation. Some preliminary investigations were also made near the summit of Mt. Evans at an elevation of approximately 14,000 ft.

Methods and materials

All instantaneous readings of temperature, wind velocity, light intensity, apparent radiation temperatures and net radiation were taken at 30 minute intervals.

Plant temperatures were measured by 30 gauge wire, copper-constantan thermocouples placed in the leaves, petioles, stalks or bases of the plants and connected to a reference cell in a potentiometer system. The thermocouples were inserted in the plant parts so that at least the first junction proximal to the leads was imbedded in the tissue. Plant temperatures measured in this manner differed at most by 2 C from simultaneous measurements using a Stoll-Hardy commercial radiometer.

Air temperatures were measured by a shaded thermocouple and a Wallac-Thermex GGA2 directional temperature and air speed indicator. These values were generally very close and an average of the two readings was used in the analysis. In one study a shaded mercury thermometer was also used. The air temperatures were usually measured at the plant level (about 6 cm from the ground). Air movement was also measured at this height using the Wallac-Thermex unit.

Net radiation was measured over the vegetation by a Goodell Pinball totalizing net radiometer (75), from which average readings were taken over 30 minute intervals. Light intensities were measured using a Weston photometer in conjunction with Kodak neutral density filters for

very high intensities. Maximum intensity readings were obtained by aiming the meter directly at the sun, and zenith light readings were taken with the meter horizontal. A Stoll-Hardy radiometer was also used to measure the apparent temperature of points of radiation. Correlations and multiple regressions were made with the data by the Colorado State University Computing Center.

Results and discussions

Preliminary studies.--The results of a nine hour study on June 21, 1961, and a 21.5 hour study between 1200 July 14, and 0930 July 15, 1961, made near the summit of Mt. Evans show that there can be a significant difference between ambient (or air) and plant temperatures in the alpine. This difference was as much as 22 C when the plants are exposed to the full amount of insolation and may be 3.5 C lower than the air temperature in the heavy shade of large rocks. The actual plant temperatures recorded ranged from 32.5 C during the day to 0.0 during the night.

From the patterns of variation in plant temperatures and air temperatures, it might be concluded that plant temperature fluctuations are influenced to a large extent by the radiation environment in certain cases and more by the air temperatures in other circumstances. This is illustrated by the graphs in Figs. 17 and 18, which show plant temperatures deviating to a considerable extent from air temperatures during the first study period when it was relatively clear all day, while during the second study period when clouds covered most of the sky much of the time and a snow storm occurred, the temperature patterns of the plants and the air were very similar and the actual values relatively close.

Fig. 17.--Air and various plant temperatures (*Geum turbinatum*, *Bessya alpina*, *Gentiana romanzovii*, *Oxyria digyna*) measured near the summit of Mt. Evans on June 21, 1961.

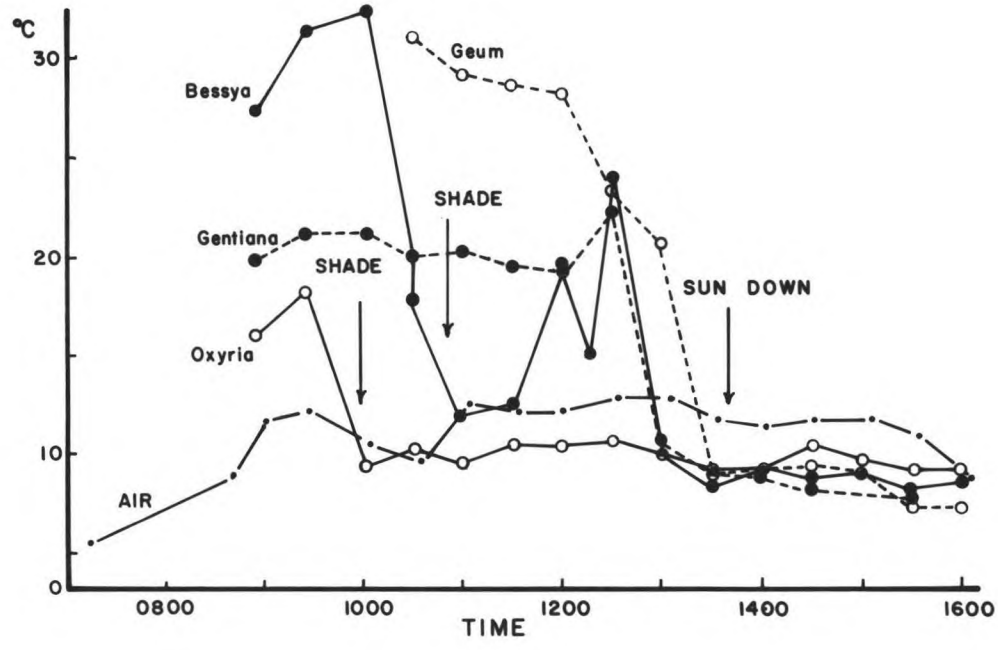
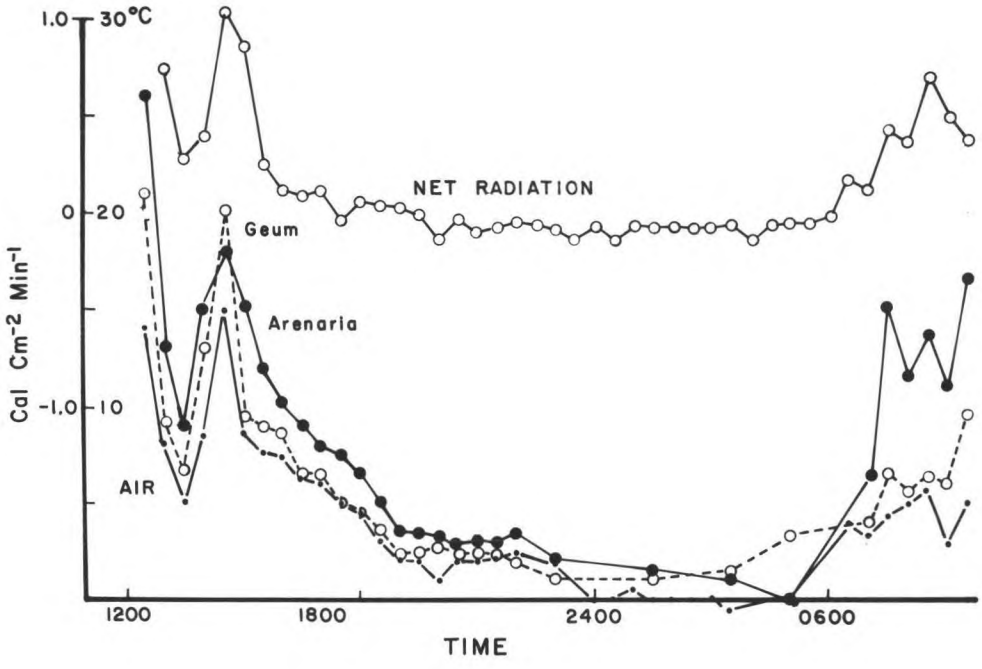

°C
30
20
10
0
Bessya
Geum
Gentiana
Oxyria
AIR
SHADE
SHADE
SUN DOWN
0800
1000
1200
1400
1600
TIME

Fig. 18.--Air temperature, net radiation and the temperatures of *Geum turbinatum* and *Arenaria obtusiloba* during a 21.5 hour period on July 14-15, 1961, near the summit of Mt. Evans.


1.0
30°C
0
20
-1.0
10
Cal Cm⁻² Min⁻¹
NET RADIATION
Geum
Arenaria
AIR
1200
1800
2400
0600
TIME

It should also be noted that plants in the shade during the first period, although lower than the air in temperature, followed the same trends in temperature variations.

It is not clear whether snow cover, ground warmth or metabolic heat was operating during the night of the second period to maintain the plant temperatures above the freezing point even though air temperatures dipped below 0 C. The net radiation values were also probably affected by the snow cover and cloud cover so that the values are possibly not good indications of the "usual" net radiation conditions.

Trail Ridge Road studies.--After the preliminary studies on Mt. Evans, more critical studies were made on four occasions on Trail Ridge Road in an attempt to evaluate the correlations between plant temperatures and environmental factors more closely. Ten thermocouples were used to record over 360 plant temperature. The plant temperatures and environmental factors were measured over 30 minute intervals during the day. In the subsequent analysis the temperatures of "mat" plants were treated separately from those of "upright" plants.

The R values in Table 4 show that plant temperatures correlated best with ambient temperatures in comparison with the other individual factors considered. The relative effect of air (= ambient) temperatures on upright plants according to these values was greater than the effect of this factor on mat plant temperature. This difference would probably be expected on the basis of the relative amounts of plant-air contact of each type of plant.

Table 4.--RESULTS OF THE CORRELATION AND MULTIPLE REGRESSION STUDIES ON THE FACTOR-PLANT TEMPERATURE INTERACTION.

	Mats			Uprights		
	R	R sq.	Loss SS	R	R sq.	Loss SS
Ambient temperature	0.6368	0.4055	142.3	0.6422	0.6422	203.5
Maximum light	-0.0149	0.0002	15.8	0.5645	0.3187	26.7
Mean wind	-0.2326	0.0541	1.7	-0.0272	0.0007	8.1
Net radiation	-0.0745	0.0056	2.2	0.3854	0.1485	0.3
Above 4 factors together	---	0.7422	---	---	0.8391	---
Zenith light	0.4456	0.1986	---	0.4194	0.1759	---
Maximum wind	-0.2579	0.0665	---	0.0215	0.0005	---

The relative differences between the effect of the maximum light intensity and zenith light on the temperatures of the mat and upright plants is very interesting and might be explained on the basis of orientation. Since most of the alpine mats are relatively horizontal, they receive light in the same way as the meter when it is placed in a horizontal position for the zenith light reading. The upright's leaf being measured, on the other hand, would at some time be oriented normal to the sun's rays and at other times parallel to them. When the leaves are normal to the sun's rays, the maximum intensity reading should more closely indicate the energy being received by them.

The correlation between net radiation and plant temperatures is actually the reverse of what might be expected, since the temperature of the mat was almost completely independent of the net radiation while the upright plant temperature showed a slight correlation. No explanation is offered for this result.

The data seem to indicate that wind has a greater influence on mat plant temperature than on upright temperature. This is also paradoxical, since the upright species would seemingly be more exposed to air movement. It is important to note, however, that the correlation between winds and plant temperatures is very slight in both cases, and it might be concluded that wind plays a very minor role in determining plant temperatures in the field.

It is unfortunate that total incoming radiation from the sun and clouds, etc. could not also be recorded during these studies. The total radiant heat load must surely be very significant in determining alpine plant temperatures. Some apparent sky and cloud temperatures were measured using a Stoll-Hardy radiometer, but since the whole radiation sphere about the plants could not be integrated, no correlations between these readings and plant temperatures were apparent.

Results of the multiple regression analysis in which the net radiation, ambient temperature, maximum light intensity, and the mean wind speed were treated as independent variables and the plant temperatures as the dependent variable, R square values for mat and upright plants were approximately 0.84 and 0.74 respectively. This in a sense means that 84 "per cent" of the temperature of a mat plant is determined by these four factors, while only 74 "per cent" of the upright temperature is the result of these factors. Thus, in the case of upright plants only about 10 "per cent" in determining the plant temperature is gained by measuring all four factors as opposed to only the ambient temperature. Yet, a 45 "per cent" better indication of the mat plant temperature is gained by measuring all four factors simultaneously. It is felt, however,

that the measurement of the total radiation would contribute significantly to plant temperatures in both cases.

Prediction equations derived from the multiple regression analysis of the data are:

(1) Mat Plant Temp. = 0.293 + 2.045 NR + 1.174 AT + 0.0006 ML - 0.178 MWS;

(2) Upright Plant Temp. = 3.179 - 0.429 NR + 0.920 AT + 0.0004 ML - 0.274 MWS;

where net radiation (NR) is in langleys, ambient temperature (AT) in degrees C, maximum light (ML) in ft-c, and mean wind speed (MWS) is in ft/sec.

The set of values for the loss in the sums of squares "Loss SS" in Table 4 may be used as another means of ranking the factors according to their relative importance in determining plant temperatures. Again the ambient temperature has the highest correlation with plant temperature; however, in this ranking the relative positions of net radiation and wind are reversed in respect to upright plant temperatures and the maximum light and mean wind are reversed in the case of the mat plants.

Nearly all of the approximately 360 plant temperatures recorded on Trail Ridge were higher than the corresponding air temperatures. The relative effect of the various factors measured on this difference in temperatures was determined by a regression analysis of the data. Net radiation, ambient temperature, maximum light intensity, zenith light intensity (ZL), and mean wind speed were considered as independent variables, and the difference between plant and air temperature was regarded as the dependent variable. The results are indicated in Table 5

Table 5.--LOSS IN THE SUMS OF SQUARES FOR THE DELETION OF THE VARIOUS FACTORS IN RELATION TO THE TEMPERATURE GRADIENT BETWEEN THE TWO PLANT FORMS AND THE AIR.

Factor	Mat plants	Upright plants
Maximum light intensity	57.32	19.30
Mean wind speed	15.22	11.08
Zenith light intensity	29.20	0.54
Ambient temperature	22.79	0.0017
Net radiation	4.85	0.28

where the loss in the sums of squares is used to rank the various factors. The prediction equations derived in this analysis are:

(1) Diff. Mat-air = -2.86 - 3.24 NR + 0.50 AT + 0.002 ML - 0.001 ZL - 0.53 MWS;

(2) Diff. Upright-air = 2.58 - 0.44 NR - 0.003 AT + 0.0004 ML - 0.0001 ZL - 0.33 MWS.

Since essentially all of the plant temperatures measured were higher than those of the air, we may assume that negative coefficients in the equations above indicate factors which reduce the difference in temperatures with an increa se in the intensity of the factor. The factors, then, which seem to be operating to diminish the plant-air temperature gradient in both cases include net radiation, zenith light intensity, and mean wind speed, while ambient temperature tends to slightly decrease the difference in the case of the upright plants. On the other hand, an increase in maximum light intensity tends to increase the gradient in both cases, while an increase in ambient temperature is correlated with an increase in the mat plant-air temperature gradient.

Maximum light intensity had the greatest relative influence upon both gradients based upon the values in Table 5. Net radiation, on the other hand, in the case of mat plants, and ambient temperature in the case of upright plants had the least influence of the factors under consideration. The relative effects of the other factors varied according to the type of plant.

It should be recognized, however, that the ranking of factors in this manner is based upon the assumption that the relation between the difference in plant-air temperature (as well as the determination of plant temperatures) and the various factors is linear, which may not be the case. For example, Mellor (118) has found a logarithmic relation between the wind speed and the temperature gradient, and it is probable that the other factors may likewise be acting in a non-linear fashion. It should also be pointed out that net radiation, maximum light intensity, zenith light intensity, and ambient temperature were regarded as independent variables, when in fact they are not. Still, the ranking described above does indicate something about the relative importance of these factors in determining the temperature gradient under alpine conditions.

The R squared values derived from the analysis were 0.169 for the mat plant-air temperature gradient and 0.082 for uprights. Thus only about 17 "per cent" of the difference between the mat temperature and the air temperature is the result of the factors considered, while these same factors account for only eight "per cent" in the case of upright plants. Total incoming radiation, humidity, and the transpiration potential (the vapor pressure gradient between the leaf and the air),

which were not measured, might well account for the remaining 83 and 92 "per cent" respectively. One evidence favoring this idea is the relative importance of the maximum light factor which is actually a measure of part of the visible light radiation but at the same time is excluding the infrared which may have a larger influence upon the air temperature. Some recent work by Mellor (118) also indicates that the radiation measured on an absolute energy basis coupled with the transpiration of a leaf have a large influence upon the plant-air temperature gradient. It is also possible that some physiological feature of the plant may allow it to regulate its temperature and consequently influences the gradient to some extent. It is evident that a good deal more work is needed in this area to determine the exact influence of each of the environmental factors on the plant-air temperature gradient.

In general, the regression analysis is rather disappointing. In some instances the results seem contrary to known physical mechanisms. Probably this is due to incomplete measurements of certain environmental factors. Total radiation, humidity and transpiration potential have been mentioned. Probably leaf orientation in relation to the sun's rays is also an important factor. Wind speed is very difficult to measure because of rapid fluctuations--a problem common to measurement of many alpine factors.

Plant temperatures in the chambers.--It is as important to this physiological ecology study to know what the plant temperatures actually are in a controlled environment as it is in the field. Thus, the temperatures of alpine plants in relation to chamber temperatures were evaluated.

Temperatures of the plants were measured in essentially the same manner that they were in the field using thermocouple equipment. Air temperatures were read from the Bristol recorder since this is used to record the air temperatures in most of the chamber experiments. Geum turbinatum was the only plant species studied, and eight thermocouples were divided equally between the crown and the leaves of four plants. Lights were on during the taking of temperatures.

Table 6 summarizes the results of the measurements. Generally there was no significant difference between the average leaf temperature and the air temperatures, and individual readings did not vary over 1.1 C from the air temperatures. The temperatures of the bases of Geum turbinatum, in contrast, were consistently about 5 C warmer than the air, probably the result of near contact with the warmer soil (warmed by radiation from the lights, less air movement, and less transpiration). Although these readings were taken over 15 minute intervals, it is believed that longer exposures to a given air temperature in the chambers, particularly at night, would result in a much smaller gradient between the soil and air, and consequently the base temperatures and the air temperatures.

Table 6.--RESULTS OF PLANT TEMPERATURE MEASUREMENTS IN THE CHAMBERS.

Chamber temperature	19.8 C	18.5 C	16.6 C	14.2 C
Average leaf temperature	19.5	18.5	17.1	14.2
Range of leaf temperature	19.0-21.1	17.4-19.5	16.7-17.5	14.1-14.8
Average base temperature	24.8	24.4	23.2	21.9
Range of base temperature	23.0-25.8	22.6-25.5	21.9-24.0	19.9-23.1

Root temperatures.--The discussion to this point has largely been concerned with the temperatures of the aerial portions of plants. However, since the soil, a relatively dense material, may differ radically in temperature from the air, and since the underground portions of the plant are in intimate contact with the soil, it is logical to assume that the temperatures of the roots and other underground parts of alpine plants are essentially the same as the temperatures of the soil, and that they may differ radically from air and shoot temperatures. In alpine plants this would mean that the underground organs of the plants would often be at a lower temperature during the day and at a higher temperature during the night than the shoots.

It would be interesting to know the exact effect this has on the free energy gradients in the plant itself, especially since there is usually a very steep gradient in soil temperatures between the lower roots and the soil surface. This may be a difference of 40 C during the day in the alpine (161). One also wonders if the cool ground water taken up by the plants had a significant effect upon plant temperatures. (This factor might account for the elimination of a little less than one per cent of the radiation absorbed by the plants).

Conclusions

The implication of this work seems to be that the temperatures of alpine plants often differ significantly from the ambient conditions, and that the interaction between various environmental factors and plant temperatures is very complex. Plant form seems to be an important consideration in the determination of plant temperatures in the alpine. Alpine plant temperatures may, however, be determined to a large extent

through the measurement of ambient temperatures and the maximum light intensities. On the other hand, the factors which determine plant temperatures to a large extent do not seem to have much influence upon the plant-air temperature gradient. Thus the factors which were not measured and those which influence air temperatures are probably the same factors that determine the temperature gradient...e.g. total radiation, infrared radiation, and transpiration potential. It may be assumed in this study that leaf temperatures of plants in the growth chambers are essentially the same as the air temperatures, and even though the base and probably the root temperatures tend to be somewhat higher, they fluctuate much the same as the air temperatures in the chambers.

Chapter IV

ALPINE PLANT GROWTH AND DEVELOPMENT

The influence of the environment upon the general vegetative growth and development potential of a plant is probably the most important feature in determining the distribution of a species. Variations in the growth and growth form of a species distributed in a wide latitude of habitats might also be used to indicate the unique environmental features of each habitat as well as those features which are common to all of the habitats. Thus from a study of the general vegetative growth and development of alpine plants we may learn something of the nature of the environment and microenvironments characterizing the alpine and, perhaps, something of the features of alpine plants which limit them to this zone.

Growth will be used according to Sinnott's definition, i.e. a permanent increase in size (157). Development in this work will be defined as the growth and differentiation of an organ or organs usually associated with a phenological stage in the seasonal progression of a plant.

Geum turbinatum

Geum turbinatum is found in nearly every habitat in the alpine but is rarely found extending far into the subalpine zone or at lower elevations (79, 198). For this reason it was felt that the vegetative growth and development of this species might be a good test for the unique factors characterizing the alpine zone.

Methods.--Plants of Geum turbinatum were photographed from fixed positions once or twice each week in the field for two seasons. These photographs, which were for the most part in color, were viewed and compared for phenological development, and photo-weights and plant image areas were used as an indication of the relative growth in the field (149, 161). Plants were chosen from both station 4 and station 12 for micro-environmental comparison.

In addition to photographs, dormant plants were also collected on Loveland Pass and in the False Mummy Pass area. These were potted and grown under different controlled conditions. The first controlled environment experiment was the simulated season described in Chapter II. In addition plants were grown in six chambers with the temperature conditions listed below in Table 7. This set of conditions was the first phase of a two part study on growth, development, and dormancy (see Chapters V and VI). The general phenological development and rate of growth of these plants were recorded. Individuals of Geum turbinatum collected on Mt. Evans were transplanted directly into an outdoor garden in Englewood, Colorado, and observations on general behavior and ability to survive were made.

Table 7.--TEMPERATURES OF THE CHAMBERS FOR THE STUDY ON THE BREAKING OF DORMANCY AND GROWTH RATE (WITH 16 HOUR PHOTOPERIODS).

Chamber	Temperatures			
	Day (10 hr)	Evening and morning	Night (8 hr)	Average per day
1	27 C	27 C	27 C	27 C
2	27	22	18	23
3	27	16	5	17
4	18	12	5	12
5	18	14	10	14
6	18	18	18	18

Results.--The rate of breaking of dormancy in the field seemed to be temperature dependent as illustrated by the relatively slow development of plants in the proximity of late lying snow at station 12 (Table 8).

Table 8.--PHENOLOGICAL DEVELOPMENTS IN GEUM TURBINATUM AT STATIONS 4 AND 12 DURING 1961.

Date	Station 4	Date	Station 12
5/22	Plants just sprouting.		
5/29	Plants larger.		
6/5	Buds evident in some		
6/12	Buds well developed.		
6/19	Buds just opening, some flowers.	6/19	Plants have broken dormancy and have grown some.
6/23	Plants in full bloom	6/23	Some plants just sprouting, others about half grown.
6/26	Plants still blooming	6/26	Some plants have buds.
6/29	Some plants producing seed.	6/29	One plant just blooming.
7/3	More plants producing seed.	7/3	One plant vegetative, one in bud stage, and another blooming.
7/7	All plants have seed.	7/7	Two plants blooming.
7/10	Ibid.	7/10	Plants from bud to have seed.
7/24	Bases of plants becoming red.	7/17	Plants in bloom and seed.
7/31	More red along midribs	7/24	All plants have seed, two showing red at the base.
8/14	Midribs are bright red. A late flower appeared on one plant.	7/31	More red along midribs.
8/24	More red, but still some green in leaves.	8/24	Two plants with bright red petioles, but a third is still essentially green.
9/18	Dormant. Losing red color.		

The results of the breaking of dormancy in the chambers also indicate the temperature dependency of the initial "spring" growth (Fig. 19). The data show that the breaking of dormancy is essentially the same in the average temperature range from 14 C to 23 C, but it is accelerated by 27 C temperatures, while the relatively low average temperature of 12 C delayed development three to four days.

After the breaking of dormancy, vigor and growth rates are altered to a considerable extent by the temperatures and possibly other factors. Fig. 20 shows the growth curves for two plants of Geum turbinatum at each station during 1961. Those at station 12 started later under higher temperatures and then progressed at a more rapid and even rate, while at station 4 there were periods of relatively little growth (roughly during flowering).

Development of the one plant at station 12 which was photographed both years was essentially the same (Table 9). The growth rate in 1960 was measured photographically and showed the same plateaus during flowering as that for plants of Geum turbinatum from station 4 during 1961 (Figs. 20 and 21). Data from all controlled environment studies on growth rate were generally quite erratic so that no detailed comparisons could be made. The poor results obtained were probably due in large part to genetic variability, the shock of transplanting, and the removal of roots in collecting. Qualitative observations indicate that 27 C day temperatures and continuous 18 C temperatures result in the eventual death of many plants and are detrimental in general to the development of Geum turbinatum. The most vigorous plants and the plants most like those in the field in appearance were associated with the cooler temperatures in chambers 4 and 5.

Fig. 19.--Curves of the rate of breaking dormancy for Geum turbinatum under various average temperature conditions.

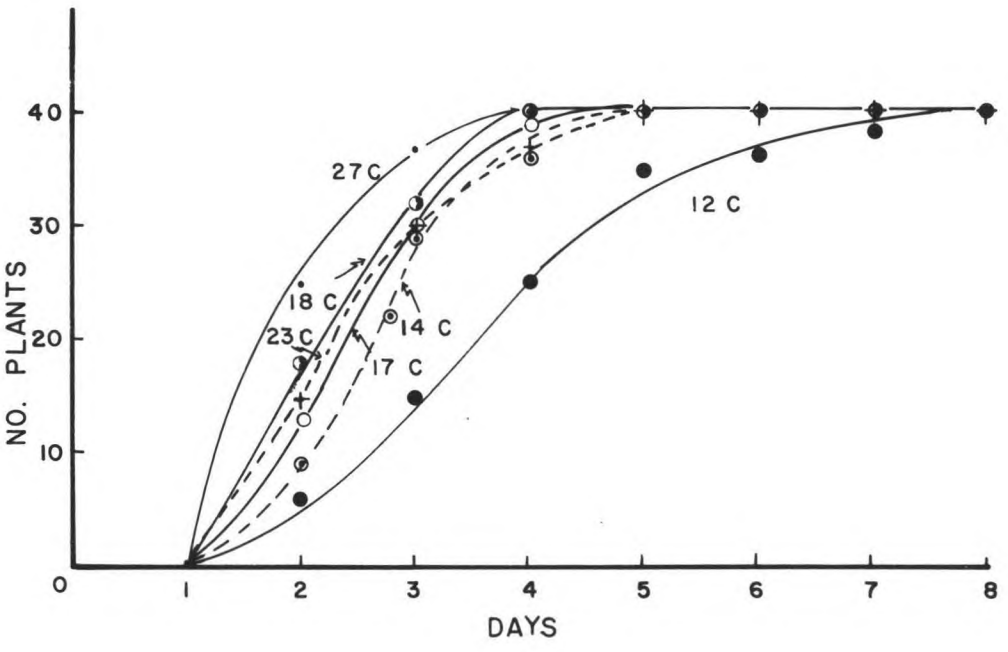

NO. PLANTS
DAYS
0
10
20
30
40
1
2
3
4
5
6
7
8
27 C
18 C
23 C
17 C
14 C
12 C

Fig. 20.--Growth curves for two plants photographed at each station (4 and 12) during the 1961 season.

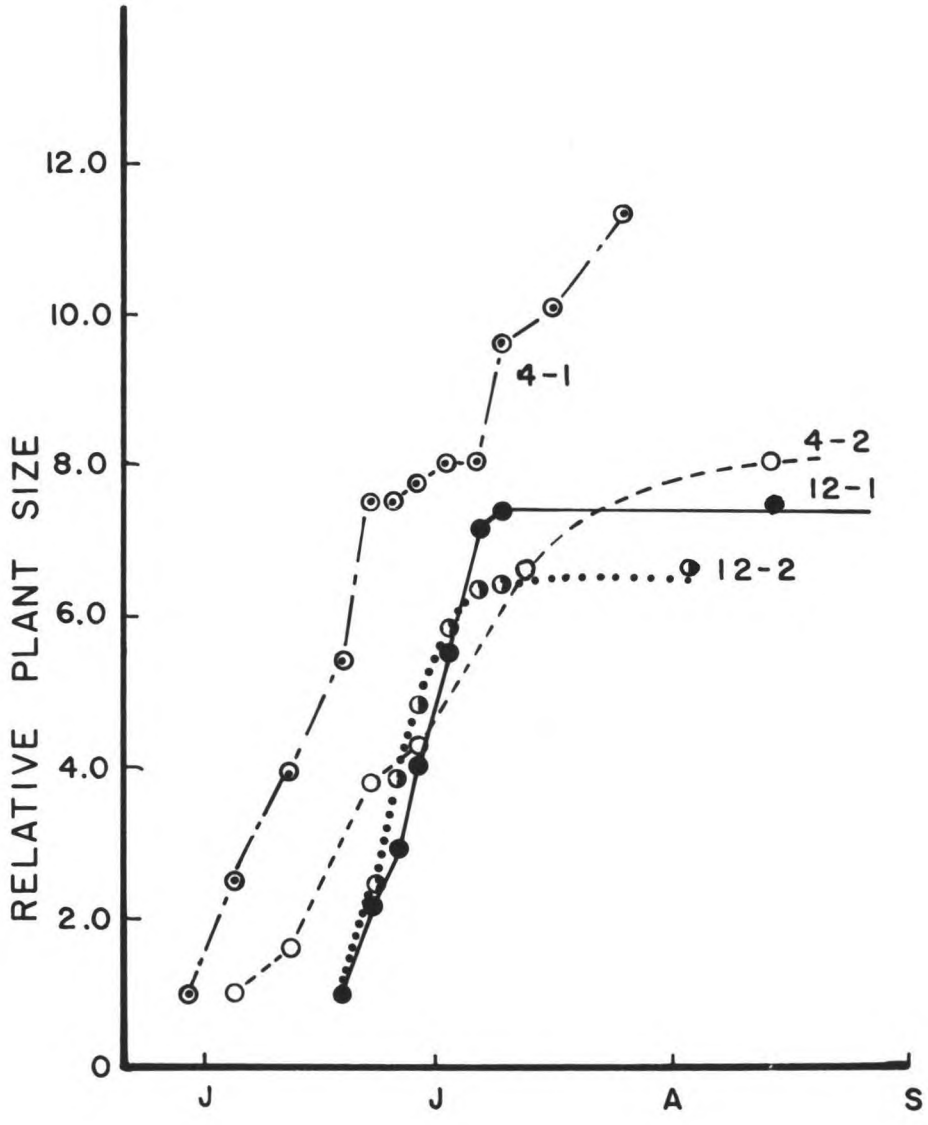
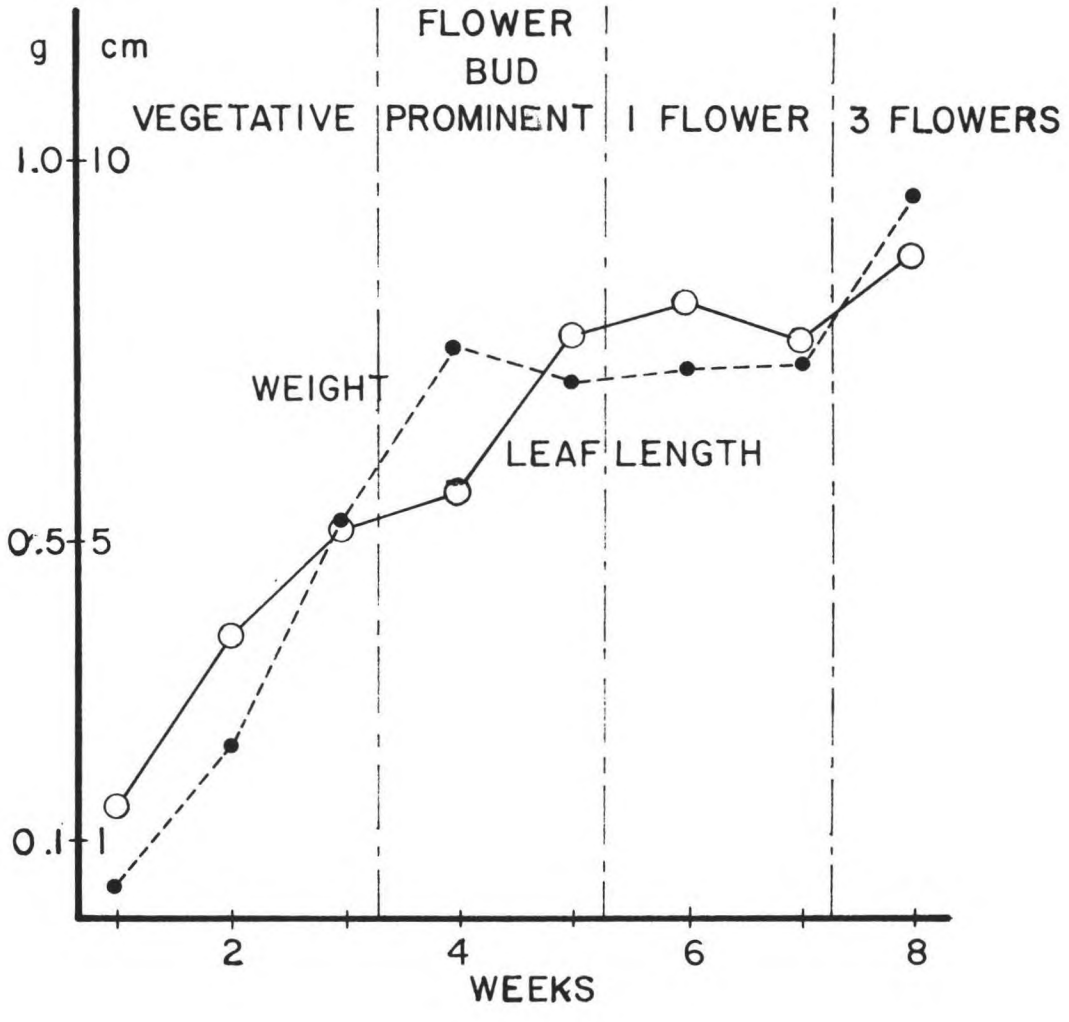

RELATIVE PLANT SIZE
12.0
10.0
8.0
6.0
4.0
2.0
0
J
J
A
S
4-1
4-2
12-1
12-2

Table 9.--PHENOLOGICAL DEVELOPMENT OF A GEUM TURBINATUM PLANT PHOTOGRAPHED AT STATION 12 BOTH SEASONS.

Date	1960	Date	1961
6/14	Just breaking dormancy.	---	
6/21	Much bigger with some red on midribs.	6/23	About the same size as in previous season at this time.
6/28	Almost full size.	6/26	Still bigger.
7/5	Neighboring plants blooming.	6/29	Like in the 1960 season.
7/12	Buds fully expanded.	7/3	Buds apparent, neighboring plants blooming.
7/19	Plant in full bloom.	7/7	Beginning to bloom.
7/26	About finished blooming. Neighboring plants in seed.	7/10	Still blooming, neighboring plants going to seed.
8/2	Still blooming, some red showing.	7/17	Some red showing, still in bloom.
8/15	Petioles and midribs bright red, leaves still green.	7/24	Ibid.
8/22	Leaves turning red.	7/31	Going to seed.
9/5	Entire plant bright red.	8/7	More red on the lower portions of the midribs.
9/12	Not much change	8/14	Petioles and midribs bright red, leaves still green.
		9/18	Plant all red, beginning to lose its red color.

Fig. 21.--The 1960 growth curve for the Geum turbinatum (12-1) photographed at station 12 during both seasons.


g
cm
FLOWER BUD PROMINENT
VEGETATIVE
1 FLOWER
3 FLOWERS
1.0
10
0.5
5
0.1
1
WEIGHT
LEAF LENGTH
2
4
6
8
WEEKS

Plants growing under greenhouse conditions and in the outdoor garden were also usually more vigorous and more nearly like field specimens than those in the warmer chambers. In the spring of 1962, however, day and night temperatures in the greenhouse were raised in connection with photoperiodism studies on another project. This seemed to sharply reduce the vigor of growth of Geum turbinatum plants.

A few specimens of Geum which were placed about 45 cm below a clock operated General Electric sunlamp (a source of UV radiation) with a six hour operating period during the middle of the day in the greenhouse, seemed to grow better than plants without this radiation. An eight hour irradiation period, however, produced the characteristic bronzing and glossy appearance associated with death of the epidermis (6) and eventually resulted in the death of the leaves.

Discussion and conclusions.--The results of the growth studies on Geum turbinatum are interesting in light of the results of Chapter III, which show that the temperatures of these plants may exceed 30 C in the field. There are two ways in which Geum turbinatum might overcome these high temperatures. First, high light intensities have been shown to increase the heat resistance of a plant (50, 155), and second, Highkin (87) has results which indicate heat resistance may also be induced by low temperatures...e.g. each night. Furthermore, these high temperatures probably have relatively short durations in the alpine so that the average kinetic energy status of the plants is actually quite low.

It is difficult to see how ambient temperatures could be limiting the extension of Geum turbinatum into the subalpine, since the ambient temperatures in the immediate subalpine and in mountain valleys which extend

close to the alpine are also quite low. It might be reasoned that the shading by the subalpine timber reduces the effectiveness of light in increasing heat resistance, but this argument fails in relation to subalpine meadows. Nevertheless, the present work indicates that Geum turbinatum is adapted to low temperatures, especially during the day, and future detailed work may indicate that this is an important factor in restricting this plant to the alpine.

Mat plants

The mat or cushion like growth form in plants is one of the characteristics usually associated with alpine vegetation. Yet there have been very few studies made on this form of alpine plant, except for work in the "puna" of the South American Andes (90, 133). An interesting feature of this type of plant is that the mat form may be lost or at least becomes much less compact at lower elevations. This may be indicative of the difference in some factor group or factors between the alpine and lower elevations, but it may also be related to genetic differences.

Description of the plants and habitat.--The plant species which may assume the cushion form in the Colorado alpine include Silene acaulis, Arenaria obtusiloba, Paronychia pulvinata, Trifolium nanum, and Phlox caespitosa. These plants are often found on open, wind blown, well drained ridges and hillsides where the surface typically consists of a pebble pavement.

Station 5′ in the False Mummy Pass area was used as a field study site. It is located between stations 4 and 5 (161) on the northwest slope near the crest of a ridge. The area is dominated by mat plants of

several species, and wind action is quite evident. Plants of this growth form were also collected in winter from a ridge on Loveland Pass, but no summer field studies were made in this area.

Methods.--It is conceivable that the mat growth form of these plants is the result of wind action, high light intensity, or an environment induced lack or destruction of stem elongating hormones such as auxins or gibberellins. To test each of these possibilities ten mats of different species were shielded from the wind by a 30 cm wide strip of relatively transparent hardware cloth supported on the west (windward) side by wires pushed into the ground, ten mats were shaded by one or two layers of window screen fashioned in the shape of a dome supported about 15 to 20 cm above the plants to allow free air movement over the plants, and about 20 plants were treated with solutions of about 2×10^{-2} M gibberellic acid. Hardware cloth had only a negligible effect on late evening light intensity, but the window screen domes reduced the light intensities by factors of three-fourths and one-half without appreciably altering its quality. Photographs were also taken of five untreated plots at station 5'.

During the winter and spring of 1962, several Paronychia pulvinata plants along with a few Trifolium nanum and Arenaria obtusiloba mats were brought down from Loveland Pass in the dormant state and potted in deep plastic trays. Half or a third of several individual mats were treated with various concentrations and combinations of gibberellic acid (GA), alpha-naphthalene acetic acid (NAA), (2-chloroethyl) trimethylammonium chloride (CCC), and 2,4-dinitrophenol (DNP). Plants used as controls were sprayed with the various solvents containing wetting

agents. Some Paronychia pulvinata were also grown in the chambers in conjunction with Geum turbinatum studies.

Results.--No significant differences were noted between the relative growth of plants in wind and sun shelters and plants growing in the open at station 5'. The GA treatment did not result in any significant growth in any of the species except Trifolium nanum, which extended some six cm beyond the length of untreated plants and bloomed a second time.

The results of the growth regulator studies in the greenhouse were inconclusive due to a large amount of variation in the responses of different plants to the same treatment. In general, GA promoted earlier development and more relative growth while plants treated with concentrations of from 10^{-6} M to 10^{-4} M NAA were retarded and had relatively little growth. The DNP and CCC had little affect on the growth or development of these mats. Where responses in growth were noted due to the treatment of GA or NAA, the difference between the treated and untreated portions of the plants indicated that there was little or no translocation of these growth regulators.

Temperatures in the chambers, on the other hand, seemed to have a great deal of influence upon the relative growth of Paronychia pulvinata. Plants growing under average temperatures of 12 to 17 C had shoots of only about 3 to 5 mm in length and in most respects resembled those in the field. Plants in chambers where the average temperatures were generally between 18 C and 27 C were killed to a large extent, but the shoots surviving were approximately 5 to 6 cm long. The mat growing

in the 18 C continuous temperature conditions, while not killed back to any degree, was still very elongate.

Discussion and conclusions.--These results do not support the ideas that wind or high light intensities produce the cushion habit, but it is conceivable that ultraviolet light penetrating the screens might contribute to the retention of the cushion form. Temperature (particularly average daily temperatures) does seem to strongly influence the growth habit of these plants.

Positive conclusions as to the possible mechanisms involved in creating the cushion habit in the alpine cannot be drawn, but low temperatures may contribute, and Trifolium nanum, at least, may assume the mat form when some environmental factor (low temperature?) reduces its natural gibberellins. These possibilities will have to be tested by further work such as analysis of gibberellin status as a function of environment.

In connection with the growth regulator studies, it is interesting to note that Arenaria hookeri which is found in wind blown areas of the plains of Colorado also forms tight mats which are unaltered by greenhouse conditions or 10^{-3} M GA. This may also indicate that the habit of these plains cusions is not the result of wind action but is a genetic feature, expressing an adaption for windy places. In this case, GA may not enter into the metabolism of these plants. In some of the alpine cushions, however, there was an effect of GA on dormancy (see Chapter VI) but not on growth. This rather unusual situation seems to be without precedent.

Ranunculus adoneus

Ranunculus adoneus represents a unique form of alpine vegetation in that it is generally associated only with snow banks. The interesting feature of plants of this species is their ability to actively grow under several feet of snow and penetrate and bloom through the thinner edges of snow fields. For this reason some preliminary experiments and speculations were made concerning the mechanisms involved.

Methods.--Most of the information on R. adoneus was collected in the field. Some data were also obtained on general growth and development in the greenhouse and chambers. To determine if this species could produce chlorophyll in the dark, i.e., under deep snow, some plants in the dormant state were placed in pots and covered by black polyethylene supported by wire frames. These pots were then placed under greenhouse benches to prevent excessive heating by sunlight.

In another experiment, plants growing under the snow, plants in full bloom, and plants in seed were collected on the same day in a snow field area of the False Mummy Pass study area. Plants were frozen in the field almost immediately between layers of dry ice, then extracted in 80 per cent alcohol in the laboratory. The extracts were chromatographed one dimensionally in a water, n-butanol, acetic acid solution (5:22:1 by volume) and developed with analine diphenylamine (Sigma Co.) to qualitatively analyze for the sugars present.

Results and discussion.--From observations of green R. adoneus under about a meter of snow on Niwot Ridge, it was originally surmised that this plant could produce chlorophyll in the dark. Observations of green leaf primordia in the quiescent perenniating buds of Geum turbinatum

and green grass blades under 170 cm of snow seemed to support this possibility. None of these plants, however, are able to produce chlorophyll under the black plastic in the greenhouse. Also, many etiolated and chlorotic plants were found under the snow during the growing season. From these results and observations, it is believed that the finding of green plants earlier under the snow during the winter is the result of cold preservation of actively growing plants which were trapped under the fall snows before becoming dormant.

The results from the chromatographs did not indicate any qualitative differences in the types of sugars found in the three developmental stages of Ranunculus adoneus. The sugars which were tentatively identified (by comparison with "known" sugars) as being present were fructose and maltose and perhaps glucose and sucrose. No morphological features normally associated with food storage in plants were noted in field specimens, so that the source of energy for the growth of this species under the snow was not determined.

Snow bank conditions are apparently not necessary for the well being of the plant since specimens in the greenhouse have been grown continuously with periodic spells of flowering for nearly three years. It was noted, however, that plants in the dormant state were killed by high temperatures in the greenhouse applied during the initial part of their growth, indicating one possible explanation for their snow bank associations in the field.

More extensive studies are needed to determine the nature of this type of plant growth.

General conclusions

It may be concluded from the results of the three studies that alpine plant growth rates and development are largely a function of temperature. This does not exclude the possibility that light intensities and perhaps ultraviolet radiation are also important in determining the growth of alpine plants.

Chapter V

THE FLOWERING OF ALPINE PLANTS

The distribution and general adaptability of a higher plant as a species probably is quite dependent upon its ability to flower and reproduce sexually in any given environment. Thus a study of the factors controlling flowering could indicate the factors which are important to the distribution of alpine plants.

Geum turbinatum is of particular interest in this case since relatively few flowers have been observed in plants transplanted to lower elevations. For this reason an attempt was made to discover the unique factors which are present in the alpine environment and which could induce flowering in Geum turbinatum.

Initiation in this paper will be defined as the physiological change in meristematic tissue which results in the development of a differentiated tissue or organ. In Geum turbinatum this is indicated by the presence of primordia, but it does not depend upon whether or not they develop into flowers.

Methods

General studies.--Plants were observed and dissected in the field as part of the field study to determine the time of flowering and floral initiation. Also, Geum turbinatum from the alpine—simulated season study were placed in a deep freeze at about -10 C for a period of ten

months after which several were dissected and some were placed in the greenhouse and observed for indications of floral initiation.

Temperature studies.--To investigate the possible influence of temperature on the initiation and development of flowers, Geum turbinatum were placed in six growth chambers with the temperatures described in Table 7 in the previous chapter. The rate of development and the number of buds and flowers produced were recorded during this time. After 43 days in these conditions the temperatures were changed according to Table 10. The plants in each chamber were also divided into six groups of six plants at this time and each group was placed in a different chamber as part of an investigation on dormancy. After a four week period, these plants were dissected to determine if flower primordia had been initiated.

Table 10.--SECOND CONDITIONS FOR THE CHAMBERS.

Chamber	Day temperature	Night temperature	Photoperiod
1	18 C	18 C	12
2	18	0	12
3	10	0	12
4	10	0	16
5	18	0	16
6	18	18	16

Growth regulator studies.--Initially five plants were treated with a 10^{-3} M solution of CCC and three plants each were treated with 2×10^{-3} M solution of GA and a solution of Roberts' "anthogen" (143). After it was determined that CCC may have some influence upon flowering, a 2 ml aliquot of a 10^{-2} M solution was applied to 25 Geum turbinatum plants that had been growing in the greenhouse for about four weeks

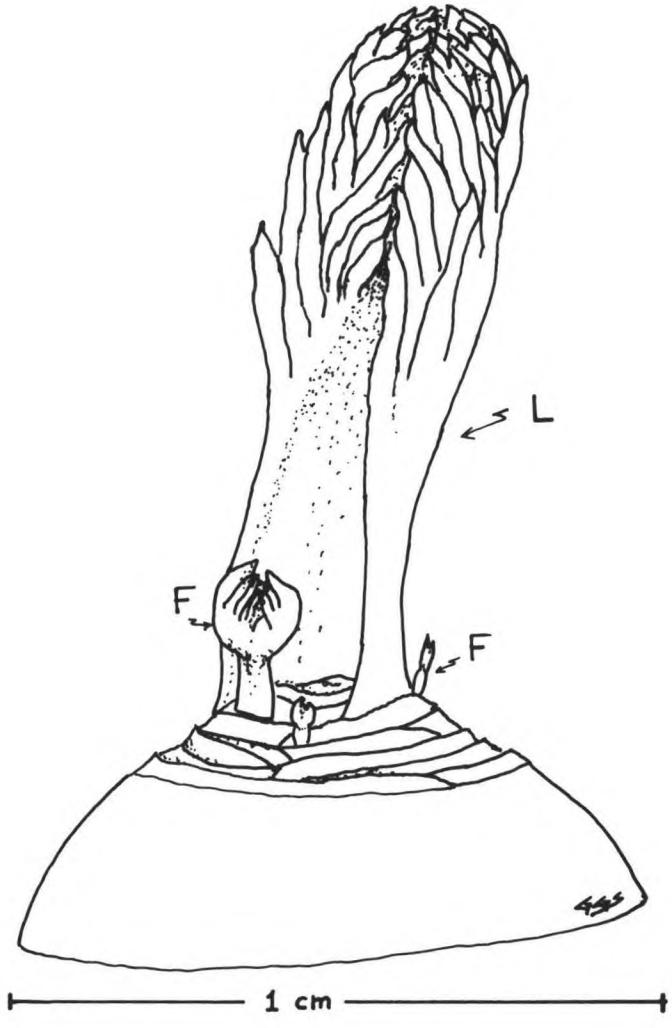
after being collected on Loveland Pass in the dormant state. The same amount of CCC was applied to the axils of four Geum turbinatum which had been growing in the greenhouse for about one year. About half of the plants treated were placed in a chamber at 18 C days and 0 C nights while the other half were left in the greenhouse.

Light studies.--Some of the plants from the simulated alpine season, previously described, were exposed to ultraviolet radiation in the greenhouse for approximately two weeks and then dissected for floral primordia. The UV irradiation periods were originally set between the hours of 0700 and 1800; however, after it was noted that this damaged the plants, the period was reduced to the hours of 0900 to 1500. The source used was a clock operated General Electric sunlamp placed about 45 cm from the plants.

Results

General observations.--Field dissection and dissection of plants collected in the field indicate that the primordia are formed about the middle of July of the year previous to the one in which the flowers develop (R. V. Parke, personal communication). Flower primordia in Geum turbinatum characteristically arise in the axils of the slightly expanded leaf primordia. They are distinguished from the leaf primordia by a much narrower, more cylindrical base (the peduncle) and a "head" which develops into the bracts and flowers (Fig. 22). Generally about 80 per cent or higher of the plants sampled had at least one and sometimes as high as eight primordia. Plants in the field usually bloomed 10 to 23 days after the initial spring growth depending upon the location and lateness of the season (see Tables 8 and 9). Many individual plants in the

Fig. 22.--Schematic drawing of the apical region of Geum turbinatum showing a leaf primordium (L) and three flower primordia (F).


L
F
F
1 cm

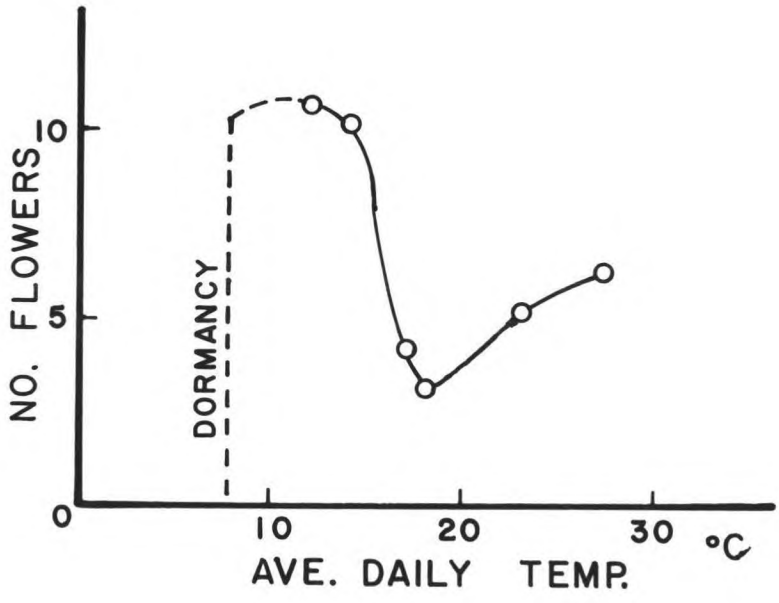
field were also noted blooming in the fall although they were apparently dormant. These blossoms were essentially sessile or with very short peduncles. Geum turbinatum usually bloomed more copiously in the alpine than in controlled situations, although there was some year to year variation (92).

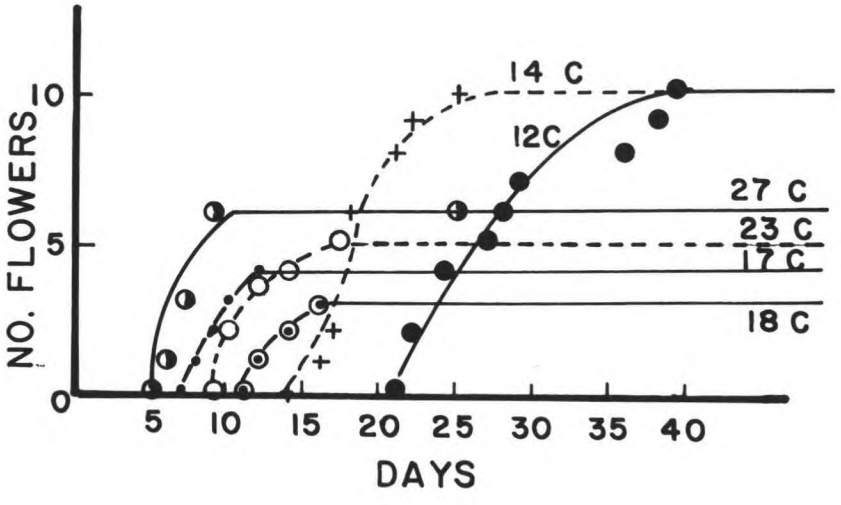
Temperature experiments.--No temperature combinations were found that would initiate primordia with one exception: Some plants that had been growing in the greenhouse for nearly nine months and had subsequently been put into dormancy in chamber 3 of the experiment described in Table 10 and kept in this state for about two months initiated primordia. Temperatures, on the other hand, did have a considerable influence upon the rate and number of flowers developing. Generally, plants which were collected from the field in early spring (with buds already initiated) flowered more rapidly in response to increased air temperatures, but the increase in temperatures decreased the total numbers of flowers which developed, (Fig. 23). This decrease in the number of flowers seemed to be the result of flower bud and primordia aborting. Abortion occurred in buds with peduncles of up to 6 cm, apparently due to high temperatures. Flowers produced in the cooler conditions of chamber 5 and particularly chamber 4 were also large and seemingly more similar to flowers found in the field.

Low temperature pretreatment seems to be necessary for development of buds initiated in summer. Plants brought down from the alpine in the dormant state in the fall did not flower after breaking dormancy when placed directly in the greenhouse; however, plants which were placed in cool chambers and then stored at -20 C in a commercial

Fig. 23.--Graph of the number of flowers produced by Geum turbinatum under various average temperatures in the growth chambers.

Fig. 24.--Curves showing the development of flowers of Geum turbinatum under various average temperatures in the growth chambers.


NO. FLOWERS
10
5
0
DORMANCY
10
20
30
°C
AVE. DAILY TEMP.


NO. FLOWERS
10
5
0
14 C
12C
27 C
23 C
17 C
18 C
5
10
15
20
25
30
35
40
DAYS

frozen food center flowered when returned to growing conditions. The pretreatment (or storage) temperatures required for flower development were not determined.

Growth regulator experiments.--No flowers were formed in response to the treatments of GA or Roberts' anthogen. Three of the five plants first treated with CCC, however, produced a tall flowering stalk and flowers, while the leaves of all five plants showed reduced growth associated with this compound (36, 177, 178, 170). All four of the plants from the greenhouse in the second group of plants treated also produced abundant primordia and flower buds. Only one developing primordium was found, however, in the group of Geum turbinatum brought down later from Loveland Pass. Still, these plants had swollen bases and much flattened apical meristems which are characteristics generally associated with the flowering of this species. In contrast, the controls had long tappered apical meristems and relatively narrow bases.

Light experiments.--None of the photoperiods in conjunction with the temperature studies indicated in Tables 7 and 10 were effective in inducing floral primordia at the light intensities of the growth chambers. The ultraviolet light did, however, result in flower primordia in about 50 per cent of the plants exposed.

Discussion and conclusions

Floral initiation.--From the results of the preceding experiments and observations on Geum turbinatum, it appears that flower initiation might result from treatments which would be expected to retard vegetative growth and elongation of the apical meristem. In the alpine,

these might include ultraviolet light, low temperatures, and perhaps the higher light intensities. CCC is considered a gibberellin "antagonist" compound because of its inhibition of internode elongation and its ability to overcome the effects of applied gibberellins (178, 179). Thus it is especially striking that this compound caused flower initiation in some test plants. P. Chouard (personal communication) indicated that low temperatures are essential in the initiation of flowers in certain European species of Geum.

Many of the failures in initiating flowers under controlled environments may be due to the destruction of roots in transplanting and the subsequent poor condition of the plants in some experiments. Still, no Geum turbinatum has been observed to flower in outdoor gardens, nor did the plants in the greenhouse flower even after they had become well established. Although application of GA resulted in increased leaf growth in such plants, flowering did not occur unless they were also treated with CCC. Obviously more work is necessary to unscramble the facts, but the hypothesis that flowers are initiated when vegetative growth and elongation of the meristematic internodes is inhibited seems worthy of further testing.

Floral development.--The higher temperatures at lower elevations would apparently inhibit flower development even if primordia were initiated. The abortion of primordia and flower buds in this way is very interesting in light of Yarwood's work with the translocation of a heat damage substance (219). He found that a compound, whose effects are reversed by kinetin, may be translocated from a site of temperature damage

and cause the same effects in tissue which has not been exposed to these high temperatures. If bud abortion is the result of a heat produced substance, its preferential influence on flower primordial tissue rather than leaf primordia may have some interesting consequences.

It is noteworthy that the chambers with temperature conditions most similar to those found in the alpine produced the maximum number of flowers and relatively slow rates of development very similar to those in the field. This seemingly optimum range of temperatures for flower development in Geum turbinatum is just above the maximum average temperature needed to "force" dormancy (see Chapber VI). The increased number of flowers in the two warmest chambers might be the result of genetic variation and small sample numbers, yet it also agrees with the idea of the accumulation of a heat damage substance. If there is a critical temperature above which a flower aborting substance gradually accumulates, then at high temperatures flowers might develop rapidly before an effective level of the substance could be built up, thus resulting in more flowers than in plants growing more slowly just above the critical temperature.

The curves in Fig. 24 also imply that day temperatures may be more important than night temperatures in determining the rate and time of initial flower development. This, then, in conjunction with the above hypothesis might explain the lower flower yields in chamber 6 at 18 C temperatures.

Flowering of alpine plants in general

The plants flowering at lower elevations and the conditions under which they flowered are listed in Table 11. It may be seen that many species do flower at lower elevations while others, like Geum turbinatum evidently require some factor combination that is present only in the alpine. The problems of initiation and development have not been studied for most of these species, however. Thus appearance of flowers at lower elevations is not always proof of initiation under these conditions. Furthermore, some of these species may not have flowered simply because they could not grow under the conditions imposed upon them... e.g. Senecio soldenella.

In general the alpine temperatures appear to be an important factor in flowering as it is in the growth of alpine plants. Furthermore, ultraviolet light should be studied from the standpoint of flower initiation.

Table 11.--PLANTS GROWN AT LOWER ELEVATIONS. (G = OUTDOOR GARDEN, GH = GREENHOUSE, AND CH = CHAMBER).

Species	Growing conditions	Able to grow	Flowering
Androsace subumbellata	Gh	Yes	Yes
Arenaria obtusiloba	Gh, Ch	Yes (Also from seed)	Periodic
A. fendleri	Gh	Yes	After field initiation
Artemisia norvegica (?)	Gh, Ch	Yes	Periodic
Caltha leptosepala	Ch	Yes (3 years)	None
Castilleja occidentalis	Ch	Yes	Field initiation
Chionophila jamesii	Gh	Yes (More branching)	None
Claytonia megarrhiza	Gh	Yes	Periodic
Deschampsia caespitosa	Gh, Ch	Yes	Periodic
Draba spp.	Gh, Ch	Yes	Periodic
Dryas octopetala	Gh, Ch	No	None
Erigeron spp. (2)	Gh, Ch	Yes	Periodic
Eritrichium elongatum	Gh	No	None
Gentiana romanzovii	Gh	Yes	Periodic (Abnormal flowers)
Geum turbinatum	Gh, Ch, G	Yes (Also from seed)	Under special conditions
Hymenoxys acaulis	Ch	Yes	Field initiation
H. grandiflora	Gh, Ch	Yes (Also from seed)	Field initiation

Table 11.--PLANTS GROWN AT LOWER ELEVATIONS. (G = OUTDOOR GARDEN, GH = GREENHOUSE, AND CH = CHAMBER).--Continued

Species	Growing conditions	Able to grow	Flowering
Juncus spp.	Gh, Ch	Yes	Periodic
Kobresia bellardi	Gh, Ch	Yes	Undetermined
Paronychia pulvinata	Gh, Ch	Yes	Periodic
Penstemon spp.	Ch	No	None
Phlox caespitosa	Ch	No	None
Poa spp.	Gh, Ch	Yes	Periodic
Polemonium viscosum	Gh, Ch	Yes (?)	None
Potentilla diversifolia	Ch	Yes (?)	None
Ranunculus adoneus	Gh, Ch	Yes	Periodic
Sedum integrifolium	Gh, Ch, G	Yes	Annually
S. rhodanthum	Gh, Ch, G	Yes	Annually
S. stenopetalum	Gh, Ch, G.	Yes	Annually
Senecio soldenella	Gh, Ch	No	None
Silene acaulis	Gh, Ch	Yes	Periodic
Solidago spp.	Ch	Yes	Field initiation
Stellaria spp.	Gh, Ch	Yes	Periodic

Chapter VI

DORMANCY

Dormancy is the phenological stage of a perenniating plant in which growth and development are essentially stopped as the result of radical changes in plant function, allowing the plant to escape or evade unfavorable growing conditions. This is the last stage in the annual flush of growth of a plant and is often characterized by such features as the accumulation of anthocyanins and sugars, death of the expanded leaves, and the formation of protective structures around the shoot meristems.

Very few studies known to the author have been carried out on the dormancy of alpine plants, although in the case of Oxyria digyna dormancy develops in response to short days (122). Dormancy in this region could be especially critical due to the rapidity with which the relatively harsh winter conditions set in. Thus a knowledge of the dormancy response in alpine plants may indicate another process which is crucial in the distribution of these plants.

Methods

Field studies included the photography described in Chapter IV and incidental observations from the application of GA solutions on mat plants at station 5'. Dormancy observations were also made on Geum turbinatum growing under the conditions listed in Tables 9 and 10

of the previous two chapters. In addition, Geum turbinatum, Kobresia bellardi, and Paronychia pulvinata plants which had been growing in the greenhouse during the first phase of the experiment were placed in chambers 2 and 3 during the second phase of this experiment. Part of these plants were then subjected to one minute of red light in the middle of the dark period, while another part was given five minutes of far-red light. A third group acted as controls.

Another experiment on the dormancy response of Geum turbinatum was carried out in the six chambers with plants which had been transplanted from Loveland Pass and allowed to develop in the greenhouse for four weeks prior to the start of the experiment. The day temperatures of each of the chambers is indicated in Table 12. The night temperature in each case was 0 C, and 16 hour photoperiods were used. During the first week of the experiment, three plants each were transferred from the first five chambers to chamber 6 each day at the beginning of the photoperiod. The amount of dormancy which had developed in the plants of each chamber was noted daily for a two week period, after which the experiment was terminated.

Table 12.--PHOTOPERIOD TEMPERATURES AND AVERAGE DAILY TEMPERATURES IN EACH OF THE CHAMBERS USED IN THE SECOND DORMANCY EXPERIMENT.

Chamber	1	2	3	4	5	6
Day temperature	8	10	12	14	16	18 C
Average temperature	5	6	7	8	9	10.5 C

Results

Dormancy in the field and simulated season.--Dormancy in Geum turbinatum is characterized first by the reddening of the petioles and midrib of the leaves, which is followed by a gradual reddening of the whole plant. Sections of Geum turbinatum midribs and leaves from a freezing microtome showed that the reddening was due to the accumulation of anthocyanins in the epidermis and first few layers of cortical tissue and in the phloem fibers of the vascular bundles. Plant development essentially stops at this time, yet some flowers may appear as described in Chapter V (probably a fraction of one per cent of the total population). The young leaf and flower primordia at the apical region of the plant are protected by the sheath-like petioles of the old leaves and the youngest partially expanded leaf (= "first leaf"), and this forms the perenniating bud. The older leaves eventually lose the red color, die and may be weathered away during the winter.

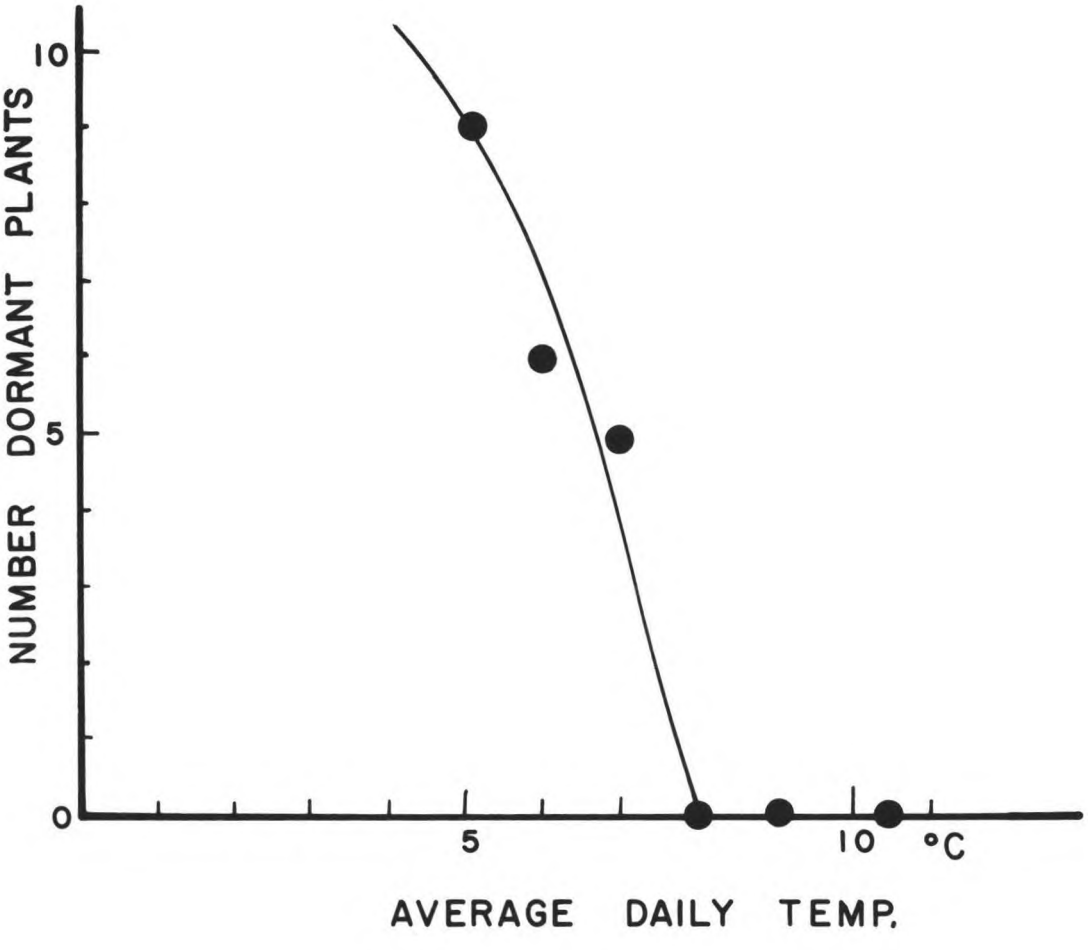
Dormancy usually begins to appear in Geum turbinatum and in many other alpine species during the first week in August. There is much variation, however, and Geum turbinatum plants in close proximity to each other may differ in time of dormancy by a month or more. Geum turbinatum plants were also photographed on August 7, 1961, in phenological stages varying from early flower bud and flowering to "deep" dormancy. Many Geum turbinatum and perhaps other species apparently do not become dormant until covered by snow or exposed to a period of intense winter cold. This was also true of the plants growing in the outdoor garden in Englewood.

No correlations were found between the time of dormancy of Geum turbinatum in the field and variation in environmental factors. The dormancy response was noted during periods in which the weekly average daily temperatures ranged from 8 C to 14 C, or mostly around 12 C. In the simulated alpine season experiment dormancy in Geum turbinatum and most of the other plants was evident some 13 days following the initial drop in temperatures and four days after the shortening of the day length (Fig. 16 and Table 3) when the average daily temperatures had dropped to 10 and 12 C.

Dormancy in controlled environments.--No Geum turbinatum or other alpine species were observed to go dormant in the greenhouse, although some periodic reddening and flushes of new growth were noted in Geum turbinatum. Most plants in the first series of chamber experiments went into dormancy in response to 10 C days and 0 C nights regardless of the photoperiod. Some slight indications of dormancy were also noted in some of the species (mostly Hymenoxys grandiflora seedlings) growing in chambers 2 and 5. There were no differences noted in the plants treated with red light or far-red light and the controls.

Fig. 25 shows the results of the second experiment after a period of two weeks. Of the plants transferred to chamber 6 only those taken from chamber 1 during the 6th and 7th days and those from chamber 2 on the 7th day showed signs of going dormant. Other plants transferred from the first three chambers which had begun to accumulate anthocyanins lost much of their red color and put out new leaves which were essentially green.

Fig. 25.--Graph of the dormancy reponse of Geum turbinatum under various average temperatures.


NUMBER DORMANT PLANTS
10
5
0
5
10
°C
AVERAGE DAILY TEMP.

All of the chamber experiments indicated that dormancy is induced by average daily temperatures of less than 8 C and the strongest responses in Geum turbinatum were obtained by temperatures of less than 7 C. It was also evident that at least six days of 5 C temperatures is required to bring about a response. It should be noted that the occurrence of freezing temperatures will not necessarily induce dormancy.

Growth regulator studies.--Most of the results reported here have already been discussed in previous chapters, but they have direct bearing upon the possible mechanisms in the dormancy response of some alpine plants.

The applications of 2×10^{-2} M GA in the field on July 12, 1961, prevented the plants treated from going into dormancy as late as September 18, while the majority of the untreated mats in this area started turning brown about August 14, and were dormant by September 18 (Table 13). A second application of 10^{-2} M GA on August 7, to some previously untreated cushions and some that were previously treated did not result in any appreciable differences in the dormancy responses of these plants. The application of GA in the greenhouse, as previously noted, hastened the breaking of dormancy in Paronychia pulvinata while NAA treated plants were delayed.

In connection with the dormancy experiments with Geum turbinatum in the chambers, the "first leaf", i.e., the youngest partially expanded leaf in the fall and the first leaf to become green in the spring (see the description of dormancy in the first section of "Results"), usually did not expand much beyond its fall proportions, although it did lose most of its red color and became green again. This leaf usually died within

Table 13.--PHENOLOGICAL DEVELOPMENT OF MAT PLANTS PHOTOGRAPHED AT STATION 5' DURING 1961.

Date	Description
5/29	Silene acaulis, Trifolium nanum, and Arenaria obtusiloba are just breaking dormancy. Paronychia pulvinata still appears dormant.
6/5	All four species turning green.
6/19	All plants still greening up. Flower buds evident on Trifolium plants.
6/23	All plants are fully green. Silene acaulis flower buds evident. Trifolium nanum is beginning to bloom.
6/26	Plants of all four species blooming.
7/3	More plants of each species blooming.
7/10	Plants still flowering.
7/17	Still some flowers present. Arenaria obtusiloba and Paronychia pulvinata browning some in one plot.
7/24	Most of the plants becoming more brown. Some Paronychia pulvinata appears to be almost dormant.
8/7	A Silene acaulis plant has a late flower.
8/14	Most of the plants appear to be going dormant.
8/24	Some Geum turbinatum plants are bright red in one of the plots.
9/18	All of the mats appear dormant with the exception of some Trifolium nanum plants which still have a few green leaves.

one or two weeks after the breaking of dormancy but remained with the plant. In dissected specimens from the field this leaf was found at different distances from the apical meristem. Removal while it was alive seemed to increase the rate of development of the young leaves and flower buds in a few instances, but no critical studies were made of this phenomenon.

Discussion and conclusions

It should be recognized that while in Geum turbinatum and probably other plants there is a great deal of variation in the dormancy response due to genetic variation or other factors, the majority of the plants still follow certain patterns of response.

Anthocyanin production and dormancy.--Dormancy is usually characterized by the accumulation of anthocyanin, probably in response to accumulations of sugars, but this does not mean to imply that anthocyanin accumulation is always an indication of dormancy. Quite the contrary, anthocyanins in Geum turbinatum and probably other species are also produced in response to low temperatures any time during the growing season. In agronomic practice, anthocyanins are often an indication of a mineral deficiency. Young sprouting plants in the spring are commonly red, especially in association with cold snow melt waters.

A group of more than 300 Geum turbinatum plants was also discovered in a small area between station 4 and 5' in the False Mummy Pass study area. These plants accumulate anthocyanins in the epidermis only, as revealed by sections from a freezing microtome. This is the result, apparently, of genetic differences. They are found interspersed with the more typical green Geum turbinatum plants and there are no plants of

intermediate color. They probably constitute a small population of a separate genetic race. They seem to resemble the green plants in every other respect as far as was determined. Other similar but distinct specimens were found about 100 m to the east. In going dormant these plants take on a deeper red color which might be the result of the accumulation of anthocyanin in the outer cortical layers and phloem fibers or the destruction of chloroplasts. It was determined as an incidental observation in the experiment to determine whether chlorophyll was produced in darkness in Geum turbinatum and other species mentioned in Chapter IV, that the anthocyanin in this race is produced only in light. The period of exposure necessary was not determined, but it apparently is less than a day. Light conditions, possibly by increasing the chlorophyll content of the leaves, tend to lessen the redness of this race under greenhouse conditions. Low temperatures in the chambers did not increase the color to any extent over that which is associated with greenhouse conditions.

General considerations.--In the growth chamber studies, aside from the simulated season, average temperatures of 8 C or higher did not induce dormancy, yet in the field and in the simulated season, dormancy was initiated and completed at higher temperatures. In general, the plants in the field and those responding in the simulated season were more vigorous than the other Geum turbinatum plants used, and root disturbuance was negligible. As a result these plants had more opportunity to accumulate carbohydrates. This implies that there is a significant difference between the response of plants which do not have time to reach a certain nutritional level and those that have. This same line of reasoning could also help to explain the difference between plants

developing late in the field and those developing earlier in the season.

The results of the first growth chamber experiment indicate that the dormancy response is not influenced by photoperiod. However, the plants used in this experiment were largely at the nutritional level where more "harsh" conditions are needed to "force" dormancy, and light intensities in the chambers were much below those in the field. Therefore, photoperiodic response is not completely eliminated as a possible means of initiation. Also, the plant at station 12 which was photographed both years went into dormancy about the same time both seasons, and this would be one evidence in favor of a photoperiodic response, since the two seasons differed in their temperature regime. Gradually changing daylengths were not tested as an independent variable, although they do change gradually in the field and in the simulated season.

Mechanisms.--The results from the growth regulator studies are too tentative to draw any conclusions as to the mechanisms involved in the dormancy response, yet some of the results are interesting in light of some of the work which has been reported in the literature. Two basic mechanisms have been suggested for the initiation of dormancy in plants (23, 102, 191). These are (a) the production of an inhibitor, and (b) depletion of some growth promoter. The production of an inhibitor may be initiated by some external environmental factor or it may be accumulated continuously throughout the growing season until a critical level of concentration is reached.

The results indicated by the removal of the "first leaf" suggest that inhibitors may be accumulated in this particular organ much

like the accumulation of inhibitors in the scales surrounding dormant buds (102, 191). Since no dormancy was observed under greenhouse conditions, and since dormancy can be a response to low temperatures, the inhibitor must be produced in response to an external stimulus rather than being continuously accumulated throughout the season. However, the periodic reddening of leaves in plants in the greenhouse may indicate that there is some factor of age or apical dominance involved. It is also interesting that the Geum turbinatum growing in Englewood had to be "forced" into dormancy by winter conditions.

The results of the GA treatments support the hypothesis that dormancy occurs in response to depletion of a growth promoter. The response to GA applied 60 days before the onset of dormancy is especially interesting. Two implications might be tested in future experiments: First, if we assume that the GA was immediately incorporated into the metabolism of the plants and had a direct effect at this time and for a short period following, we can infer that the dormancy response had already been initiated some two months before the plants actually became dormant. Second, if we assume that the dormancy process was not underway at this time, then the GA must have remained in the plant in an active form until the onset of dormancy. The early growth response of Trifolium nanum (see Chapter IV) and the apparent ineffectiveness of the late application to various species would tend to favor the former hypothesis, but is not conclusive. In either case the mechanism involved might be a promoter-inhibitor balance, where an increase in "promoter" (GA) would induce growth and thus inhibit dormancy while an increase in the "inhibitor" over a certain level would induce dormancy.

The retardation of the breaking of dormancy by the concentrations and treatments of NAA described in Chapter IV has some very interesting implications in that auxins are generally considered as being growth promoters and many times promote the breaking of dormancy (63, 191). It will now be interesting to see if NAA applications will induce dormancy in these mats in the field. Surely, the response of mat plants to auxin is radically different for most other reported auxin effects. An exception is the inhibition of lateral bud growth, of which auxin induced dormancy in potato tubers seems to be an example. Are we to infer that breaking of dormancy in cushion plants is a matter of lateral bud activity?

Although most of the results of these experiments and observations are tentative, we may conclude that temperatures and nutritional levels are important factors in the dormancy response of alpine plants. Yet it is obvious that this response is very complex, and that there are apparently other factors unique to the alpine, such as high light intensity photoperiods, which may be involved in this process. The striking effects of the growth regulators on alpine plants indicate that their physiology may be somewhat unique compared to the plants normally studied. These factors together may be very significant in determining the boundaries of the alpine zone. They certainly afford ample material for further investigations.

Chapter VII

SUMMARY

A study was made in the alpines of Rocky Mountain National Park and Mt. Evans and in controlled environments to determine something of the plant-environment interactions which are unique to and help to distinguish the alpine as a vegetational zone.

1. Several factors in the alpine environment, including radiation, temperature, wind, and moisture, were measured during the growing seasons of 1960 and 1961. It was determined that the total and visible radiation in the alpine is quite high during the day and may, under proper conditions, surpass the solar constant. Temperatures in the air and soil were low relative to those at lower elevations. Precipitation and moisture availability were low in 1960 compared to 1961. Wind speeds were generally high depending upon the height above the soil surface, and the winds were characteristically quite gusty.
2. Plant temperatures and the factors of light, net radiation, wind and air temperature were measured simultaneously on Trail Ridge Road and analyzed for possible correlations. Plant temperatures often deviated widely from ambient conditions. The plant temperatures, particularly those of

upright plants, were most closely correlated with ambient temperatures. Although none of the factors considered seemed to correlate strongly with the plant-air temperature gradient, maximum light intensity correlated most closely with this gradient.

3. Studies in the field and in controlled environments seem to indicate that alpine plant growth and development is strongly affected by temperature. There is also some indication that UV light may influence the growth of some alpine plant species. High light intensities in preliminary field studies did not seem to have much direct influence upon the growth habit of alpine mats. The application of GA in the field also did not affect the growth of cushion plants with the exception of Trifolium nanum.
4. It was found that many species of alpine plants, including Geum turbinatum, do not initiate flowers under the natural conditions at lower elevations; however, flowers develop on G. turbinatum at lower elevations if they have been initiated in the field prior to being brought down and have also been subjected to a period of cold. G. turbinatum may also initiate flowers if plants are treated with CCC, UV light, or possibly cold temperatures. This suggests that the inhibition of vegetative growth from the meristem results in the initiation of flower primordia. A certain nutritonal level may also be important to the initiation of primordia.

5. Dormancy in the field was not correlated with any specific changes in environmental factors, although it may be the result of a gradual lowering in temperatures and shortening of photoperiods. Dormancy may be induced in controlled environments by daily average temperatures of less than 8 C regardless of the photoperiod. The temperature required for induction seems to depend largely upon the nutritional condition of the plants. In the field, dormancy in mat plants was retarded by GA applied 60 days prior to the actual dormancy response of untreated plants. In controlled environments GA increased the rate of the breaking of dormancy while NAA retarded it in some mat plant species.

No final conclusions were drawn as to the exact nature of the alpine zone, but temperature and radiation conditions seem to be especially important in characterizing this region. It is these factors interacting with plant processes that may determine to a large extent the distribution of alpine plants.

This study constitutes a preliminary and exploratory investigation into the physiological ecology of the alpine. Thus the need for more extensive studies into certain aspects of the alpine environment and vegetation has become evident during the course of this investigation. Some possible future studies are listed below.

1. Measurement of the alpine environment should be continued and expanded to include more intensive measurement of the edaphic factors and the qualitative aspects of radiation. In addition more attention should be given to

the internal conditions of the plants themselves, such as plant temperature and water relations.

2. The photoperiodic responses of alpine plants, if they exist, should be investigated with particular reference to the high light intensities which occur in the alpine.
3. The problems of germination of alpine seeds and seedling establishment, especially under field conditions, have received relatively little attention in the past and should be considered more in future studies.
4. A great deal of work is needed on the problems of plant processes such as photosynthesis, frost resistance, growth regulation, pigment production, etc., particularly as they relate to the general growth and development of alpine plants in the field.
5. Studies on the anatomical, environmental, and hormonal relations to the flowering process of Geum turbinatum and other alpine plant species need more attention and could contribute much to the basic knowledge of the nature of the alpine.
6. The relationship between environmental factors as they occur in the field and the dormancy response of alpine plants needs to be worked out. In addition, the nature of the hormonal balance in the plants in relation to dormancy should be investigated more extensively.

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ABSTRACT OF DISSERATION

PHYSIOLOGICAL ECOLOGY OF ALPINE PLANTS

A physiological ecology study was made in the alpine areas of Mt. Evans and Rocky Mountain National Park, Colorado and in controlled environments. Alpine environmental factors were measured and analyzed. Growth chambers and other controlled environment facilities that were used to study plant processes are described.

Alpine plant temperatures were measured in the field along with certain environmental factors, and the data were analyzed for correlations. Plant temperatures of up to 32 C were recorded, and differences between the plant and air temperatures were frequently more than 20 C. The plant temperatures correlated most strongly with air temperatures, while the plant-air temperature gradient had the highest correlation with maximum light intensity, although the factors considered did not have a large effect on the plant-air temperature gradient. In both cases the form of the plant influenced plant temperatures and the gradient to a considerable degree.

The growth and vegetative development of alpine plants were affected to a considerable extent by the average daily temperature. Temperatures of 18 to 27 C increased the initial growth rate and development but were found to be detrimental to the plants after a prolonged length of exposure. Temperatures of around 12 to 14 C seemed to be optimal for the overall growth of alpine plants. Treatments with GA,[1/]

1/ Gibberellic acid.

shading, or wind shielding did not alter the cushion plant form in the field except that GA caused the internodes of Trifolium nanum to elongate. These mat plants usually lost their cushion form at lower elevations.

The flowering of Geum turbinatum was investigated extensively since this species normally does not flower at lower elevations unless it has initiated flower primordia in the field and has also received a period of cold temperatures. CCC[2/], however, promoted the initiation of flower primordia and flower development in many individuals under greenhouse conditions. Cold treatment and UV radiation may also result in the initiation of flower primordia.

Dormancy of several species of alpine plants was studied in the field but no correlations were found between environmental factors and the dormancy response. Dormancy in some species was induced by average daily temperatures of less than 8 C depending upon the nutritional state of the plants. No plants were induced to go into dormancy by photoperiods alone, nor was there any effect from the treatments of red and far-red light. GA retarded the dormancy of mat plants in the field when applied 60 days in advance of the time of dormancy. GA also increased the rate of breaking dormancy in some mat plant species under greenhouse conditions while NAA[3/] retarded growth and the breaking of dormancy in these same cushion plants.

2/ (2-chloroethyl) trimethylammonium chloride.

3/ Alpha-naphthalene acetic acid.

George G. Spomer
Department of Botany and
Plant Pathology
Colorado State University
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