DISSERTATION

PHENOLOGY OF COLORADO ALPINE PLANTS

Submitted by

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DEPARTMENT OF BOTANY AND PLANT PATHOLOGY

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May, 1962

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INTRODUCTION

The extent of land in Colorado classified as alpine tundra amounts to almost 2 1/4 million acres (Schwan and Costello, 1951), an area greater than that of Delaware and Rhode Island combined. The assets afforded by the alpine type in the state are numerous and varied. It is estimated that over twenty per cent of all the stream flow in the state originates in the alpine (Schwan and Costello, 1951). The sheep industry is highly dependent upon the use of the tundra as summer grazing range, and the important game animals elk (Cervus canadensis), deer (Odocoileus hemionus) and mountain sheep (Ovis canadensis), summer in the alpine. The aesthetic and recreational aspects are of increasing value, as evidenced by the ever greater number of visitors to the Trail Ridge area of Rocky Mountain National Park each year.

The alpine tundra is of particular botanic interest for several reasons. Its treelessness is immediately obvious, and there has been considerable discussion of the phenomenon of timberline. Perhaps the most unique character of the alpine plant life is the substantial reduction in internodal lengths resulting in the consistently stunted growth of the vegetation. As yet, few detailed analytical studies have been conducted which reveal the adaptive advantages of this growth form, but it probably reflects an evolutionary development that has resulted in the most efficient form suited to living in the harsh environment of the alpine. The alpine species are adjusted to extremely severe winters and cool, short growing seasons. They exist under unusually high light intensities, where there is also a significant increase in ultraviolet rays. In some of the more exposed sites the moisture regime approaches that found in deserts, while in other areas very wet conditions prevail. There is much to be learned about the physiological and morphological responses and adaptations of the alpine flora.

The purpose of the present study was to examine the phenologic behavior of many alpine species in a variety of natural situations. During the summers of 1960 and 1961, data were recorded on the times of initiation of vegetative growth, microscopic appearance of floral bud, flower expansion, fruiting, dispersal, and first signs of dormancy for 85 major species of Angiosperms in the False Mummy Pass alpine region.

Data of this type are important from the descriptive standpoint in that they increase considerably our basic knowledge of the vegetation and the cyclic patterns of the component species. They also provide a very important record of the natural behavior which can be used for comparison in any test of the effects of environmental manipulations in growth chamber studies.

From the more practical standpoint a phenological record aids in the utilization of the alpine range. This is so, both from the standpoint of when to allow grazing, and in predicting changes in vegetational composition under different grazing patterns. A record of this type gives the park naturalist a better understanding of the vegetation and enables him to better preserve and interpret the area.

DESCRIPTION OF THE AREA

The area chosen for the study lies just within the northern boundary of Rocky Mountain National Park in the area known locally as False Mummy Pass (Range 74 West, Township 7 North, Section 36, Larimer County, Colorado) (Fig. 1). This area was selected primarily because it satisfied the requisite of no recent disturbance due to grazing by domestic livestock, a condition which is virtually non-existent in unprotected areas of the state. The wide variety of sites in a relatively small area, plus the opportunity to utilize the facilities of the Colorado State University Forestry Camp at Pingree Park were further positive attributes. A survey of the literature indicates that no previous ecological studies have been conducted in the area.

History

In 1905 the area was made a part of the Colorado National Forest, which in 1910 was redesignated the Roosevelt National Forest. In 1915 Rocky Mountain National Park was formed by an act of Congress. Technically this act imposed immediate restrictions of use on the approximately 255,000 acres that make up the park. These restrictions prohibited, among other things, use of the lands for the grazing of domestic livestock, lumbering, or agricultural projects. It is conceivable, perhaps even probable, that in the early days of the Park there were infractions of these rules by shepherds and others, but it is likely that the area has been essentially free from domestic grazing for some

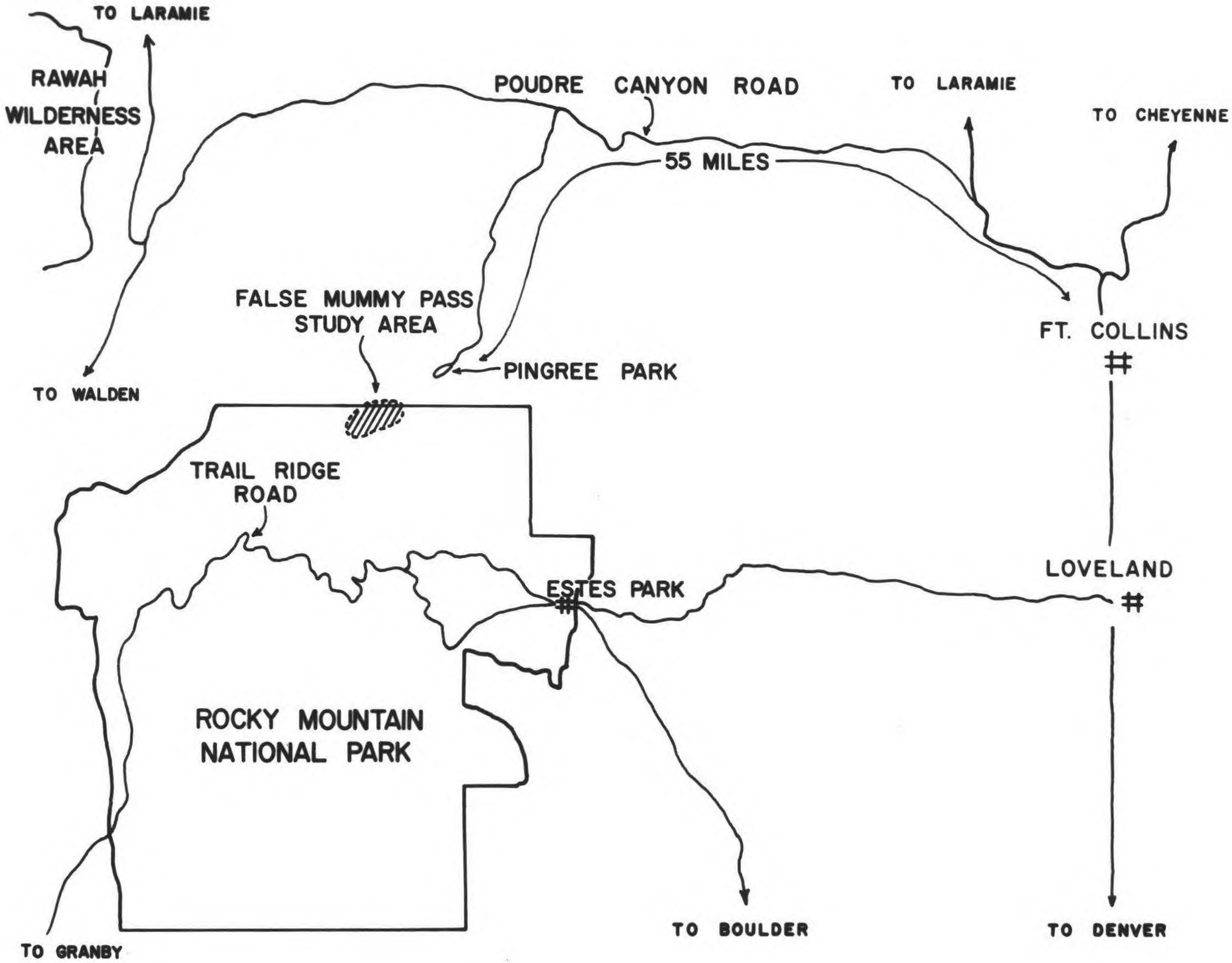

Fig. 1.--Map showing location of the study area.

time. A trail leading from Pingree Park to Mummy Pass was constructed in 1930, but the remoteness of this area of the National Park has kept human influence to a minimum.

Physiography and Geology

The study area is located in the section of the Rocky Mountains known as the Front Range of Colorado. This range extends northward from Canon City, Colorado to Wyoming where it merges with the Larimar Range. Near the center, where it is most rugged, summit elevations are generally from 12,000 to 14,000 feet. The primary study site lies slightly to the north of this in the Mummy Range portion of the Front Range.

The western slope falls quickly away from the crest of the Front Range, but the eastern slope is characterized by a series of bench-like erosion surfaces which descend in a step-like fashion to the plains and form the prominent physiographic features of the range. This general form resulted from the great period of mountain building called the Laramide Revolution which occurred in the upper Cretaceous and lower Tertiary. The pre-revolution topography and structure greatly localized and influenced the folding and faulting during this orogeny. The eastern slope was subjected to much less deformation than the western slope, but was the site of many localized northwesterly folds and persistent, steep, northwesterly faults. Its structure is dominantly that of a steep monoclinal fold, although, as illustrated by the well known "flat irons" near Boulder, Colorado, thrusting has taken place. Post-orogenic block thrusting is known to have occurred in Colorado as recently as the Pliocene (Lovering and Goddard, 1949).

These authors describe the base structure of the Front Range as being essentially crystalline pre-Cambrian granites, schists, and gneisses, with the Tertiary period represented mainly by clastics to the north and by interbedded shales, algal limestones, tuffs and lavas to the south. Associated with the lavas in Rocky Mountain National Park are intrusive rocks representing the middle Tertiary period.

Little is known of the glacial history of the Front Range, but it is generally accepted that all of the high mountain valleys have at some time had extensive ice fields and glaciers. The presence of many cirques, hanging valleys, and morainal deposits serves as evidence of past glacial activity.

Alpine Soils

The Rocky Mountain region is so geologically young and unstable that soil forming processes have not even approached the development of mature soils over the greater portion of the alpine. The principal soil forming processes involved in the alpine are physical factors including wind, gravity, and frost action, rather than chemical factors. This is due to the high chemical resistance of the predominantly siliceous substrata. The same physical factors involved in soil formation act to prevent the development of good soils in the alpine. The strong winds, melt-water flow, and the steep slopes prevent the accumulation of the fine particles and organic matter necessary for soil development. The soils that do result are, therefore, generally very stony or gravelly with little incorporated organic matter. Areas of greatest soil accumulation and conditions approaching maturity are found where these removed particles and organic matter are deposited or protected against removal, such as along the margins of streams, in bogs, at the base of steep slopes, and in locations of nearly even topography. Both the chemical nature of the substrata and the decelerated rate of organic matter breakdown under the environmental conditions found in the alpine contribute to the generally acidic reactions of the soils.

Few analytical investigations of alpine soils have been made; Burdelorf 1970's the trend has been merely to group all of the soil variations encountered into one broad Soil Group. Jenny (1930) used the Soil Group term Alpine Humus soils and listed under this more than a dozen, widely variable types, e.g., raw humus soils, grass-mor soils, pioneer-vegetation soils, and tundra-like high-mountain soils. Retzer (1956), after an analysis of alpine soils in Colorado, proposed three classes in the Great Soil Group category which made the classification of alpine soils more meaningful. The groups are the Alpine Turf soils, the Alpine Meadow soils, and the Alpine Bog soils. Of these, only the Alpine Turf type approaches a mature soil in that it possesses the normal A, B, C horizons, and is the only one that has been subjected to a thorough laboratory analysis. The other two have not developed beyond the A, C horizon stage typical of immature soils. No provision is made to include "skeletal" soils and areas made bare by wind, water, or gravity. He classifies these as areas of landscape degradation and as such are not considered to be soils. As with so many other facets of the alpine, the soils are in need of more investigation.

Soil Phenomena

There are certain physical happenings characteristic of the alpine tundra which profoundly affect the vegetation. The interactions of gravity, repeated freezing and thawing patterns, and saturated soils lead to the development of a variety of soil disturbances. Washburn (1956) described terraces, stone garlands, sorted nets, stone stripes, polygons, and frost boils. Osburn (1958) discussed the influences of solifluction, congeliturbation, snow cover and pocket gophers on alpine vegetation in Colorado.

Billings and Mooney (1959), working in the Medicine Bow Mountains of Wyoming, described polygon patterns and discussed their cyclical nature. They also referred to the sequential plant changes that accompanied the formation of these polygons.

Climate

Since it is quite difficult and expensive to maintain year around stations at high altitudes, climatological data of alpine regions of the alpine regions of the Front Range are very scarce. Researchers at the University of Colorado have been engaged in such a study, and a brief summary of climatic conditions at their Niwot Ridge alpine area is presented by Marr (1961). Cox (1933) presented what is perhaps the most detailed climatic analysis of the Front Range alpine environment presently available. Based on personal field observations, discussions with the researchers at the University of Colorado, and on the data in Cox, the following generalizations on climate are presented.

The first snows usually come in the months of September or early October, the exact time varying from year to year. These early snows may not persist over the entire area, but the snow-accumulation pockets usually maintain some snow from then on. By the end of October the snow is well deposited in its ground patterns; it lasts generally through the early part of June in the less protected areas, but persists into August in the wind sheltered, heavy accumulation areas. Those portions of the tundra that are exposed to the prevailing westerly winds are generally snow-free throughout the major part of the winter and achieve their maximum cover when the wet and heavy spring snows occur; these accumulations are usually of short duration, however, usually lasting only into early May.

The months of June and July are characterized by moderate to strong winds and frequent thunderstorms, some of which deposit a transient covering of pellet snow called graupel. Daytime air temperatures are cool, and night time frosts are not uncommon, particularly in June. The wind becomes less intense and the frequency of storms decreases during the month of August and the first part of September.

Certain studies have compared the environmental conditions of different altitudinal zones, thus providing some data indicative of the conditions in the alpine. Whitfield (1933), in a study of the Pike's Peak region of Colorado, and Holch, et. al. (1941), in Rocky Mountain National Park, found that air and soil temperatures, vapor pressure deficit, and evaporation rate all show a general depression with increases in elevation. Conversely they found that wind velocity, precipitation, and soil moisture generally increase with increases in altitude. Whitfield (1932) reported that transpiration decreases with increases of altitude. Daubenmire (1943) reported that the date of the last killing frost in the spring is delayed approximately 14 days by each 1000 foot increase in altitude. He also noted that the diurnal variation in relative humidity was found to be rather great in the alpine, and concluded that the degree of reradiation is significantly greater at higher elevations.

Based on environmental data recorded in the James Peak alpine region, Cox (1933) concluded that evaporation rates, relative humidity, precipitation, light intensities, and reradiation are all higher in the alpine than at lower elevations. He found evaporation rates from Livingston atmometers of only 13.2 cc/day in the spruce-fir forest, and 13.7 cc/day in the wind timber, as compared to values of 31.0 cc/day in a mesophytic meadow and 46.5 cc/day in an exposed fell field during the period of July 9th through August 26th, 1928. In 1928 he recorded ten freezing temperatures during the summer as opposed to no such readings in 1929. He speculated that the growing season ranged from three and one-half months in the most favorable spots to a few days or no period at all in snowdrift areas; for most of the region he felt that it was between six to ten weeks.

Hayward (1952) reported environmental data taken during a study of the alpine in the Uinta Mountains of Utah. Although noting a considerably higher light intensity in the alpine than at lower elevations, he doubted that the effect on photosynthesis is significant. Diurnal variations in the relative humidity were found to be rather great; a range of from 25 to 75 per cent was recorded, with the high readings around 2:00 A.M. and the low values around 4:00 P.M. Early afternoon thunderstorms were frequent and seemed to benefit the vegetation mostly by greatly increasing the relative humidity.

Bliss (1956), in a study of the alpine of the Medicine Bow Mountains of Wyoming, found the light intensity and ultra violet radiation to be very high. Precipitation in 1954 and 1955 amounted to 4.1 and 5.3 inches, respectively. The summer winds were predominantly from the southwest and west, with an average velocity of 6.3 mph. In addition to further consideration of climatic factors, the effects of physical factors, such as slope and exposure, as related to microenvironments were discussed. Billings and Bliss (1959), also in the Medicine Bow Mountains, investigated the effects of an alpine snowbank on the adjacent vegetation. They presented a considerable amount of microenvironmental data including soil moisture, soil temperature, and air temperature at various proximities to the snowbank. Data of this sort are greatly needed for a better understanding of plant-environment relationships in the alpine.

Weather Record

During the summers of 1960 and 1961 data on the general weather conditions of the study area were accumulated by members of the research project. Precipitation, instantaneous wind velocities, present temperatures and relative humidity were recorded at each station every Monday and on as many days thereafter throughout the week as time and personnel would allow. In addition, at Stations 4, 8 and 12 in 1960, and at 4 and 12 in 1961, recording hygro-thermographs and maximum-minimum thermometers were maintained on a similar schedule.

Precipitation was measured by the use of standard type rain gauges which were buried so that the catchment surface was about six inches above the ground. Wind velocities were measured by means of a hand-held Dwyer Wind Meter. A sling psychrometer was used to obtain the relative humidities and the dry bulb readings were used for later conversions of relative humidity to vapor pressure deficits. The psychrometer was swung in such a manner that the recorder's body shielded it from the direct rays of the sun, thus avoiding the heating effects of direct radiation. The comparisons of data for the two summers indicate that the two years were strikingly different in regard to weather.

In both years the great majority of storms came from the west or southwest. On rare occasions clouds pushed upslope from the plains to the east, resulting usually in foggy or drizzly conditions.

Total precipitation varied considerably between the two years and in view of the high evaporative rates reported for the alpine, the difference might well have been compounded. In 1960 for a period of 14 weeks, June 10th to September 19th, an average total of 4.97 inches of precipitation was recorded for the study area stations, as compared to an average total of 8.45 inches for a similar period in 1961, June 10th to September 18th. This gives an average of 0.32 inches of precipitation per week for the period in 1960 and 0.60 inches per week in 1961. It should not be inferred that the rain was evenly distributed throughout the 14 week period. The general pattern of summer distribution and the average recorded amounts are presented in Figs. 2, 3 and 4.

The distributional pattern of precipitation throughout the area was relatively uniform although certain points are worthy of mention. Stations 4, 8 and 10 recorded consistently less total precipitation than did the other stations (Fig. 5). These three stations along with Station 1 also had the highest average wind velocities (Figs. 6 and 7). At Station 1 the highest velocity winds were usually upslope winds from the northeast and were generally not associated with rain. On the other hand, the winds of highest velocities at the other three stations were usually out of the southwest, west or south and were frequently accompanied by thundershowers. It appears that the increased wind velocities at the more exposed stations had a direct effect on the amount of rainfall striking a unit area, in this case the area of the mouth of the rain

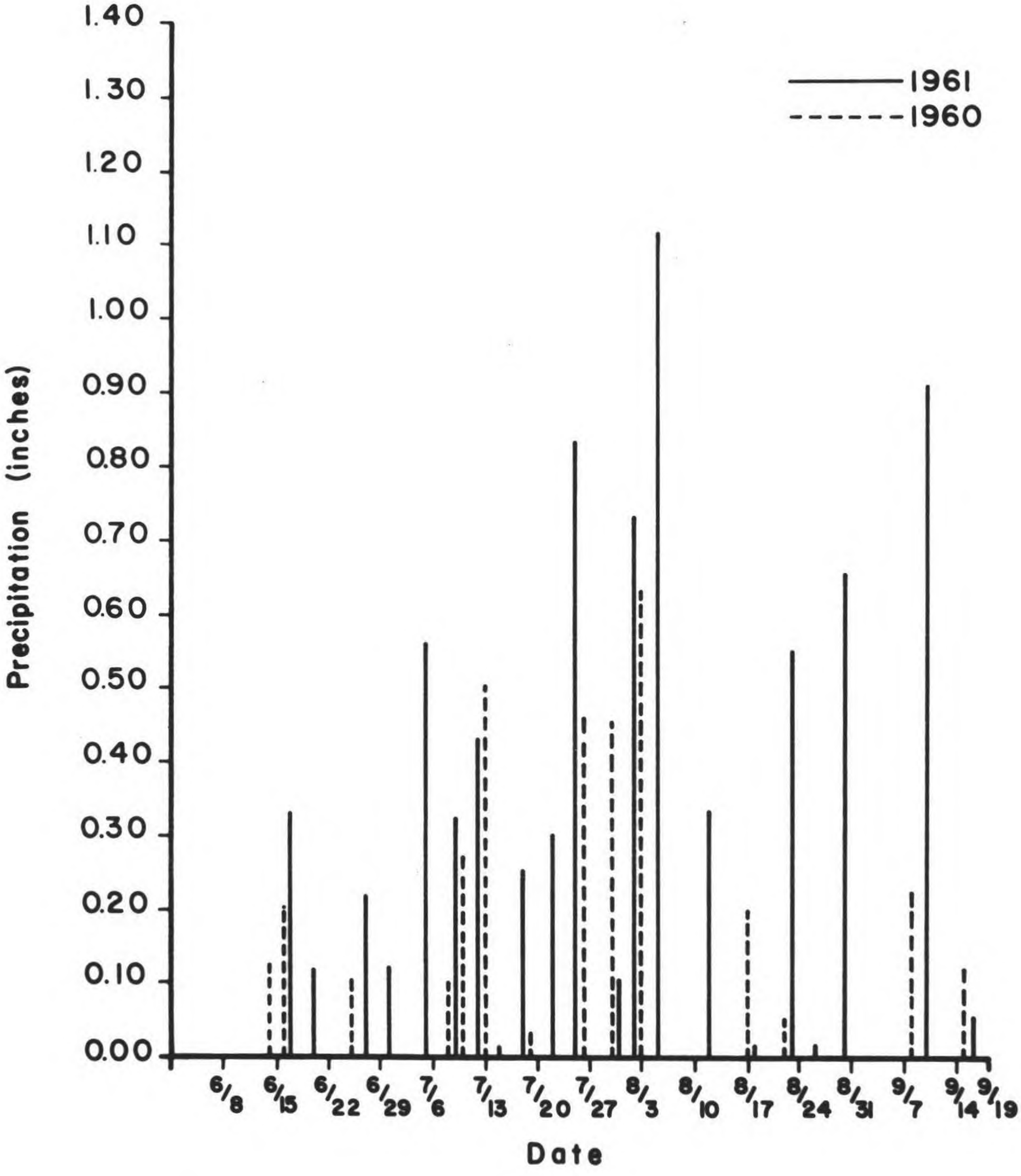

Fig. 2.--Precipitation data averaged for all stations.

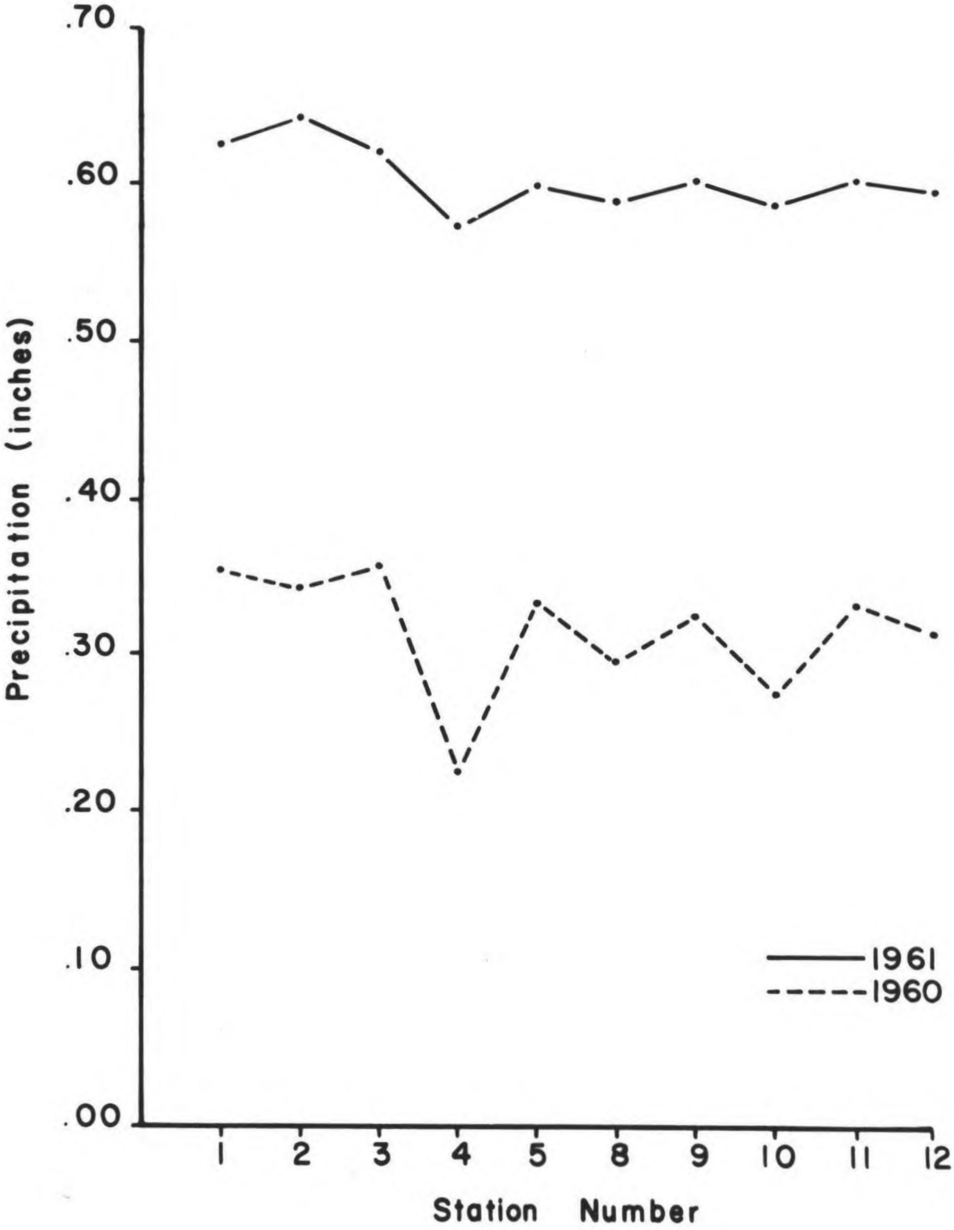

Fig. 3.--Average weekly precipitation (June 10-September 19).

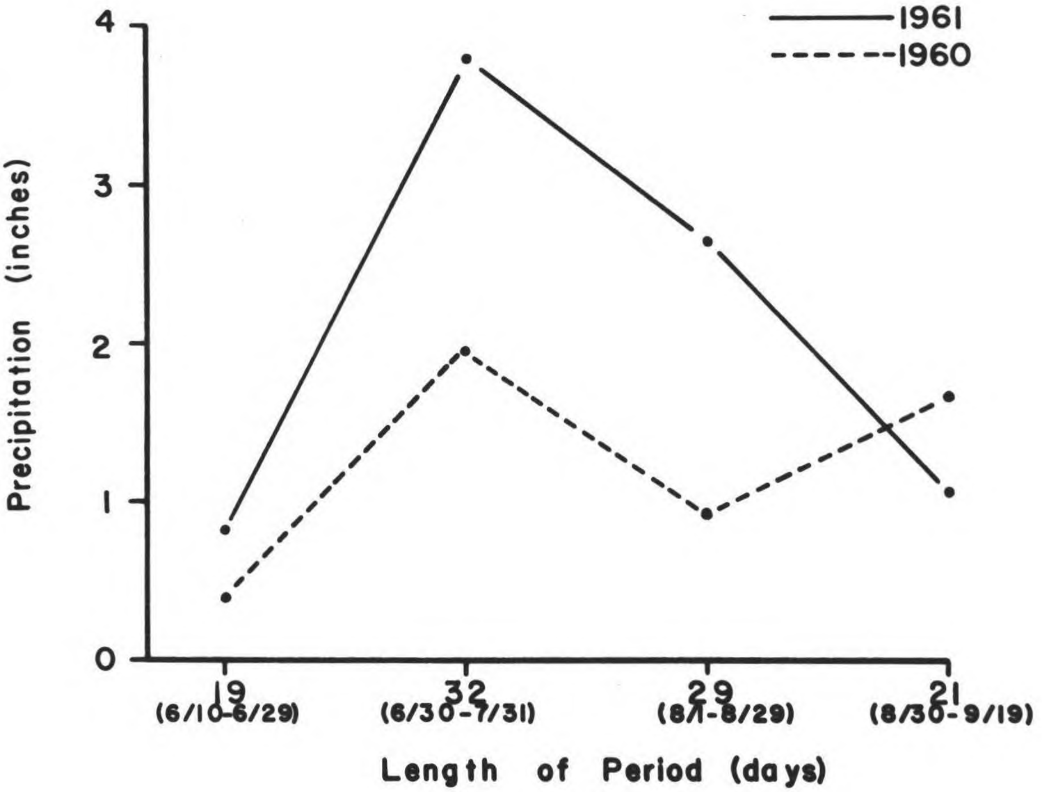

Fig. 4.--Average total monthly precipitation of all stations recorded during the study period.

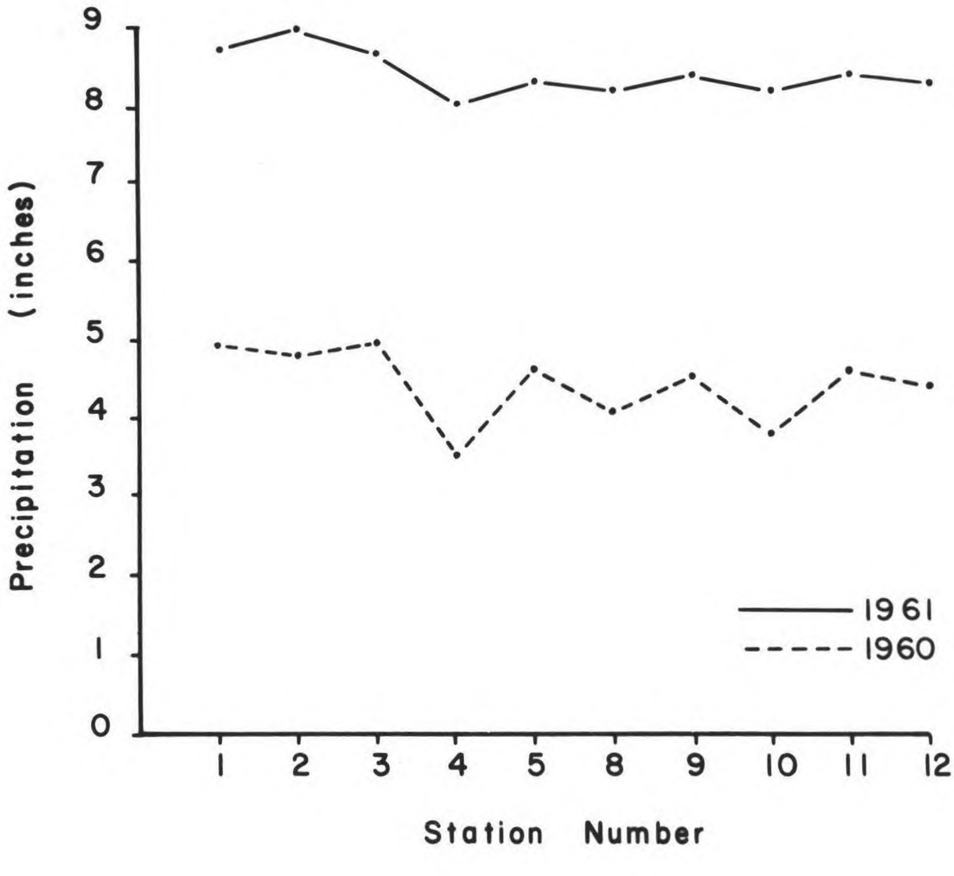

Fig. 5.--Total precipitation for period of June 10 to September 19.

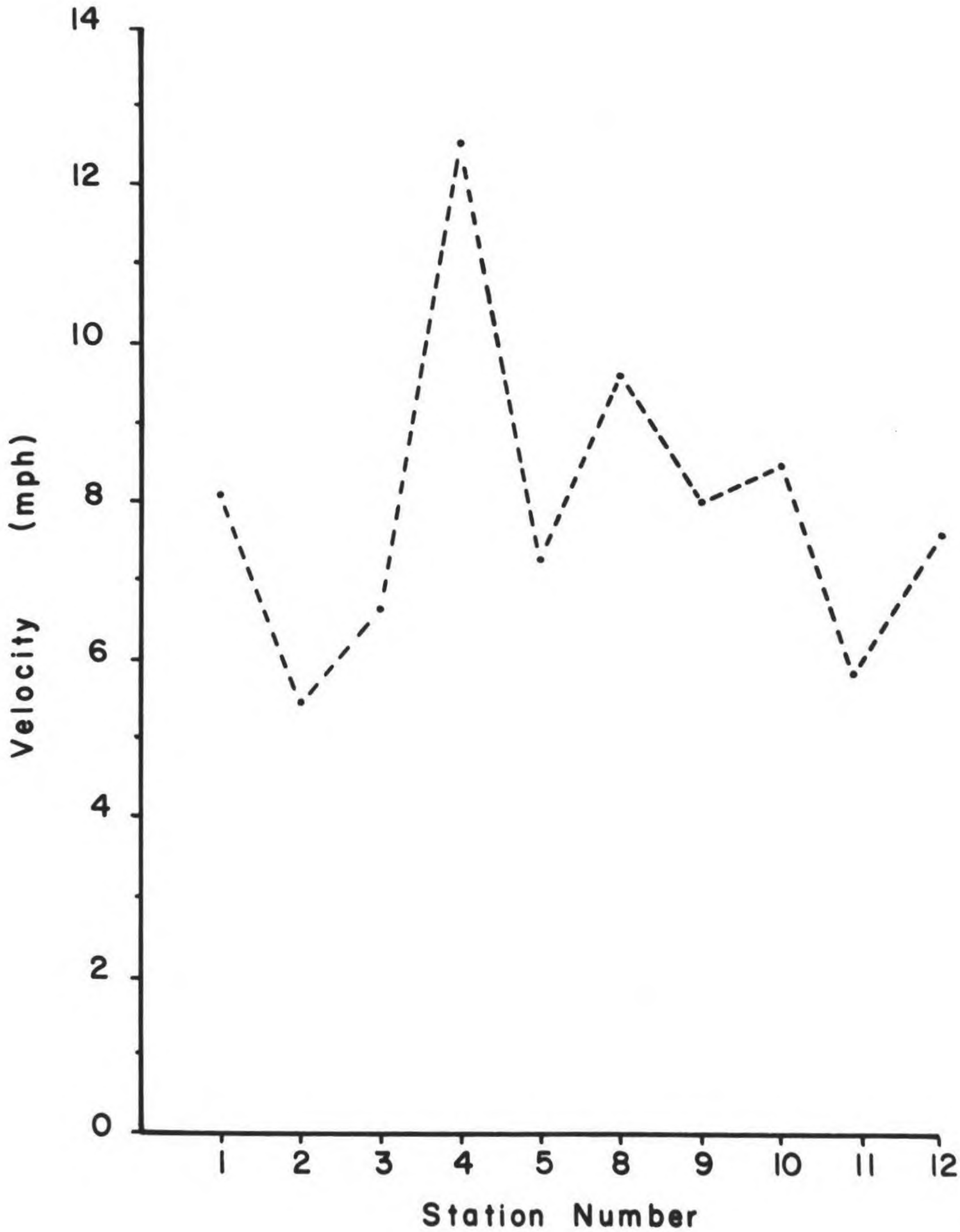

Fig. 6.--Average wind velocity breast height (June 27-September 19, 1960).

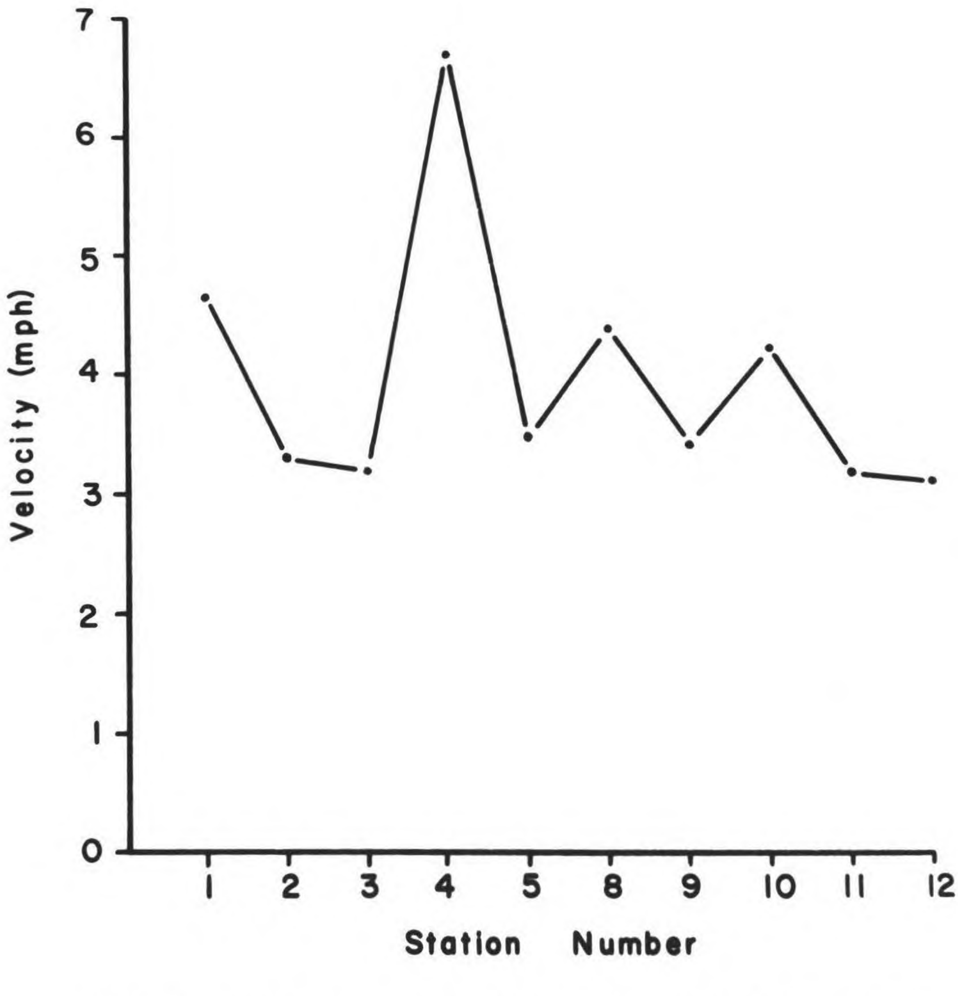

Fig. 7.--Average wind velocity at eight inches above ground level (June 5-September 19, 1961).

gauge. It was not uncommon to see the rain moving in a nearly horizontal plane at these stations on some of the more windy days.

Wind velocities between the two years cannot be critically compared because the readings were taken at different distances above the ground. In 1960 the wind meter was held at chest height and the velocity range over a two minute interval recorded. In 1961 it was held for a similar time period at about eight inches above the ground and the extremes of velocity as well as the direction were recorded. Although the difference in levels at which the records were taken voids any exact comparisons, the change to the eight inch level seemed necessary as it would allow a more accurate account of the velocities that the vegetation was subjected to. Stocker (Warren-Wilson, 1959) found that in alpine Lappland the winds speeds at 10 cm averaged only about 15 per cent of the speeds at 170 cm. Warren-Wilson (1959) and other investigators have substantiated these reductions in other arctic and alpine areas in subsequent investigations.

The general concensus of the people involved in the research program both summers is that there were many more days of high winds in 1960. Several times in 1960, particularly in the early part of June, gusts of 30 mph or higher were recorded. On June 15th, the indicator ball of the wind meter was blown into the top of the gauge and held there, although the meter records a maximum velocity of 70 mph. The highest recorded wind in 1961 was 20 mph at Station 1 on June 23rd. Figs. 6 and 7 show the differences in the average velocities for the two years, but it must be reemphasized that direct comparisons are not possible because of the discrepancies in heights between the two sets of readings.

In 1961 the wind was predominantly from the southwest, west or south. Wind direction was not recorded in 1960 but personal recollection, confirmed by other members of the unit, is that the patterns, particularly for the stronger winds, was very similar to that observed in 1961. Winds from the north and northeast were most frequently recorded at the lower stations early in the day. By early afternoon the winds at these lower stations were usually from the southwest.

The wind composite, Fig. 8, shows the relative wind values for the area in 1961. To arrive at a value that represented not only the velocity of the wind but also the direction, the average velocity of wind from a particular direction was multiplied by the number of occurrences in that direction. If all of the wind readings had been taken in the afternoon it is likely that the winds from the southwesterly directions would have been even further emphasized due to the shift from easterly and northeasterly winds to southwesterly winds at the lower stations as the day progressed.

The maximum and minimum temperatures are perhaps the best indicators of temperature for comparison of the two years; Fig. 9 indicates the average extremes recorded at Stations 4 and 12. The summer of 1960, in addition to being much drier, was somewhat warmer than that of 1961. In 1960 the mean maximum temperature was 18.4^{o}C and the mean minimum was 3.6^{o}C, whereas in 1961 the means were 17.6^{o} and 2.2^{o}C. The highest temperature recorded in 1960 was 25^{o}C on September 12th at Station 4. The lowest of the same year was 0^{o}C on June 21st at Station 4 and on June 24th at Station 12. In 1961 a high temperature of 21^{o}C was recorded on August 7th at Station 4 and at Station 12, and on August 10th at Station 12. The 1961 low was -5^{o}C on September 6th at both stations.

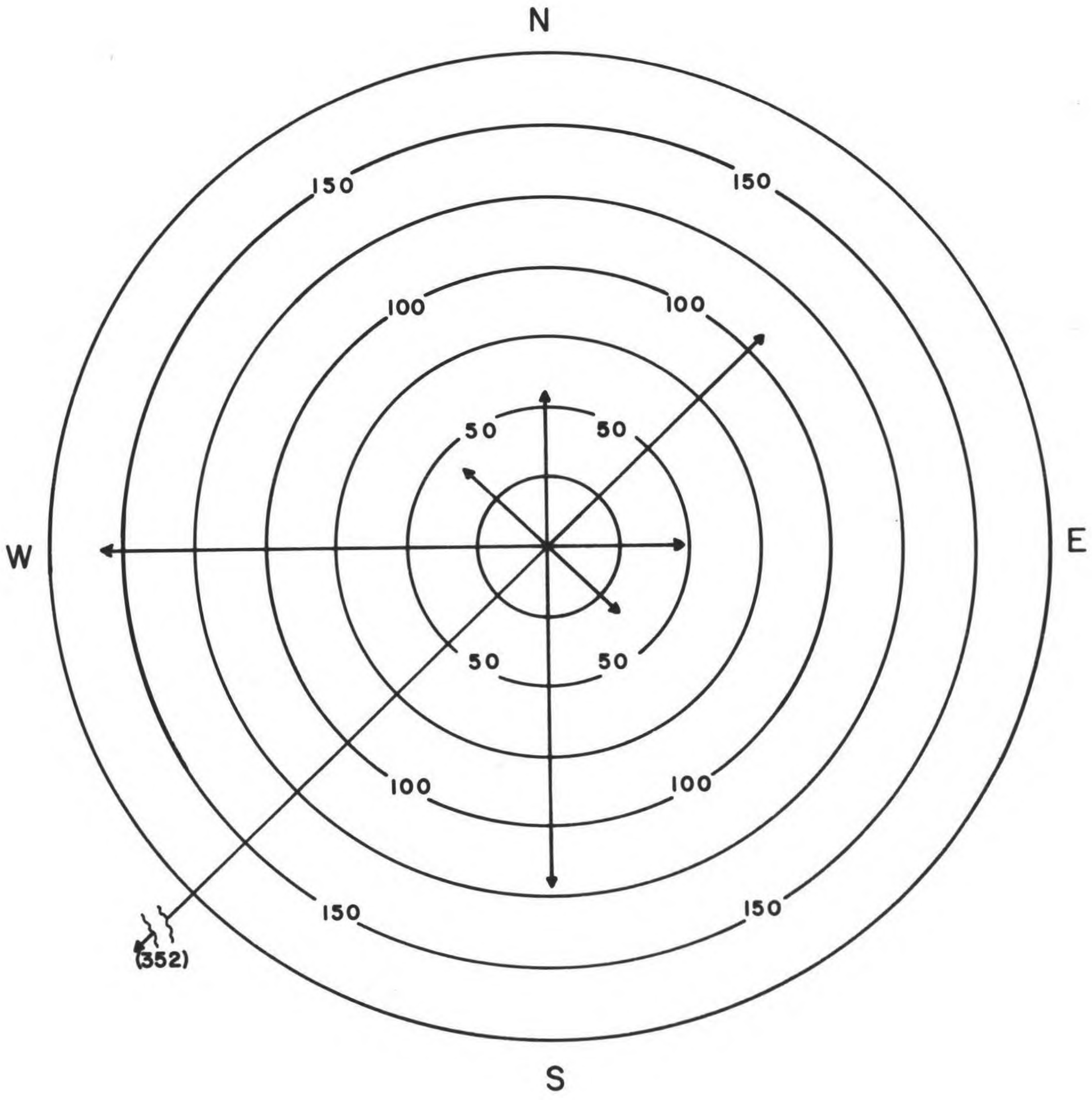

Fig. 8.--Composite of surface wind direction and velocity determined by multiplying the numver of times a wind occurred from a direction by the average velocity of the winds reached in that direction in 1961. (Arrows point into the wind.)

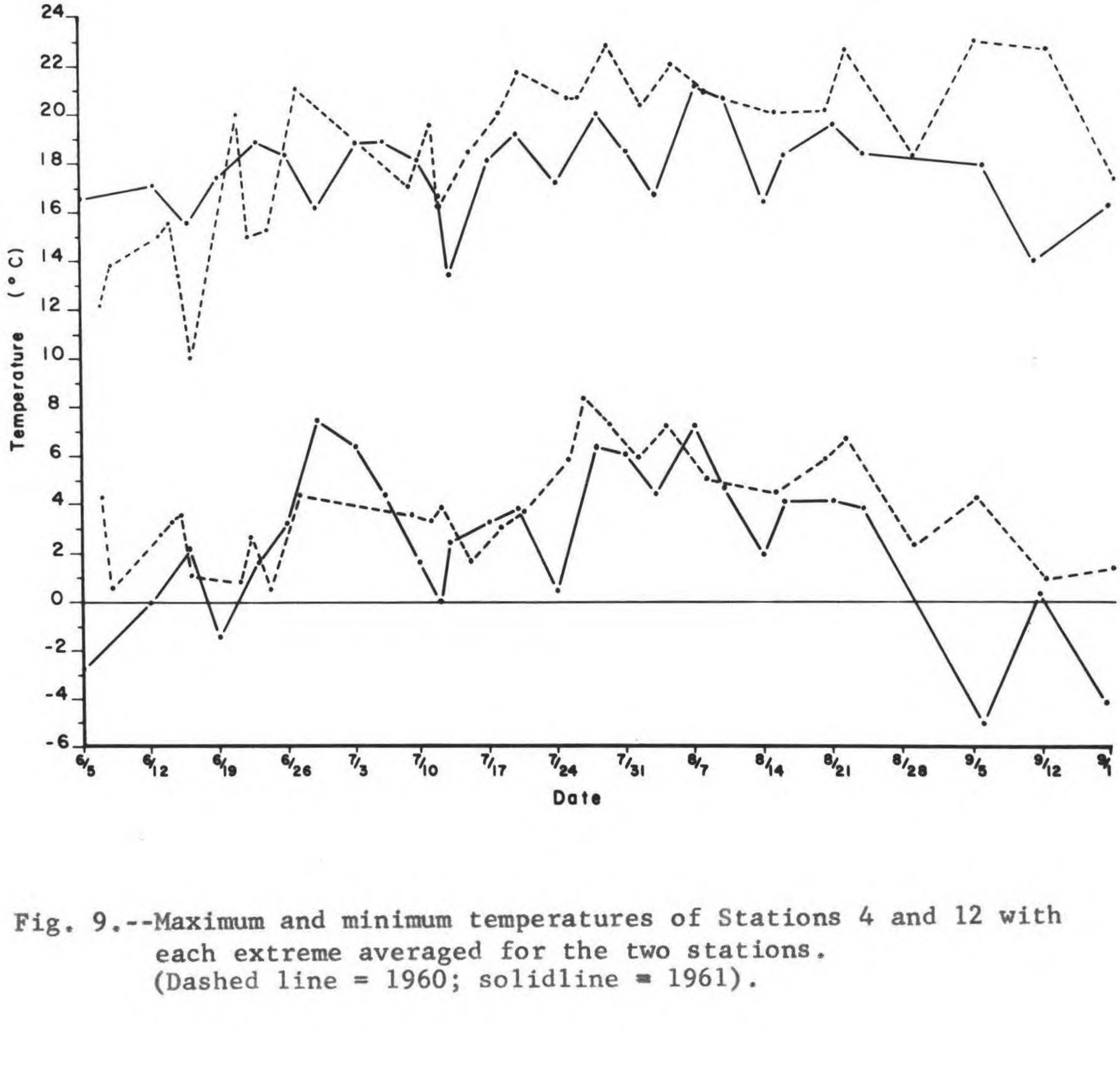

Fig. 9.--Maximum and minimum temperatures of Stations 4 and 12 with each extreme averaged for the two stations. (Dashed line = 1960; solidline = 1961).

There were no days in 1960 on which the average minimum temperature for the two stations was zero or below, while there were six such days in 1961.

The average vapor pressure deficits for 1960 and 1961 (Fig. 10) reflect the effects of the lower precipitation, higher temperatures, and higher winds that occurred in 1960. Evaporation losses from the soil, and transpiration losses from the vegetation must have been significantly greater in 1960 than in 1961. Cox (1933) found differences of 31 cc/day at the same station between a dry and a wet week.

The microclimate of snow accumulation areas differs substantially from that of snow-free stations. The soil moisture relationships and the early growing season soil temperatures differ greatly in the two sites and will be discussed in greater detail in the chapter on description of stations. It was estimated that the spring snow cover in the two years was quite comparable both as to depth and extent. However, the higher frequency of rains in 1961 seemed to have an accelerating effect on the melting of the snow, so that Stations 2, 11 and 12, areas of accumulation, were opened up about a week earlier than in 1960. The first fall snows in 1960 occurred sometime between visits of October 15th and the 31st. On the 31st the winter accumulation patterns were well defined, with the exposed ridges and leeward slopes displaying their typical winter characters. In 1961 the fall snows were considerably earlier, coming during the first week in September; on the 6th of that month much of the area was under the snow. By the 11th, however, most of the snow was gone except for residual amounts in some of the more protected pockets. On September 18th the area was virtually snow-free again, but on the October 15th visit the winter accumulation patterns were again present.

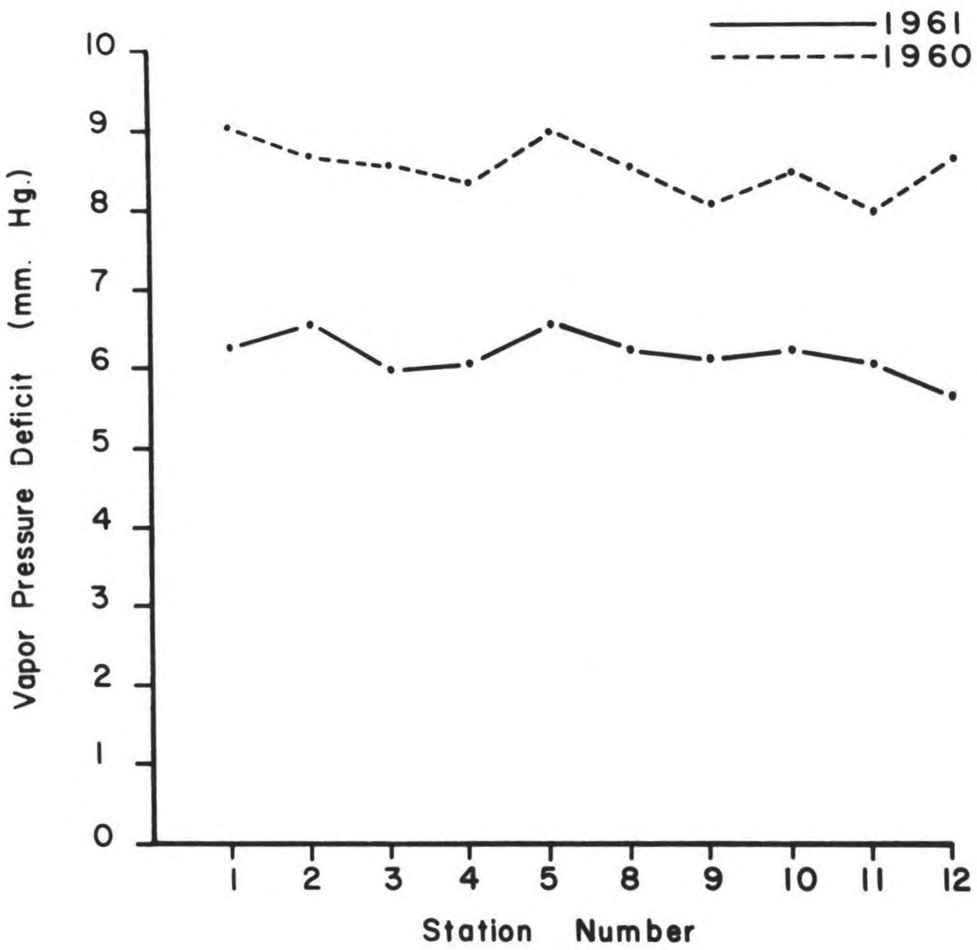

Fig. 10.--Average vapor pressure deficit (June 13-September 19).

REVIEW OF LITERATURE

The alpine tundra of the southern Rocky Mountains has been studied periodically by ecologists for at least 50 years, and has perhaps received more attention than similar vegetation in other areas of North America. Nevertheless, the number of ecological investigations is relatively few, particularly when compared to the number of studies of other major vegetation types such as the prairie or the deciduous forest. The tundra of the southern Rockies is still a substantial unknown.

Origin of Flora

Rydberg (1914), writing about the alpine of the Rocky Mountains, proposed that the flora had originated from several sources including circumpolar, American Arctic, and American endemic. Holm (1927) believed that there were four major sources of origin for the alpine flora -- alpine, endemic, arctic and circumpolar. Of the 170 vascular plants of the alpine tundra that he considered, 63 were classified as arctic in origin, 31 circumpolar, and nearly 100 endemic. For 28 of these species he also listed the probable geographic origins. Daubenmire (1943) considered only two basic origins, the alpine endemic and the arctic. A discussion of several circumpolar species, including the various locations where they may be found today, as well as the possible means of migration was presented by Bocher (1951).

Morphology

On this continent, Holm (1908, 1927) has probably contributed as much as anyone to our knowledge of alpine plant morphology. In the first paper, concerned with the Gramineae of the alpine, he concluded that none of the alpine species showed any distinct variations from the species of the lower elevations. In the later paper he discussed at some length the general morphology of many of the representative alpine species. The majority of forms are caespitose, forming dense mats or cushions; rosette types are the next most common. Vegetative reproduction was found to be mostly by means of over-wintering buds. The characteristic brilliance of the flowers was noted and the general predominance of the various colors listed. Leaves were found to be mostly glabrous and entire. No saprophytes, epiphytes, or climbers were found, and only one parasite, a green genus in the Scrophulariaceae, was noted. Root systems were described and a series of plates provided considerable detail concerning the general structure of many of the more common species.

Holch, et. al. (1941) presented a general account of the morphology of alpine species and gave detailed and illustrated accounts of the root systems of 34 common herbaceous forbs. He noted that nearly all species were perennials, and exhibited a low growth form. The leaves were found to have an extremely thick cuticle to which he assigned dual functions. First, it protected the plant against water loss by evaporation, and second, it protected the chlorophyll from light breakdown by reducing the intensities reaching the palisade layer. The root systems of plants in protected and exposed sites, as well as in dry and wet habitats, were examined. On the average, the root system comprised about 72 per cent of the total length of the plants; moreover, they were quite shallow in distribution, often being confined to the upper three to six inches of soil. Rhizomes were the most common type of underground system encountered; they perhaps provide the best method of propagation and food storage in the severe alpine environment. A short taproot was found to be the most common root type, while fibrous roots were almost entirely lacking.

Daubenmire (1941) presented descriptions and drawings of the root systems of 24 of the more common alpine species of Colorado. Of these, 20 appeared to reproduce by seed rather than vegetatively, 16 had their shoots proliferated at or near the ground resulting in mat-like or cushion-like plants, and 6 had well developed underground storage organs. No strikingly uniform subterranean adaptations to the alpine environment were found. The average depth of the roots was 25 cm, with a range of 9 to 55 cm.

Bonnier (1895) was perhaps the first to propose an explanation for the dwarfing of the alpine flora. His theory was based on the belief that the higher light intensities found in the alpine, in conjunction with the drier air and lower temperatures, were responsible for the stunting of the vegetation. Clements, Martin and Long (1950) questioned the accuracy of Bonnier's measurements, and concluded instead that the water content of the soil was of first importance in dwarfism. In those cases where water was not a factor, the length of the growing season appeared to assume the major influence.

Wager (1938) stated that dwarfing in arctic species was due primarily to low temperatures and low carbohydrate production rather than to low water or mineral content. Daubenmire (1954) proposed a heat budget theory that offers an explanation for the phenomenon of timberline, and at the same time indirectly explains why the low growth form would be most efficient in the severe alpine environment. A study involving the effects of wind on arctic-alpine vegetation by Warren-Wilson (1959) appears to offer possible support to the low temperature theory of dwarfism. The report does not attempt to offer an explanation for the dwarfness of the flora, but rather attempts to explain why only plants with a low growth form may survive in an arctic or alpine environment. He points out that the alpine vegetation is already near the critical point of seed plant survival, and that the lower temperatures encountered only slightly above the ground level might be sufficient to prohibit growth.

In all probability, it may never be established that any one factor is responsible for the dwarfing of alpine vegetation, but rather that the condition is an adaptive response to the entire environmental complex. Billings (1952) points this out in his statement, "Any study of plant growth and distribution in relation to environment must consider each factor in relation to the others of the complex."

Phenology

There are very few studies related to the phenology of apline species in the southern Rocky Mountains. Cox (1933), although not concerned directly with phenology, presented some indication of flowering aspects in the various habitats of the James Peak area. Hayward (1952), in the Uinta Mountains of Utah, found the biotic activity to start around the middle of June, and to reach the peak generally by the middle of July. In the Medicine Bow Mountains of Wyoming, Bliss (1952) observed that the peak of flowering occurred from sometime before June 22nd, the date on which he initiated the study, through the first week in July. He stated that generally the phenological events took place first on the south-facing slopes, one to two days later on the ridges, with an additional one to two day delay on north slopes. Wet meadows were three to seven days behind the south-facing slopes largely as the result of late-lying snow.

In a more specific study in the same area, Billings and Bliss (1959) studied the effects of snowbank environment on alpine vegetation. A comparison of the lengths of the phenological phases for Geum turbinatum as affected by snow release dates was made, and there was some indication that a compression of some phases occurs as the release dates become progressively later.

Mooney and Billings (1961) have studied the physiological and morphological variations in Oxyria digyna, both in the field and in the laboratory, with collections from Alaska to the southern part of the Colorado Rockies. Representatives from different latitudes had different phenological responses which were primarily influenced by photoperiod.

Phytosociology

The phytosociology of the tundra has received a considerable amount of attention. The emphasis has been mostly on descriptive accounts of the physical habitats and the competitive and successional sequences encountered in these various habitats.

Cooper (1908), in his study in the vicinity of Long's Peak, Colorado, was probably the first to describe community structure for the tundra of the Colorado Rockies. Based on the moisture content of the soil, the tundra was divided into two major types. The first, Dry Meadow, he subdivided into four minor classifications depending upon the size of the rock fragments in the soil. The second category, Wet Meadow, was not further subdivided.

Clements (1920) listed 62 dominant species for the Petran Alpine Meadow Association as represented in the Colorado Rockies. Of these, 30 were sedges, 23 were grasses, and 8 were rushes. He further listed 80 societies of which 29 are endemic, 32 are also represented in the Pacific Association, 32 are found in the American Arctic, and 32 occur in Eurasia. Clements points out that the identity in number in the last three is merely coincidence, for the species are not the same throughout.

A most intensive and useful description of the alpine and its characteristics was given by Cox (1933). He likewise divided the alpine into two major categories, the alpine desert and the alpine grassland. The alpine desert is subdivided into three types based on the size of the rock fragments and the degree of slope; these are the boulder field, the fellfield, and the talus slide. The alpine grassland consists of six sub-groups based primarily on the amount of moisture available to the sites. These are the alpine scrub, snow-flush association, wet meadow association, mesophytic meadow association, dry meadow association and the climax alpine meadow. The species common to each of these different associations are listed, and their relative importance given.

Daubenmire (1943) described the boulder fields, fellfields, and alpine meadow of the tundra and listed the species characteristic of each. In a study which considered the alpine from an economic standpoint, Schwan and Costello (1951) provided a general description of the alpine associations of Colorado.

A recent analysis of the communities or associations of the alpine of Colorado is presented by Marr (1961). He described nine of the more conspicuous stand types and listed the species common to each. Proposed were the Kobresia Meadow, Hairgrass, Parry's Clover, Adoneus

Buttercup, Snowbank Complex, Cushion Plant, Dryas, Sedge-Grass Wet Meadow, and Willow-Sedge Hummock stand types.

Essentially the study of alpine tundra has been approached on the basis of a community concept. Ward (1961), however, presented evidence to show that the structure of alpine vegetation is not one of community delineation, but rather is a continuum.

Perhaps the stands in which Kobresia bellardi is a major component have received the most attention in recent Colorado alpine studies. This species is thought by some to be the climax dominant over much of the alpine region of the state (Cox, 1933; Osburn, 1958; Willard, 1958; Marr, 1961). Osburn (1958) described the Kobresia bellardi meadow ecosystem in the Front Range of Colorado, and Willard (1958) evaluated the role of Kobresia bellardi in the Rocky Mountain alpine, Lappland, and in the European Alps. In the latter two areas the species is considered to be an important constituent of the sub-climax vegetation.

Outside of Colorado, studies of the alpine tundra of North America have been few. Hayward (1952), in a discussion of the community types of the Uinta Mountains of Utah, divided the area into the wet meadow, dry meadow, sub-climax, and climax portions. He presented a species list numbering 127, with indication as to occurrence in the American Arctic, Canadian Rockies, and the Colorado Rockies. All but nine of the species found in the Uintas had been listed either by Cox (1933) or Holms (1927) for Colorado. Kobresia bellardi is mentioned in the species list, but is not listed as a dominant feature of any of the proposed community types for the Uintas. The alpine of San Francisco Mountain in Arizona was divided into the alpine rock field and the alpine meadow by Little (1941). Of particular interest in this study is the fact that Kobresia bellardi was not listed as present. Cain (1943) did not encounter Kobresia during his study in the Medicine Bow Mountains in Wyoming, an area of even closer proximity to tundra areas in Colorado.

Succession

In a study concerned with competition and succession in the Colorado Rockies, Griggs (1956) established an invasion order for 36 species associated with a fellfield. Careful observations allowed him to determine which species were the first to invade a barren area, then by continued observations he was able to detect which species would invade the pioneers and in turn be invaded by others. With these data in mind, he proposed a "tentative" competitive ladder for all the species involved. Further checking of these species in different locations indicated that the trend of succession was always in the same direction. In his sequence the typical cushion plants were the early invaders, with the erect stalked types appearing last.

Cooper's (1908) study, while not primarily concerned with succession, described successional trends in wet meadow areas. He stated that succession was from two directions, with the mesophytic forms moving up into the meadow from below, and the xerophytic forms moving down into the meadow from above. He felt that the mesophytic rather than the xerophytic forms were to play a more important role in the final climax vegetation. Cox (1933) described the successional patterns that might be expected in each of his meadow types which lead ultimately to the Kobresia climax. In wetter areas the accumulation of litter and organic matter tends to gradually lift the ground surface higher above the water table causing more mesic conditions which are suitable to the Kobresia. At the other extreme, the accumulation of litter and soil in the xeric meadows allows greater water retention and provides more mesic conditions suitable to the Kobresia climax.

METHODS AND MATERIALS

In order that the progression of phenological events might be followed in a number of habitats, ten primary stations were selected early in the growing season of 1960. A substantial variation in such things as elevation, slope direction and inclination, length of the snow-free period, vegetational composition and cover was sought in the choice of these. The direction and degree of slope of each of these stations was found by the use of a Brunton compass. Altitudes were determined by averaging the readings obtained by carrying a calibrated altimeter into the field on several clear days. In addition, the frequency and cover of the vegetation at each station, with the exception of Station 9, was also determined. In 1961 two additional stations were established. The first was chosen to allow observations on the effects of surface melt-water on phenological progression. The second was located in a snow accumulation area, and was studied to provide a measure of the effects of retreating and late lying snow on phenological progression and vegetational composition. Although the majority of the research was carried out at these project stations, comparative observations of a general nature were made throughout the study area as well as at other more remote alpine areas.

Phenological Studies

To facilitate the locating of a sizable number of plants for periodic observations, ten quadrats, 25 cm on a side, were laid out at each station, with the exception of the late snow station (Station 16) where seven groups of ten quadrats each were established. The quadrats, again with the exception of Station 16, were located in a subjective manner. In the selection of a quadrat an effort was made to include at least two of the species which appeared characteristic of the vegetational dominants of the station. The remaining species considered in the quadrats were merely chance inclusions. In Station 16 the quadrats were located at various intervals along one side of the retreating snow at a distance of approximately one foot onto the snow. This effectively eliminated any selectivity of species to be included in the quadrats.

Each quadrat was marked by two galvanized wire pegs placed at opposite corners. One peg was fitted with a numbered, metal identification tag and a strip of brightly colored surveyor's flagging tape (Fig. 11). The 25 cm square quadrat size was found to be sufficient to include a number of individuals and at the same time was small enough to facilitate accurate and rapid examination. The phenology of an average of between seven and eight species per quadrat was followed throughout the two growing seasons in the original ten stations. In the melt-water and snow accumulation stations data were obtained for the 1961 season only.

At the time of each weekly reading a 25 cm square quadrat frame was placed in position by means of the corner wire pegs. The frame was constructed from medium gauge welding stock, which has the advantages of strength, rigidity and light weight.

Fig. 11.--Photo illustrating quadrat frame, locating pins, flagging and metal identification tag.

The stages of plant development are merging phenomena, but there are certain reasonably distinct phases that can be meaningfully described and used as reference points in the analysis of time-environment relationships. The phases used in this study and the interpretation given them are as follows:

Vegetative.--Plants in a green state with no external evidence of a flower bud. Some of the species were already in this condition when exposed by the receding snow, thus for these the date of first appearance from under the snow was recorded. Many others were already snow free and green when the area was first visited in May. For these the date that the quadrats were first read was noted. Finally, for those species that began new growth from beneath the ground, the time of emergence was considered to be the beginning of the vegetative condition.

Appearance of flower bud.--Visible to the naked eye.

Flower maturation.--The first appearance of a completely expanded flower.

Fruiting.--The time of first visible enlargement of the ovary or the time that the flower first showed signs of shedding or shrivelling of perianth parts.

Dispersal.--The earliest date upon which the plant dispersed some of its seed or fruits (e.g., the pods of _Trifolium parryi_).

Beginning of dormancy.--The time at which a species first exhibited any systemic signs of fall color change, usually browning, of the vegetative portions of the plant.

Dormancy.--This term applied when all of the representatives of a given species within a given quadrat were virtually devoid of green coloration. The quadrats were visited at weekly intervals, at which time the most advanced state of any individual representing the species under consideration was recorded for that species. Inspection was also made for newly appearing individuals that might be added to the study list. Often the new shoots were too small to allow identification, in which case the shoot was marked by a colored toothpick and so noted on the data form. Later development usually revealed the species identity. When field identification was not possible, a representative of the same species was collected outside the quadrat for determination.

At the end of each season the data were analyzed to determine the extreme dates for each of the phenological phases within each of the stations. The data from each station and for each year were then compared for indications of significant time differences that might be related to environmental differences between stations and between years.

In an effort to obtain some idea of the degree of phenological correspondence of the small quadrats and the overall station area, general observations of the aspect were made each week.

Melt-water Investigation

To determine the effects of prolonged surface melt-water on phenological development, irrigation water was applied to a portion of a small area of homogeneous vegetation in close proximity to the principal springtime drainage stream that flows through the lower part of the general study area.

A dam was constructed at a point a short distance above the experiment site, using a heavy gauge, flexible sheet plastic of the type used in standard irrigation practices. One end of a fifty foot garden hose was placed under the dam and extended up into the pool of water.

A coarse screen filter was fitted around the end to prevent larger pieces of debris from entering and clogging the hose. A 25 foot length of canvas soaker was attached to the other end. The hose was placed down along the margin of the upper portion of the area, and then the soaker was laid at right angles to the slope at about the midway point of the area. Small slits were made in the soaker just above the location of the quadrats so that the maximum amount of water would flow directly over the quadrat area. Even with the screen filter, the soaker holes had to be cleaned and the soaker flushed several times a week. The quadrats were examined twice a week until the water in the stream ceased to flow. From that point on they were read once a week throughout the remainder of the season.

Snow Retreat Investigation

To study the response to progressively later lying snow, the most persistent snow accumulation pocket in the general study area was selected for individual study. For this, a series of seven groups of ten quadrats each were set out at various intervals along the eastern periphery of the snow area. To determine the location of the quadrats the frame was thrown at intervals about one foot in from the edge of the snow. Two wire pegs were driven down through the snow into the ground at opposite corners of the quadrat frame, and the quadrats were first read for species presence on the day that they appeared from under the snow. The first group was set out on July 5th and was read two days later. As the rate of snow retreat differed from day to day, the time interval between the establishment and reading of new quadrat groups became a function of the melting rate of the snow. The snow was allowed to retreat from between five to ten feet between the establishment of successive quadrat groups. This was done to allow maximum coverage of the area with a reasonable number of quadrats.

Differences in the rate of phenological progression for the same species were looked for as well as changes in the general vegetational composition from the outside to the center of the snow area.

Vegetational Analysis

The vegetation at each station, with the exception of Station 9, a thick willow-scrub area, was sampled systematically for frequency and cover by means of 50 quadrats 20 cm on a side. This size quadrat was deemed suitable because it resulted in maximum frequencies of around 90 per cent, and the number of quadrats is believed to provide accurate information, particularly for the most important species.

Cover was interpreted to be the percentage of the quadrat that would be compactly filled by the vegetation present. In an effort to increase the accuracy of the estimate, two smaller quadrats were employed in conjunction with the 20 cm square one. These were equal to one-fourth and one-sixteenth of the area of the main quadrat. The smaller quadrats were placed over clumps and the leaves lifted vertically. An estimate was then made as to how many of the smaller quadrats were completely filled. These were then summed to provide a total per cent cover for the 20 cm square quadrat. In addition to the total cover, the species that constituted the major portion of that cover and their per cents were also estimated and recorded for each quadrat.

Community association indices were computed for all of the primary phenology stations, except Station 9, by combining the frequency and the species cover data. The formula used in these computations was presented by Kulczinski (1927). In this, Association Index = 2W/a = b; "W" is equal to the sum of the least frequency or species cover value of those species common to the two stations being compared, "a" represents the total frequency or species cover value for the first station, and "b" a similar value for the second station. For this evaluation, Kulczynski's index was determined using first the frequency and then the cover values. The results were averaged to represent the index value for two stations. These data provided an indication of the relative affinity or dissimilarity of the vegetation at the phenology stations.

Soil Studies

Soil cores were taken by a standard coring tool at each of the ten phenological stations established in 1960. Ten corings were taken at each station, the locations of which were determined by objective tossing of the tool. Since the agreement with the Rocky Mountain National Park officials was to disturb the area as little as possible, this method of soil sampling was chosen in lieu of the usual cut profiles.

Where sufficient depths were attained, a striking transition zone from dark to light soil was noted. The latter was apparently very low in humus and for discussion purposes was designated as mineral soil as opposed to the term humus-soil which was assigned to the upper, darker brown soil. The average depth of each soil phase, and the total soil depths were found for each station.

Relative soil moisture and soil temperatures were obtained through the periodic reading of Colman Units buried at 15 cm at each station. These wafer-like units are fiberglass, monel-metal strips containing a thermistor. The conductivity of the wafer portion varies with changes in soil moisture, and thus the amount of current recorded on the battery operated, alternating-current microammeter is indicative of the moisture conditions in the soil. The thermistor portion permits soil temperature measurements by which resistance can be converted to temperature (Colman, 1947). Determinations of field soil moisture were made periodically by others in the research team. Plugs of soil were taken by use of the soil corer and immediately sealed in plastic bags. Upon return to Pingree Park the wet weights were determined, and after drying for at least 24 hours at 105°C, the dry weight was found. Field moisture as a per cent of dry weight was then computed. Later the soils were pulverized and the volumes computed. Weight to volume ratios were determined and these values were multiplied by the per cent dry weight figures to give a relative indication of the soil moisture/unit volume for each of the stations.

DESCRIPTION OF STATIONS

The locations of all stations pertaining to this study are shown in Fig. 12. Data concerning the physical characteristics of the ten primary phenology stations are summarized in Table I, and the most important species based on frequency and cover values are listed in Table II. The stations represent an elevational range of from 3,208 m (10, 600 feet), at Station 1, to 3,390 m (11,200 feet), at Station 11. They were chosen to provide a wide array of exposures, slopes, snow conditions and vegetative cover.

The depth of the soil in the ten primary stations varied considerably. The shallowest soil encountered was in the bare terraces at Station 2. Here the humus was only superficial, but the mineral soil beneath was as deep as 30 cm. Beneath the vegetation at Station 2 the incorporated humus layer was considerably deeper. The deepest soil was at Station 11, where the depths frequently exceeded 50.8 cm (the length of the soil coring tool).

Soil temperature data derived from Colman Units are independent of soil characteristics and are, therefore, considered to give reliable indications of the temperature regimes of the stations. The average temperatures at 15 cm depth, as well as the seasonal trends at stations chosen to represent the main habitat types (dry, mesic, wet, and bog) are presented in Figs. 13, 14 and 15. The patterns for the

Fig. 12.--Aerial photo of study area in early spring showing location of study stations. (Photo courtesy of F. B. Salisbury.)

Table I.--PHYSICAL CHARACTERISTICS OF THE PRIMARY PHENOLOGY STATIONS.

Station	Elevation	Exposure	Slope	Average depth of top-soil	Relative soil moisture and temperature condition	Approximate time of snow departure
1	3,208 m (10,590 ft)	S85°E	15°	10-22 cm	Dry and cool	Mostly winter free
2	3,223 m (10,650 ft)	N75°E	14°	2-17 cm	Moist and cool	Mid-June
3	3,268 m (10,800 ft)	N41°E	15°	9-25 cm	Dry and warm	Early May
4	3,299 m (10,900 ft)	W	12°	14-34 cm	Dry, mod. warm	Mostly winter free
5	3,344 m (11,050 ft)	N35°E	9°	5-10 cm	Mod. moist, warm	Late May, early June
8	3,367 m (11,125 ft)	None	Level	15-20 cm	Moist, mod. warm	Late May, early June
9	3,367 m (11,125 ft)	None	Level	12-20 cm	Wet and cool	Late May, early June
10	3,382 m (11,175 ft)	S	13°	8-15 cm	Dry and warm	Mostly winter free
11	3,390 m (11,200 ft)	S60°E	8	25-50+ cm	Wet, mod. warm	Mid-June
12	3,375 m (11,150 ft)	S45°E	16	20-40 cm	Moist and warm	Mid-June

Table II.--VEGETATIONAL CHARACTERISTICS OF THE PRIMARY PHENOLOGY STATIONS.

Station	Species with highest frequency per cents	Per cent	Species with highest cover per cents	Per cent	Per cent total cover
	Campanula rotundifolia	50	Trifolium dasyphyllum	4	
1	Sedum stenopetalum	38	Arenaria obtusiloba	4	20
	Trifolium dasyphyllum	36	Phlox caespitosa	2	
	Vaccinium caespitosum	86	Vaccinium caespitosum	11	
2	Danthonia intermedia	78	Geum turbinatum	3	22
	Artemisia norvegica	38	Danthonia intermedia	1	
	Trifolium dasyphyllum	81	Trifolium dasyphyllum	8	
3	Potentilla diversifolia	52	Arenaria obtusiloba	5	26
	Sedum stenopetalum	43	Geum turbinatum	5	
	Trifolium dasyphyllum	85	Trifolium dasyphyllum	11	
4	Arenaria obtusiloba	63	Arenaria obtusiloba	6	36
	Artemisia scopulorum	62	Geum turbinatum	6	
	Dryas octopetala	54	Dryas octopetala	14	
5	Carex elynoides	52	Arenaria fendleri	1	21
	Arenaria obtusiloba	34	Arenaria obtusiloba	1	
	Geum turbinatum	86	Geum turbinatum	10	
8	Festuca ovina	76	Festuca ovina	5	41
	Polygonum bistortoides	66	Trifolium dasyphyllum	5	
	Trifolium dasyphyllum	82	Trifolium dasyphyllum	19	
10	Oreoxis alpina	60	Oreoxis alpina	4	37
	Carex drummondiana	50	Poa rupicola	2	
	Polygonum bistortoides	90	Deschampsia caespitosa	24	
11	Deschampsia caespitosa	90	Geum turbinatum	11	45
	Geum turbinatum	74	Sibbaldia procumbens	3	
	Geum turbinatum	70	Deschampsia caespitosa	19	
12	Deschampsia caespitosa	66	Artemisia norvegica	4	31
	Polygonum bistortoides	44	Geum turbinatum	2	

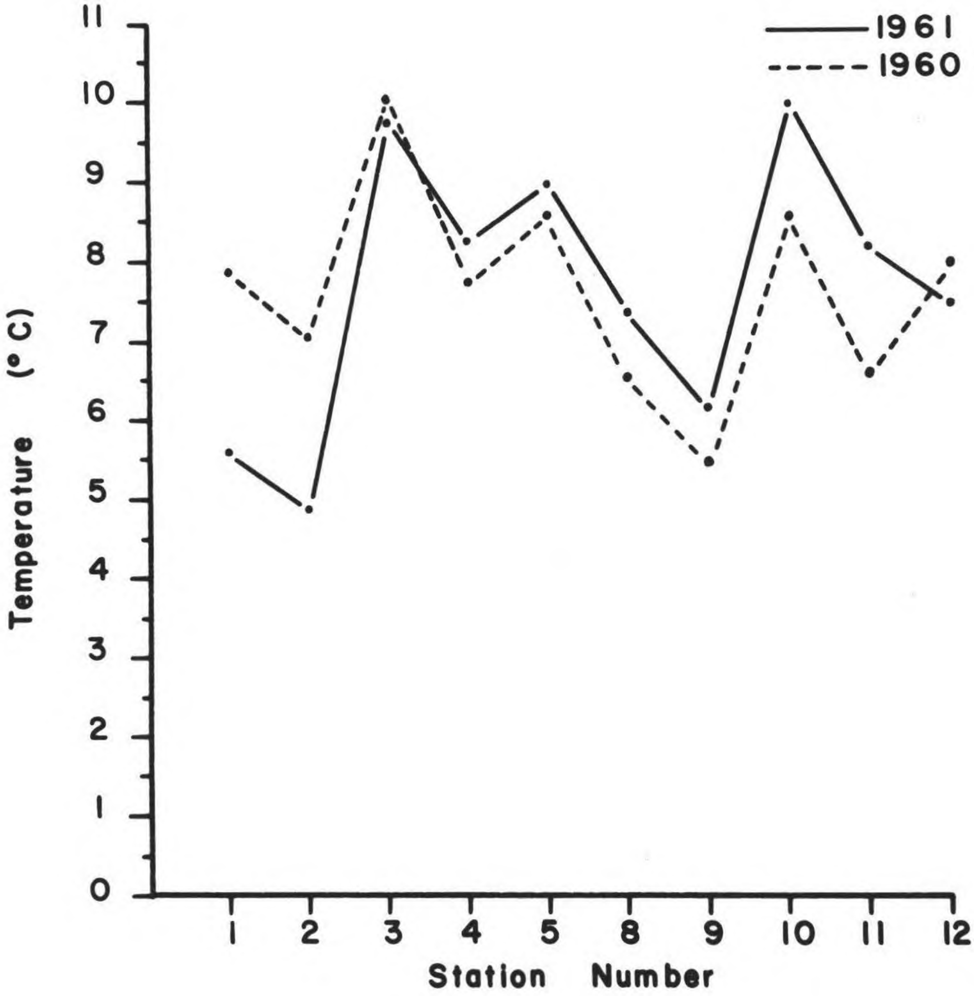

Fig. 13.--Average soil temperatures at 15 cm depth (June 22 - September 19).

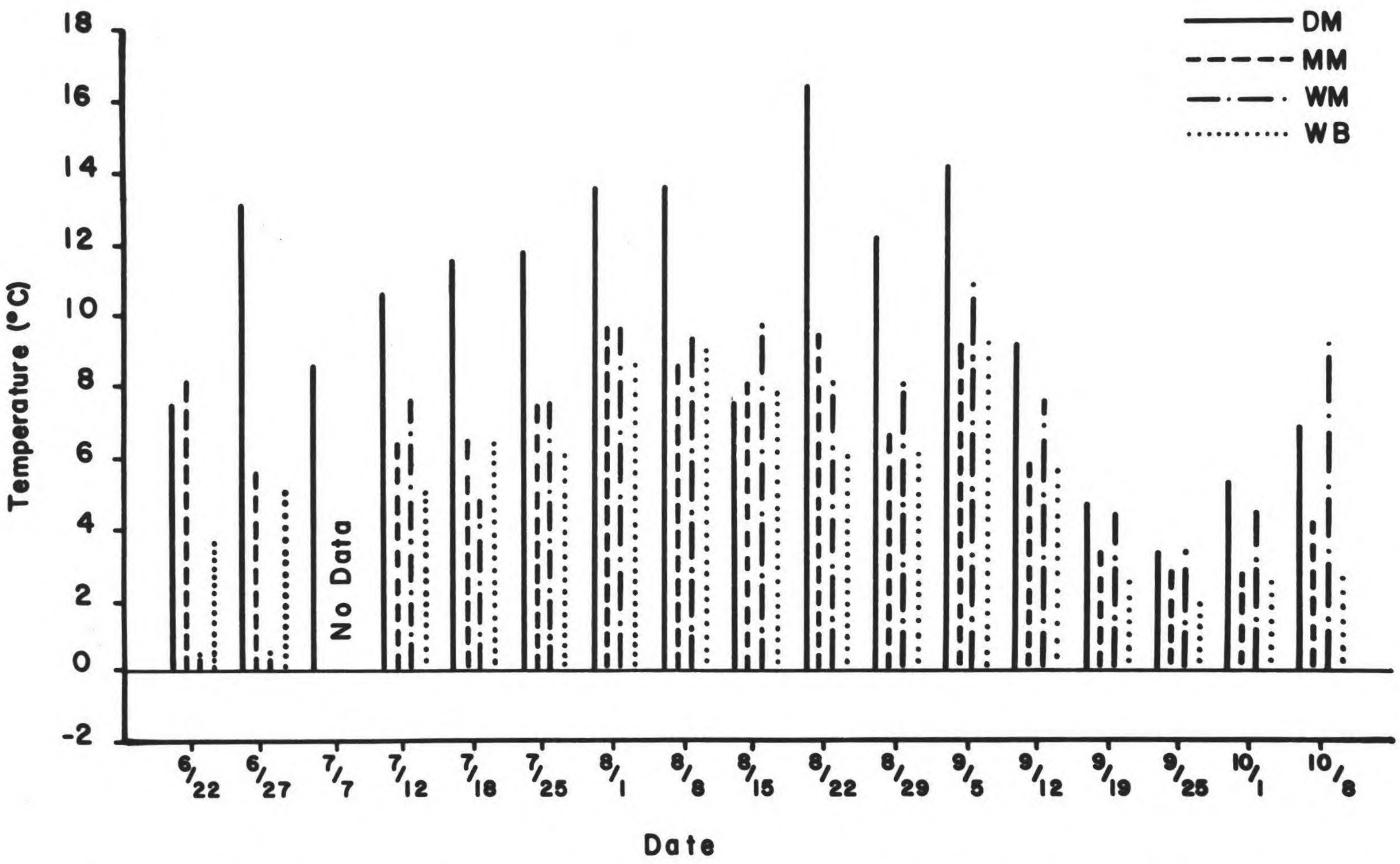

Fig. 14.--A comparison of the 1960 soil temperatures in stations representing the dry meadow, mesic meadow, wet meadow and willow bog station groups (15 cm depth).

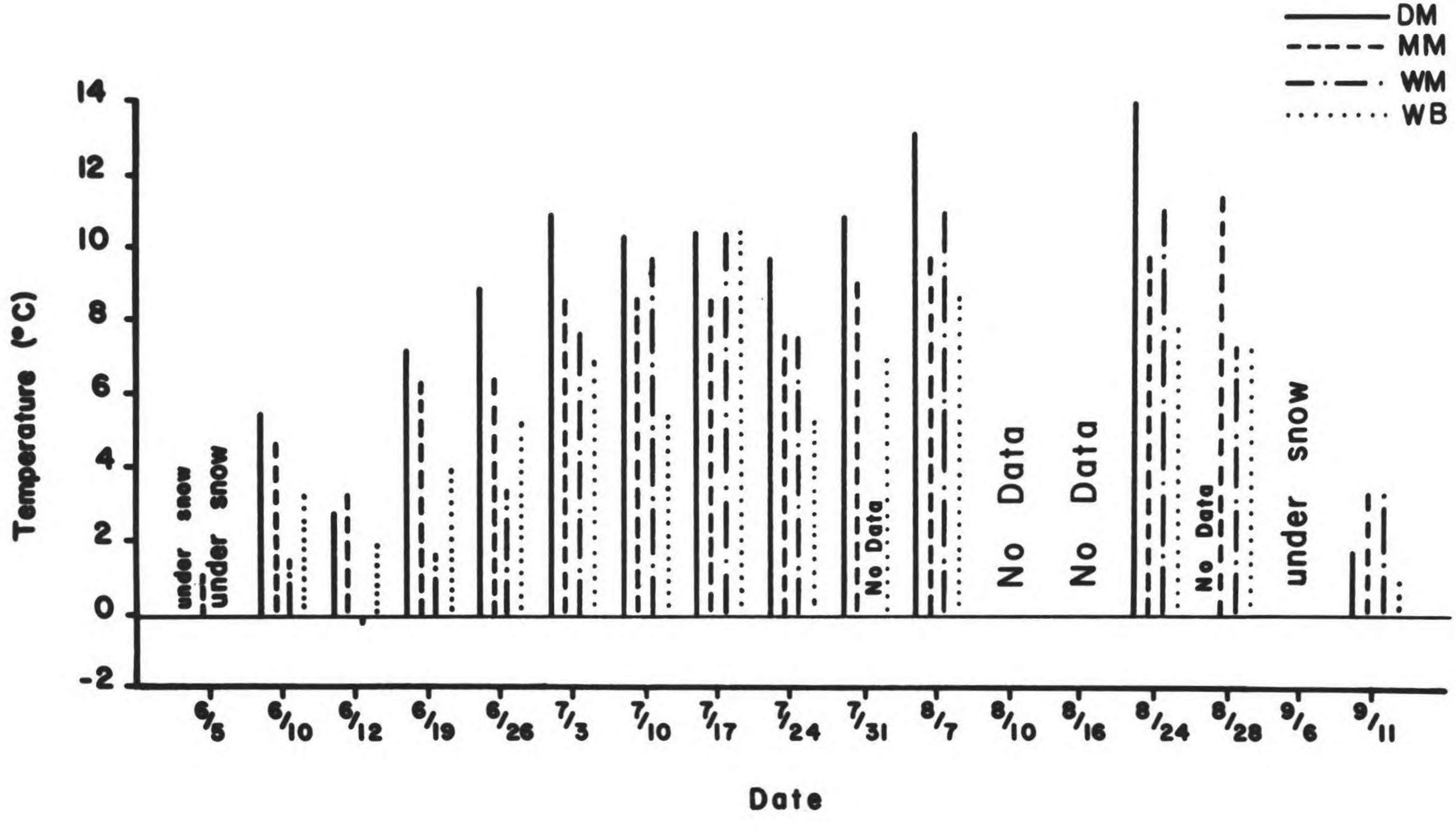

Fig. 15.--A comparison of the 1961 soil temperatures in stations representing the dry meadow, mesic meadow, wet meadow and willow bog station groups (15 cm depth).

two seasons were quite similar, although the general trend was toward cooler temperatures in 1961. The maximum-minimum air temperatures (Fig. 9) of the two years indicate a similar trend.

Variations in soil temperature were most pronounced at the drier stations, especially in the latter part of the growing season. Wetter stations showed temperature depressions during cooler periods, but the deviation from the mean was not so great as in the drier stations.

The measurement of amounts of soil moisture with Colman Units is dependent upon the physical characteristics of the soil as well as the amount of water present in the soil. Therefore, to obtain valid indications each unit must be calibrated to the soil type in which it is used, a process which is difficult and which time did not permit. More important ecologically is the moisture tension, the tenacity with which water is held by capillary and other forces in the soil. The relationship of Colman readings to moisture tension is now being studied in the laboratory by another member of the research group, and it appears that the units may be reliable indicators of this soil property.

The Colman moisture record for the first two years (Fig. 16) is of uncertain value, however, in view of some inconsistencies between it and other evidence. The extreme flattening of the curve in 1961 seems highly suspect since stations that were obviously soggy underfoot for much of the season were indicated to be only slightly more moist or even drier than stations with no free water. There is little agreement between the 1961 Colman Unit record and the direct measurements

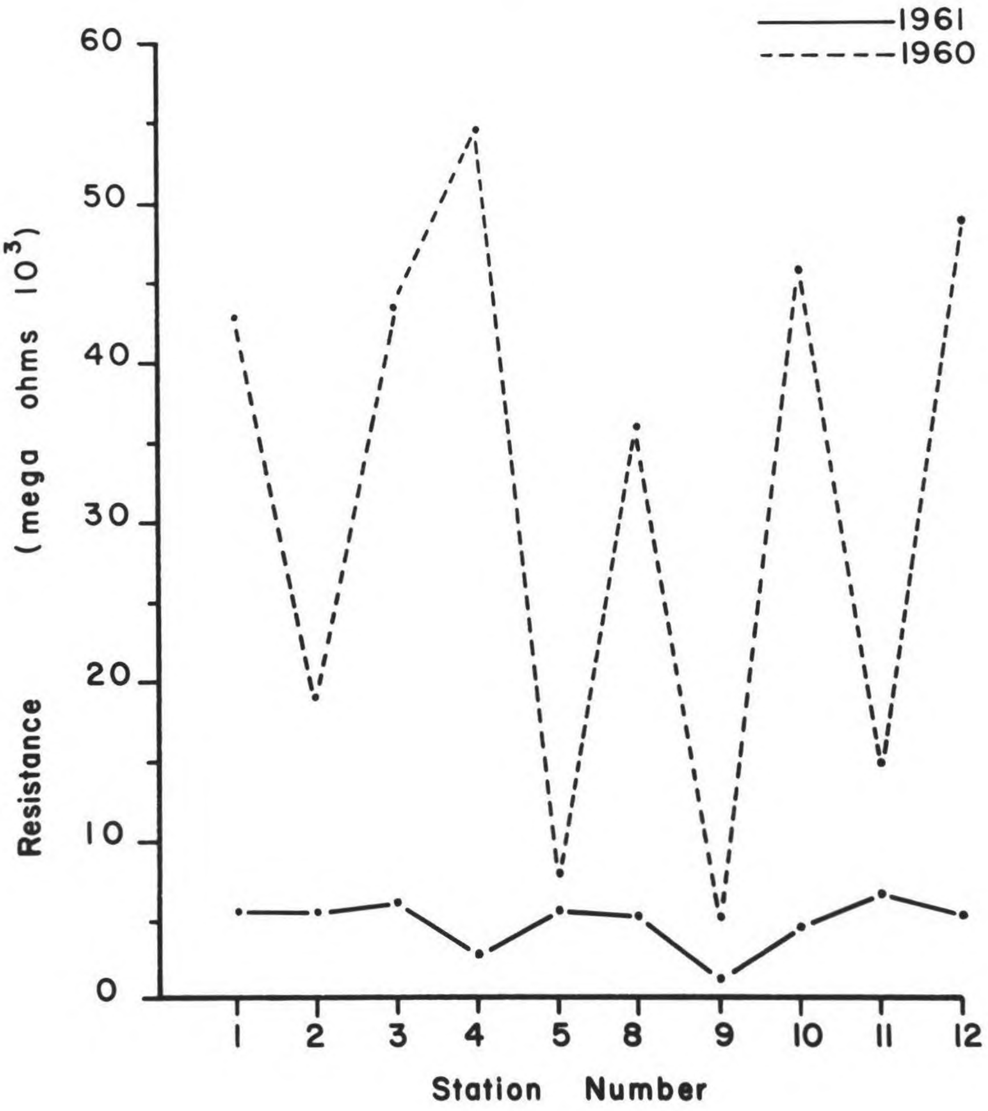

Fig. 16.--Average soil moisture as determined by Colman Units at 15 cm depth (June 22-September 19).

of field moisture (Fig. 17) in the same year, but the correspondence of station relationships is good when the comparison is made with the record of 1960. Obviously the available data do not allow any final conclusions as to the soil moisture regimes. The inferences drawn for later discussions are based largely upon general field observations and the data from direct measurement of field moisture.

The composition of the vegetation at the various stations is quite different, as indicated by the values for frequency and cover. Data were not taken for Station 9 because of the heterogeneous nature of the vegetation and the difficulties encountered in applying the methods used at the other stations to a willow scrub vegetation. This station is interesting, however, in that it is an area where species typically associated with dry habitats were found with those most commonly associated with wet habitats. Examples of this were the joint occurrence in phenology quadrats of <u>Trifolium</u> <u>dasyphyllum</u>[1] and <u>T</u>. <u>parryi</u>, and <u>Sedum</u> <u>stenopetalum</u> and <u>S</u>. <u>rhodanthum</u>. The first of each generic pair is typical of mesic or dry sites, while the second is most often found in moist areas.

The degree of affinity or dissimilarity of stations based on the Association Index of Kulczinsky (1927), in which Association = 2W/ a = b, using the frequency and cover data for each station is indicated in Fig. 18. It is readily apparent that the stations show degrees of affinity that can be quite closely correlated with winter snow conditions. Fig. 12 shows the winter snow pattern for the general study area and the phenology stations. The photographs of stations representing the dry, mesic, wet and bog habitat groups show the mid-summer appearance (Fig. 19).

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[1]Taxonomic nomenclature according to Harrington, 1954.

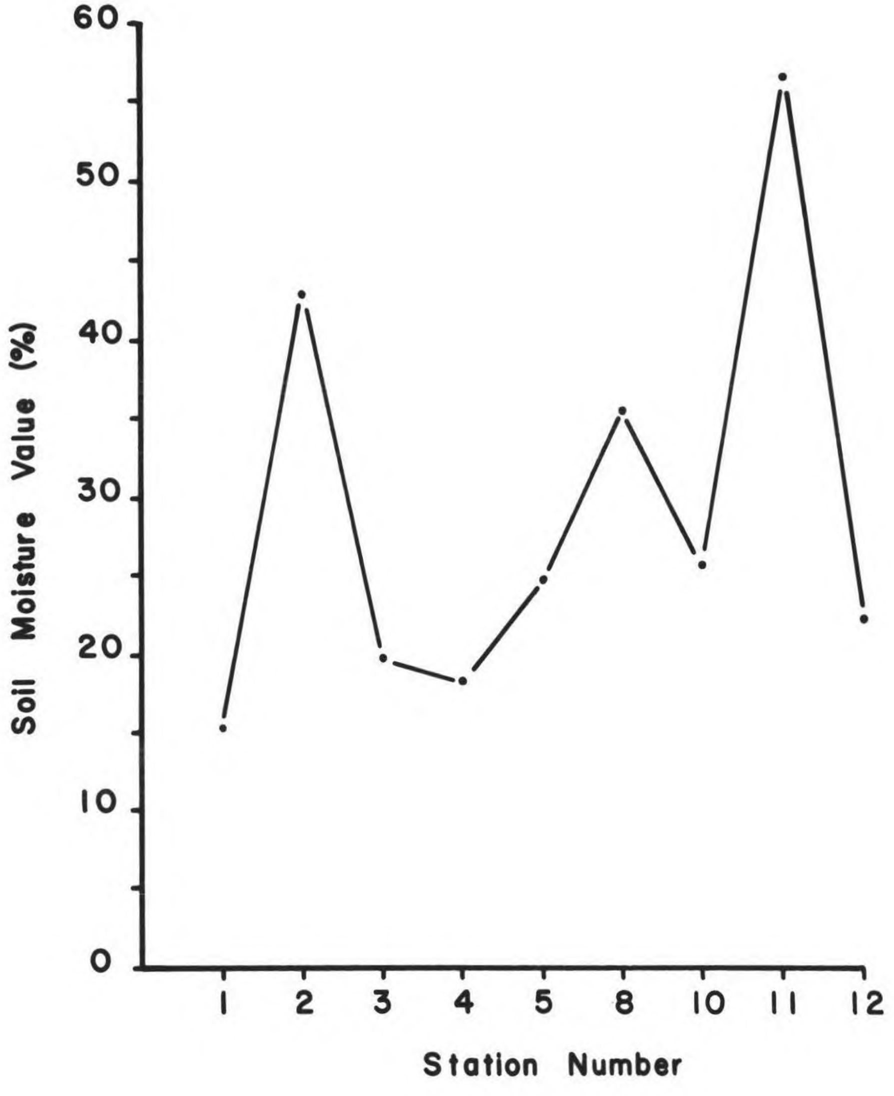

Fig. 17.--Soil moisture as indicated by weight/volume ratio times per cent dry weight (1961).

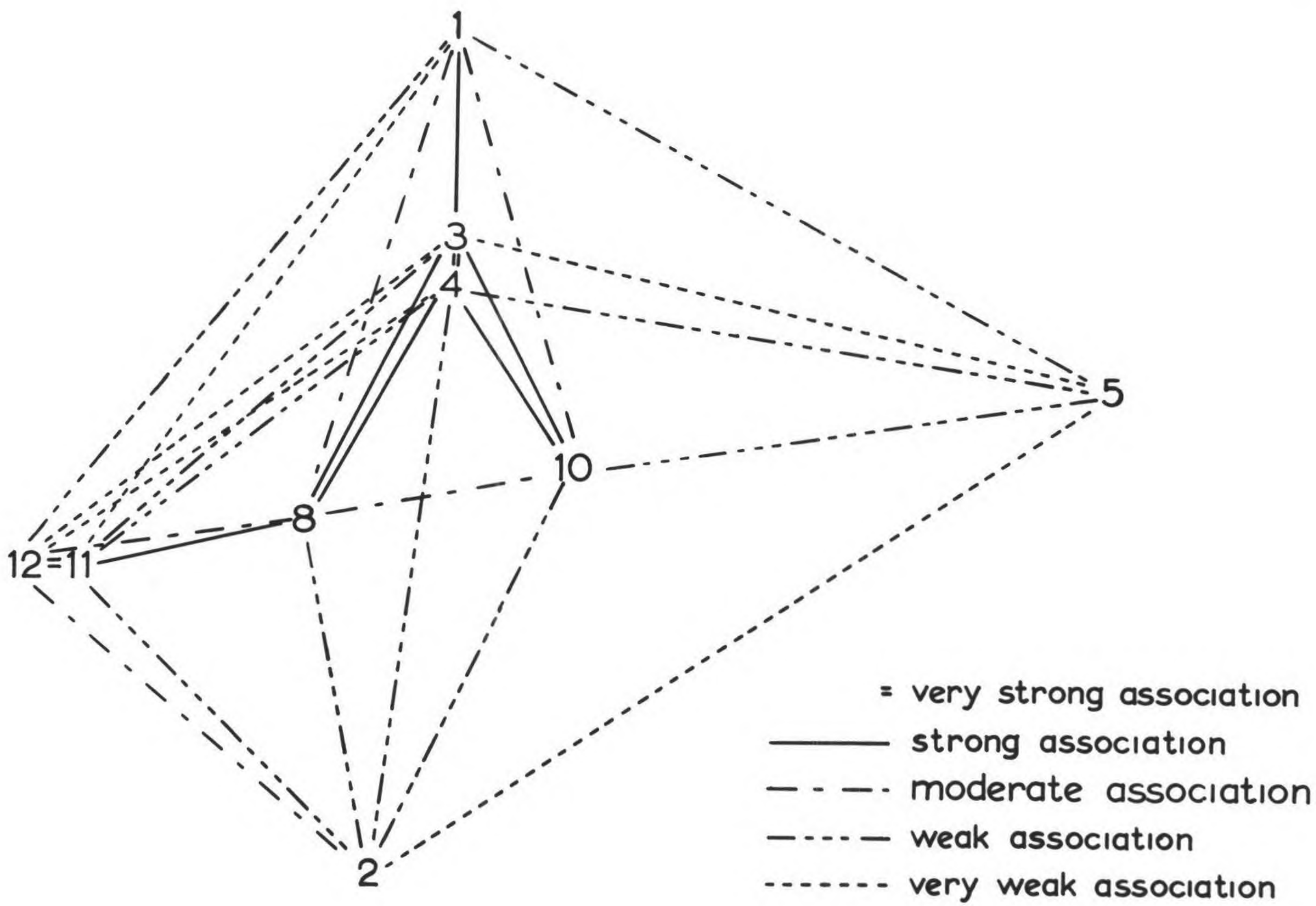

Fig. 18.--Constellation illustrating the relative affinities of vegetation for the primary phenology based on frequency and cover data applied to Kulczinski's Association Index.

Fig. 19-1.--Photo of Station 4 representing exposed, early-dry station group (July 24, 1961).

Fig. 19-2.--Photo of Station 8 representing the mesic station group (July 24, 1961).

Fig. 19-3.--Photo of Station 11 representing the snow accumulation, late-wet station group (July 24, 1961).

Fig. 19-4.--Photo of Station 9 representing the willow-bog station group (July 24, 1961).

Stations 1, 4, and 10 were snow free in the middle of May in both 1960 and 1961, and the airplane flights over the area during the winter indicated that they were essentially snow free throughout the winter. Further, they were subjected to only minimal or no surface or sub-surface drainage from upslope snow accumulations. For purposes of discussion they are classified as early, dry stations, or dry meadow areas. Station 3 had moderate snow depths during part of the winter and early spring, but summer moisture conditions, and species composition seemed to indicate that this station belongs in this category of early, dry or dry meadow.

Stations 5, 8, and 9 are areas in which there were shallow to moderate depths of snow throughout most of the winter, and in which the snow was usually gone by mid to late May. Station 8 is classified as a mesic meadow, while Station 9, because of the position of the water table and the resultant predominence of willows, is classified as a willow bog. Station 5 is a slightly terraced area, with mats of *Dryas octopetala* separated by very coarse and barren gravelly soil stripes. This station, while covered with only moderate depths of snow during the winter, was subject to considerable surface and sub-surface drainage early in the season from an upslope accumulation of snow.

Stations 2, 11 and 12 were areas of deeper snow accumulations which persisted into the middle or latter parts of June. Station 11 is a typical wet meadow, whereas Stations 2 and 12 appeared to be wet early in the season, but dried out considerably more than Station 11 later in the season. The reservoir of water at Station 11 was provided by an upslope snowbank that lasted into the latter part of August and produced considerable amounts of streamflow and subterranean drainage. Such an upslope influence was conspicuously lacking in the areas of Stations 2 and 12. Station 2 remained somewhat cooler and more moist than Station 12 in the latter part of the season.

Station 14, the melt-water investigation station, is at an altitude of 3,240 m (10,725 feet) with a slope of about 15° facing N 10°E. The area was free of snow June 19th, 1961, and surface melt-water influences were negligible in the non-irrigated portion by June 23rd. Irrigation was applied to the lower portion of the area from June 20th to July 10th, the day that the source stream ceased to flow for the summer. During the week previous to the 10th, the flow was only intermittent with the stream flowing only in the afternoons when snow melting was at its peak. Generally the area can be described as a wet or wet-mesic meadow.

The frequency and cover sampling at Station 14 included 27 species. Of these, 15 species had frequency values greater than 20 per cent, and 10 had values over 30 per cent. *Danthonia intermedia* and *Potentilla diversifolia*, each with 72 per cent frequencies, were the most common. *Geum turbinatum* and *Artemisia norvegica* were next with 60 per cent, followed by *Anemone zephyra* and *Trifolium parryi* with frequencies of 48 per cent. The average basal cover per quadrat was 22 per cent. There were only three species which made up more than 10 per cent of the plant cover. These were *Geum turbinatum* (17%), *Danthonia intermedia* (16%), and *Artemisia norvegica* (14%).

Station 16, the snow-retreat study area, lies at an altitude of 3,320 m (10,975 feet). The area is a basin shaped depression on a hillside with a north-northeast exposure and a slope of from 12° to 15°. The margin of the station came out from under the snow on July 7th and the center on August 4th, 1961.

Because of the obvious differences in the composition of the vegetation around the periphery and in the center of this station, frequency and cover were determined for outer and inner areas. The line of demarcation was arbitrarily taken to be the zone between phenology quadrat Groups 4 and 5. The outer portion, consisting of the general area of the first four quadrat groups, had 24 species. Of the five species with frequencies over 50 per cent, Trifolium parryi with a frequency of 92 per cent was highest. Next were Geum turbinatum (76%), Deschampsia caespitosa (72%), Ranunculus adoneus (68%), and Festuca ovina (56%). The average per cent basal cover in this portion was 20 per cent. There were only three species which made up more than 10 per cent of the plant cover; these were Deschampsia caespitosa (43%), Geum turbinatum (24%), and Trifolium parryi (15%).

The central part of the area had only 16 species. The species with highest frequencies were Carex pyrenaica (100%), Erigeron melanocephalus (92%), Deschampsia caespitosa (72%), Poa alpina (48%), and Trifolium parryi (32%). It will be noted that the first two species, with frequencies of over 90 per cent, were not among the most frequent species of the marginal area. E. melanocephalus had a frequency of 36 per cent in the outer region, but C. pyrenaica had a frequency of only 4 per cent. P. alpina had a frequency of 8 per cent in the outer area. Another species which illustrates the sudden shift in composition is Juncus parryi which did not occur in the frequency quadrats of the outer area, but had a frequency of 20 per cent in the inner area. The cover data emphasize even more the change in composition from the outside to the inside of the station. In the middle, the average basal cover was only 14 per cent, and of this, two species, Carex pyrenaica (72%) and Deschampsia caespitosa (17%), accounted for about 90 per cent. Several species were greatly reduced in cover near the center.

RESULTS

The results presented here are based primarily on data collected at regular intervals throughout two growing seasons at the primary phenology stations, and during one season in the melt-water and snow retreat study areas. These data, together with information from general observations, provide a better understanding of the phenological patterns of the alpine species.

Primary Phenological Stations

Of the 85 species studied at the ten primary phenology stations, two were observed at all stations, while some were observed at only one (Table III). The majority were studied at between three and six stations. In a few instances a species was represented in only one quadrat at a given station; however, this ranged upward to 10 quadrats of occurrence per station.

For purposes of phenological comparisons between stations the growing season was arbitrarily divided into four periods. Although without calendar meaning, they represent somewhat natural periods of flowering at all stations. The first period (late May to June 23) extended from the time the study area was initially visited until the time the snow left the accumulation stations (2, 11 and 12). The second (June 24 to July 9) ended with the completion of flowering of Geum turbinatum in the dry stations (1, 3, 4 and 10). The third period (July 10 to July 22) extended to the time of flowering for

Table III.--THE NUMBER OF INDIVIDUALS OF A SPECIES STUDIED PER PRIMARY PHENOLOGY STATION AND THE TOTAL FOR ALL STATIONS.

	1	2	3	4	5	8	9	10	11	12	Total
BORAGINACEAE											
Eritrichium elongatum	-	-	-	4	3	-	-	-	-	-	7
Mertensia alpina	-	-	-	1	-	3	-	4	-	-	8
CAMPANULACEAE											
Campanula rotundifolia	4	1	-	-	-	-	-	-	-	1	6
CARYOPHYLLACEAE											
Arenaria fendleri	3	1	3	5	5	1	-	6	-	1	25
Arenaria obtusiloba	4	2	8	6	8	2	-	1	2	3	36
Cerastium beeringianum	-	-	-	-	-	1	3	1	-	-	5
Silene acaulis	-	-	-	3	3	-	1	-	-	-	7
Stellaria longipes	-	-	-	-	-	1	1	1	-	2	5
COMPOSITAE											
Achillea lanulosa var. alpicola	2	2	-	-	-	-	-	2	-	-	6
Agoseris aurantica	-	-	-	-	-	-	-	-	-	1	1
Antennaria microphylla	1	3	-	-	1	-	1	1	2	2	11
Artemisia norvegica	1	6	2	-	-	1	-	-	-	6	16
Artemisia scopulorum	3	1	4	5	5	-	-	2	-	-	20
Artemisia spithamaea	-	-	-	-	-	7	7	-	3	4	21
Cirsium scopulorum	-	-	-	-	-	-	-	1	-	-	1
Erigeron compositus	2	-	-	-	-	-	-	-	-	-	2
Erigeron pinnatisectus	3	-	2	-	2	-	-	-	-	-	7
Erigeron simplex	1	-	-	2	1	7	6	-	-	2	19
Haplopappus pygmaeus	1	-	1	3	-	-	-	-	-	-	5
Hymenoxys acaulis	-	-	-	2	-	-	-	-	-	-	2
Hymenoxys grandiflora	-	-	-	1	1	3	-	1	-	-	6
Senecio crassulus	-	-	-	-	-	-	-	-	-	1	1
Senecio dimorphophyllus	-	-	-	-	-	-	-	-	2	-	2
Solidago decumbens	-	-	-	-	-	1	-	-	-	3	4
CRASSULACEAE											
Sedum integrifolium	-	-	-	-	-	-	1	-	-	-	1
Sedum rhodanthum	-	-	-	-	-	-	3	-	-	-	3
Sedum stenopetalum	7	2	7	1	4	1	1	2	-	2	27
CRUCIFERAE											
Draba aurea	-	-	1	3	-	-	-	1	-	-	5
Draba crassifolia	-	1	-	-	-	-	-	-	1	3	5
Draba streptocarpa var. streptocarpa	-	-	2	-	-	-	-	-	-	-	2
Erysimum nivale	2	1	-	-	-	-	-	1	-	-	4
Thlaspi alpestre	-	-	-	-	-	1	-	1	-	-	2

Table III.--THE NUMBER OF INDIVIDUALS OF A SPECIES STUDIED PER PRIMARY PHENOLOGY STATION AND THE TOTAL FOR ALL STATIONS.--Continued

	1	2	3	4	5	8	9	10	11	12	Total
CYPERACEAE											
Carex chalciolepis	-	-	-	-	1	-	-	-	-	-	1
Carex chimaphila	-	1	-	-	-	1	6	-	4	-	12
Carex drummondiana	-	1	-	8	4	1	-	5	-	-	19
Carex elynoides	3	-	1	-	3	4	1	6	-	3	21
Carex haydeniana	-	1	-	-	-	1	-	-	-	-	2
Carex nigricans	-	-	-	-	-	-	-	-	5	-	5
Carex rossii	-	1	-	-	-	-	-	-	-	1	2
Kobresia bellardi	-	-	-	-	-	-	1	-	-	-	1
ERICACEAE											
Vaccinium caespitosum	-	9	-	-	-	-	-	-	-	-	9
GENTIANACEAE											
Gentiana prostrata	-	-	-	-	-	-	3	-	-	-	3
Gentiana romanzovii	-	-	-	-	-	2	4	-	-	-	6
GRAMINEAE											
Agropyron scribneri	8	-	1	-	-	-	-	-	-	-	9
Calamagrostis purpurascens	2	-	1	1	-	-	-	-	-	-	4
Danthonia intermedia	-	7	-	-	-	-	-	-	-	-	7
Deschampsia caespitosa	-	-	-	-	-	-	1	-	10	4	15
Festuca ovina	1	-	1	-	1	3	1	1	2	2	12
Helictotrichon mortoniana	1	-	-	3	1	-	-	2	-	-	7
Poa alpina	-	-	-	-	-	-	1	-	1	-	2
Poa pattersoni	2	2	2	-	-	1	1	2	-	-	10
Poa rupicola	4	-	-	1	-	2	1	1	-	-	9
Trisetum spicatum	-	1	1	-	-	1	1	-	1	3	8
JUNCACEAE											
Juncus parryi	-	2	-	-	-	-	-	-	1	-	3
Luzula spicata	-	1	1	3	4	-	-	-	2	-	11
LEGUMINOSAE											
Trifolium dasyphyllum	7	2	10	8	2	4	3	9	-	1	46
Trifolium nanum	-	-	-	2	-	-	-	-	-	-	2
Trifolium parryi	-	-	-	-	-	-	9	-	3	3	15
LILIACEAE											
Llyodia serotina	-	-	-	1	1	1	4	2	-	2	11
POLEMONIACEAE											
Phlox caespitosa	5	-	6	9	1	-	-	3	-	-	24
Polemonium viscosum	1	-	-	-	-	3	-	3	-	-	7
POLYGONACEAE											
Polygonum bistortoides	1	5	2	2	3	8	3	1	10	6	41
Polygonum viviparum	-	-	-	-	-	-	5	-	-	-	5
PORTULACEAE											
Lewisia pygmaea	-	3	-	-	-	-	-	1	1	2	7
PRIMULACEAE											
Androsace septentrionalis var. subumbellata	2	6	3	-	3	1	1	1	-	9	26
Primula angustifolia	-	-	-	2	1	1	-	1	-	-	5

Table III.--THE NUMBER OF INDIVIDUALS OF A SPECIES STUDIED FOR PRIMARY PHENOLOGY STATION AND THE TOTAL FOR ALL STATIONS.--Continued

	1	2	3	4	5	8	9	10	11	12	Total
RANUNCULACEAE											
Anemone zephyra	-	-	-	-	-	1	8	-	-	4	13
Aquilegia caerulea	-	-	-	-	-	-	-	1	-	-	1
Caltha leptosepala	-	-	-	-	-	-	3	-	2	-	5
Pulsatilla ludoviciana	1	-	-	-	1	-	-	-	-	-	2
Ranunculus adoneus	-	2	-	-	-	-	-	1	2	-	5
Ranunculus pedatifidus	-	-	-	-	-	5	-	2	-	-	7
ROSACEAE											
Dryas octopetala	-	-	-	-	8	-	-	-	-	-	8
Geum turbinatum	3	5	6	10	7	9	8	3	8	5	64
Potentilla diversifolia	4	2	7	1	-	-	3	2	-	3	22
Sibbaldia procumbens	-	1	-	-	-	-	-	-	4	4	9
SALICACEAE											
Salix sp.	-	-	-	-	1	-	-	-	-	-	1
SAXIFRAGACEAE											
Heuchera nivale	1	-	1	2	-	-	-	-	-	-	4
Saxifraga rhomboidea	-	-	-	-	5	2	5	3	-	4	19
SCROPHYLARIACEAE											
Castilleja occidentalis	-	-	-	-	-	6	3	-	1	-	10
Pedicularis groenlandica	-	-	-	-	-	-	1	-	-	-	1
Pedicularis parryi	-	1	-	-	-	-	-	-	-	1	2
Penstemon whippleanus	-	1	-	-	-	-	-	1	-	1	3
UMBELLIFERAE											
Oreoxis alpina	1	-	-	-	-	3	-	6	-	-	10
VIOLACEAE											
Viola adunca var. bellidifolia	-	-	-	-	-	-	-	-	1	-	1
	---	---	---	---	---	---	---	---	---	---	----
Total - Species	30	30	23	26	27	33	35	36	22	32	85
Individuals	81	74	73	89	79	89	107	82	67	94	826

Campanula rotundifolia, the first of the late season species. The last period (July 23 to end of season) was considered to end with the completion of flowering by Gentiana romanzovii at Station 8.

The data in Table IV indicate the period and station in which the species flowered. Fig. 20 shows the number of species in flower at each station at the time of the weekly reading of the quadrats. These data provide an indication of the flowering activity within a station throughout the growing season, as well as the per cent of species present that flowered in each of the two seasons.

Typically there were a considerable number of species in bloom during the first period in the early, dry stations, a lesser number in the mesic stations, and fewer still or none in the bog and wet stations. The flowering in the wet stations was generally concentrated in the last two periods. By this time the flowering activity at the early, dry stations was gradually approaching a minimum. In the mesic and bog stations flowering was fairly evenly distributed through the second, third and fourth periods.

A comparison of the data for the two growing seasons indicates certain differences and similarities in the phenological patterns between the two years (Fig. 21). In 1961, the earliest species responded somewhat later than in 1960. This was most pronounced at the early, dry stations (1, 3, 4 and 10), which were virtually snow-free at a time when the areas of snow accumulation were still quite deeply buried. Most species of the snow accumulation areas, and those species that normally bloomed in the middle or latter part of the season in all areas, showed quite similar patterns for each of the

Table IV.--FLORAL PERIOD AND STATIONS IN WHICH FLOWERING OCCURRED.

First floral period - From late May to June 23.
Second floral period - From June 23 to July 9.
Third floral period - From July 10 to July 22.
Fourth floral period - From July 23 to end of season.

	Floral period		Stations in which flowering occurred	
	1960	1961	1960	1961
Pulsatilla ludoviciana	1	1	1-------5-------------	1---------------------
Thlaspi alpestre	1	1	----------8---10------	----------8---10------
Eritrichium elongatum	1	1-2	------4-5-------------	------4-5-------------
Primula angustifolia	1	1-2	------4-5-----10------	------4-5-8---10------
Ranunculus adoneus	1-2	1-2	--2-----------10-11---	--2--------------11---
Trifolium nanum	1-2	1-2	------4---------------	------4---------------
Oreoxis alpina	1-2	1-2-3	1---------8---10------	1---------8---10------
Phlox caespitosa	1-2	1-2-3	1---3-4-------10------	1---3-4-------10------
Caltha leptosepala	1-2	2	------------9----11---	------------9----11---
Erysimum nivale	1-2	2	1---3---------10------	--------------10------
Ranunculus pedatifidus	1-2	2	----------8-----------	----------8-----------
Androsace septentrionalis var. subumbellata	1-2-3	1-2-3	1-2-3---5-8-9-10----12	1-2-3---5-8-9-------12
Llyodia serotina	1-2	2-3	------------9-10------	----------8-9-10----12
Polemonium viscosum	1-2	2-3	1---------8---10------	1-------------10------
Draba aurea	1-2-3	2-3	----3-4-------10------	------4-------10------
Mertensia alpina	1-2-3	2-3	------4---8---10------	----------8---10------
Potentilla diversifolia	1-2-3	2-3	1-2-3-------9-10----12	1---3-4-----9-10----12
Saxifraga rhomboidea	1-2-3	2-3	--------5-8-9-10----12	--------5-8-9-10----12
Carex drummondiana	1-2-3-4	1-2-3	------4-5-8---10------	--2---4-5-----10------
Carex elynoides	1-2-3-4	1-2-3	1---3---5-8-9-10----12	1---3---5-8-9-10----12
Geum turbinatum	1-2-3-4	1-2-3-4	1-2-3-4-5-8-9-10-11-12	1-2-3-4-5-8-9-10-11-12
Festuca ovina	1-2-3-4	2-3-4	1---------8-9-10----12	1---3---5-8-9----11-12
Arenaria obtusiloba	1-2-3-4	2-3-4	1-2-3-4-5-8------11-12	1-2-3-4-5-8---10-11-12
Trifolium dasyphyllum	1-2-3-4	2-3-4	1-2-3-4-5-8-9-10------	1---3-4---8-9-10------
Poa pattersoni	1-2-3-4	2-3-4	1-2-3-----8---10------	1-2-3-------9-10------
Poa rupicola	1-2-3-4	2-3-4	1-----4---8-9-10------	1-----4---8---10------
Helictotrichon mortoniana	1-2-3-4	2-3-4	------4-5-----10------	1-----4-5-----10------

Table IV.--FLORAL PERIOD AND STATIONS IN WHICH FLOWERING OCCURRED.--Continued

	Floral period		Stations in which flowering occurred	
	1960	1961	1960	1961
Erigeron compositus	1-2	2-3-4	1-------------------	1-------------------
Agropyron scribneri	2-3	1-2-3-4	1---3---------------	1-------------------
Draba streptocarpa var. streptocarpa	2	2-3	1-------------------	----3---------------
Heuchera nivalis	2	2-3	1-----4-------------	1-----4-------------
Calamagrostis purpurascens	2-3	2	1---3-4-------------	1-----4-------------
Aquilegia caerulea	2-3		-------------10------	-------------10------
Carex haydeniana	2-3		--2-------8----------	---------------------
Carex chalciolepis		2-3	---------------------	--------5------------
Salix sp.		2-3	---------------------	--------5------------
Anemone zephyra	2-3	2-3	----------8-9------12	----------8-9------12
Dryas octopetala	2-3	2-3	--------5------------	--------5------------
Vaccinium caespitosum	2-3	2-3	--2------------------	--2------------------
Draba crassifolia	3	2-3	--2----------------12	----------------11-12
Carex chimaphila		2-3-4	---------------------	--2-------8-9----11---
Luzula spicata	2-3	2-3-4	--2-3-4--------------	--2-3-4----------11---
Silene acaulis	2	2-3-4	------4-5------------	------4-5------------
Sibbaldia procumbens	2-3-4	2-3	--2-------------11-12	--2-------------11-12
Trifolium parryi	2-3-4	2-3	------------9---11-12	------------9---11-12
Hymenoxis grandiflora	2-3-4		------4-5-----10------	----------8----------
Arenaria fendleri	2-3-4	2-3-4	1-2-3-4-5-----10------	1---3-4-5-8---10----12
Artemisia spithamaea	2-3-4	2-3-4	----------8-9----11-12	----------8-9----11-12
Erigeron pinnatisectus	2-3-4	2-3-4	1---3---5------------	1---3----------------
Erigeron simplex	2-3-4	2-3-4	1-----4---8-9------12	1-----4---8-9------12
Lewisia pygmaea	2-3-4	2-3-4	--2-----------10----12	--2-----------10-11-12
Polygonum bistortoides	2-3-4	2-3-4	1-2-3-4---8------11-12	1---3-4---8---10-11-12
Carex nigricans		2-3-4	---------------------	----------------11---
Hymenoxis acaulis	2-3	3-4	------4--------------	------4--------------
Antennaria microphylla	2-3-4	3-4	1-2-----5--------11-12	--2-----5-----10-11---
Artemisia norvegica	2-3-4	3-4	1-2----------------12	1-2-3--------------12
Artemisia scopulorum	2-3-4	3-4	1---3-4-5------------	1-2-3-4-5------------
Castilleja occidentalis	2-3-4	3-4	----------8-9----11---	----------8-9----11---
Carex rossii	3-4	2-3	--2----------------12	--2------------------
Juncus parryi	2-3-4	4	--2-------------11---	----------------11---

Table IV.--FLORAL PERIOD AND STATIONS IN WHICH FLOWERING OCCURRED.--Continued

	Floral period		Stations in which flowering occurred	
	1960	1961	1960	1961
Sedum integrifolium		3	---------------------	------------9--------
Achillea lanulosa var. alpicola	3-4	3-4	1-2----------10------	1--------------------
Deschampsia caespitosa	3-4	3-4	----------------11-12	----------------11-12
Kobresia bellardi	3-4		------------9--------	---------------------
Viola adunca var. bellidifolia		3-4	---------------------	----------------11---
Sedum rhodanthum	3-4	3-4	------------9--------	------------9--------
Haplopappus pygmaeus	3-4	4	1---3-4--------------	1-----4--------------
Penstemon whippleanus	3-4	4	-------------10---12	-------------10---12
Polygonum viviparum	3-4	4	------------9--------	------------9--------
Sedum stenopetalum	3-4	4	1---3-4-5-8-9-10------	1-2-3-4---8---10------
Stellaria longipes	3-4	4	----------8-9-10------	------------9-10----12
Cerastium beeringianum	4	3-4	----------8---10------	------------9-10------
Poa alpina	4	3-4	------------9--------	------------9----11---
Trisetum spicatum	4	3-4	--2-3-------9-------12	----3-----8------11-12
Agoseris aurantica		4	---------------------	------------------12
Campanula rotundifolia	4	4	1------------------12	1--------------------
Cirsium scopulorum	4		-------------10------	---------------------
Danthonia intermedia	4	4	--2------------------	--2------------------
Gentiana prostrata	4	4	------------9--------	------------9----11---
Gentiana romanzovii	4	4	----------8----------	----------8----------
Pedicularis groenlandica		4	---------------------	------------9--------
Pedicularis parryi	4	4	--2------------------	-------------------12
Senecio crassulus	4		-------------------12	---------------------
Senecio dimorphophyllus	4	4	----------------11---	----------------11---
Solidago decumbens	4	4	-------------------12	-------------------12

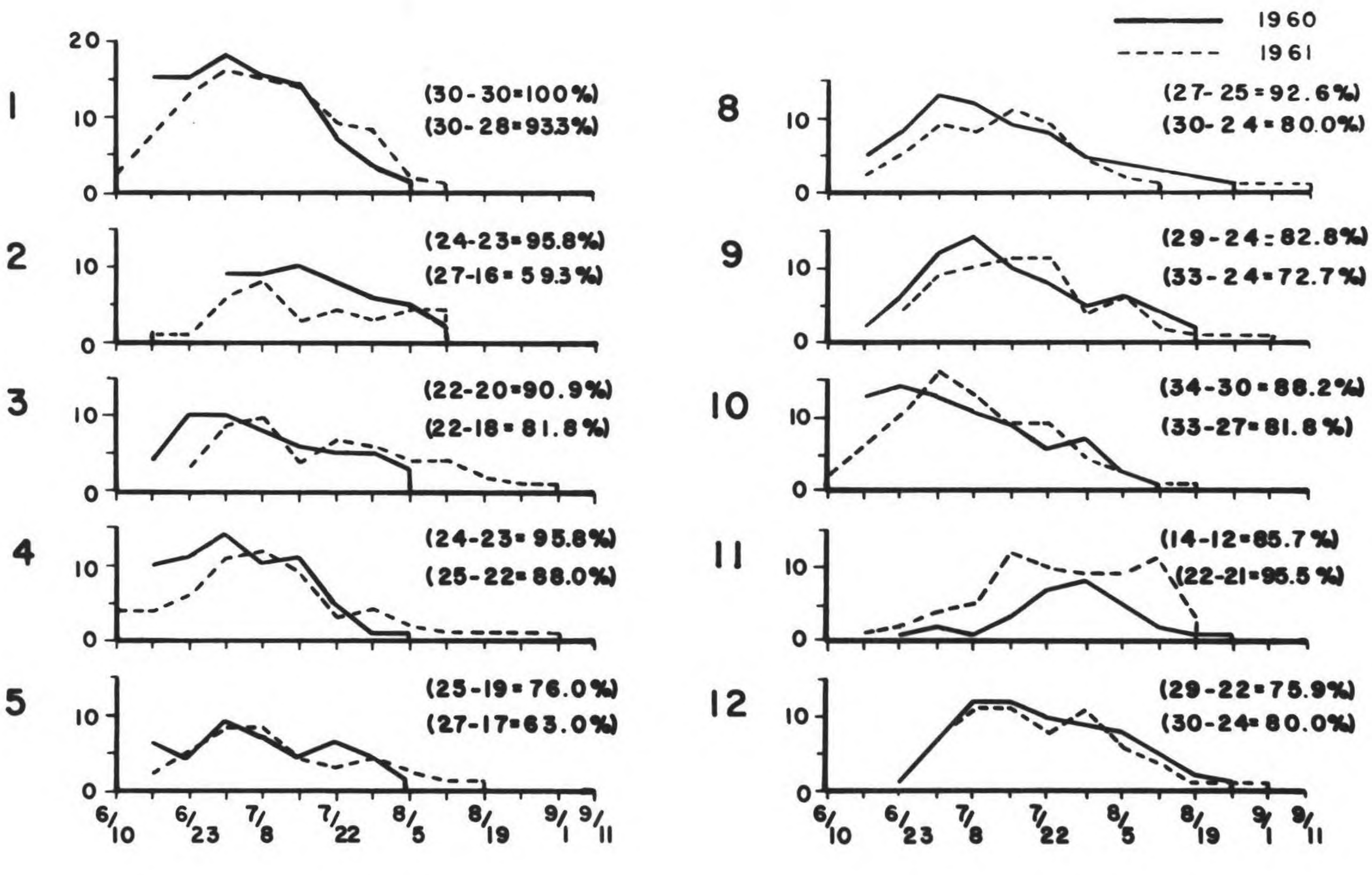

Fig. 20.--Number of species in flower at each station at the time of the weekly readings, and the per cent of species studied that flowered each season.

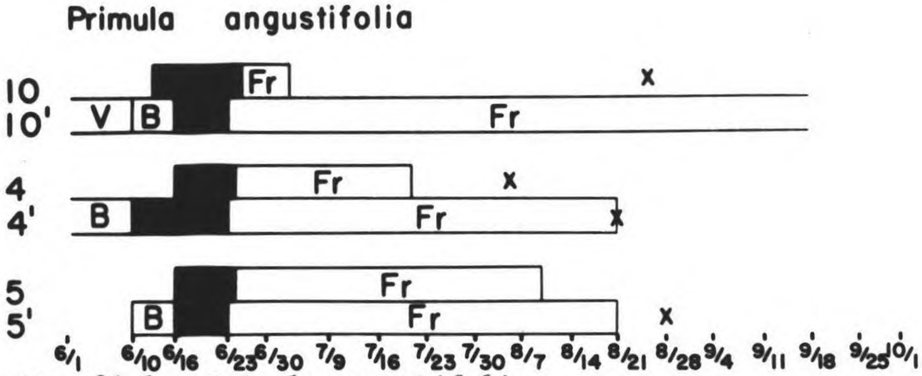

Fig. 21-1.--Primula angustifolia.

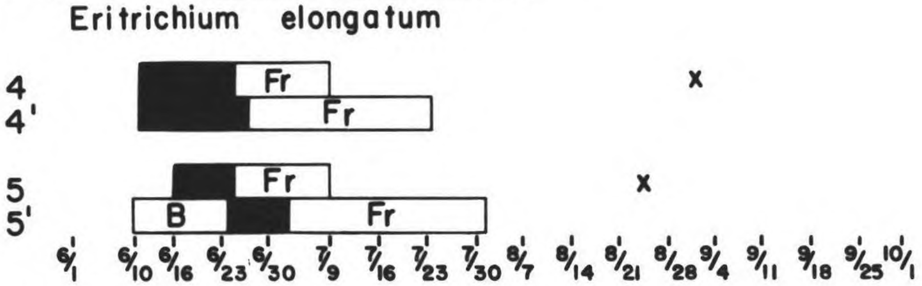

Fig. 21-2.--Eritrichium elongatum.

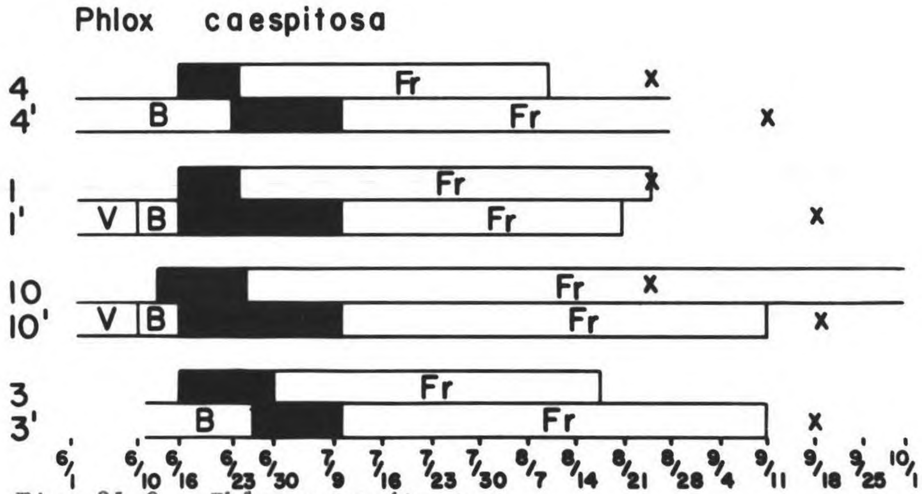

Fig. 21-3.--Phlox caespitosa.

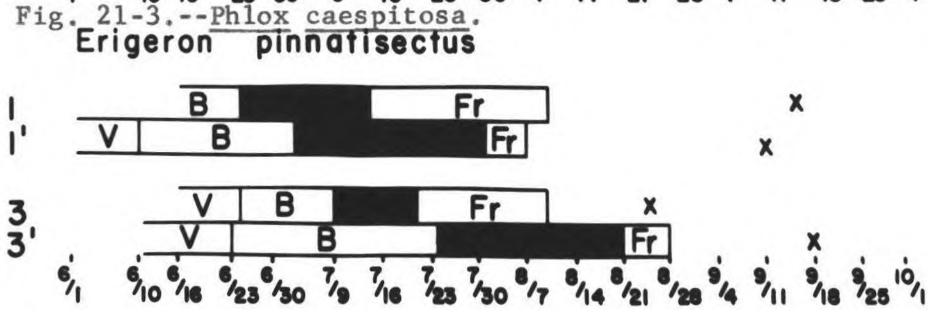

Fig. 21-4.--Erigeron pinnatisectus.

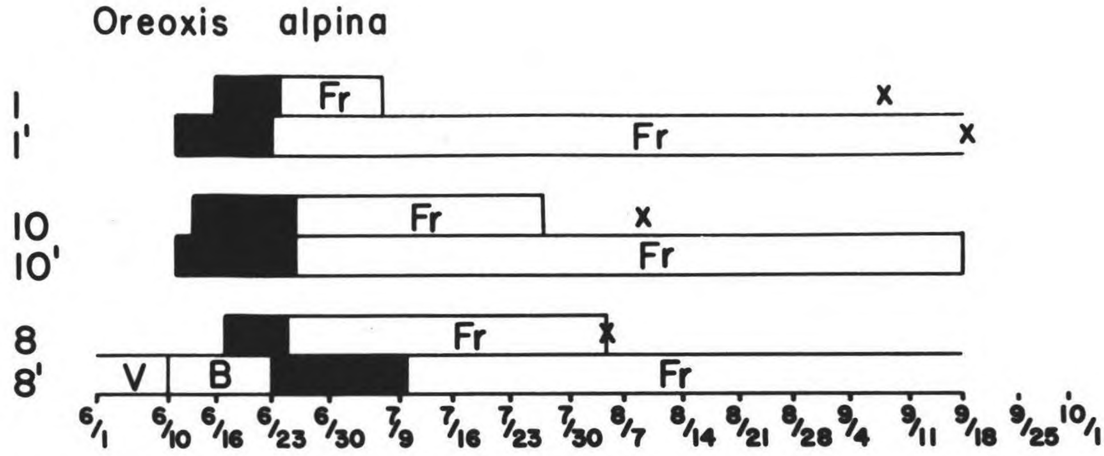

Fig. 21-5.--Oreoxis alpina.

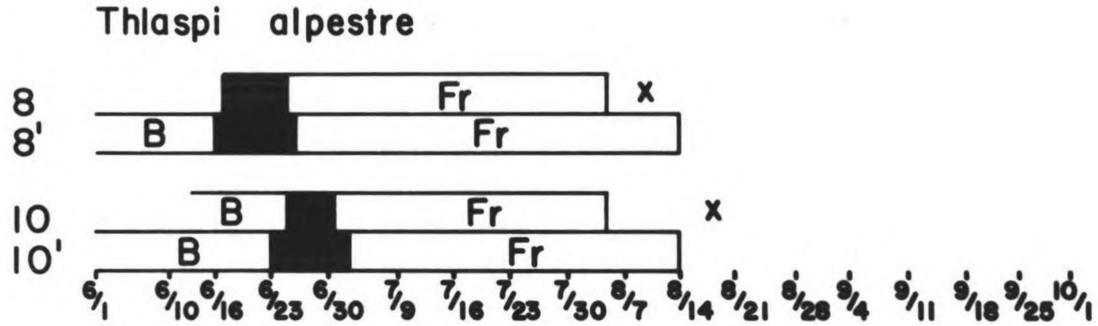

Fig. 21-6.--Thlaspi alpestre.

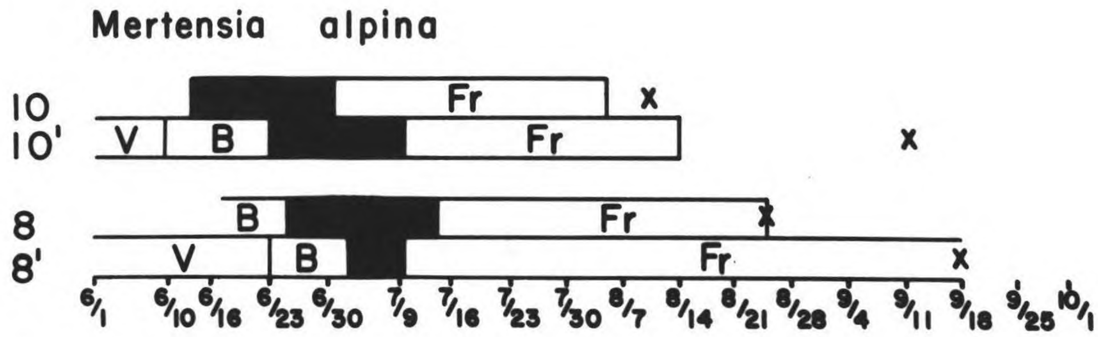

Fig. 21-7.--Mertensia alpina.

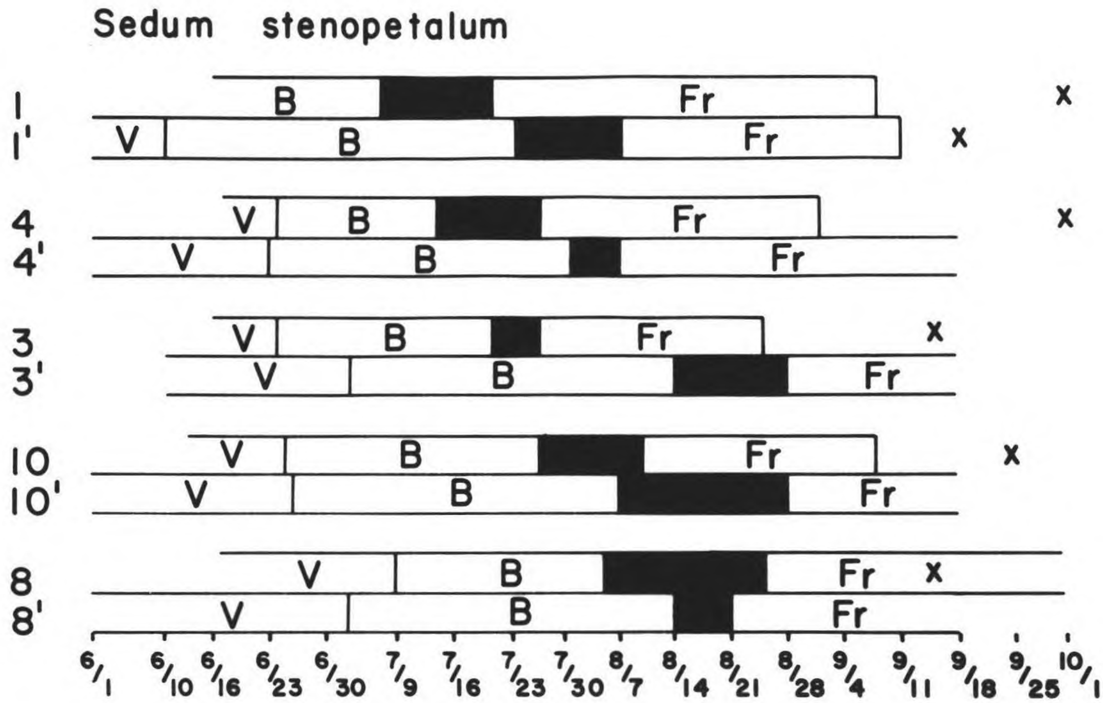

Fig. 21-8.--Sedum stenopetalum.

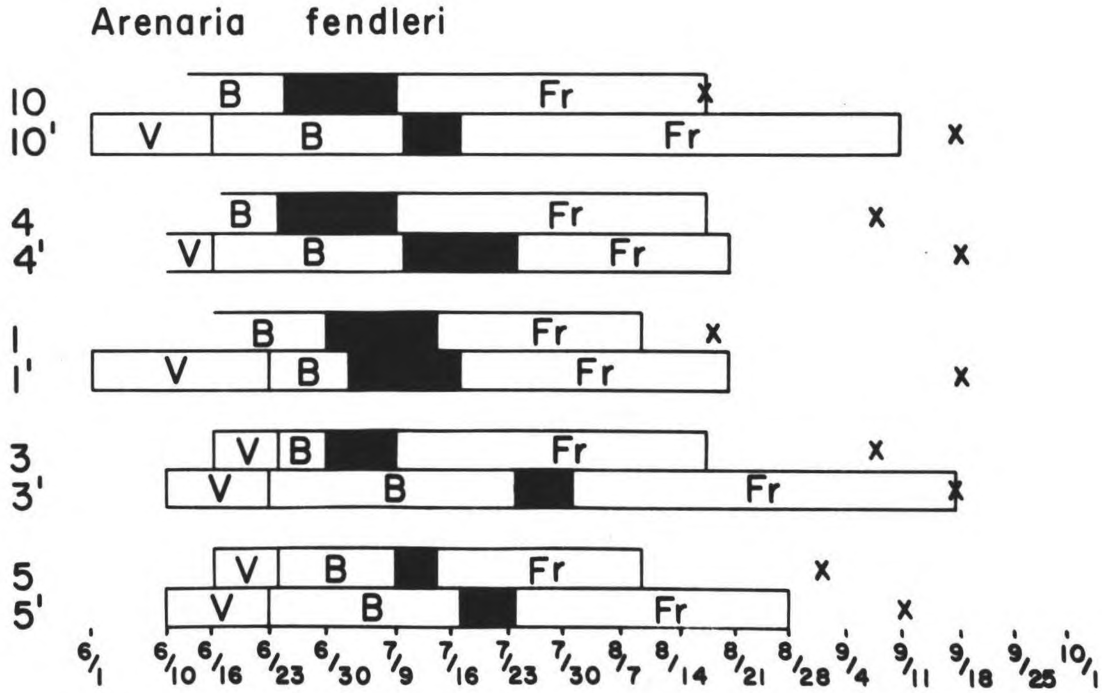

Fig. 21-9.--Arenaria fendleri.

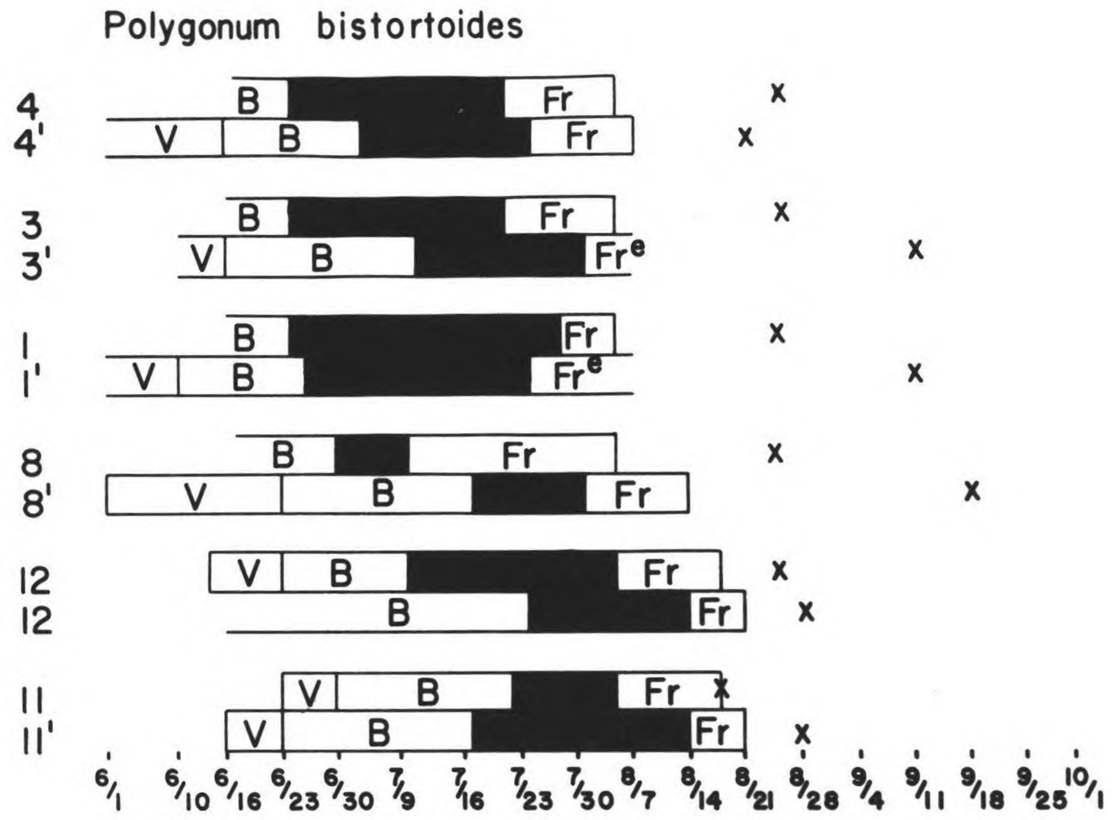

Fig. 21-10.--Polygonum bistortoides.

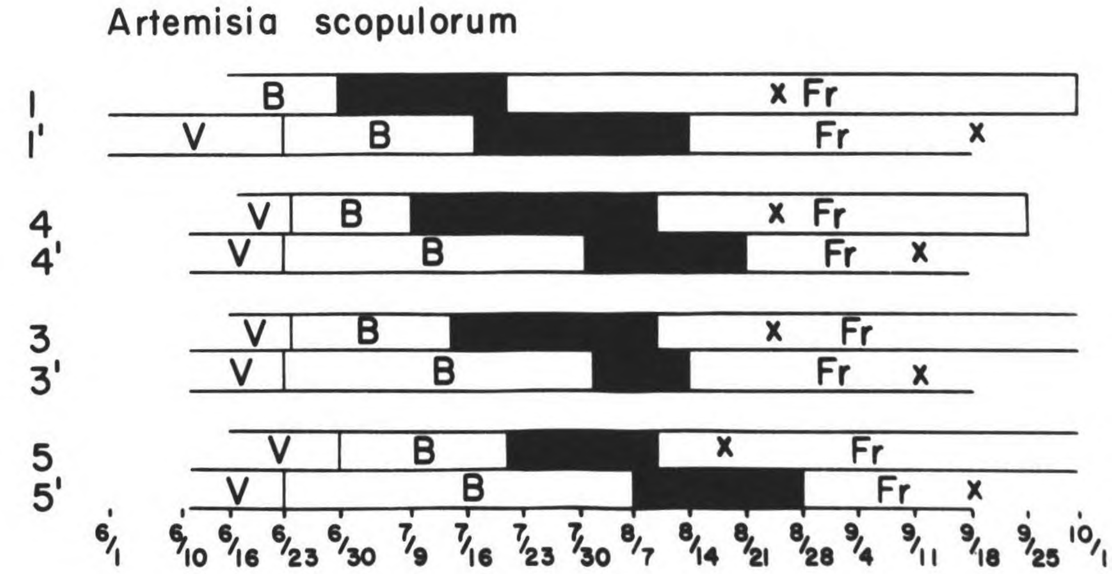

Fig. 21-11.--Artemisia scopulorum.

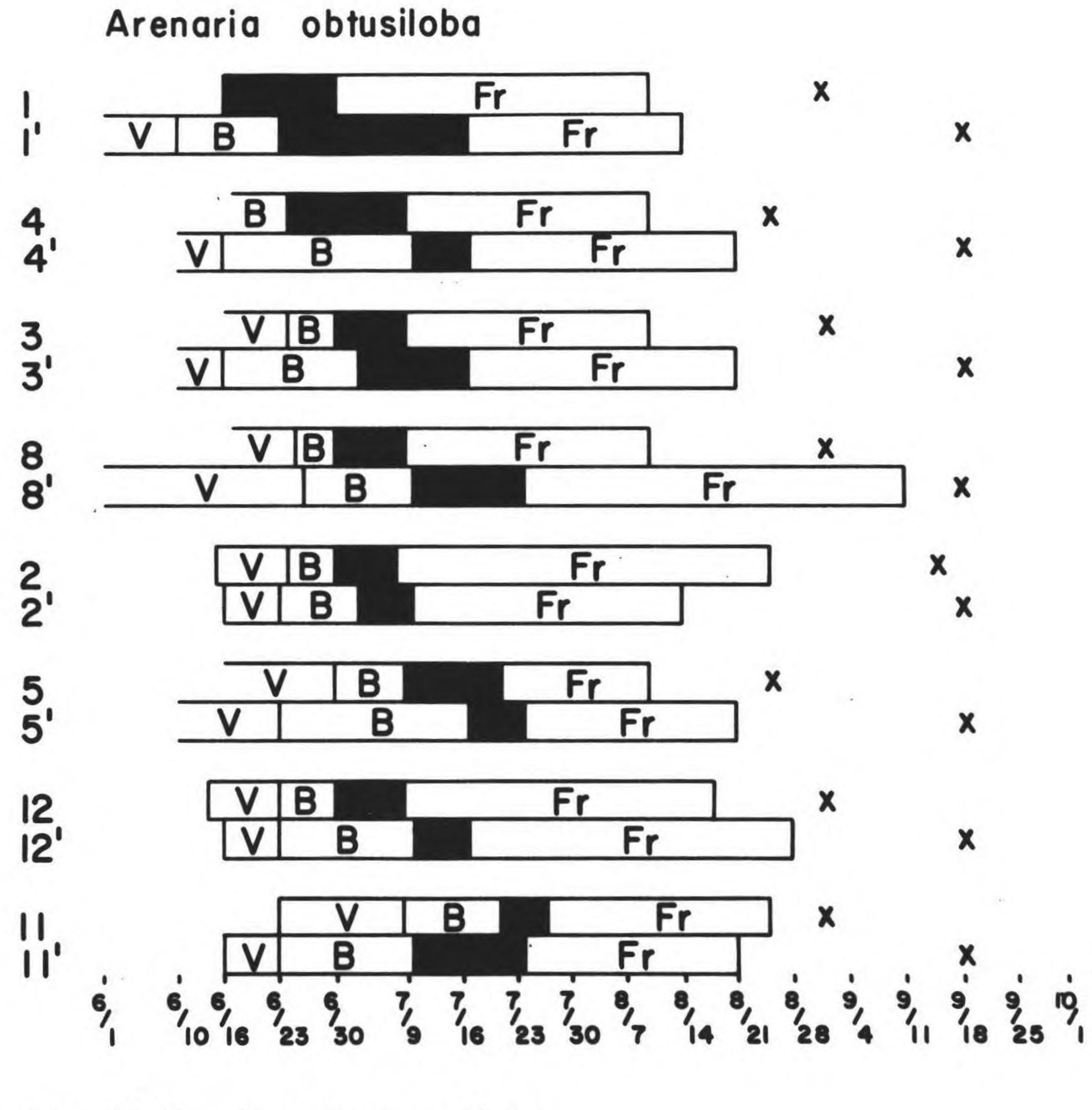

Fig. 21-12.--Arenaria obtusiloba.

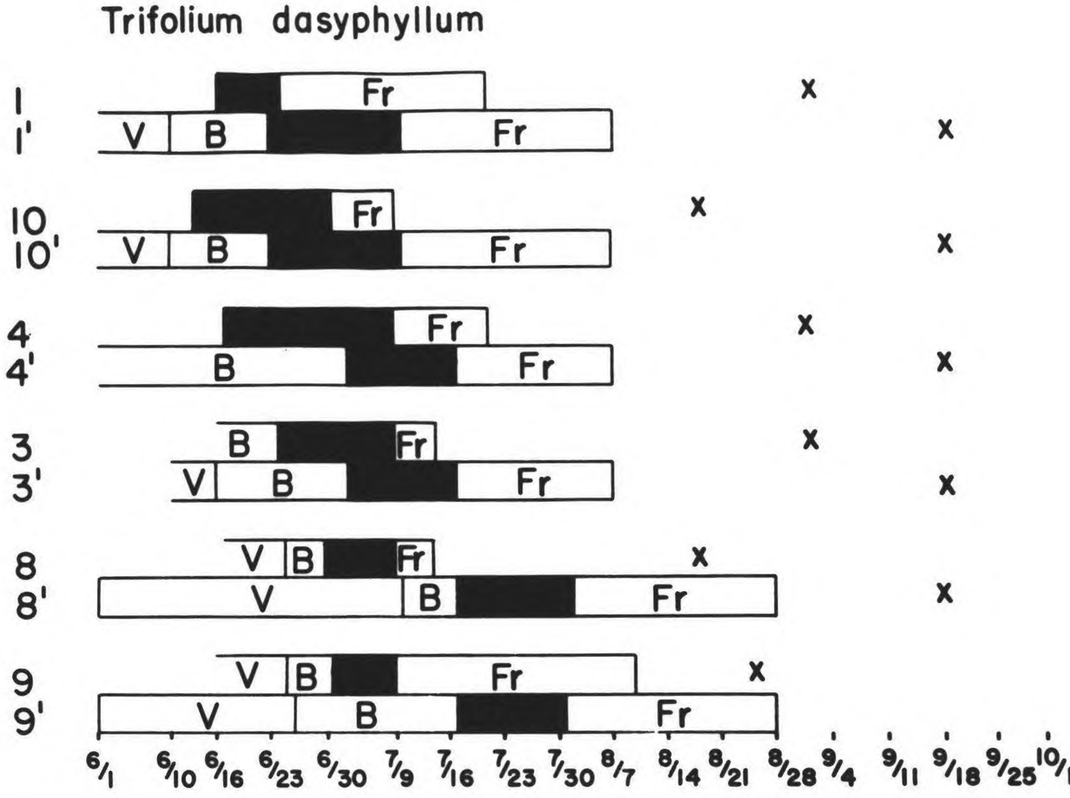

Fig. 21-13.--Trifolium dasyphyllum.

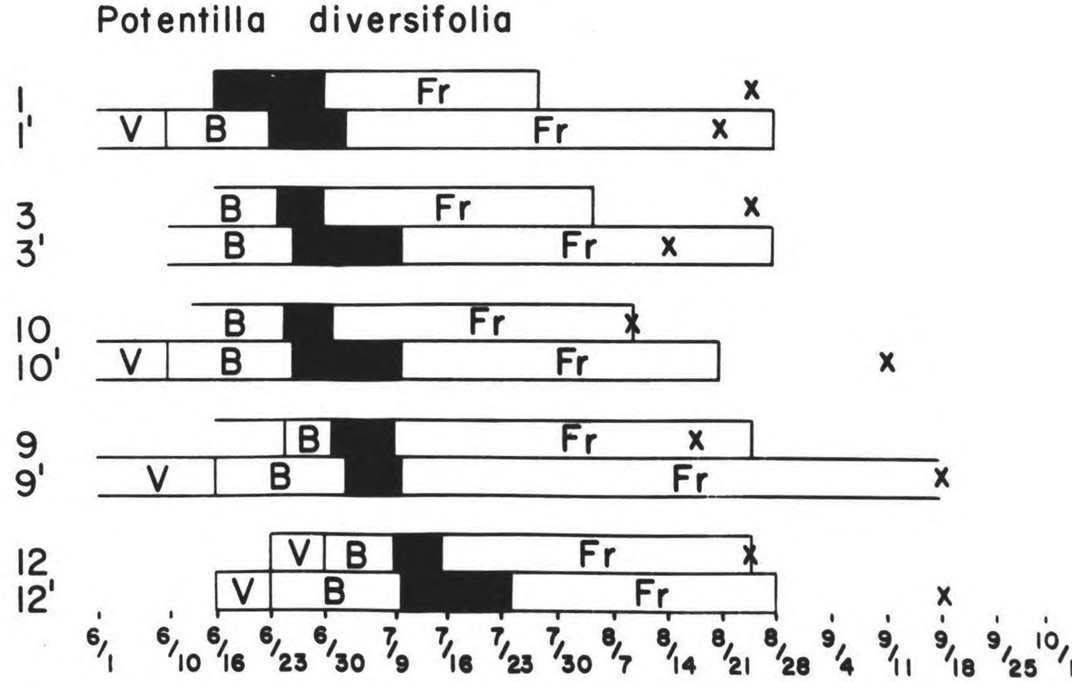

Fig. 21-14.--Potentilla diversifolia.

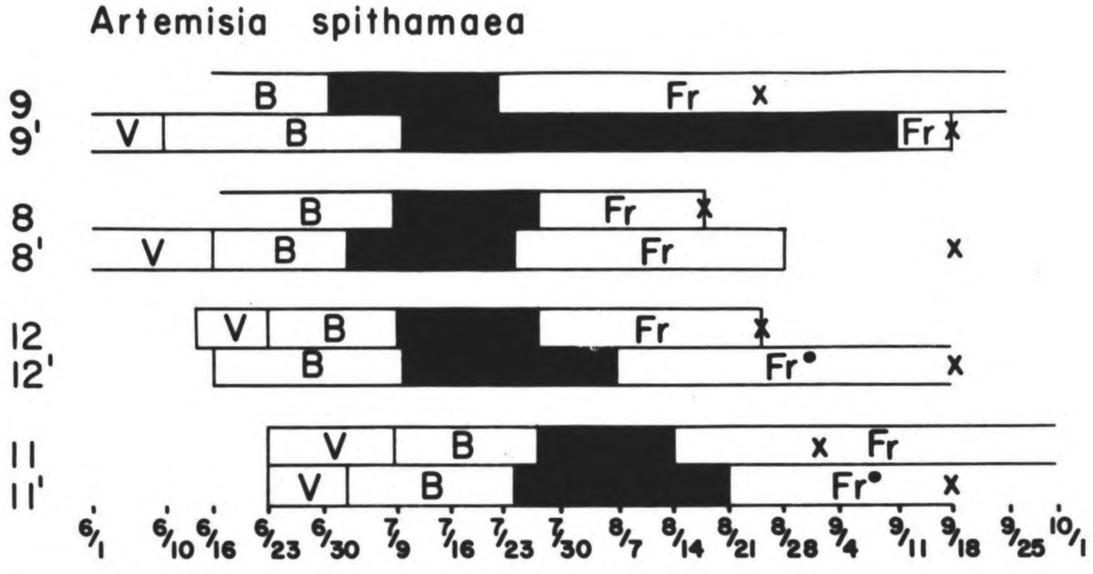

Fig. 21-15.--Artemisia spithamaea.

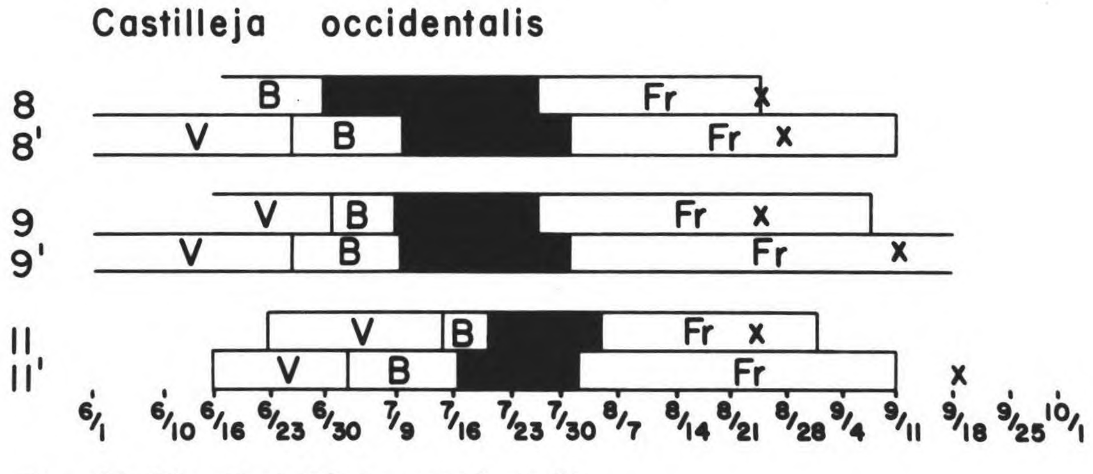

Fig. 21-16.--Castilleja occidentalis.

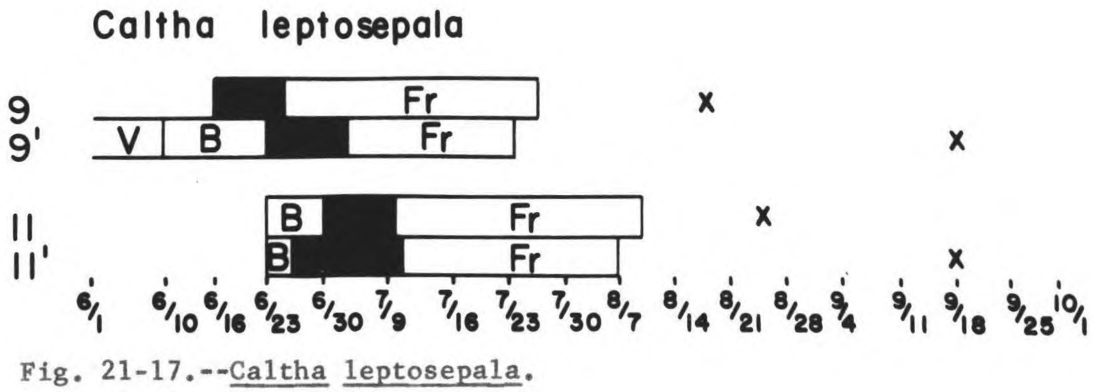

Fig. 21-17.--Caltha leptosepala.

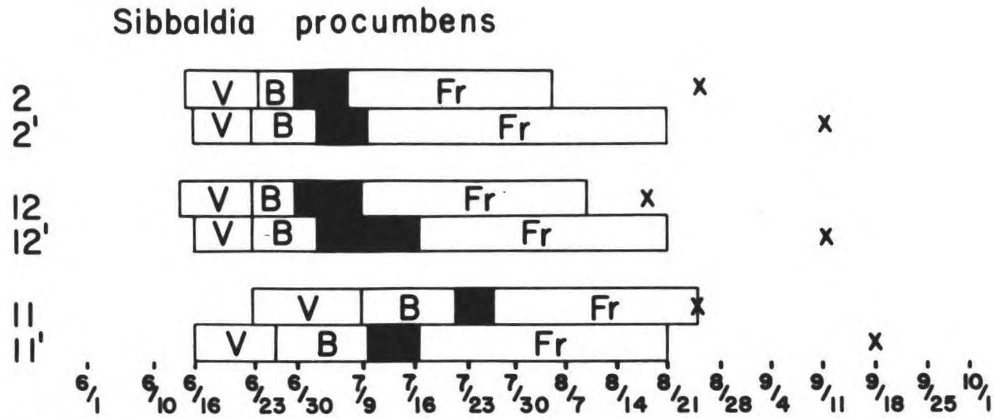

Fig. 21-18.--Sibbaldia procumbens.

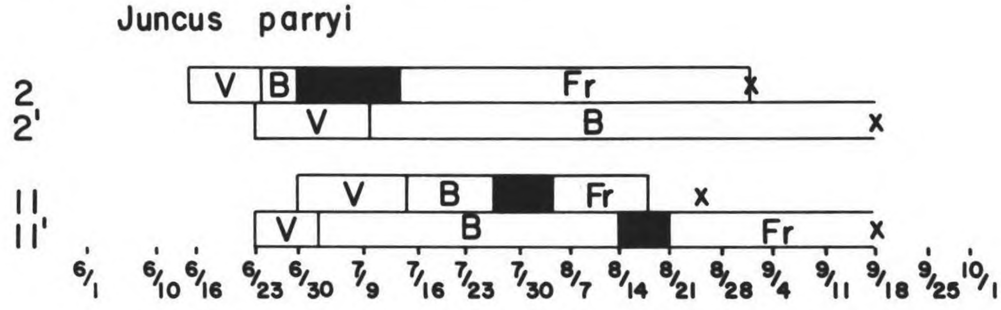

Fig. 21-19.--Juncus parryi.

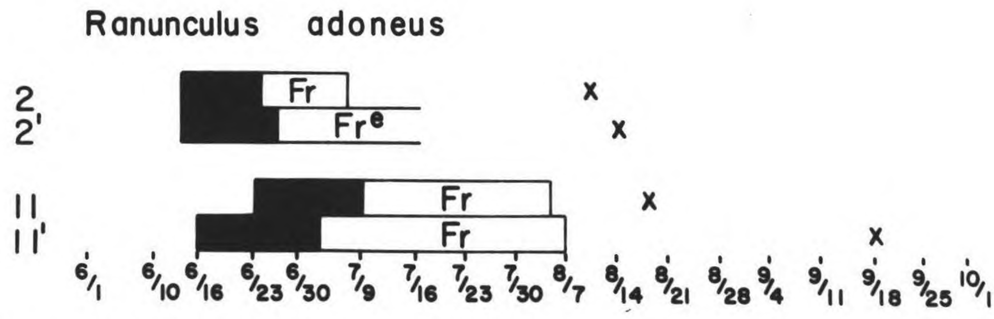

Fig. 21-20.--Ranunculus adoneus.

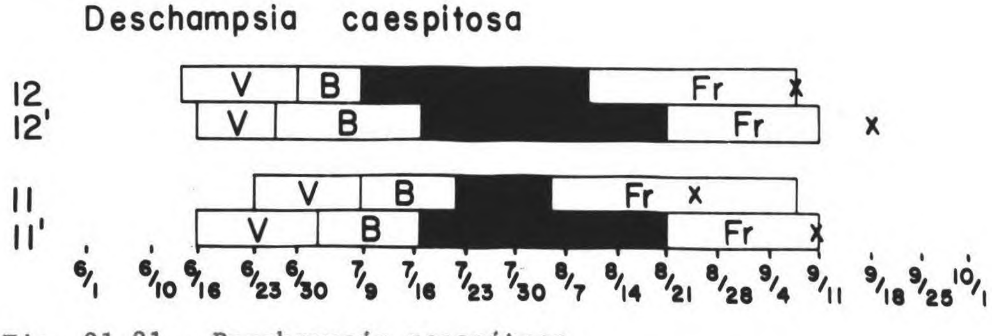

Fig. 21-21.--Deschampsia caespitosa.

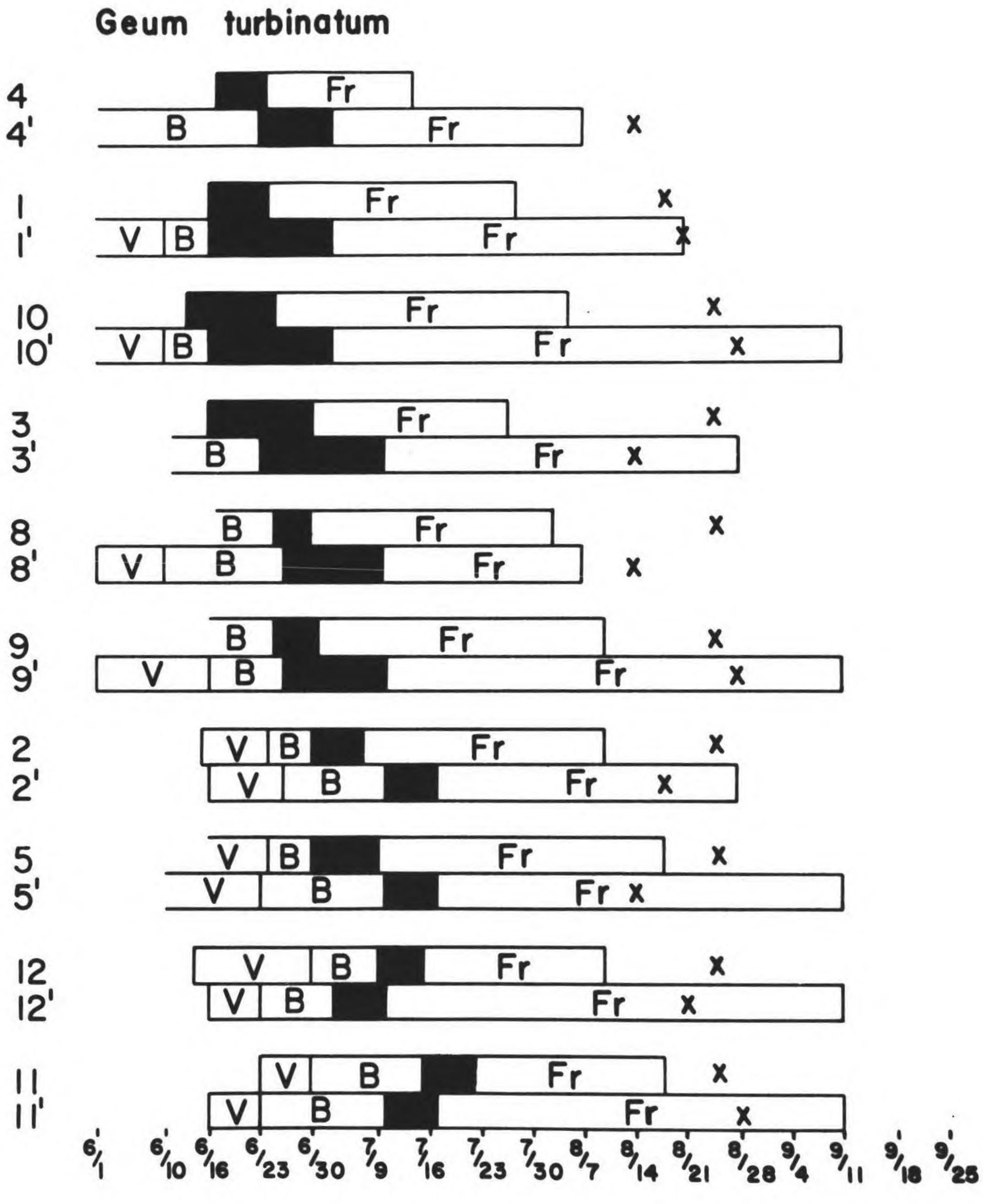

Fig. 21-22.--Geum turbinatum.

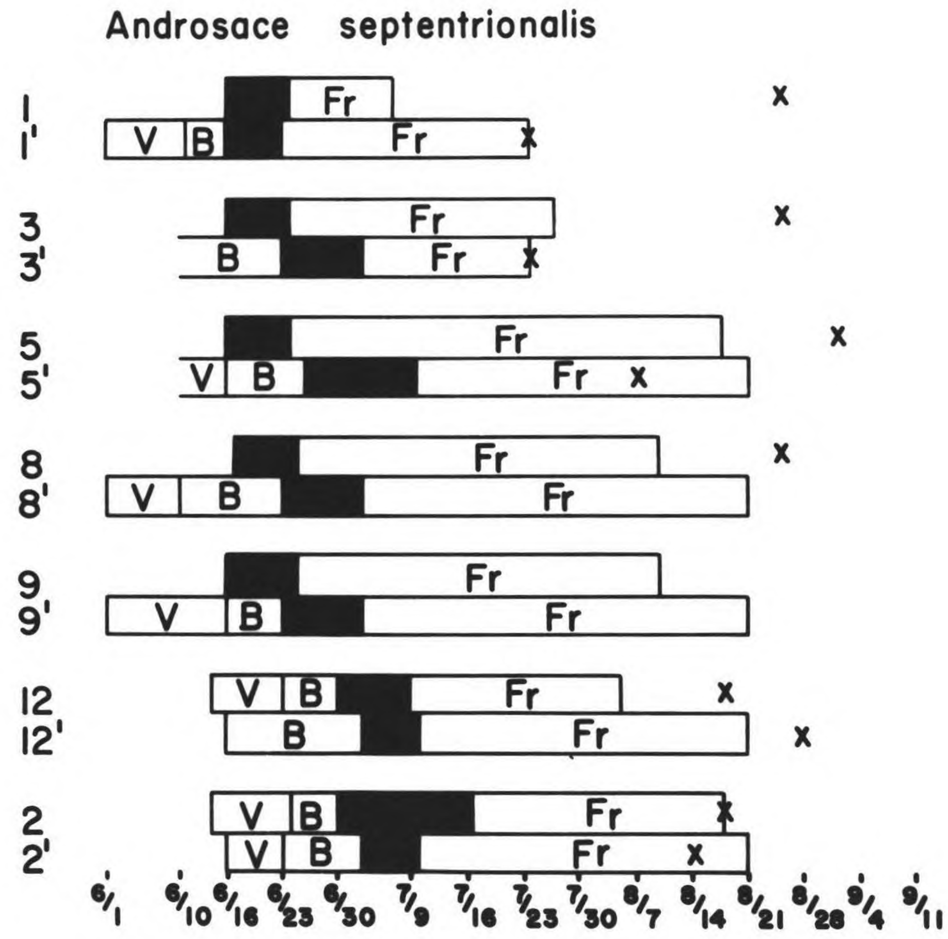

Fig. 21-23.--Androsace septentrionalis var. Subumbellata.

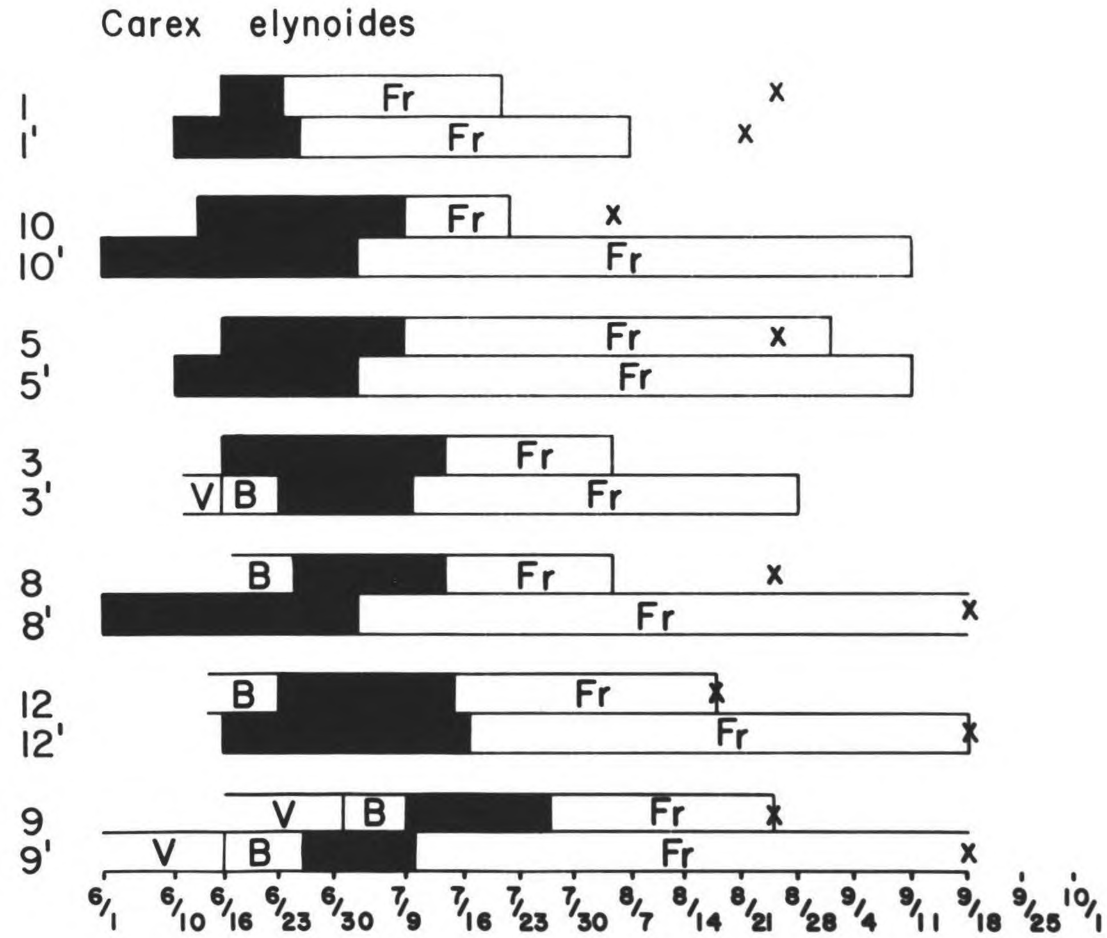

Fig. 21-24.--Carex elynoides

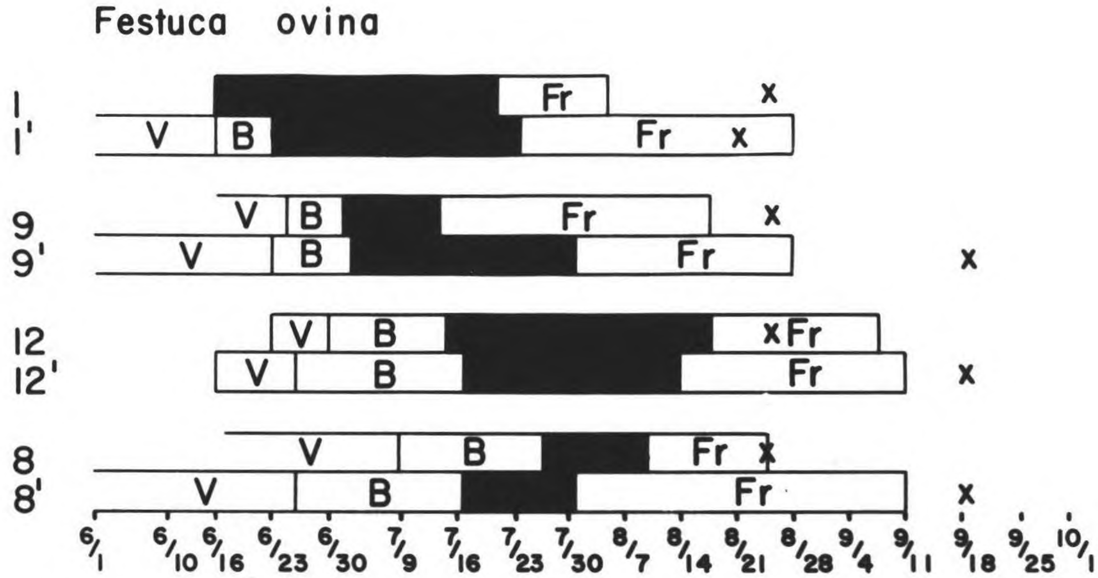

Fig. 21-25.--Festuca ovina.

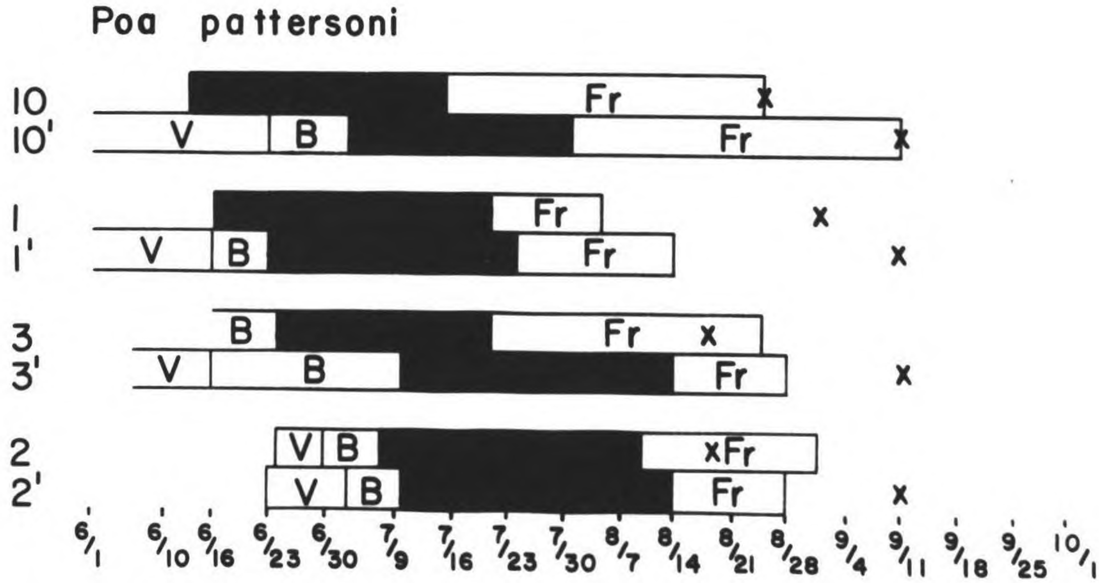

Fig. 21-26.--Poa pattersoni.

two growing seasons. Carex elynoides (Fig. 21-24) is the only species observed that appeared to be consistently earlier at all stations in 1961.

Examples of species restricted to the early, dry stations which showed prominent delays from 1960 to 1961 were Phlox caespitosa and Erigeron pinnatisectus (Figs. 21-3 and 21-4). Several species, found in both dry and mesic stations, exhibited the same pattern of delayed flowering in 1961. Included were Arenaria fendleri, Artemisia scopulorum, Eritrichium elongatum, Mertensia alpina, and Sedum stenopetalum (Figs. 21-9, 21-11, 21-2, 21-7 and 21-8).

Some of the species common to wet and dry areas showed late flowering at the early stations and similar or even somewhat earlier flowering in the late, wetter stations. Androsace septentrionalis var. subumbellata, Arenaria obtusiloba, Festuca ovina, Poa pattersoni, and particularly Geum turbinatum had this pattern (Figs. 21-23, 21-12, 21-25, 21-26, and 21-22). G. turbinatum flowered a week or more later at each of the dry stations in 1961. In Station 8 and Station 9, mesic and bog stations respectively, it flowered at about the same time in 1961, while at Stations 2 and 5 it flowered over a week later, due primarily to an extended bud stage in 1961. In two of the wet stations, Stations 11 and 12, G. turbinatum was nearly a week earlier in 1961.

Flowering patterns of species generally limited to the wet stations were usually less predictable, although species at Station 11 were most frequently earlier in 1961, while these same species were often similar or somewhat later in date of response at Stations 2 and

12. Species illustrating this were Deschampsia caespitosa, Juncus parryi, Ranunculus adoneus and Sibbaldia procumbens (Figs. 21-21, 21-19, 21-20 and 21-18).

Many species also showed a second phenomenon of notable consistency. In 1961 a large majority of the species remained in the bud stage for a longer time period than they did in 1960. This was particularly true of the early season species, although the trend was noted throughout the season and in some species from all stations. As mentioned, Geum turbinatum was more than a week longer in bud in Stations 2 and 5 in 1961. Erigeron pinnatisectus was over two weeks longer in bud in 1961 at Station 3 (Fig. 21-4) and Androsace septentrionalis var. subumbellata was about a week longer in bud at Stations 11 and 12 in the second season (Fig. 21-23). Arenaria obtusiloba was longer in bud at all stations in 1961, with period differentials ranging from about half a week at Station 11 to nearly three weeks at Station 5 (Fig. 21-12). Examination of the data in Fig. 21 for several other species indicates the frequency of this occurrence in 1961.

Although the general floral patterns were quite similar for each of the station groups (dry, mesic, wet and bog), minor station to station variation in phenological timing within the station groups was not uncommon. For example, the flowering times of Arenaria obtusiloba at Stations 1, 3 and 4 were quite different. In 1960 at Station 1 it flowered at the beginning of the third week in June, at Station 4 about six days later, and at Station 3 still another six days later, for a total variation of 12 days. In 1961 the variation for the same species at these stations amounted to 10 days between Stations 1 and 3, and 16 days between Stations 1 and 4. Within the wet stations (2, 11 and 12) similar variations were noted for species in common, especially for the early species.

As would be anticipated, the greatest variation in phenological phases was recorded for those species which were common to both the relatively dry and the wet, snow accumulation areas. Such species often lagged in their development by as much as two, three, and even four weeks in the latter sites. Comparisons of the Figs. 22-1 to 22-10, showing the patterns of phenological progression of all species at each of the stations, illustrate this point. For example, in 1961 Polygonum bistortoides flowered on June 26 at Station 1, but did not flower until July 17 and 24 at Stations 11 and 12, respectively. Geum turbinatum flowered on June 16 at Station 1 and 10 and was 25 days later at Stations 2 and 11. The degree of difference in flowering time was less pronounced in those species which respond toward the latter part of the season in the drier areas. As an example, Erigeron simplex flowered on July 10 at Stations 1 and 4, and the following week on July 17 at Station 12. Anemone zephyra flowered on July 3 in both Station 8 and Station 12.

Melt-water Investigation

The artificial application of melt-water by irrigation (Fig. 23-1) had marked effects on the rate of phenological development of most of the species examined (Figs. 23-2 and 23-3). Of 14 species which flowered in both the irrigated and non-irrigated quadrats, 12 were earlier in the non-irrigated quadrats (Fig. 24). This earliness ranged from 7 days in Geum turbinatum, Penstemon whippleanus, and

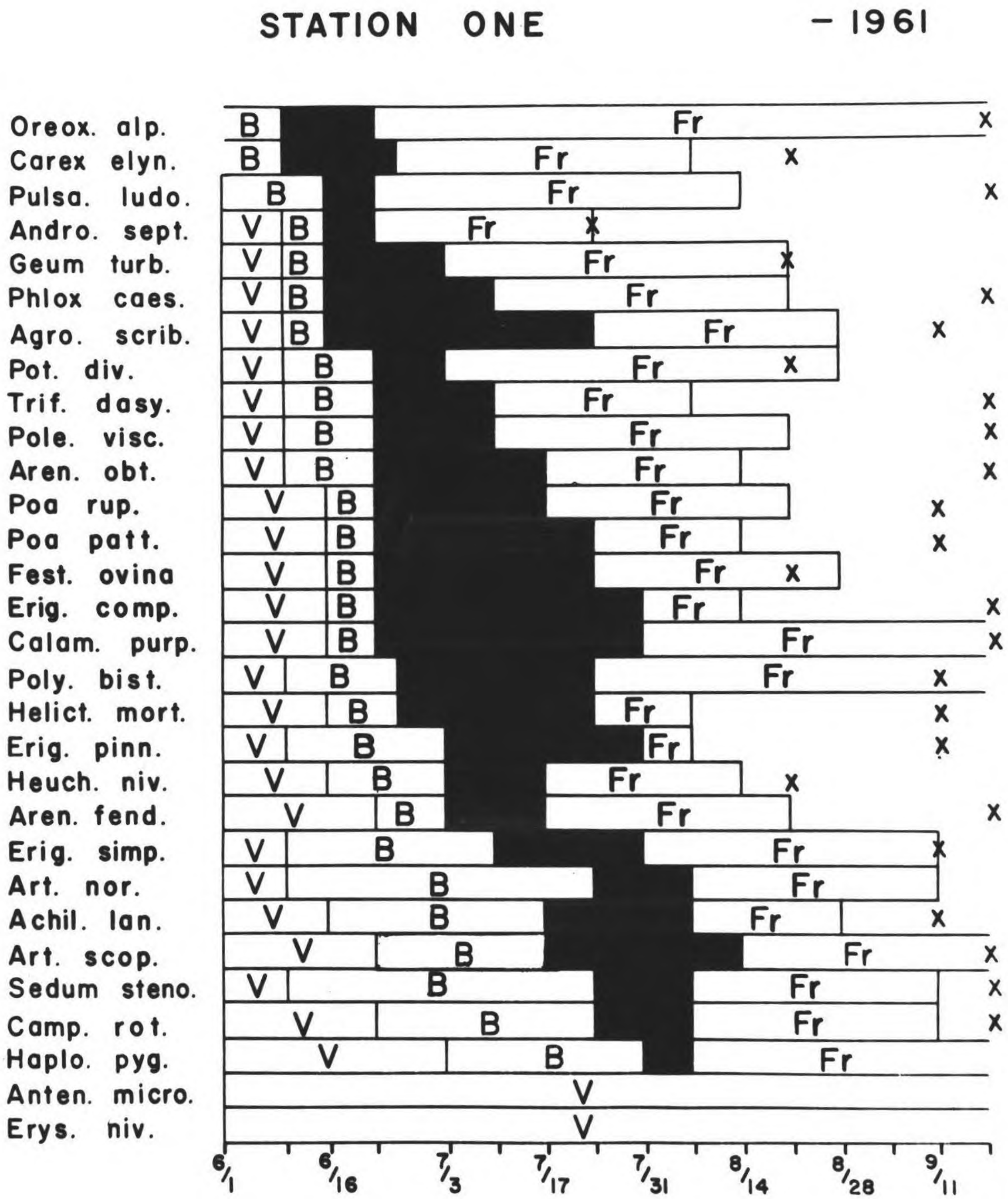

Fig. 22-1.--Station 1.

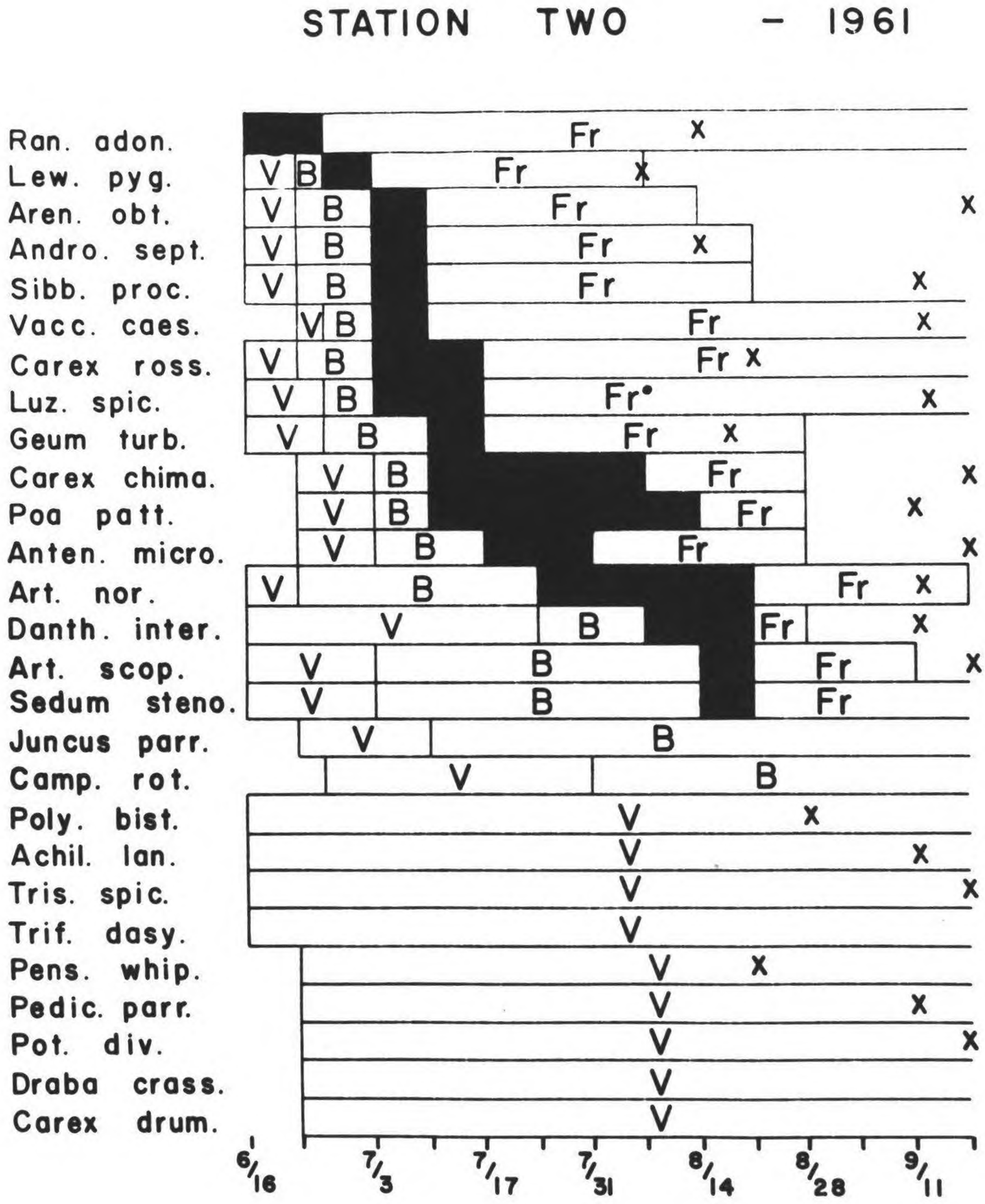

Fig. 22-2.--Station 2.

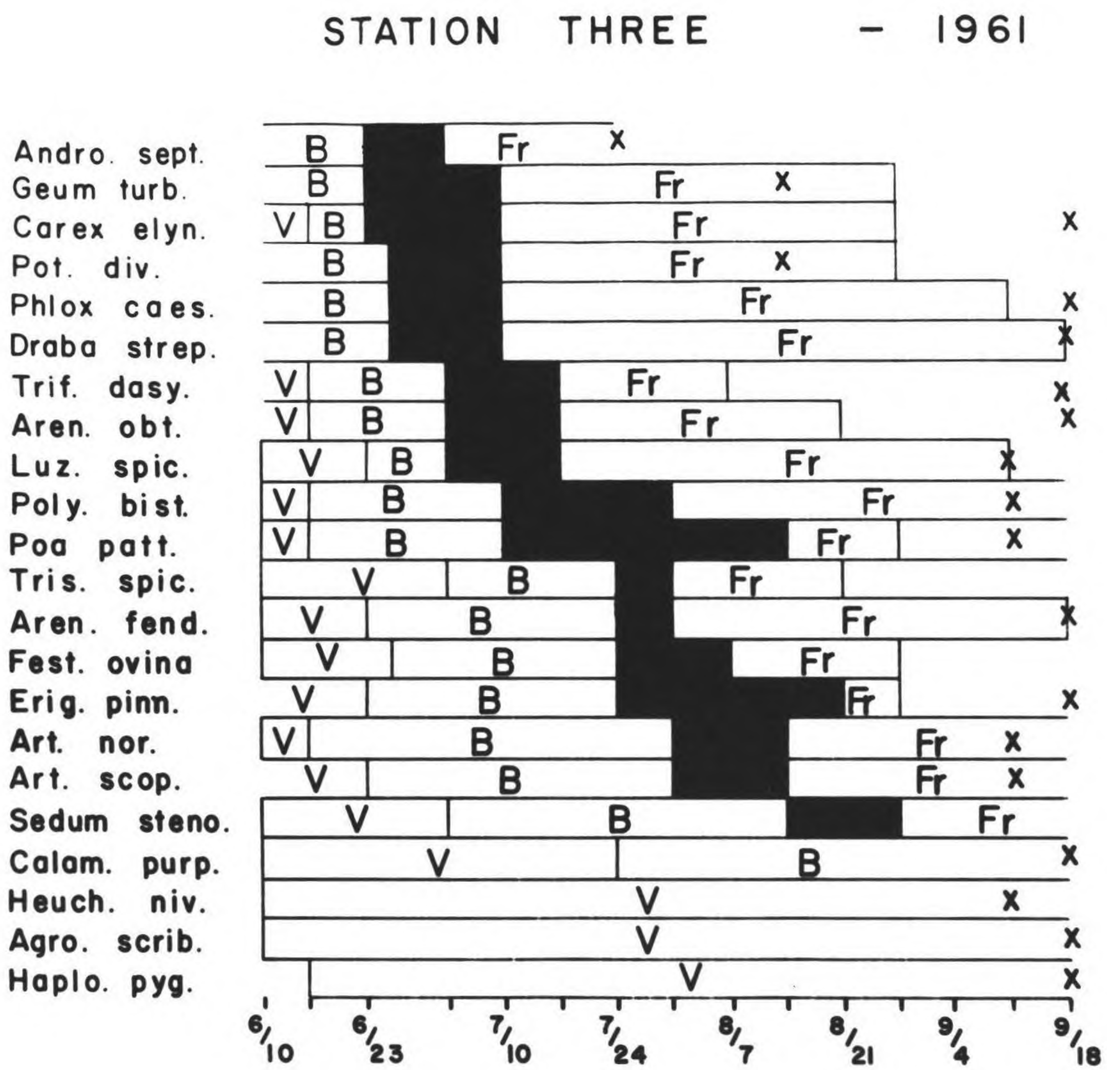

Fig. 22-3.--Station 3.

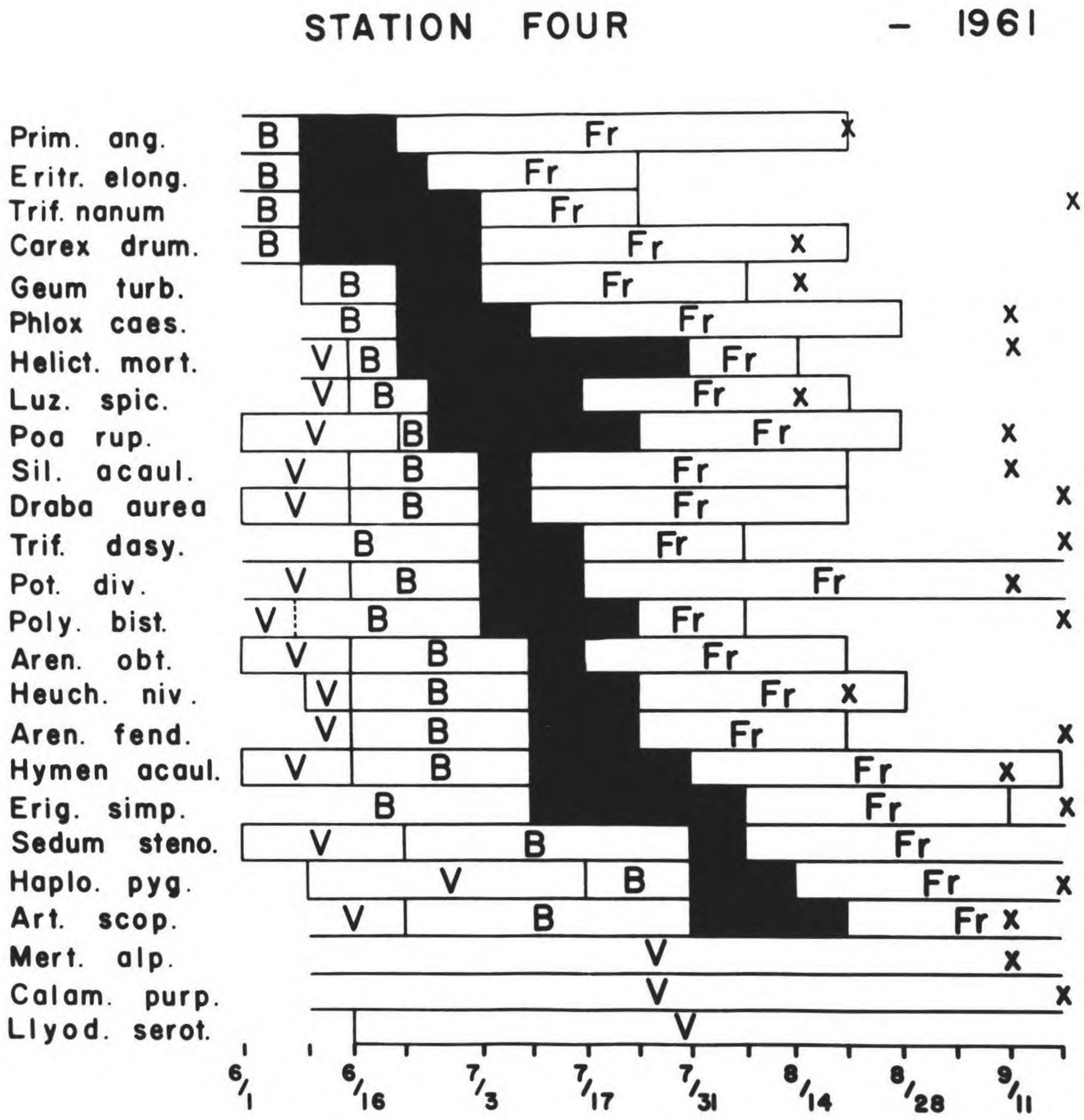

Fig. 22-4.--Station 4.

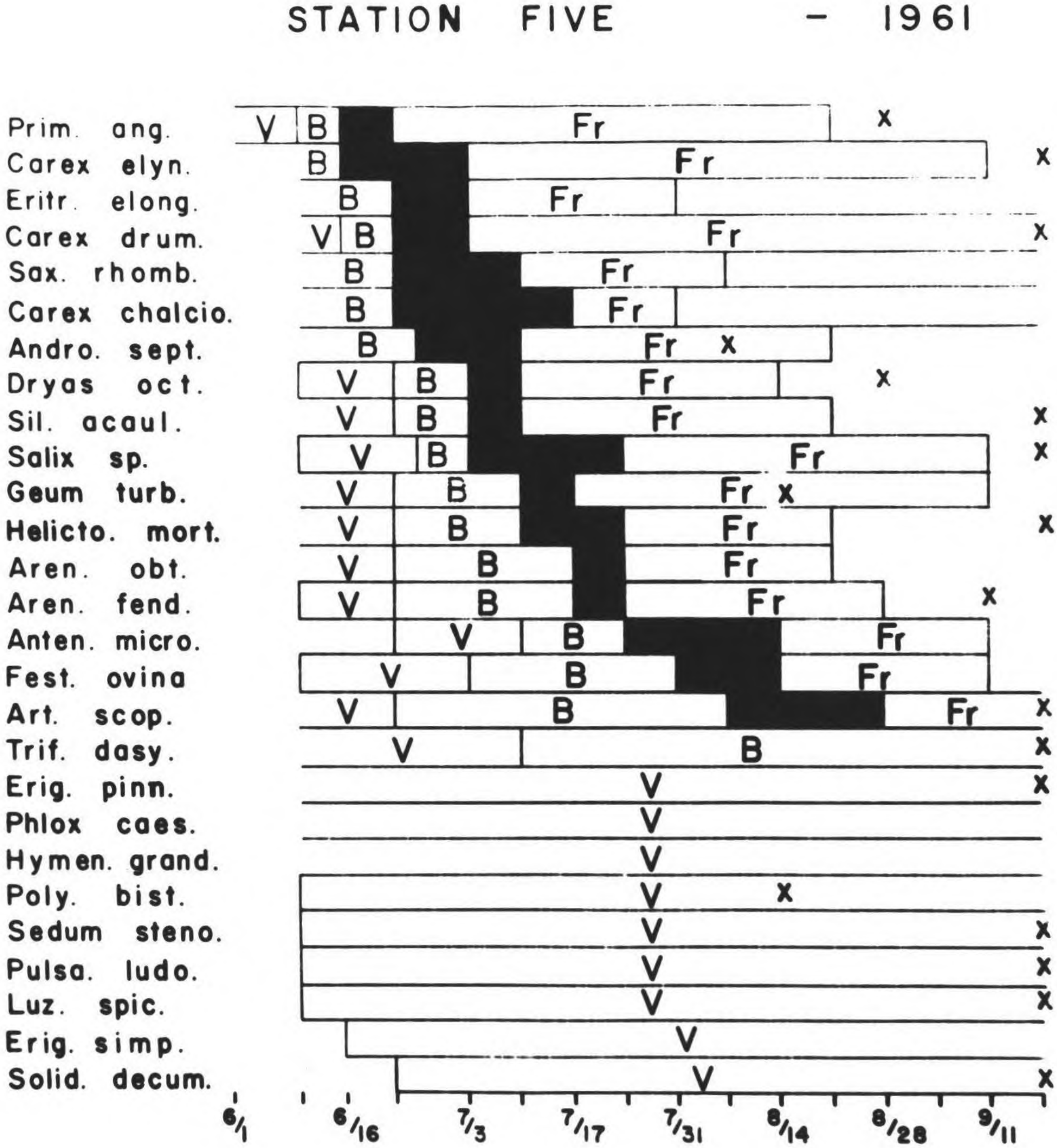

Fig. 22-5.--Station 5.

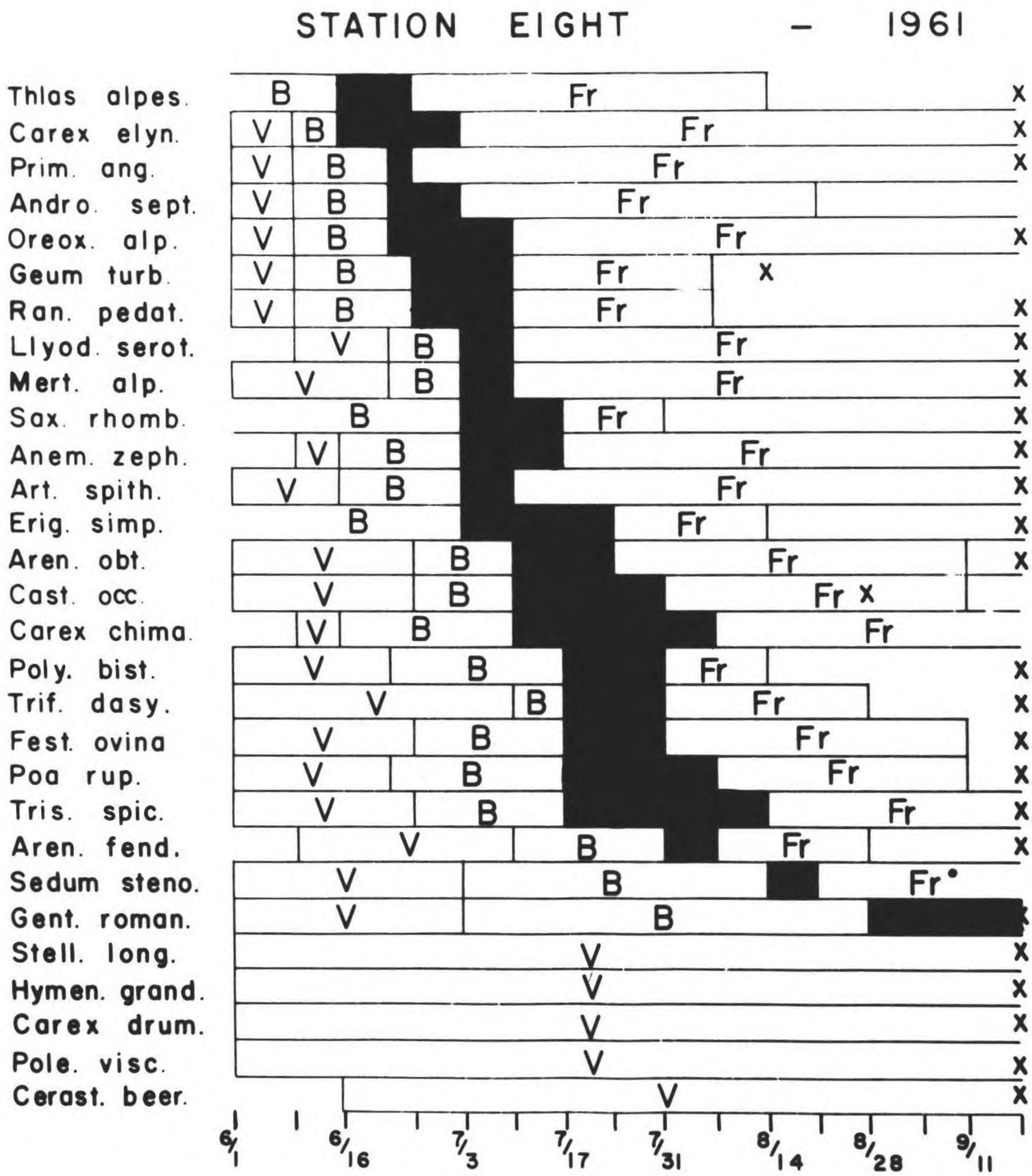

Fig. 22-6.--Station 8.

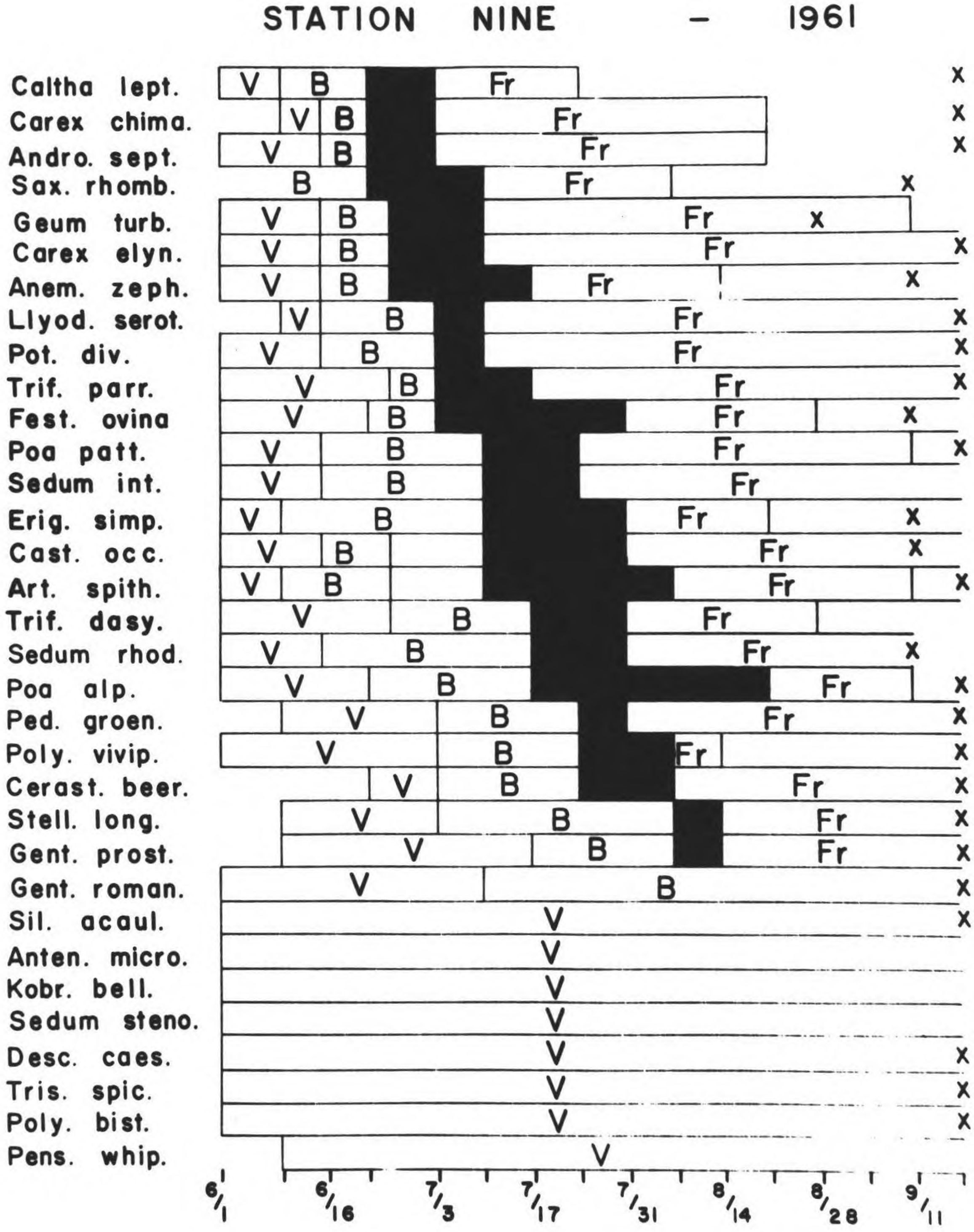

Fig. 22-7.--Station 9.

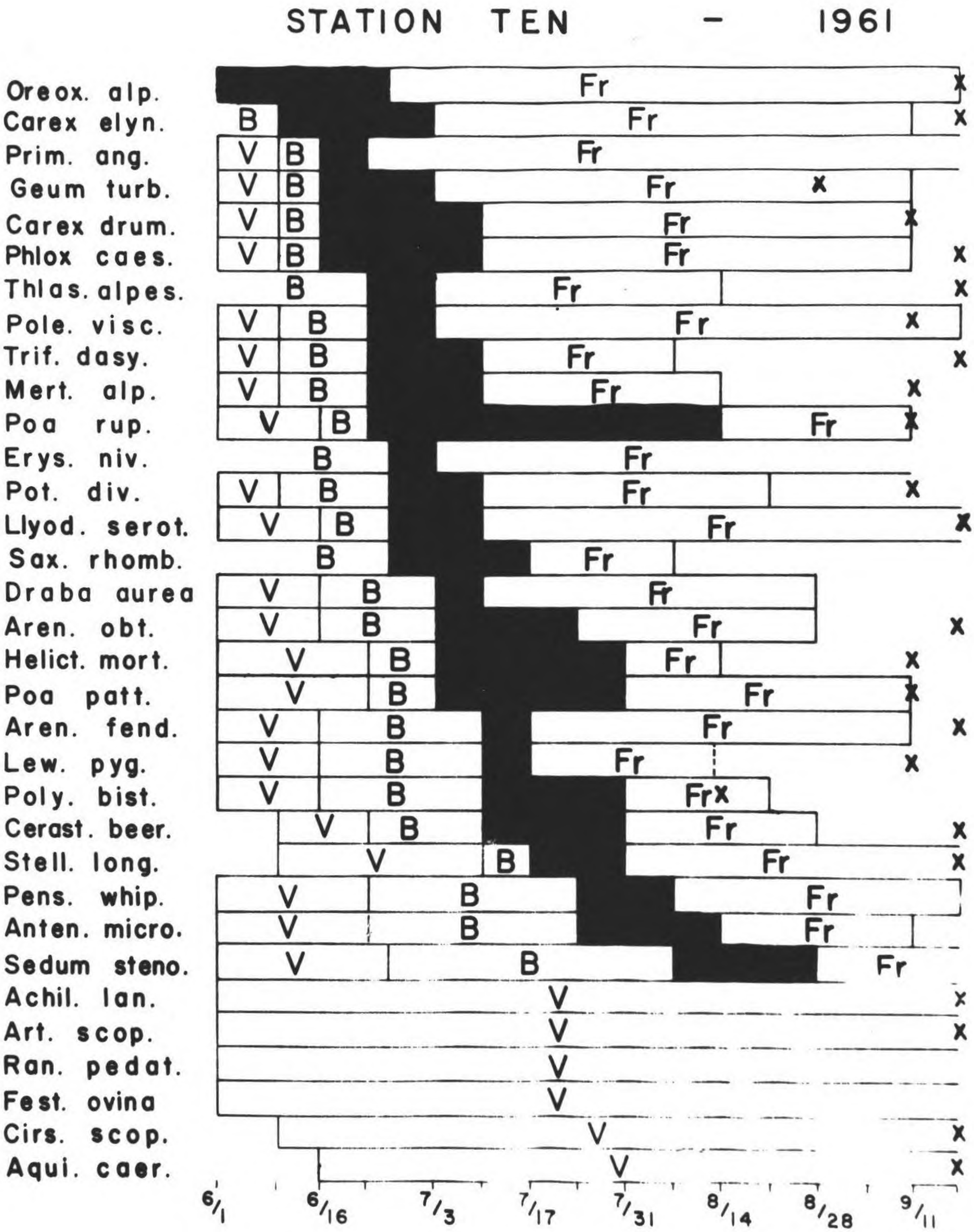

Fig. 22-8.--Station 10.

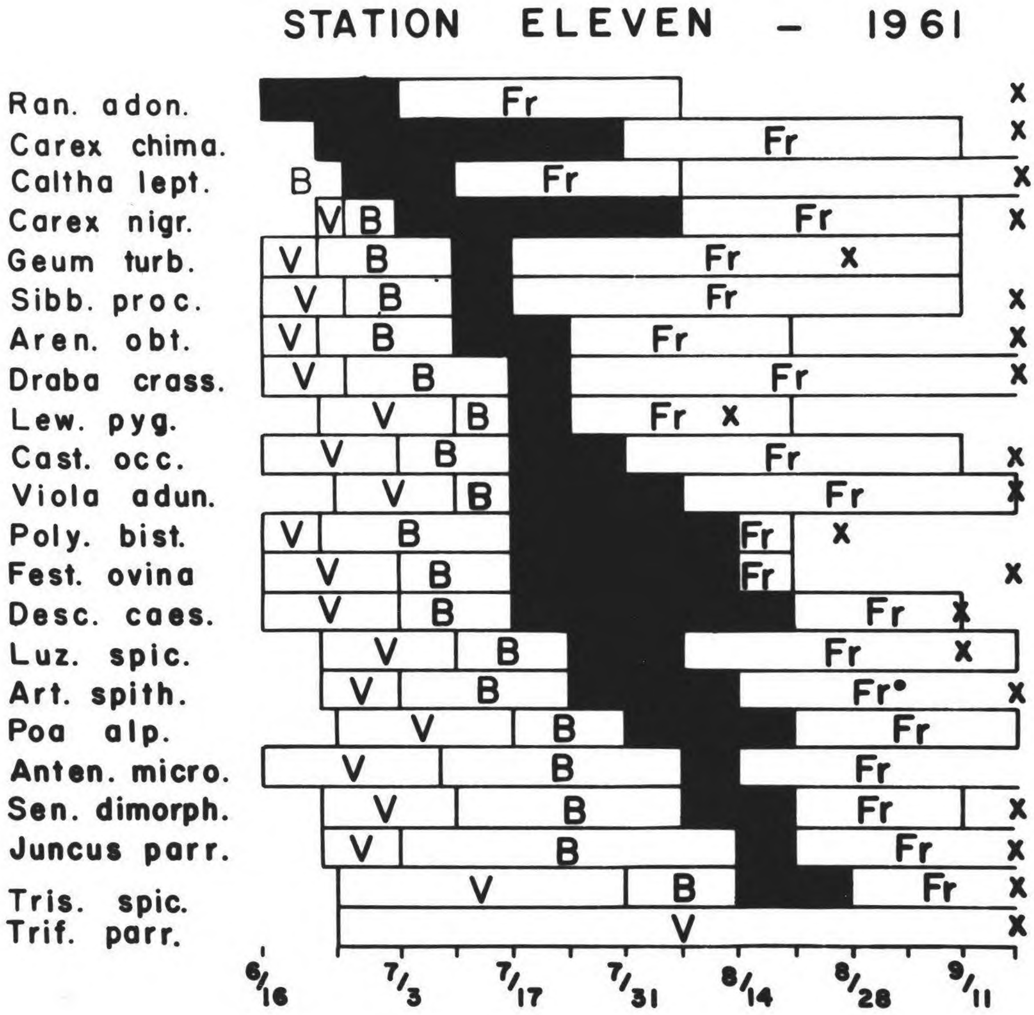

Fig. 22-9.--Station 11.

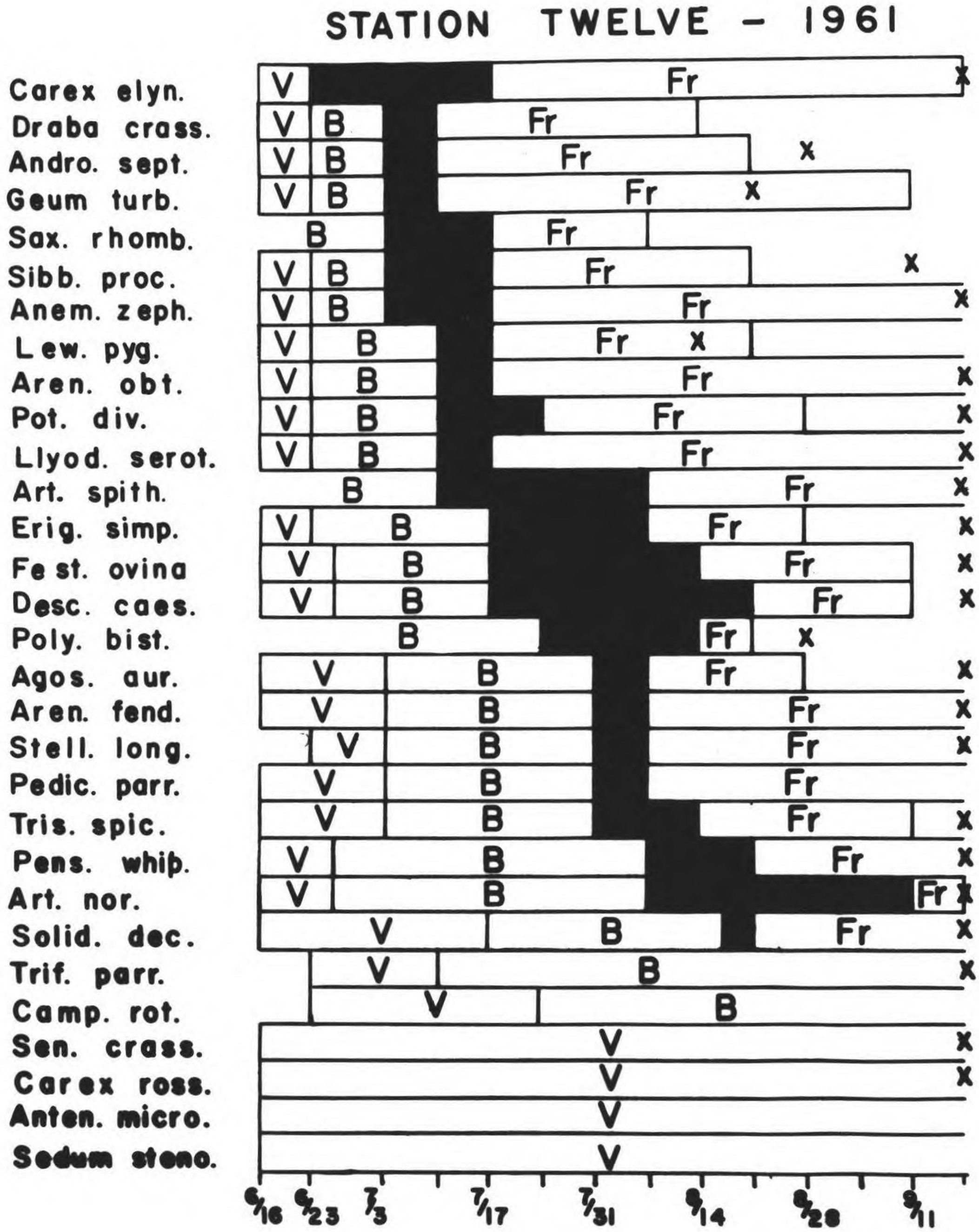

Fig. 22-10.--Station 12.

Fig. 23-1.--Photo illustrating position of the irrigation hose at Station 14.

Fig. 23-2.--Quadrat above soaker hose showing degree of vegetative development on July 10, 1961.

Fig. 23-3.--Quadrat below soaker hose showing degree of vegetative development on July 10, 1961.

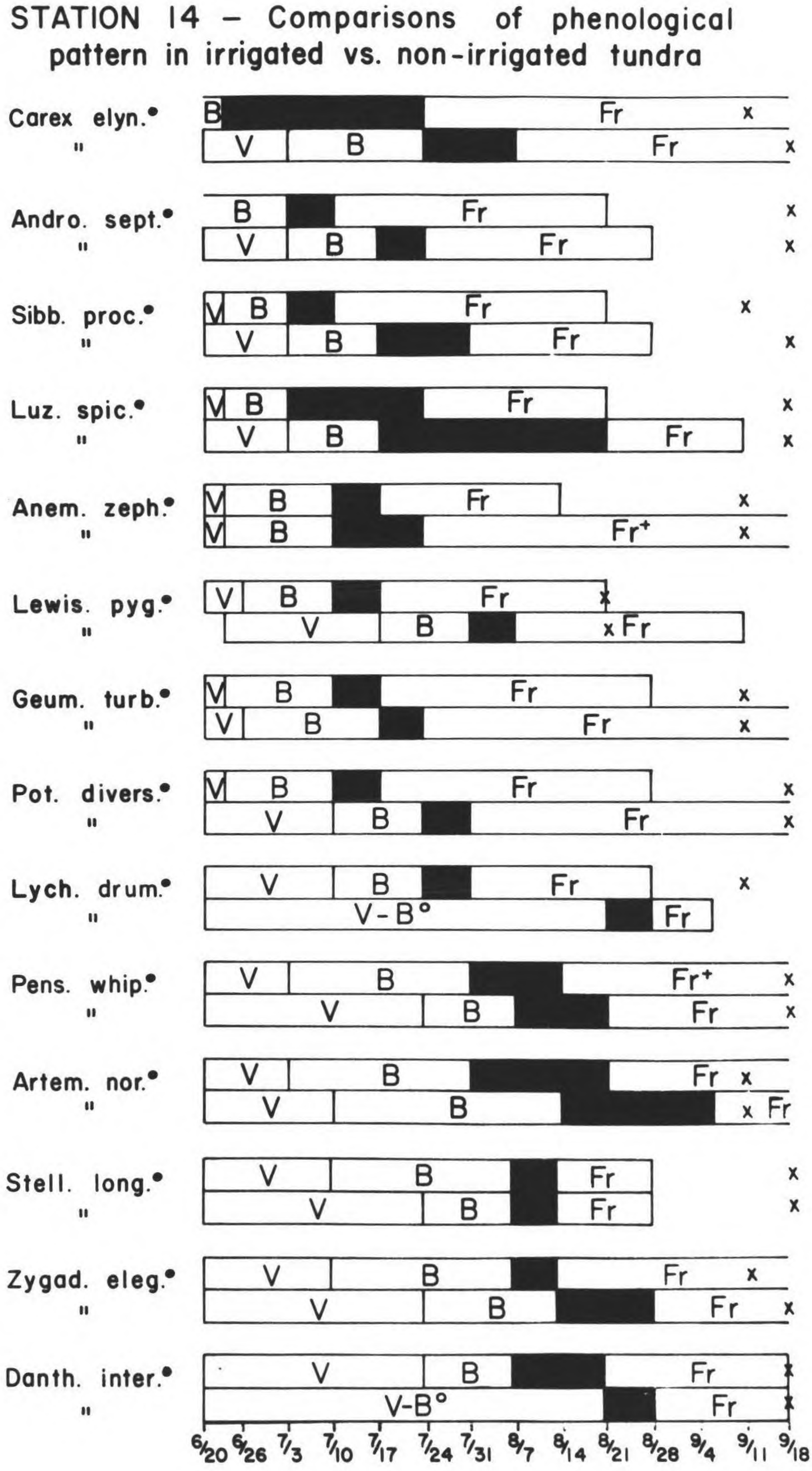
STATION 14 – Comparisons of phenological pattern in irrigated vs. non-irrigated tundra
Carex elyn.•
Andro. sept.•
Sibb. proc.•
Luz. spic.•
Anem. zeph.•
Lewis. pyg.•
Geum. turb.•
Pot. divers.•
Lych. drum.•
Pens. whip.•
Artem. nor.•
Stell. long.•
Zygad. eleg.•
Danth. inter.•
V
B
Fr
Fr+
V-B°
x
6/20 6/26 7/3 7/10 7/17 7/24 7/31 8/7 8/14 8/21 8/28 9/4 9/11 9/18

Fig. 24.

Zygadenus elegans to 31 days for Carex elynoides. Anemone zephyra bloomed on the same date in both quadrat situations, but in the irrigated quadrats it did not produce normal, mature fruit. Stellaria longipes also flowered on the same date under both conditions, but in both areas it budded after the irrigation water had ceased to flow for the season, and the specimen in the non-irrigated quadrat was in bud 14 days longer than was the one in the irrigated area.

In general, budding periods followed no set pattern under the two sets of conditions. Some species, Carex elynoides, Sibbaldia procumbens, Artemisia norvegica, and Geum turbinatum, were somewhat longer in bud in the irrigated plots, while others, Potentilla diversifolia, Zygadenus elegans, and particularly Penstemom whippleanus and Stellaria longipes were longer in bud in the non-irrigated plots.

Of the 14 species followed, 10 dispersed fruit or seeds on or before September 18 in the non-irrigated quadrats as compared to only 7 in the irrigated quadrats. Five species, Androsace septentrionalis var. subumbellata, Sibbaldia procumbens, Luzula spicata, Lychnis drummondii and Danthonia intermedia, were longer in the fruiting phase in the non-irrigated quadrats, and only two, Geum turbinatum and Potentilla diversifolia, which dispersed only in the non-irrigated quadrats, spent more time in fruit in the irrigated area. The fruiting period of only Stellaria longipes was the same in both situations.

Snow Retreat Investigation

The snow retreat study reveals that progressively later lying snow has pronounced effects on phenology and vegetational composition. From a Deschampsia caespitosa-Geum turbinatum-Trifolium parryi complex in the outer portion of the basin, the transition to the center terminated in an almost pure stand of Carex pyrenaica. Table V shows the vegetational pattern encountered in the seven groups of quadrats as well as the number of quadrats in which a species occurred in each group. Geum turbinatum occurred in all of the quadrats of peripheral Groups 1 and 2 but did not occur in Group 7. Deschampsia caespitosa, on the other hand, was most frequent in Groups 3-5, but was found in the majority of quadrats throughout the basin. Carex pyrenaica did not occur in the outer quadrat groups but was abundant in all quadrats of Groups 6 and 7.

Of the species found only in the inner portion of the Station, two, Antennaria microphylla and Oxyria digyna were considered to be chance inclusions rather than representative species. Neither was encountered in the frequency and cover quadrats, and they were quite characteristic of other habitats.

Many species that were common to the outer and inner portions, and some individuals of species found only towards the center of the area, did not have time to complete fruiting and dispersal in the center part (Table VI). Some of these did not progress beyond the bud or flower stage before the first snows of fall. Deschampsia caespitosa, Geum turbinatum, and Trifolium parryi, which occur in the peripheral groups as well as in limited amounts toward the center of the area, were able to complete their life cycle in the outer areas, but the degree of completion was progressively less nearer the middle. Several individuals of Carex pyrenaica and Erigeron melanocephalus were unable to complete the life cycle in the center part of the inner area.

Table V.--SPECIES DISTRIBUTION AND NUMBER OF QUADRATS OF OCCURRENCE IN QUADRAT GROUPS AT STATION 16.

Species	Quadrat Group Number						
	1	2	3	4	5	6	7
Llyodia serotina	2						
Senecio crassulus	1						
Anemone zephyra	1	1					
Potentilla diversifolia		1					
Sedum stenopetalum		1					
Arenaria fendleri		1					
Carex elynoides	1		1				
Erigeron simplex	1		3				
Trisetum spicatum	2	1	1	2			
Castilleja occidentalis	3	4	1	2			
Lewisia pygmaeus			2	1			
Polygonum bistortoides		3	1		1		
Luzula spicata	2	1		1	1		
Festuca ovina	6	6	4	4	4		
Artemisia spithamaea	1	1	2	2		2	
Sibbalbia procumbens	3	2	4		2	4	
Arenaria obtusiloba	3	1	1		2	1	
Androsace septentrionalis var. subumbellata	4	2		3	1	1	
Artemisia norvegica	7	3		1	2	3	
Trifolium parryi	9	9	10	10	10	3	
Geum turbinatum	10	10	8	6	7	1	
Draba crassifolia	1	4	3	4	8	2	
Erigeron perigrinus				1			
Deschampsia caespitosa	6	8	10	9	10	7	8
Ranunculus adoneus	5	8	8	6	8	4	1
Erigeron melanocephalus		1	2	3	8	9	10
Carex pyrenaica			2	4	1	10	10
Senecio dimorphophyllus			2	1			1
Poa alpina			1	1	2	5	3
Juncus parryi				1			5
Antennaria microphylla						1	
Oxyria digyna						1	
Epilobium alpinum							2

Table VI.--SPECIES DISTRIBUTION AND MAXIMUM STAGE OF DEVELOPMENT REACHED IN QUADRAT GROUPS AT STATION 16. (V = vegetative, B = flower bud, Fl = flower, Fr = fruit, D = dispersal).

Species	Quadrat Group Number						
	1	2	3	4	5	6	7
Llyodia serotina	V						
Senecio crassulus	V						
Anemone zephyra	V	V					
Potentilla diversifolia		V					
Sedum stenopetalum		V					
Arenaria fendleri		B					
Carex elynoides	Fr		Fr				
Erigeron simplex	Fr		D				
Trisetum spicatum	V	V	V	V			
Castilleja occidentalis	Fr	Fr	B	Fr			
Lewisia pygmaeus			Fr	Fr			
Polygonum bistortoides		D	D		Fr		
Luzula spicata	Fr	D		V	Fr		
Festuca ovina	D	Fr	Fr	Fr	Fr		
Artemisia spithamaea	Fr	V	V	Fr		Fl	
Sibbaldia procumbens	Fr	Fr	Fr		Fr	Fr	
Arenaria obtusiloba	D	Fr	Fr		Fr	Fr	
Androsace septentrionalis var subumbellata	Fr	Fr		Fr	Fr	B	
Artemisia norvegica	D	Fr		Fr	Fr	B	
Trifolium parryi	V	V	D	Fr	Fr	V	
Geum turbinatum	D	D	D	Fr	Fr	Fr	
Draba crassifolia	D	D	D	Fr	Fr	Fr	
Erigeron perigrinus				Fl			
Deschampsia caespitosa	D	D	D	Fr	Fr	Fr	Fl
Ranunculus adoneus	D	D	D	D	D	D	V
Erigeron melanocephalus		D	D	Fr	Fr	Fr	Fr
Carex pyrenaica			Fr	D	Fr	D	Fr
Senecio dimorphophyllus			Fr	Fr			V
Poa alpina			Fr	V	Fr	Fr	Fr
Juncus parryi				Fr			Fr
Antennaria microphylla						V	
Oxyria digyna						V	
Epilobium alpinum							Fl
	---	---	---	---	---	---	---
Total number species	19	20	19	19	15	15	8

The number of species encountered in each of the quadrat groups was relatively uniform throughout the first four groups (19, 20, 19 and 19). A reduction to 15 species occurs in Groups 5 and 6, followed by a sharp decrease to only 8 species in Group 7.

No evidence was found to indicate that there was a compression of any of the phenological phases for those species that were found in more than one of the quadrat groups. It was noted, however, that the species in the center of the station were very quick to respond to snow release. Carex pyrenaica and Erigeron melanocephalus, species almost exclusive to the inner area, consistently appeared with buds in an advanced state. Certain individuals of Deschampsia caespitosa were noted to have the floral boot ruptured at the time of snow release.

Phenological Summary

The phenological patterns of the alpine species are highly variable and difficult to classify. The length of time a species was in a particular phenologic phase varies a great deal between species, between stations, and between years. Plants which went through the complete life cycle showed variations in timing of particular phases, but generally these variations were within rather narrow limits for a given species. The variations encountered between species were of considerable more consequence.

Table VII shows a general phenological summary for the species studied. In addition, the station types in which each was found, and the relative amounts of seed production is given.

In general, the budding period lasted from two to five weeks, but for certain species it was somewhat shorter and for others it was

	Station Group of Occurrence				Time of Flowering				Time in Bud (weeks)					Time in Flower (weeks)				Time in fruit (weeks)					Seed Production		
	1	2	3	4	V	E	M	L	1	2	3	4	5	1	2	3	4	1	2	3	4	5	A	M	P
BORAGINACEAE																									
Eritrichium elongatum	x	x			x				x*	m				o	m						x	x		x	
Mertensia alpina	x	x			o	x			x*	x				m	x	o					m	x+			x
CAMPANULACEAE																									
Campanula rotundifolia	x		x					x				x	x	x	m							x+			x
CARYOPHYLLACEAE																									
Arenaria fendleri	x	x	x			x	x	x	o	x	m	m		x	x						x	x	x		
Arenaria obtusiloba	x	x	x		o	x	x		o*	x	m			x	x						x	x+	x		
Cerastium beeringianum	x	x		x			m	x	o	m	m				x	m			o		m			x	
Lychnis drummondii			m					m		m	m					m				m	m			m	
Silene acaulis	x	x		x		x			o	x				x								x		x	
Stellaria longipes	x	x	x	x			x	x			o	x	m	x	m				o			m		x	
COMPOSITAE																									
Achillea lanulosa var. alpicola	x		x				x	x		o	o	m	m		o	x				x	o				x
Agoseris aurantica			x					m			m	m		m					m	m				m	
Antennaria microphylla	x	x	x	x		o	x	x	o	x	o				m	x	o			o	x	x		x	
Artemisia norvegica	x	x	x			o	x	x		o		m			m	x	o				m	x		x	
Artemisia scopulorum	x	m	x			o	x	x		o	o		m		x	x	o				m	x+	x		
Artemisia spithamaea		x	x	x		m	x	x		o	x	m				x	x				m	x			x
Cirsium scopulorum	x						o					o		o						o				o	
Erigeron compositus	x				x	x			o*	m	m				o	x	m		o	m	m		x		
Erigeron melanocephalus			m					m			m*	m*			m	m				m	m			m	
Erigeron pinnatisectus	x					x	x	x	o*	o	m	m			o	x	m	x					x		
Erigeron simplex	x	x	x	x		x	x	x		o	x	m			o	x	m			x	o	o		x	
Haplopappus pygmaeus	x						o	x		o	x	m		x	x						m	x+		x	
Hymenoxys acaulis	x					o	x		o*		m					x					m	x+		x	
Hymenoxys grandiflora	x	x				o	o		o	o						o				o	o		o		
Senecio crassulus			x					o				o			o					o				o	
Senecio dimorphophyllus			x					x			o	m		o	m				m	m	o			x	
Solidago decumbens		x	x					x		o	o	m		m		o						x+		x	

	Station Group of Occurrence				Time of Flowering				Time in Bud (weeks)					Time in Flower (weeks)				Time in fruit (weeks)					Seed Production		
	1	2	3	4	V	E	M	L	1	2	3	4	5	1	2	3	4	1	2	3	4	5	A	M	P
CRASSULACEAE																									
Sedum integrifolium				m			m				m				m						m				m
Sedum rhodanthum				x			x	m				x			x							x		x	
Sedum stenopetalum	x	x	x	x			o	x				x	x	x	x						x	x^+	x		
CRUCIFERAE																									
Draba aurea	x				o	x			o*	m	m			x								x^+		x	
Draba crassifolia			x			x			o	m	m			x						o	x	o		x	
Draba streptocarpa var. streptocarpa	x					x			o	m				o	m							x		x	
Erysimum nivale	x				o	x			o*		m			x								x^+		x	
Thlaspi alpestre	x	x			x	x			x*	m				x*	m							x^+	x		
CYPERACEAE																									
Carex chalciolepis		m				m			m							m						m^o		m	
Carex chimpahila		m	m	m		m	m		m							m	m				m	m^o		m	
Carex drummondiana	x	x			x	x			x*							m	x					x^o		x	
Carex elynoides	x	x		x	x	x			x*						x	x						x^o		x	
Carex haydeniana		x				o			o						o							o^o	o		
Carex nigricans			x			m	o	o	x						x	m	m					x^o		x	
Carex pyrenaica			m					m	m*					m	m							m^o		m	
Carex rossii			x			m		o		x	o				x	o						x^o			x
Kobresia bellardi				x		o			o	o					o							o^o		o	
ERICACEAE																									
Vaccinium caespitosum			x			x			x*					x								x^o			x
GENTIANACEAE																									
Gentiana prostrata				x				x		o	m			m	o							x^o		x	
Gentiana romanzovii		x		x				x				m	x	o		m						x^o		x	

	Station Group of Occurrence				Time of Flowering				Time in Bud (weeks)					Time in Flower (weeks)				Time in fruit (weeks)					Seed Production		
	1	2	3	4	V	E	M	L	1	2	3	4	5	1	2	3	4	1	2	3	4	5	A	M	P
GRAMINEAE																									
Agropyron scribneri	x				m	x			x*							o	m					x^o		x	
Calamagrostis purpurascens	x					x			m*	x					x	o						x		x	
Danthonia intermedia			x					x		x				o	m					x	m			x	
Deschampsia caespitosa		x	x				x	x		x	x					o	x			x	x			x	
Festuca ovina	x	x	m	x	o	x	x	x	o*	x	m	m			x	x	x		o	x	x			x	
Helictotrichon mortoniana	x	x			x	x			x*	m					o	x	x	o	x	m				x	
Poa alpina			m	x			m	x	o*	x	m					x	m			m	x			x	
Poa pattersoni	x	x	x	m	o	x	x		x*	m	m						x		o	x	x	x	x		
Poa rupicola	x	x			o	x	x		x*	m						x	x		o		m	x	x		
Trisetum spicatum	x	x	x	x			m	x		x	x				m	x	o		o	x	m			x	
JUNCACEAE																									
Juncus parryi			x			o	o	x		o	o		m	x	o					o	o	m^o		x	
Luzula spicata	x	x	x			x	x	m	x	x				o	x	m					o	m	x		
LEGUMINOSAE																									
Trifolium dasyphyllum	x	x	x	x	o	x	x	m	o*	m	m			o	x					o	x				x
Trifolium nanum	x				x				x*					o*		m				m	o				x
Trifolium parryi			x	x		x	x		x						x						o	m^o			x
LILIACEAE																									
Llyodia serotina	x	m	x	x	o	m			o*	m				x	x							x^o			x
Zygadenus elegans			m					m				m		m								m^o		m	
ONAGRACEAE																									
Epilobium alpinum			m					m		m				m	m					m^o				m	
POLEMONIACEAE																									
Phlox caespitosa	x	x			x	m	m		x*	m				o	o	m	m					x^+		x	
Polemonium viscosum	x	x			o	x	m		o*	m				o	x							x^+		x	
POLYGONACEAE																									
Polygonum bistortoides	x	x	x	x		x	x	x	o*	x	x	m			x	x	x	x	x	m				x	
Polygonum viviparum				x			x	x		o	m				x			m	o				x		
PORTULACEAE																									
Lewisia pygmaea	x		x			x	x	m	x	x				x						o	x	m		x	

	Station Group of Occurrence				Time of Flowering				Time in Bud (weeks)					Time in Flower (weeks)				Time in Fruit (weeks)					Seed Production		
	1	2	3	4	V	E	M	L	1	2	3	4	5	1	2	3	4	1	2	3	4	5	A	M	P
PRIMULACEAE																									
Androsace septentrionalis var. subumbellata	x	x	x	x	x	x	x		x*	m				x	x					x	x	x^+	x		
Primula angustifolia	x	x			x				x*	m				x	x						o	x^+		x	
RANUNCULACEAE																									
Anemone zephyra		x	x	x		x	x		o*	m	m				x	m					m	o	x		
Aquilegia caerulea	x					o			o							o						o		o	
Caltha leptosepala			x	x	o	x			x*					o*	x					m	x	o	x		
Pulsatilla ludoviciana	x	x			x				x*					x*								x^+	x		
Ranunculus adoneus	x		x		x	x			x*					x*	m						o	m	x		
Ranunculus pedatifidus	m	x			o	x			o*	m*				o*	m							x^+		x	
ROSACEAE																									
Dryas octopetala		x				x	x		x	x				x							x	x	x		
Geum turbinatum	x	x	x	x	x	x	x	x	x*	x				x	x						o	x^+	x		
Potentilla diversifolia	x		x	x	o	x	x		o*	x				x	x						x	x^+	x		
Sibbaldia procumbens			x			x	x	o	o	x				x	x						o	x^+	x		
SALICACEAE																									
Salix sp.		x		x		m			m							m						m^+	m		
SAXIFRAGACEAE																									
Heuchera nivale	x					x			o*	m					x					o	m	m			x
Saxifraga rhomboidea	x	x	x	x	o	x			o*	x	m				x	m				x	x	x		x	
SCROPHULARIACEAE																									
Castilleja occidentalis		x	x	x		o	x	x	o*	x					x	x						o	x^+		x
Pedicularis groenlandica				x				m			m			m								m^o		m	
Pedicularis parryi			x					x			o	m	x								o	m^o		x	
Penstemon whippleanus	x		x			o	o	m			o	x	m^+	m	x						o	m^o		x	
UMBELLIFERAE																									
Oreoxis alpina	x	x			x	x			x*						x							x^+		x	
VIOLACEAE																									
Viola adunca			m				m			m						m						m^+		m	

longer. For example, many of the very early season species took less than a week to develop a bud into an open flower. Eritrichium elongatum, Oreoxis alpina, and Phlox caespitosa are species of dry areas that flowered in a short time after bud enlargement. Trifolium parryi, is an example of species that may bud and flower within a week after the overlying snow disappears. Ranunculus adoneus occasionally flowered right up through the snow; thus, for this species the length of the period of bud development is uncertain. Carex pyrenaica, Erigeron melanocephalus, and on rare occasions Geum turbinatum and Deschampsia caespitosa, came out from under the snow with the buds in an advanced state, and flowering took place in a matter of days. The carices studied seemed to proceed very quickly from the appearance of the bud to anthesis. Among the grasses, Poa pattersoni, P. rupicola, P. alpina, and Agropyron scribneri were noted to flower within a week after the first detection of a floral axis in the boot of fertile culms.

Species which exhibit periods longer than five weeks in the bud phase included Gentiana romanzovii, Penstemon whippleanus and Sedum stenopetalum. The latter two were generally in bud from five to six weeks, while the gentian was commonly eight weeks in the bud.

The flowering time for most species ranged from two to three weeks. This period was not easily determined in the grasses, but floral durations of four weeks seemed to be common. Several composites and carices were in flower nearly four weeks. Individuals of Phlox caespitosa and Polygonum bistortoides were also noted to flower for four weeks. Several species completed the flowering phase within a week. Dryas octopetala, Gentiana prostrata, Lewisia pygmaeus, Primula angustifolia, Pulsatilla ludoviciana, Silene acaulis, Solidago decumbens, Juncus parryi, many of the Drabas, and in many instances Geum turbinatum, Potentilla diversifolia, and Sibbaldia procumbens were examples of this.

The time for fruit development and maturation was also quite variable, but usually lasted from four to five weeks. Notable exceptions exhibiting shorter periods were Erigeron pinnatisectus and Polygonum viviparum which frequently dispersed seed within a week after flowering. Polygonum bistortoides was also noted to do this on occasion, but more commonly it required about three weeks in the fruiting stage. Phlox caespitosa, Polemonium viscosum, Primula angustifolia, Pulsatilla ludoviciana, and Thlaspi alpestre were often in fruit for more than five weeks. Individuals of Polemonium viscosum at Station 10 took from 8 to 11 weeks from flowering to seed dispersal. The developing seeds of nearby plants of this species were examined throughout this period and were found to be quite green up until about two weeks before dispersal. Androsace septentrionalis var. subumbellata often required eight to nine weeks, but almost as frequently dispersed seed within three weeks. This was an extreme case of the variation encountered in the length of time for a particular phase in a given species.

Phenological Deviations

Several phenomena were noted during this study relating to deviations from normal phenological patterns. Certain individuals, especially of Geum turbinatum and Artemisia norvegica, showed apparent vigorous vegetative growth, but no floral bud development.

Many times a species produced floral buds which did not go on to develop flowers. This was frequently noticed in Artemisia spithamaea, Trifolium dasyphyllum, T. parryi, Castilleja occidentalis and Campanula rotundifolia, and was less common in Dryas octopetala, Erigeron simplex, E. melanocephalus, Gentiana romanzovii, Geum turbinatum, Saxifraga rhomboidea and Zygadenus elegans.

Many individuals produced abundant flowers but then failed to develop mature fruit or seeds. Most notable in this group was Trifolium parryi; the examination of several hundred pods of this species yielded only 28 seeds. Artemisia spithamaea and Campanula rotundifolia were two more exceptionally poor seed producing species. Some individuals of Anemone zephyra and Trifolium nanum often did not produce any seed, while others set abundant seed. Other species which occasionally exhibited this behavior were Artemisia norvegica, Carex drummondiana, C. rossii, Castilleja occidentalis, Erigeron simplex, Eritrichium elongatum, Heuchera nivale, Llyodia serotina, Luzula spicata, Mertensia alpina, Oreoxis alpina, Phlox caespitosa, Ranunculus adoneus, Sedum integrifolium, S. stenopetalum, Silene acaulis and Vaccinium caespitosum.

Several species, especially certain grasses and carices, had not dispersed at the time of the last fall observations in mid-September. Agropyron scribneri and Carex elynoides, prominent in this group, were apparently ripe a month or more before these last observations. Heads of A. scribneri shattered readily when touched, however, and slight pressures on the heads of the C. elynoides caused the fruits to drop off. With the herbaceous species the failure to disperse seeds appeared to be the result of insufficient time to mature fruit or seeds rather than the retention of mature disseminules.

Late Season Activity

A late reblooming was commonly noted in both years by individuals of several species, however, the number of flowers produced was significantly less than in the normal floral period. Phlox caespitosa, which began a major floral period on June 16 exhibited a rebloom on August 28. Trifolium dasyphyllum flowered on July 1 in 1960 and rebloomed on October 1, and in 1961 bloomed on July 3 and again on September 11. Erysimum nivale flowered first on June 26 and again on September 18th, and a still later individual was seen flowering on October 15, 1961, when much of the area was already under snow. Other species frequently exhibiting this late season reblooming included Androsace septentrionalis var. subumbellata (7/3 and 9/11), Arenaria obtusiloba (7/17 and 9/18), Geum turbinatum (7/3 and 8/28) and Haplopappus pygmaeus (7/31 and 9/18); all dates were for 1960 although each of these species also rebloomed late in 1961.

The re-initiation of vegetative growth near the end of the growing season was a common occurrence. Saxifraga rhomboides produced a new, reduced rosette of leaves very similar in size and pattern to that exhibited by the species when it first appeared from under the snow in spring. Similar vegetative development was noted for Caltha leptosepala, Hymenoxys grandiflora, Ranunculus adoneus, Primula angustifolia, Thlaspi alpestre, Potentilla diversifolia, Erysimum nivale, Artemisia scopulorum, Erigeron compositus, E. pinnatisectus, Achillea lanulosa var. alpicola, Sibbaldia procumbens, Heuchera nivale, Draba aurea, Silene acaulis, Arenaria fendleri, and Anemone zephyra. Most of this activity took place during the latter part of September or very early October. Arenaria obtusiloba added new, reduced, green leaves to the cushions as late as October 1.

In addition to a period of vegetative production late in the season, some species developed a prominent perennating bud with apparently all of the primordia for development in the following season. Species in which a perennating bud was observed with certainty were Geum turbinatum and Potentilla diversifolia. By general appearances, it seems that Artemisia norvegica, Pulsatilla ludoviciana, and Erysimum nivale also developed this structure.

Dormancy Responses

The onset of dormancy in alpine species appeared to be a highly variable response. Individuals of some species, especially Saxifraga rhomboidea, showed signs of browning up very early in the year, and yet a portion of the plant stayed green and apparently photosynthetically active throughout the season. Other species, for example Sedum stenopetalum, seemed to change very little from the beginning to the end of the season, giving the impression of an evergreen. Often reddish in color when first observed, the plants gradually became green in summer, and in late fall many of them again took on the reddish appearance. Other species which tended to be almost evergreen included Eritrichium elongatum, Arenaria obtusiloba, Phlox caespitosa, and the branches of Vaccinium caespitosum. All were somewhat chlorotic appearing early in the spring, and again late in fall, but a considerable amount of green tissue was present.

Damage by Animals and Fungi

Certain of the alpine species seem to be selectively affected by higher animals, insects, or fungal diseases. At each of three widely separated stations *Penstemon whippleanus* was found to suffer heavy leaf damage caused by an unidentified caterpillar. This caterpillar was not observed feeding on any other species. In addition, grasshopper nymphs seemed to feed rather heavily on the *P. whippleanus*.

Another example of extreme selectivity of a species by some animal was seen in *Erigeron compositus*. This species and *E. pinnatisectus* had several flowering heads in bloom during the same time interval at Station 1. Shortly after the onset of fruiting it was noted that several heads of *E. compositus* had been removed, while none of those of *E. pinnatisectus* were disturbed. A week later all heads of the first species were gone, and still none of the heads of the latter species had been touched. Unfortunately, the agent responsible for the removal of the heads of *E. compositus* was not discovered.

Polygonum bistortoides, *Saxifraga rhomboidea* and *Ranunculus adoneus* also suffered heavy losses of seed heads to birds or other animals. While searching for seeds of *R. adoneus* in an area of heavy plant concentrations, it was often necessary to examine as many as twenty or thirty plants before finding one with the seed head still intact. In all three species the seed head had usually been removed just below the receptacle. Some of the developing fruits of *Vaccinium caespitosum* were taken by birds. *Luzula spicata*, *Carex drummondiana*, *C. elynoides*, *Primula angustifolia* and *Hymenoxys grandiflora* suffered relatively minor losses due to the action of birds or animals.

Hymenoxys appeared to be a favorite food of the marmot (Marmota flaviventris), and in places the damage was extensive. The marmots pulled up the plant, ate the taproot, and discarded the rest.

Fungal infections were uncommon but highly selective, and in susceptible species the incidence was often quite high. Most prevalent was a smut found in the ripening seeds of many of the carices studied, especially Carex elynoides and C. rossii. In certain locations nearly the entire population was infected and seed production was nil. Of the forbs, only three species, Erigeron simplex, Potentilla diversifolia, and Trifolium dasyphyllum, were commonly noted to be infected. The latter two species were subject to the orange or yellow stage of an unidentified rust. There was no apparent loss of vigor as a result of the infection, and the plants flowered and fruited normally. The Erigeron, especially in wetter areas, was commonly infected with a smut-like fungus which affected achene production.

Species Account

Certain of the alpine species have characteristics that make them worthy of greater individual discussion. The following accounts, in part summary of previous statements, are concerned with such species.

Geum turbinatum - This species is one of the most ubiquitous of alpine species. It was found in the very dry habitats as well as in areas that came out from under the snow as late as the first week in August.

Examination of the perennating bud in early fall indicates that the leaf and floral primordia for the following year were already present. In late fall and during the winter the perennating bud was sheathed in the old leaf bases of the preceding season's growth. In early spring, or upon coming out from under the snow, the new shoots were very small and chlorotic appearing, resembling the heart of a bunch of celery. Comparisons of the number of floral primordia seen by dissection or perennating buds in fall with the average number of flowers per plant in the growing season indicate that several buds did not develop.

G. turbinatum was one of the first species to bloom wherever it occurred. In late snow areas it sometimes appeared with the flower bud in an advanced state of development. This species formed a flowering aspect, either major or minor, in a great number of alpine habitats.

G. turbinatum commonly produced abundant vegetative growth with no subsequent flower development. On the other hand, the record within the phenology quadrats indicates that some individuals had both early and late season blooming periods. For example, in 1960 at Station 3 it bloomed on July 3, dispersed seed on August 18, and then had a rebloom on August 28. Similar patterns were noted for both seasons at other stations.

Other points of interest concerning G. turbinatum are the dispersal habit and dormancy responses. The species was usually in fruit five or more weeks before dispersal, at which time the calyx reflexed slightly and the achenes were carried away by the wind. Some individuals have been noted to retain the achenes until the fall snows, and on rare occasions individuals have been found to contain a few achenes the following spring.

Dormancy responses were quite striking. In late August in 1960, G. turbinatum turned red in a matter of days over most of the area. No freezing temperatures were associated with this change, in fact it occurred during the warmest period of that season. Notable exceptions to the dormancy response were found in those individuals that had come out from under the snow very late in the summer. These showed no signs of dormancy until late September. Plants in full flower sometimes occurred only a few feet from dormant appearing individuals. In 1961, only a few scattered individuals turned red in late August; it was not until mid or late September that the majority, including those of the late snow areas, showed the reddish appearance.

In 1961 a patch of G. turbinatum exhibited reddish leaves throughout the entire growing season. The plants otherwise developed in a normal manner, flowering, fruiting, and dispersing at a rate similar to the neighboring green plants.

Hymenoxys grandiflora - This species is one of the most interesting of those included in the study. In early spring the rosettes expanded rapidly, and the flowering shoots began to elongate. As the flowers developed they pointed straight upward, but as they approached maturity the flower stem bent and the heads faced generally towards the east. As the flowers began to dry up and the fruits enlarged the stems bent so that the heads once again faced upward. From this final position the abundant achenes were readily dispersed by wind.

Of even further interest is the fact that of over 500 Hymenoxys plants examined that had flowered in 1960, one had survived into the 1961 growing season. The dried up flowering stalks from the previous year remained erect, but the slightest pull on the stem removed the entire dead plant from the ground. A study plot was established to further study this characteristic.

Ranunculus adoneus - This species is very interesting because of its ability to respond at low temperatures, as indicated by its common practice of flowering up through shallow snow cover, or coming out from under the snow in full flower. R. adoneus was encountered only in areas that have winter snow cover, usually of considerable depth. Seed production was quite high, but many of the seed heads were taken by birds or other animals.

Erigeron melanocephalus - This species was found only in areas where snow persisted late into the summer. It came out from under the snow with the floral bud well developed and flowered in about three weeks. Many individuals did not complete the life cycle before the fall snows.

Carex pyrenaica - This species was also found only in areas where snow persisted until the latter part of July or early August. It appeared from under the snow with the spike well developed, and anthesis occurred as quickly as three days later. A period of about six and a half weeks after snow release was evidently adequate for seed to be produced and dispersed, with all of the activity taking place when the soil was cold and nearly saturated.

Saxifraga rhomboidea - The rosettes of this species were apparently initiated near the end of the growing season and then over-wintered. The floral buds embedded in the center of the rosettes became evident very early in the spring. Upon release from the snow, there was a very rapid elongation of the floral axis, the species reaching heights of from 80 mm to 150 mm within two to four weeks. Growth measurements of individuals at different locations averaged out to about 5 mm/day. Floral maturity was very closely associated with maximum elongation of the peduncle. Shortly after flowering the leaves dried up considerably and the plants appeared nearly dead. At the end of the growing season, however, these same plants developed another new, reduced rosette, and the cycle continued the following season.

Polygonum bistortoides - This species was also characterized by rapid elongation of the floral axis. In early spring the plants were first evident as two red, linear leaves, often with a visible bud at the base. There was a great deal of variation in the final heights noted, and consequently the average growing rates per week are not too meaningful. One individual that attained a final height of 300 mm elongated 140 mm in a one week period. Others, however, did not even reach a height of 140 mm. Despite the great variation in final heights, the time required to reach maximum elongation was fairly uniform for all individuals. Flower maturation occurred somewhat prior to the time of ceasation of floral axis elongation. Several individuals developed large leaves but did not produce flower buds.

Trifolium nanum - This species displayed different growth habits in different habitats. It was most common in places where it was exposed to strong winds. Here the leaves and flowers were sessile or very short petioled and peduncled, resulting in a tight cushion. In areas where there was protection from the wind, as in the lee of hummocks or rocks, the leaves were generally quite long petioled and the flowers were borne on peduncles that often exceeded the leaves in length. The growth habit in these circumstances was quite lax and spreading, no longer resembling a cushion.

Seasonal Aspects

Although the flowering of early season species was somewhat later and subdued in 1961, the general flowering peaks at the various stations were essentially similar in the two years. Descriptions of flowering aspects are subjective, with the emphasis placed on the most conspicuous species, while the less conspicuous but often abundant plants of grasses and carices are frequently overlooked.

At Stations 1, 3, 4 and 10, in the early part of June, the bloom was predominantly that of *Phlox caespitosa*, a species with petals of various hues of blue. Other species which added to the overall blue coloration were *Eritrichium elongatum*, *Mertensia alpina* and *Pulsatilla ludoviciana*. *Primula angustifolia* with its reddish-pink flowers, and *Oreoxis alpina* with yellow flowers added some variety.

The yellow flowered *Geum turbinatum* dominated the next general aspect of the season at these early stations, and was in fact the only species to contribute at least a minor aspect to all of the ten phenology stations, as well as to Station 14 and the outer part of Station 16. The two to three week yellow flush of *G. turbinatum*, further emphasized in some stations by *Potentilla diversifolia*, was followed by a predominance of the white flowered *Arenaria obtusiloba*. Somewhat later flowering than *A. obtusiloba*, but contributing to the same general aspect was *A. fendleri*. Many of the important grasses were at the peak of anthesis during this period.

The next aspect to characterize some of the dry stations was provided by Sedum stenopetalum, a yellow flowered species. At Station 1 the blue Campanula rotundifolia accompanies and tends to overshadow the yellow of S. stenopetalum, while at Station 10 the deep purple of Penstemon whippleanus heightens the period. After the S. stenopetalum bloom, which terminated toward the end of July in 1960 and in the middle or latter part of August in 1961, the flowering activity of the season was relatively minor in the dry stations. A few species rebloomed, and a few new species came into flower, but such activity was spotted and did not provide general coloration.

Station 5 needs separate consideration because of the nature of the vegetation and the habitat. Snow seemed to collect and persist to a much greater degree, at least along the upper margins, than at Stations 1, 3, 4 and 10, however, in the nearly bare soil stripes between the Dryas octopetala mats, soil moisture and temperature conditions appear to resemble those of these dry stations. Evidence for this conclusion is seen in the presence of such species as Eritrichium elongatum, Primula angustifolia, Artemisia scopulorum, Erigeron pinnatisectus, Helictotrichon mortoniana, Phlox caespitosa and Pulsatilla ludoviciana, all of which were commonly associated with dry habitats. The general sparcity of plants precludes the formation of any prominent aspects; the white flowered Dryas, which bloom during the first part of July, is most conspicuous.

Station 8, a mesic meadow, had limited amounts of the white flowered Thlaspi alpestre for its first floral aspect in mid June. Shortly thereafter the species was greatly outnumbered by those of the yellow flowered species, Geum turbinatum, Oreoxis alpina and Ranunculus pedatifidus. An occasional reddish-pink flower of Primula angustifolia was seen. Carex elynoides and various other carices reached anthesis during this time, but their nature was such that they did not contribute to the aspect. The early to middle part of July was marked by the flowering of a mixture of various colored species, with little or no dominance on the part of any. Some of the more conspicuous species included Arenaria obtusiloba, Castilleja occidentalis, Erigeron simplex, Polemonium viscosum, Polygonum bistortoides, and Trifolium dasyphyllum. Many of the grasses present were in anthesis during this time. The station continued without any dominant coloration until the latter part of August at which time the off-white flowers of Gentiana romanzovii provided the final aspect of the year.

Station 9, an area of heterogenous vegetation ranging from localized Kobresia bellardi to abundant willows, had no prominent aspects. Anemone zephyra, Caltha leptosepala, Androsace septentrionalis var. subumbellata, Geum turbinatum and Saxifraga rhomboidea were all in bloom during the same period in the latter part of June. Erigeron simplex, Castilleja occidentalis, Trifolium parryi, and T. dasyphyllum were in flower in the early to middle part of July, as were most of the grasses. In late July Polygonum viviparum bloomed for about a week and was followed by Gentiana prostrata. Gentiana romanzovii although present, failed to flower in either of the two growing seasons.

Seasonal aspection within the wet Stations 2, 11 and 12 was basically different for each station. The yellow Ranunculus adoneus, which was conspicuous because of its nature of flowering up through the snow or being in flower immediately upon snow release, was the first aspect at Stations 2 and 11, ,but did not occur at Station 12.

Station 2 had perhaps the most poorly defined aspection. The relatively minor flowering of R. adoneus was followed by the progressive appearance of Lewisia pygmaeus, Geum turbinatum, Potentilla diversifolia, Androsace septentrionalis var. subumbellata, Sibbaldia procumbens and Vaccinium caespitosum. Of these, only Geum approached aspect proportions. Danthonia intermedia was very prevalent and flowered heavily, but was quite inconspicuous. There was more or less continuous flowering by a few individuals of scattered species throughout the growing season. Campanula rotundifolia produced a prominent late season aspect in 1961, failed to flower in 1961.

At Station 11, the flowering of Ranunculus adoneus was closely followed by that of Caltha leptosepala in the latter part of June and early July. The period of Caltha prominence carried slightly over into the subsequent G. turbinatum aspect, which started in the first week of July and extended over about a two week period. It in turn was replaced by the flowering of Polygonum bistortoides and Castilleja occidentalis. These two species formed the most prominent aspect of Station 11 in 1960, but their appearance was much less pronounced in 1961. The grasses reached their peak of anthesis at about the same time as Polygonum and Castilleja. In August there were scattered flowers of Artemisia spithamaea, Senecio dimorphophyllus and Antennaria microphylla. There was no well defined late season aspect.

At Station 12 the first species to flower was Carex elynoides. Several other species came into flower shortly thereafter, but of these, only G. turbinatum provided any general coloration. After this there was little floral prominence until the latter part of July when Penstemon whippleanus was quite showy. As with the P. bistortoides and C. occidentalis at Station 11, this species was much more prominent in 1960 than in 1961. In 1960 the last aspect of the season at Station 12 was a profuse flush of light blue by Campanula rotundifolia, occurring in the latter part of August. In 1961, however, the species failed to flower, and the only late flowering species was an occasional plant of Solidago decumbens.

DISCUSSION AND CONCLUSIONS

The rather marked difference in phenological timing between certain stations (Table VIII) leads to a consideration of the similarity or diversity of the floras involved. Were many of the same species present with differences in timing related primarily to inherent plastcity of the species, or were there important floristic differences, with species of different ecological amplitudes selected by the particular environments? The data indicate that both elements are present, but that the floristic differences are more significant.

A comparison between a dry, windy, exposed area (Station 4) and a later, wet area of snow accumulation (Station 11) will serve as an example. The times of numerical flowering peaks at the two stations were distinctly different, with the dry station having the greatest number of species in flower during the second floral period (June 24 to July 9), while the wet station exhibited the greatest number in bloom in the fourth floral period (July 22 to end of season). Of the approximately two dozen species studied at each of these two stations, only three species occurred at both stations. It is quite obvious that the general phenologic delay in the wet area was primarily related to a substantial selection of different species. A similar comparison could be made between all dry and wet stations of the study.

The general correspondence of phenological timing at stations with somewhat similar habitats should also be interpreted. How do the

Table VIII.--THE NUMBER OF SPECIES IN FLOWER DURING A GIVEN PERIOD AT EACH STATION.

First floral period - From late May to June 23
Second floral period - From June 24 to July 9
Third floral period - From July 10 to July 22
Fourth floral period - From July 23 to end of season

		Floral period			
		1	2	3	4
Station 1	'60	15	20	17	8
	'61	7	18	17	10
Station 2	'60	1	9	13	11
	'61	1	7	9	7
Station 3	'60	4	13	10	7
	'61	0	9	10	10
Station 4	'60	10	15	11	5
	'61	4	13	12	6
Station 5	'60	6	9	7	6
	'61	2	9	10	5
Station 8	'60	5	16	13	12
	'61	2	12	13	12
Station 9	'60	2	13	14	12
	'61	0	11	13	13
Station 10	'60	13	16	12	9
	'61	6	18	16	10
Station 11	'60	0	2	2	10
	'61	1	2	8	8
Station 12	'60	0	6	16	15
	'61	0	7	14	16

species and phenologic patterns at two similar areas compare? In an earlier chapter it was pointed out that Station 3 had slightly different snow relationships in winter and early spring than the other dry Stations 1, 4 and 10, but nevertheless the progression of phenologic events was generally comparable. The nature of the gross phenologic similarities is apparent when it realized that of the 20 study species that flowered at Station 3, 12 were observed to flower at Station 4, and 11 of these flowered in the same floral period at both stations. To a considerable degree the same species are apt to be in the same phase of development at the same time.

Factors Influencing Phenology

The phenology of plant species is not an independent response due only to internal, self-regulatory factors. Bliss (1956) emphasizes this in his statement that "The various plants grow and bloom in response to the effects of the general environment on their genetic structure. The influence of the microenvironment in modifying this is also important. Thus the same species frequently reaches an equivalent level of phenological development on different dates at various stations." It seems evident, therefore, that the later flowering time for certain populations of rather widespread species is in large part related to a corresponding delay in appropriate environmental conditions.

The exact nature of such plant-environment relationships is not known, and the potential complexity of the problem is indicated by the fact that there are already about 50 known plant-environment flowering interactions, with many more suspected (Salisbury, personal communication). Many reviews have been written on environment and the physiology of flowering, but few studies have involved native species, particularly those of the alpine. In spite of the ultimate complexity of the problem, it is worthwhile to consider the major environmental factors as they might relate to phenology.

From early visits to the study area and from flights over the area in winter, the consistent segregation of the tundra into areas of snow accumulation and areas virtually free of snow influence was apparent. The prevailing westerly winds of winter deposit large amounts of snow on lee slopes and in pockets, while at the same time sweeping the ridges and outcrops relatively clear.

For plant activity this basic difference in snow cover is of great importance. Warming (1909) recognized this fact and said:

> "In arctic countries every patch of surface from which the snowy covering is blown away by winter storms has vegetation different from that on snow clad depressions....Thus the snow is of ecological importance."

One effect of such differences in snow cover is that the areas free of snow in winter tend to be drier and warm up much more quickly. Such areas have longer growing seasons, and are often subjected to periods of drought. Vegetative activity occurs early in the season. In snow accumulation areas species are delayed by the overlying snow and also by the wetter and perhaps cooler conditions which often prevail at the ground surface when the snow is gone.

The effects of snow retreat on actual timing of phenology are not well known. Billings and Bliss (1959) reported that plants of Geum turbinatum released from snow on progressively later dates seemed to flower in slightly less time than those snow-free earlier in the season. An examination of plants of G. turbinatum released from snow over a 21 day period at Station 16 shows that partial development sometimes occurs beneath the snow in later areas, but no real evidence was found to indicate that a shorter time period is required for these late plants to develop flowers. In quadrat Groups 1, 2 and 3, at Station 16, the buds of G. turbinatum appeared in three or four days. In Groups 4 and 5 some plants had buds in evidence on the day of snow release. The time from bud to flower was always about 17 days, thus in a sense some individuals in Groups 4 and 5 were able to flower in a shorter period of time. If the amount of time spent in bud development under the snow by these individuals is taken into account, however, the time from the vegetative state to flower expansion is probably quite comparable.

At the snow accumulation stations (2, 11 and 12) the buds of G. turbinatum were evident at the time of the first weekly reading following snow release, giving a period of seven days or less for their development. Again the time from bud to flower was approximately 17 days. There is a need to study a much greater number of individuals on a shorter examination interval, and in a wider variety of sites to clarify the effects of progressively later release dates on phenology in this and other species.

A second response reported by Billings and Bliss (1959), and also noted in the present study, was the reduction in size of individuals of a species at the time of flower maturity in areas where snow persisted into late July or early August. The reduction is quite likely associated with the shorter growing season, the highly saturated and cool soils, and the resultant decrease in carbohydrate production.

Although the environment surely accounts for most of the phenological delays in a species the possibility of ecotypic variations must also be considered. Bliss (1956) points out the possible presence of ecotypes and biotypes in the alpine, especially in late snow accumulation areas.

Different slopes and exposures as they tend to correlate with variations in incoming solar radiation, soil temperature, and conditions of soil moisture might be expected to show marked differences in phenology patterns for species in common. Station 3, on a northeast-facing slope, could be expected to be later in development than Station 10, situated on a slight, south-facing slope. For the many common species found, however, the timing of phenological events was very similar. The similarity of a minimum of early snow cover, at a time when air temperatures were increasing to a level adequate for plant activity, was surely of considerable importance. Stations 2 and 3 are only slightly different in slope, exposure and elevation, but Station 2 was snow covered until mid-June and was consistently two to three weeks behind Station 3 in plant development. From the present evidence, it appears that the importance of slope and exposure may be considerably less than that of snow cover.

Lower temperatures, shorter growing seasons, higher light intensities, greater ultra violet radiation, greater reradiation, lower partial pressures, greater diurnal variations in relative humidity, lower vapor pressure deficits and higher wind velocities are among the many phenomena that have been reported with increases in altitude. It might, therefore, be expected that variations in altitude would result in differences in phenological timing. However, based upon observations of species common to areas of similar snow conditions, but located over a 600 ft range in altitude, it appears that elevation, as it represents general changes in the environment, had little influence on the timing of plant responses. On the contrary, the evidence indicates that there was no correlation between phenology and altitudinal variation, at least within the ranges of this study. In one season certain species exhibited a delay with increasing altitude, but in the other season the same species showed the reverse trend. It seems quite possible that study stations covering a greater range of elevations might reveal regular and predictable progressions for many species.

The environmental data collected have been examined and attempts made to correlate them to the phenological patterns observed. In addition the literature has been reviewed for studies that attempted to determine the factors in the environment responsible for the initiation and development of the reproductive stages of the phenological cycle.

Soil temperature (15 cm), soil moisture (15 cm), relative humidity (later converted to vapor pressure deficit), and wind velocity were recorded at each of the primary phenology stations throughout the summer, while a continuous hygrothermograph record and maximum and minimum temperatures were obtained at Station 4, a windy, dry area, and at Station 12, a late, snow accumulation site.

The specific importance of the temperature factor is not clearly indicated by an analysis of the temperature records and phenological responses, but certain relationships can be postulated. Perhaps the only requirement of soil temperature for some plants is that the ground be above freezing temperature. At Station 4 on June 5, 1961, the first temperature reading of the season showed a soil temperature at 15 cm of less than 1^{o} C, and no species were in flower. Five days later the soil temperature was up to 3^{o} C and a few species were in bloom.

Station 12 was under snow on June 10, but on June 12 a soil temperature of 0.5^{o} C was recorded. On June 26 the temperature was up to 5.5^{o} C, but only *Carex elynoides* was in anthesis. By July 3 the temperature was 8.5^{o} C, and six species were in flower.

It might appear from these data that species at the wet stations require higher soil temperatures for floral development, but this may not be so. Station 4 is apparently snow free most of the winter and spring. Here the vegetation is probably subjected to intermittent periods of sufficiently high air temperatures to allow partial vegetative activity during the month of May. By contrast, at Station 12, which was snow covered until almost mid-June both years, the species are kept at or near 0^{o} C, and probably very little plant development results until the snow melts or becomes quite shallow. The fact that the soil temperatures were higher by the time flowering occurred was probably due to the higher angle of the sun resulting in more direct solar radiation and to the air temperatures in mid-June which were significantly higher than those of early June, thus warming the ground more quickly, and also because the vegetation would require a minimum period of time to develop regardless of temperature.

The continuous record of temperature at Stations 4 and 12 do not allow conclusions regarding the importance of specific air temperatures to phenology. At Station 4 the many species were already well into the reproductive cycle when the temperature record was initiated. Thus no analysis of temperature threshholds for vegetative activity are possible. At Station 12 the higher temperatures recorded at the time of snow release seem to be unnecessary for vegetative activity in view of the fact that many of the same species were seen in flower earlier in other areas.

Surely actual plant temperatures are more important to plant development than air temperatures. Salisbury (1961) found that temperatures of alpine plants are very dependent upon incident solar radiation. Plant temperatures of from 6° to 20° C higher than air temperatures were recorded in direct sunlight. The passing of a cloud, or the advancement of the shadow of a rock over the plant, often dropped the plant temperature to a few degrees below air temperature. For plant responses, these differences in temperature between the air and the plant, and the wide fluctuations in leaf temperatures throughout the day, are probably much more significant than the air temperature.

Lindsey and Newman (1956) attempted to correlate official weather data of spring to a phenological record in Indiana, and thereby establish the ecological value of such weather records. From these data they postulated that the species studied crossed certain temperature threshholds before vegetative activity began. Once this activity was initiated the species apparently needed a certain number of days with temperatures above this threshhold to attain flowering. Any days below this threshhold merely resulted in a comparable delay in flowering time. They concluded that short time periods before flowering were associated with low temperature threshholds and early blooming dates, while long time periods were associated with high temperature threshholds and late blooming dates. It thus seemed that later blooming plants needed greater heat sums. Such indications can be paralleled in the observation of the phenological behavior of species in this study. The early responding species were in the bud stage a very short time, whereas those species that provided the late season aspects were often in bud three to four times as long. There is no evidence to allow the conclusion that the species were responding to different heat sums, but the possibility should be kept in mind.

Wolfe, Wareham and Scofield (1949) and Went (1953) feel that the principal of heat sums may be misleading in that it integrates the temperatures of night and day and does not differentiate between these. Other experimenters (cited in Hillman, 1962) have shown that the differences between day and night temperatures are often very important in the development of reproductive structures.

Bassett, Holmes and MacKay (1961) examined the influence of air temperatures on phenology of several woody and herbaceous species at Ottawa, Ontario. They report that there appears to be a base temperature below which plants do not develop flowers. Some species studied showed closer relationships to average maximum temperatures, others were more closely related to average minimum temperatures, while still others did not appear to be influenced at all by average spring temperatures. Such a wide array of responses serves to illustrate the complications involved in trying to assess importance of the temperature factor to the phenological responses of the species of this study.

Soil moisture, which varies greatly from habitat to habitat in the alpine, might be expected to have pronounced effects on the phenology of the species. Such effects might be either direct or indirect. Direct effects would be concerned with water balance; indirect effects would include such things as differences in soil temperature, oxygen tension, rates of mineral uptake, organic matter accumulation and pH. Unfortunately, this phase of the environment has not received much study in the alpine. Perhaps the best evidence of the importance of soil moisture and associated effects on phenology in this study resulted from the investigation involving the application of melt-water by irrigation to the vegetation. Such treatment resulted in less vigorous vegetative growth and a delay in flowering for 12 of the 14 species studied. The change in the environment resulting from the melt-water application was partly an increase in moisture and partly a decrease in temperature; the water on reaching the quadrats was still only a few degrees above freezing. The relative importance of these two factors is difficult to assess, and it is probable that both are influential.

Wind is certainly a factor of great significance in the alpine, particularly as it influences species distribution, but it apparently has little direct effect on phenology except for dispersal of pollen and seed. The indirect effects of wind on phenology through determination of snow patterns are of great consequence.

The importance of day length to flowering is well known. Once again, however, many of these studies have been primarily concerned with exotic vegetation. Went (1953) states that most of the plants that respond to day length are annuals, a life form that is almost entirely lacking in the alpine (alpine annuals are briefly discussed later in this chapter). Mooney and Billings (1961) have demonstrated that the circumpolar arctic-alpine species Oxyria digyna does exhibit flowering responses at different latitudes that are directly correlated to day length (probably more correctly to night length). It is quite possible that such relationships exist in other alpine species, but the data from the present study do not even allow speculation in this regard.

Phenology and Species Distribution

Absolute figures on the existing growing season are not available, but a reasonable estimate may be made considering the period of time between initial greening and general dormancy in any given area. For some of the snow-free stations the maximum period was probably between 14 and 15 weeks. The minimum was 6 to 7 weeks at Station 16, the latest seasonally of the snow accumulation stations.

For many of the species occurring in dry, snow-free areas the length of time spent in the vegetative condition before the formation of a visible bud is not known. From the observance of a bud until seed dispersal, however, the average time required for most species ranged between 6 and 9 weeks. Adding to this a period of 2 to 4 weeks to allow for the vegetative stage, the maximum time required for the majority of species to complete the cycle was from 7 to 11 weeks. This 2 to 4 week estimate is based upon known values for many of the species at later stations, but was unnecessary for those species that came out from under the snow with the bud well advanced.

Many species have cycles that would normally exceed the limits of the growing season in the late snow accumulation areas, but this alone does not seem to satisfactorily account for their absence from these locations. Surrounding drier areas produce abundant seed of many species which apparently do not even occur as seedlings in the snow sites. Further, there are many species which do not occur in the very late snow areas that have cycle requirements shorter than those of some of the characteristic species of such areas. It therefore appears that some factor or factors, such as competition or increased soil moisture are more important than the length of the phenological cycle in the selection and maintenance of species under the conditions of late snow areas.

The length of the phenological cycle may, however, be very important for alpine plants in general. Surely part of the reason why many species of lower elevations do not grow in the alpine is related to the longer time requirements for expansion of the perennating organ and seed formation. It seems worthwhile to consider what might happen to the present alpine flora of the study area if the growing seasons were gradually shortened or lengthened over a period of several years. This might result either from changes in the climate or in elevation due to orogeny or erosion.

It is readily apparent that if the season were to be curtailed to the extent that the production of viable seed is prevented, the many species dependent upon this method of regeneration (Daubenmire, 1941) would in time be eliminated. Under present conditions, particularly for the species occurring in the late-snow sites, the margin for completion of the cycle appears to be quite narrow. However, these late area species might well be among those adapted to survive a shortened growing season, providing they could migrate to and compete in dry areas that would likely become cooler and more moist with any shortening of the snow-free period. It seems reasonable to assume that the flora of the alpine area would be significantly depleted if subjected to a shorter growing season, with the dry site species which require relatively long periods for cycle completion being the first to be eliminated.

Lengthening of the growing season, on the other hand, might result in a general increase in species numbers in the alpine. If lengthening involved greater drying of wet areas in summer, then some of the species of these habitats would likely be eliminated. On the other hand, perhaps many or all of the wet area species would quickly complete the cycle and possibly aestivate during the dry periods while migratory species from more mesic or drier sites would become active. Species from lower altitudes with longer requirements for life cycle completion would probably immigrate upward into the alpine.

In general, it can be concluded that minor consistent changes in the lengths of the growing season would produce corresponding changes in the flora of the alpine. Such changes were no doubt very much in evidence during the past periods of glaciation in the Colorado Rockies.

Factors Influencing Total Flower Production

The reduction in flower production in 1961 as compared to 1960 by the great majority of species was readily apparent. However, the possible causes for such a decrease were not so evident. Some of the factors involved in the initiation of flowering responses have been discussed. The factors that seem most closely related to the total production of floral primordia by alpine species will now be considered.

Possibly the alpine species have to build up a certain amount of carbohydrate reserve material before they can produce abundant floral primordia. In favorable years of sufficient moisture and warm temperatures, maximum amounts of carbohydrate would be synthesized, resulting in higher flower production at some later time. Conversely, in poor seasons marked with drought, low temperatures and frequent frosts, the total carbohydrate reserves and subsequent flower production would be reduced. The cyclic nature of flower production in woody species is often cited, and is related to total carbohydrate production. It is probably not unreasonable to assume that similar relationships might exist for the herbaceous alpine flora.

Mooney and Billings (1960) made carbohydrate analyses on typical alpine plants, such as *Geum turbinatum*, *Polygonum bistortoides* and *Saxifraga rhomboidea*, and attempted to correlate carbohydrate levels to phenological phases. In general, carbohydrate levels were highest in underground storage organs at the time of fall dormancy. Some of these reserves were used up during the winter. Evidence that the species began to develop under the snow in spring is believed to account for the most of these losses, although the respiration of dormancy through winter would use up some reserves. Maximum depletion of reserves occurred during the initial vegetative surge of activity leading to flowering. After flowering, carbohydrate accumulated rapidly and in fall the shoot reserves were translocated to underground organs and the cycle was ready to repeat. Unfortunately, no mention is made of the total amount of flower production as a function of carbohydrate levels, but it was pointed out that even at times of lowest levels, it appeared that the species had sufficient reserves to carry them through adverse periods.

The environmental complex is known to have effects on the general phenology of species, and it is reasonable to assume that this same complex would also influence the total production of flowers. A comparison of the general weather conditions of the two summers of this study suggests some possible relationships. The summer of 1960 was quite severe with intermittent periods of drought, low total precipitation, high vapor pressure deficits, high temperatures, and high winds. This season, however, was marked by very heavy flowering by the majority of species. In 1961 there were no prolonged periods without precipitation, and the many more days of rain resulted in more total precipitation. Temperatures were slightly lower and vapor pressure deficits were significantly lower in 1961, and there were fewer days with high winds. The 1961 season seemed to be much more favorable for plant growth and development. Nevertheless, there was a significant reduction of flowers in 1961. The indication is that the environmental conditions of one season are not predominately effective in that season, but rather are reflected in the activity of some later season. Evidence that many species initiate the floral primordia for one growing season during the preceding summer strengthens this conclusion; such initiation is suggested for many of the herbaceous alpine species.

It may be that more than one year is required to build up reserves to levels necessary for heavy flowering. It also seems quite possible that relatively short term environmental extremes might be more important than the broad pattern of an entire season, such things as an extreme period of drought, or a period of sub-zero temperatures. Additional years of observation should help to clarify this point.

Late Season Activity

The reblooming of many species late in the season, often several weeks after the first floral period, is a matter of interest. Again it is not possible to make definite conclusions as to cause without further study at the species level, but the following three possibilities might be considered. First, it may be that reblooming is merely the development of a bud that for one reason or another failed to respond during the normal floral time. Second, high carbohydrate production may result in the development and expansion of new buds late in the season. Third, late flowers may result from the bolting of floral axes that normally would have been carried over into the next growing season in the perennating organ. It was noted that reblooming most often was seen in those species known or suspected to produce well defined perennating organs.

The development of new and usually smaller leaves by many species at the end of the growing season may be a mechanism that provides for quicker resumption of activity in the next season. Although it is difficult to image that these leaves, especially on plants in exposed sites, would survive the winter conditions, there is evidence to indicate that they do overwinter without noticeable damage. The evergreen habit for herbaceous plants in such a severe environment is a behavior that should be studied further.

Annuals in the Alpine

Annuals in some habitats are referred to as "evaders" since they exist through periods of adverse environmental conditions in the seed state. Desert annuals often remain as seed for years until favorable conditions occur, at which time they quickly germinate, grow and produce flowers and seed and die. In the alpine, a similar rapid response seems possible, but with the exception of the Sierra-Nevada Range, this life form seems to be rare.

The paucity of annuals in the Colorado alpine is probably related to the severity of the environment, especially low growing season temperatures. The weather in Colorado often changes abruptly from warm, sunny conditions to freezing rain or snow. Such changes likely result in the death of many plants before completion of their life cycle. Even young perennials are probably killed by adverse weather, but this life form has the advantage of being able to make repeated attempts at regeneration over a period of years, thus compensating for losses in any given year.

To survive in the Colorado alpine an annual would have to be cold hardy, or it would have to be timed very precisely (most day length response plants are annuals) to a short period in the middle of the summer when freezing temperatures are rare. Only one species encountered in this study, Gentiana prostrata, is classified by Harrington (1954) as an annual or biennial. It flowers in the early to middle part of August, a time when freezing temperatures are probably infrequent. A second species, Androsace septentrionalis, var. subumbellata, listed as an annual or short lived perennial, is one of the first species to flower and therefore must be somewhat cold hardy. Its perennial habit may provide the assurance of survival in adverse years. Without such adaptations of cold hardiness or timing of response, which appear to be uncommon in annuals, the survival potential of such species would be very poor in the Colorado alpine.

Pollination

Insect populations in the alpine, with the exception of mosquitoes, appear to be generally low in numbers. Only a few grasshoppers and bees, and an occasional spider, caterpillar, beetle and butterfly were seen. ~~Very~~ few plant species were seen attended by insects, thus it may be ~~that~~ not many are independent upon insect pollination. The various species of Trifolium are probable exceptions, and the sparsity of bees may largely account for the poor seed production in these species. The winds in the alpine are more than adequate for transport of pollen throughout the area and between it and other areas.

Suggestions for Future Studies

With the data obtained from the present study as a basis, it would now be possible to select a limited number of representative species and observe them at more frequent intervals to determine specific response patterns and possible environmental interrelationships. With fewer species to observe, it would also be possible to maintain more stations in a greater variety of sites over a greater range of elevation. It would further be possible, and desirable, to set up one or more new study areas in other alpine regions and compare phenological data for the same species from more than one area.

The present study has also given rise to many specific questions relating to the phenology of alpine species. Many of these are in apparent need of further study. For example, what is the exact nature of pollination in alpine species? To what extent are species self-sterile? What would be the effect of artificial pollination in certain poor seed producing species, for example the alpine Trifolium species? At present, little is apparently known concerning these questions.

What are the growth characteristics of the various species? How long do presumed evergreen leaves actually last? How many years does it take for a seedling to mature and produce viable seed? How does the chlorophyll content and the photosynthesis/respiration ratio in red leaved individuals of Geum turbinatum and other species compare to those found in green leaved plants?

Do the species that are found in a wide variety of habitats have wide tolerance ranges, or are there ecotypes? Little is known concerning this possibility, and yet ecotypes may be equally as important in the alpine as they appear to be in other vegetational types. The ecotypic differentiation of species found over a broad elevational range, including the alpine, needs to be studied for more species.

Perhaps the one area that needs most study concerns the determination of casual relationships of physiological responses terminating in the formation of the reproductive phase in alpine plants. Are certain alpine plants responsive to day and night lengths? What is the role of soil, air, and plant temperatures in the flowering process? How do other environmental factors relate to the phenology of alpine species? It is apparent that there are many questions that remain to be answered before a better understanding of alpine plant life can be attained.

SUMMARY

During the summers of 1960 and 1961 a study of the phenology of 85 alpine angiosperms was conducted in the vicinity of False Mummy Pass, Rocky Mountain National Park, Colorado.

Ten primary phenology study stations were selected in 1960, representing variations in slope, exposure, altitude, snow cover and composition of the vegetation. In 1961 two more stations were added, one to study the effects of the artificial application of melt-water to the vegetation, and the other to study the effects of progressively later lying snow on phenology and vegetational composition. Semi-permanent quadrats 25 by 25 cm were established at each station to facilitate relocation of individual plants and clones. An average of slightly over eight species per quadrat was observed weekly for phenological change from early June to late September.

The vegetation was sampled for frequency and cover at all stations except one, a heterogeneous area of willow scrub. The frequency and cover data for the primary phenology stations were applied to the Kulczinski Index of Association to determine station affinities.

Air temperature, wind velocity, precipitation and relative humidity (later converted to VPD) were recorded throughout both summers. Colman Units were buried at 15 cm depth at each of the primary phenology stations to record soil temperature and soil moisture, and soil cores were

taken to determine the average soil depths. In 1961 the soil moisture was also determined on a per cent dry weight/volume basis by analysis of field samples.

The growing season could be arbitrarily divided into four rather distinct periods of flowering. The first period (late May to June 23) was primarily limited to the wind-blown, snow-free, dry stations. The second period (June 24 to July 9) represented the time of major floral activity at the dry stations, and marked the onset of blooming at the later, wetter stations. The third (July 10 to July 22) and fourth (July 23 to end of season) periods showed a prominent diminishing of floral activity at the dry stations, but were the times of maximum activity at the late, wet stations.

The analysis of data showed no consistent phenological patterns which could be associated with exposure, slope or elevational differences. There were, however, consistent patterns noted with dry, exposed stations and with the wetter, late, snow accumulation stations. Species common to two or more of the dry stations were generally within a week in flowering. For the snow accumulation stations, species in common flowered mostly within a two week period. Species common to both dry and wet stations often bloomed as much as five weeks later in the wet sites.

The differences in the broad phenological patterns of dry and wet stations were concluded to be related to two basic factors. First, the covering of snow into mid-June in the snow accumulation stations delays the arrival of appropriate environmental conditions thereby delaying vegetative activity. Second, and probably most important, the differences in microenvironment in the wet sites apparently selects different species with dissimilar phenologic responses.

The maximum growing season was estimated to be 14 to 15 weeks at the dry stations, and the minimum 5 to 6 weeks in the center of a snow basin. The data indicate that the majority of species required a period of 5 to 11 weeks to develop from the resumption of vegetative activity in the spring to seed dispersal. A few species, such as Phlox caespitosa with a development time of up to 14 weeks, required significantly more than the average time. Some species with cycles shorter than those characteristic of the wet stations were not found in such areas, and it was concluded that factors other than the length of the phenological cycles were limiting. Consideration was given to the possible consequences of shortened and lengthened growing seasons. It was concluded that such changes would likely have marked effects on the flora of the alpine.

Attempts to correlate weather data to phenology were generally unsuccessful. The literature was reviewed for reports on the effects of various climatic factors on phenology, but such studies concerning native vegetation are not especially helpful. It was suggested that temperature responses will probably be found to be most important in the alpine flora.

In 1961, a sharp decrease was noted in the total flowers produced in the study area as compared to 1960. It was concluded that total carbohydrate levels, which may in turn be dependent upon the environmental conditions of some preceding growing season, are important in influencing total flower production.

Many species were observed to rebloom near the end of the growing season, often a few weeks after dispersal of fruits or seeds from the first floral production. Three possible causes for this phenomenon were discussed. First, a bud that failed to develop earlier in the season may have had a delayed response. Second, a new bud may have been produced through the influence of an excess of carbohydrate production. Third, a bud in a developing perennating organ that would normally have expanded in the following growing season may prematurely bolt and expand. Of these possibilities, it was concluded that the latter offered the best explanation. The basis for this conclusion was the fact that this reblooming was most frequently seen in species known or suspected to produce well differentiated perennating buds.

The production of new, reduced leaves near the end of the growing season was also observed in several species, most commonly those that responded very early in the spring or soon after snow release. Examination of several of these individuals in the following season indicated that these leaves overwinter without apparent harm. It was concluded that such behavior allows the species to develop more rapidly in the following spring.

Suggestions for future studies are made. The first involves the expansion and refinement of the present study. Second, the need for information concerning the exact nature of pollination of alpine species, growth characteristics, and the presence and role of ecotypes in the alpine is expressed, as is the necessity of making more specific studies relating to plant-environment responses and phenological development.

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ABSTRACT OF THE DISSERTATION

PHENOLOGY OF COLORADO ALPINE PLANTS

During the summers of 1960 and 1961 a study of the phenology of 85 alpine angiosperms was conducted in the vicinity of False Mummy Pass, Rocky Mountain National Park, Colorado.

Ten primary phenology study stations were selected in 1960, representing variations in slope, exposure, altitude, snow cover and composition of the vegetation. In 1961 two more stations were added, one to study the effects of the artificial application of melt-water to the vegetation, and the other to study the effects of progressively later lying snow on phenology and vegetational composition. Semi-permanent quadrats 25 by 25 cm were established at each station to facilitate relocation of individual plants and clones. An average of slightly over eight species per quadrat was observed weekly for phenological change from early June to late September.

The vegetation was sampled for frequency and cover at all stations except one, a heterogeneous area of willow scrub. The frequency and cover data for the primary phenology stations were applied to the Kulczinski Index of Association to determine station affinities. Environmental data, including air temperature, relative humidity, wind velocity, soil temperature, and soil moisture, were recorded at each station. The average depth of soil at each station was also determined by use of a soil coring tool.

The growing season could arbitrarily be divided into four rather distinct periods of flowering. The analysis of data showed no consistent phenological patterns which could be associated with exposure, slope or elevational differences. There were, however, consistent patterns noted with dry, exposed stations and with the wetter, snow accumulation stations. It was concluded that the differences in the broad phenological patterns of dry and wet stations are primarily related

to two basic factors. First, the covering of snow into mid-June in the snow accumulation stations delays the arrival of appropriate environmental conditions, thereby delaying vegetative activity. Second, and probably most important, the differences in microenvironment in the wet sites apparently selects different species with dissimilar phenologic response patterns.

Attempts to correlate weather data to phenology were generally unsuccessful. However, it was suggested that temperature responses will probably be found to be most important in the alpine.

The maximum growing season was estimated to be 14 to 15 weeks at the dry stations, and the minimum 5 to 6 weeks in the center of a snow basin. The data indicate that the majority of species required a period of 5 to 11 weeks to develop from the resumption of vegetative activity in the spring to seed dispersal.

Many species were observed to rebloom near the end of the growing season. The possible causes include a delay of an existing bud, production of a new bud resulting from excess carbohydrate production, and bolting of a floral bud primordium produced in a perennating bud.

The production of new, reduced leaves near the end of the growing season was also observed in several species. These leaves apparently overwinter without harm, and allow the species to respond more quickly in the spring.

There were fewer total flowers produced in the area in 1961. The possible causes were discussed, including the probable importance of carbohydrate accumulation and buildup for abundant flowering.

Suggestions for future research were made. A selection of a limited number of the more important species which could be examined more frequently over a wider variety of habitats, and in more than one major study area would provide more specific information on phenologicaresponses. Further, the need for detailed studies concerning the pollination, growth characteristics, and ecotypic potentials of alpine species was emphasized.

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