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CANOPY STRUCTURE AND PHENOLOGY OF ALPINE TUNDRA VEGETATION

by

Marcee Fareed

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Plant Ecology

Approved:

Major Professor

Committeeman

Committeeman

Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

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Marcee Fareed

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ABSTRACT

An inclined point frame was used to measure leaf area indices in an alpine tundra *Kobresia* stand and *Deschampsia* meadow on Niwot Ridge, Colorado. Measurements were made throughout the summer of 1971 at various heights in the canopy and for each species in the two communities. Maximum leaf area indices of 2.2 and 2.0 occurred in the *Kobresia* and *Deschampsia* sites, respectively. The *Kobresia* site was characterized by a single dominant species, *Kobresia myosuroides*, and a predominance of vegetation within 2.5 cm of mean ground level. The *Deschampsia* site had no single dominant species. The region of maximum foliage shifted from the 2.5 to 5 cm height zone in June to the 5 to 10 cm zone in early August. Phenological observations revealed a greater number of vegetative contacts in the *Deschampsia* site on all sampling dates. Certain shared species varied in their phenological patterns. It is suggested that differences in the duration of snow cover and surface melt-water may be related to the variation in phenological patterns in the two sites. In both communities, maximum LAI occurred when flower and fruit production overlapped. Arctic tundra LAI values, measured using similar methods, were less than half the maximum LAI values reached in the alpine communities examined here.

INTRODUCTION

A number of studies have examined the productivity of alpine tundra plants. Bliss (1962a) and Billings & Mooney (1968) have reviewed the methods and results of earlier alpine productivity studies. The chief method used in tundra productivity studies has been the harvest method. The annual above-ground productivity in most tundra ecosystems ranges from 40 to 128 gm⁻² (Bliss, 1962a). Scott and Billings (1964), working with alpine tundra communities in the Medicine Bow Mountains of Wyoming, found that above-ground standing crops were in the range of 100 to 200 gm⁻².

Considering that productivity rates for temperate region herbaceous communities vary from 1 to 10 gm⁻²day⁻¹, the annual alpine rates, when calculated on a daily basis, appear low (Bliss, 1966). If roots are included, the total net productivity may be as high as 11.1 gm⁻²day⁻¹ on mesic sites (Scott and Billings, 1964). These rates are, however, comparable to those for many temperate region communities, if daily productivity rates are calculated using the length of the growing season as a basis (Bliss, 1962a).

Another technique for tundra analysis utilizes the inclined point frame method to estimate leaf area indices for each species as a function of position in the canopy (Warren Wilson, 1960a, 1963). Leaf area index, LAI, is the ratio of the surface area of one side of a leaf to the ground area. This method has been used extensively in pasture research (Booyesen, 1966; Warren Wilson, 1960b; Brown, Blaser, and Dunton, 1966; Goodall, 1953c; Watson, 1958; Winkworth, 1955; Loomis and Williams, 1969; Hoyt and Bradfield, 1962; McCree and Troughton, 1966) and, recently, in the arctic tundra research of the IBP Tundra Biome Program (Tieszen, unpublished data). In contrast to the harvest method, the point frame

method is non-destructive. The course of development and progression of senescence of the same vegetation can be followed through time. The data acquired provide knowledge of the number of layers and orientation of photosynthetic elements in the canopy.

Leaf area index, in a strict sense, is an indicator of productivity. Successive determinations reveal leaf growth rates of individual species as well as changes in the total canopy morphology. Canopy structure affects light penetration into the canopy, amount of chlorophyll exposed to incoming radiation, aerodynamic roughness of the canopy and transfer of CO₂, water vapor, and heat (Loomis and Williams, 1969).

The present study utilizes an inclined point frame to describe the canopy structure of two alpine tundra communities on Niwot Ridge, Colorado. The phenologic response of species in these two communities was also examined during the summer of 1971. Holway and Ward (1965) reviewed the literature on alpine plant phenology.

DESCRIPTION OF STUDY AREA

Physical features

A Kobresia community and a Deschampsia meadow were selected for study on Niwot Ridge ($40^{\circ} 04'N$, $105^{\circ} 36'W$) at an elevation of approximately 3476 m in the Front Range, the easternmost range of the Rocky Mountain System in Colorado. The Kobresia site had a southwest aspect and 5° slope, as compared to the 4° slope and southeast aspect of the Deschampsia site.

Bedrock of the alpine zone is composed of Precambrian granites to granodiorites and metamorphics in large batholithic masses. Tertiary quartz monzonites to diorites occur as stocks, dikes, and sills injected into the Precambrian rocks. Schists and phyllites are also present (Marr, 1967).

The soils on Niwot Ridge have undergone one or more of the geomorphic processes associated with freeze-thaw cycles: heaving, thrusting, sorting, and down-slope movement. Kobresia meadow soils are primarily silty-loams (Marr, 1967). Where soils have been stable for a considerable time, soil profiles are well developed with upper horizons rich in humus and up to 30 cm thick. During the winter months, soil ice is present and in some areas it persists throughout the year.

Retzer (1956) has described alpine turf, meadow, and bog soils in the Rocky Mountains of Colorado. An intensive soil survey has also been made on the Fraser alpine area (Retzer, 1962).

Climate

Climatic data has been collected at tundra and subalpine stations on Niwot Ridge by Marr (1967) and summarized by Barry (1972). During the

short summer growing season, minimum temperatures above 3050 m range from 0 to 5 C and maximum temperatures range from 12 to 18 C (Figure 1). Highest temperatures have been recorded during July and August, when plant growth is most active. During the winter, temperatures may be as low as -12 C and during the months of October to May daily temperatures may never be above freezing.

Wind speeds are generally reduced during the summer season. Mean minimum monthly values are between 3 and 4 ms^{-1} during July and August. In January, average wind speeds may be 13 ms^{-1} . The prevailing wind direction is from the West, but significant amounts of precipitation come with both easterly and westerly winds. Summer convectional thunderstorms are frequent in the alpine tundra and monthly precipitation, often in the form of hail or sleet, can be as high as 102 mm. Most of the annual precipitation occurs in the spring.

Mean monthly solar radiation during the period of most active plant growth ranges from 610 lyday^{-1} in May to 290 lyday^{-1} in October (Figure 2).

Vegetation

The two major alpine community types examined here are located on a gently sloping saddle of Niwot Ridge. The vegetation within this area is characterized by low, perennial grasses, sedges, herbs and shrubs. These plants are distributed in distinct vegetation zones in which one or more species may be locally abundant.

Variations in plant cover are, in part, related to the degree of snow accumulation, soil moisture, and topography.

The Kobresia site is typical of a well-developed, mesic meadow. Here, there may be up to 250 snow-free days per year. The dominant species,

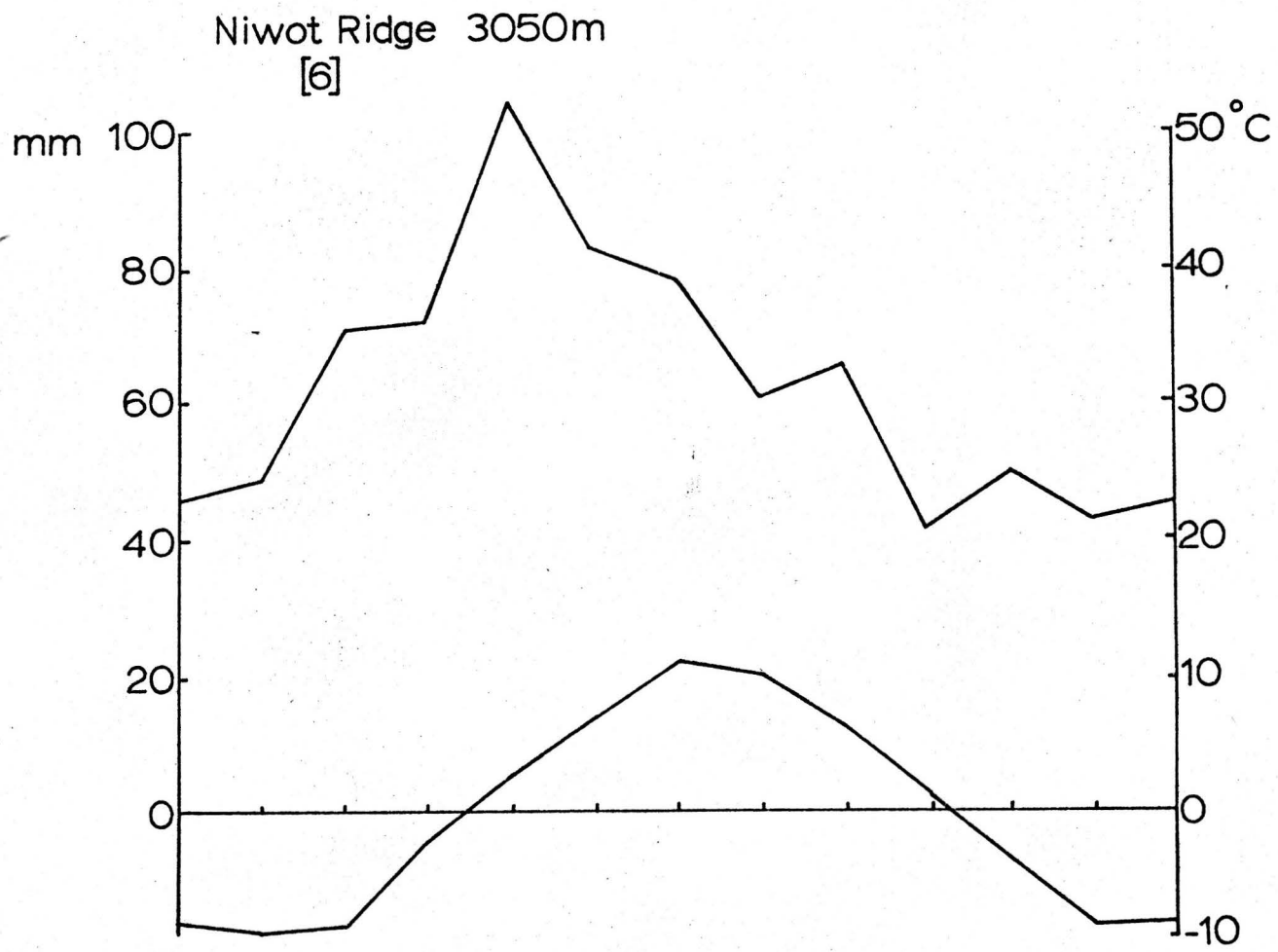


Figure 1. Climatic diagram for Niwot Ridge, Colorado. Upper line indicates mean monthly precipitation, lower line shows mean monthly temperatures (based on data from Barry, 1972).

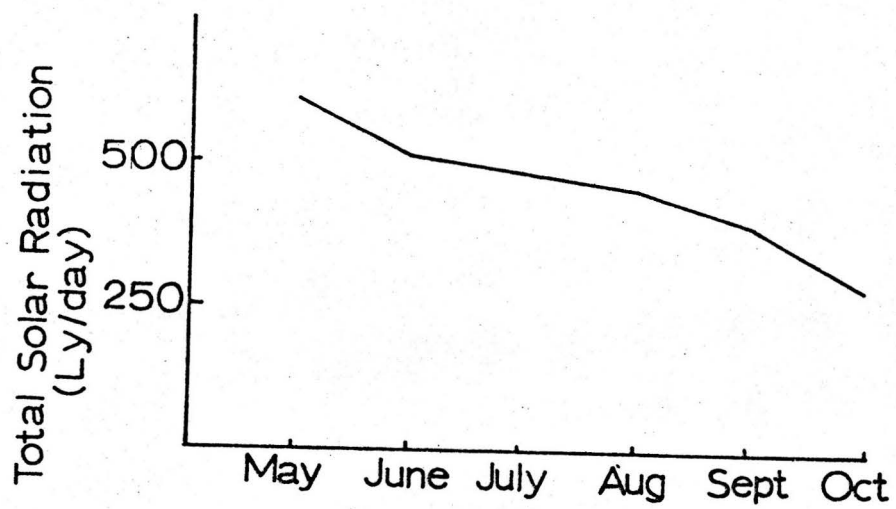


Figure 2. Mean monthly total solar radiation on Niwot Ridge, 3050 m during the summer of 1971 (Clark, unpublished data).

Kobresia myosuroides, is associated with Geum rossii, Trifolium parryi, and Polygonum bistortoides. The Deschampsia site is characteristic of areas where meltwater runoff is heavy. Only 67 snow-free days per year have been observed in this site in 1970-71 (Ebert, unpublished data). Here, Deschampsia caespitosa is commonly found with Artemisia scopulorum, and Geum rossii.

A voucher collection of all species identified is on file in the Intermountain Herbarium, Logan, Utah. Plant nomenclature follows that of Weber (1967).

METHODS

Ten one-meter square quadrats were randomly selected as non-destructive point frame quadrats within each of the two intensive alpine tundra sites.

Methods of collection of canopy structure data closely followed those used at the intensive arctic tundra site at Barrow, Alaska (Brown and West, 1970 and Tieszen, unpublished data). A modified inclined point quadrat was used to measure the leaf area throughout the 1971 growing season at various levels in the canopy for each species in the two communities (Warren Wilson, 1960a). In each quadrat, 47 pins (each 2 mm in diameter) were placed at horizontal intervals of 2 cm and passed through the low growing vegetation at an inclination of 32.5°. The frame height was held constant at 25.2 cm above mean ground level. Movement of the pin into the canopy was regulated by a small battery-operated motor.

For each contact 6 values were recorded: pin number, distance from pin point to top of frame, name of species contacted, whether living or dead, type of structure contacted (leaf, stem, or flower), and current phenological stage of the associated plant.

Leaf area index values were calculated in the two major vegetation sites: a *Deschampsia* community, and a *Kobresia* meadow. Within each site, ten 1 x 10 m plots were laid out parallel to each other and each of the 10 plots was then divided into 10 one-meter square quadrats. Ten quadrats were randomly selected from the 100 existing quadrats in each site. Leaf area index values were calculated in each quadrat, plot, and site for each species and for the total foliage. The total foliage category included all higher plants species contacted.

RESULTS

Live LAI

Tables 1 and 2 list the species contacted in the Kobresia and Deschampsia sites and their total LAI values on successive sampling dates. Species are arranged in order of decreasing values of total seasonal LAI. Table 3 shows standard deviation values for selected species and the total foliage in each site. The standard deviations indicate the marked variability in microsites within the two communities.

A total of 35 species were identified in the Kobresia site. A maximum total foliage value of 2.2 was measured at the beginning of August. Kobresia myosuroides accounted for 78% of this peak LAI value. The Deschampsia meadow was characterized by only 16 species, 11 of which were shared by the Kobresia site. A maximum total foliage LAI value of 2.0 was reached approximately 10 days earlier in the Deschampsia site than in the Kobresia site. At this time, both Artemisia scopulorum and Geum rossii accounted for approximately 30% of the Deschampsia site total foliage value, while Deschampsia caespitosa contributed 13%.

Figures 3 and 4 show the change in LAI at different heights in the canopy throughout the sampling season. In the Kobresia site, most of the vegetation was below 10 cm. The following species reached the 10-15 cm height zone: Campanula rotundifolia, Carex scopulorum, Deschampsia caespitosa, Festuca brachyphylla, and Poa glauca. Kobresia myosuroides and Polygonum bistortoides were the only species contacted above 15 cm. The greatest change in the total leaf area in the Kobresia site, occurred in the 5-10 cm zone. In this zone, there was a fivefold increase in live LAI between June 24 and August 4. Towards the end of the season there

Table 1. Live leaf area index values for the Kobresia stand site on successive sampling dates in 1971

| Species | Sampling Date | | | | | | |
|-----------------------------------|---------------|------|------|------|------|------|------|
| | 6/25 | 7/05 | 7/15 | 7/25 | 8/04 | 8/14 | 8/24 |
| <u>Kobresia myosuroides</u> | 1.04 | 1.03 | 1.07 | 1.45 | 1.68 | 1.36 | 0.83 |
| <u>Geum rossii</u> | 0.08 | 0.08 | 0.09 | 0.09 | 0.07 | 0.06 | 0.01 |
| <u>Trifolium parryi</u> | 0.05 | 0.09 | 0.08 | 0.06 | 0.04 | 0.02 | 0.01 |
| <u>Deschampsia caespitosa</u> | 0.04 | 0.05 | 0.05 | 0.07 | 0.06 | 0.03 | 0.04 |
| <u>Carex rupestris</u> | 0.04 | 0.06 | 0.05 | 0.06 | 0.05 | 0.05 | 0.02 |
| <u>Silene acaulis</u> | 0.01 | 0.03 | 0.03 | 0.02 | 0.03 | 0.03 | 0.02 |
| <u>Polygonum bistortoides</u> | 0.01 | 0.03 | 0.05 | 0.06 | 0.02 | 0.02 | 0.01 |
| <u>Oreoxis alpina</u> | 0.03 | 0.03 | 0.03 | 0.02 | 0.04 | 0.02 | 0.02 |
| <u>Festuca brachyphylla</u> | | 0.01 | 0.01 | 0.04 | 0.02 | 0.02 | 0.01 |
| <u>Minuartia biflora</u> | 0.02 | 0.01 | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 |
| <u>Campanula rotundifolia</u> | 0.01 | 0.02 | 0.01 | 0.03 | 0.01 | 0.01 | 0.00 |
| <u>Erisimum simplex</u> | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 |
| <u>Calamagrostis purpurescens</u> | P* | 0.02 | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 |
| <u>Artemisia scopulorum</u> | 0.01 | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 |
| <u>Minuartia obtusiloba</u> | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 |
| <u>Trifolium dasyphyllum</u> | P | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 | P |
| <u>Poa glauca</u> | P | 0.01 | P | 0.02 | 0.01 | 0.01 | P |
| <u>Lloydia serotina</u> | P | 0.01 | | 0.01 | 0.01 | 0.01 | 0.01 |
| <u>Carex scopulorum</u> | 0.01 | P | | 0.01 | 0.01 | 0.01 | 0.01 |
| <u>Stelaria longipes</u> | 0.01 | P | 0.01 | 0.01 | 0.01 | 0.01 | |
| <u>Polygonum vivparum</u> | P | P | P | 0.01 | 0.01 | P | P |

Table 1. Continued

| Species | Sampling Date | | | | | | |
|-----------------------------------|---------------|------|------|------|------|------|------|
| | 6/25 | 7/05 | 7/15 | 7/25 | 8/04 | 8/14 | 8/24 |
| <u>Poa arctica</u> | P | P | P | 0.01 | P | P | P |
| <u>Carex albonigra</u> | 0.01 | | P | | 0.01 | P | |
| <u>Thalspi montanum</u> | 0.01 | P | P | | P | P | P |
| <u>Carex elynoides</u> | | | P | 0.01 | 0.01 | | |
| <u>Cerastium beeringianum</u> | 0.01 | P | P | 0.01 | P | | |
| <u>Phlox sibirica</u> | | 0.01 | P | 0.01 | P | P | |
| <u>Lewisia pygmaea</u> | P | 0.01 | P | | P | | |
| <u>Draba lanceolata</u> | | | P | 0.01 | P | P | |
| <u>Helictotrichon mortonianum</u> | P | | P | | P | | |
| <u>Eretrichium aretoides</u> | P | P | P | | | P | |
| <u>Poa alpina</u> | P | | | | | | P |
| <u>Mertensia veridis</u> | 0.01 | | | | | | |
| <u>Sedum lanceolatum</u> | | | P | | P | | |
| <u>Luzula spicata</u> | | | | .01 | | | |
| Total foliage | 1.45 | 1.54 | 1.57 | 2.03 | 2.16 | 1.73 | 1.09 |

* P means present with an LAI value less than 0.01.
Blank means no contact was made.

Table 2. Live leaf area index values for the Deschampsia meadow site on successive sampling dates in 1971

| Species | Sampling Date | | | | | | |
|--|---------------|------|------|------|------|------|------|
| | 6/25 | 7/05 | 7/15 | 7/25 | 8/04 | 8/14 | 8/24 |
| <u>Artemisia scopulorum</u> | 0.16 | 0.35 | 0.64 | 0.72 | 0.67 | 0.55 | 0.37 |
| <u>Geum rossii</u> | 0.13 | 0.39 | 0.59 | 0.60 | 0.55 | 0.46 | 0.25 |
| <u>Deschampsia caespitosa</u> | 0.14 | 0.13 | 0.19 | 0.27 | 0.28 | 0.26 | 0.17 |
| <u>Polygonum bistortoides</u> | 0.03 | 0.08 | 0.12 | 0.14 | 0.16 | 0.20 | 0.13 |
| <u>Chianophilla jamesii</u> | 0.04 | 0.06 | 0.07 | 0.07 | 0.09 | 0.05 | 0.02 |
| <u>Caltha leptosepala</u> | 0.03 | 0.03 | 0.05 | 0.11 | 0.05 | 0.03 | 0.02 |
| <u>Erisimum simplex</u> | 0.02 | 0.03 | 0.05 | 0.06 | 0.04 | 0.03 | 0.02 |
| <u>Lewisia pygmaea</u> | 0.01 | 0.02 | 0.04 | 0.02 | P* | | P |
| <u>Festuca brachyphylla</u> | | 0.01 | 0.02 | 0.01 | P | P | P |
| <u>Carex scopulorum</u> | | | 0.01 | P | 0.01 | P | P |
| <u>Minuartia biflora</u> | | P | P | 0.01 | 0.01 | P | P |
| <u>Castelleja occidentalis</u> | | | 0.01 | 0.01 | P | P | |
| <u>Polygonum viviparum</u> | | | | 0.01 | | | |
| <u>Gentiana algida</u> | | | | | | | 0.01 |
| <u>Luzula spicata</u> | | | | | P | | |
| <u>Poa nevadensis</u> | | P | | | | | |
| Total foliage | 0.55 | 1.09 | 1.79 | 2.02 | 1.86 | 1.58 | 0.99 |

* P means present with an LAI value less than 0.01.
Blank means no contact was made.

Table 3. Leaf area index values and standard deviations of selected species and the total foliage in the Kobresia and Deschampsia sites during 1971

| | <u>Sampling Date</u> | | | | | | | | | | | | | |
|-------------------------------|----------------------|-----|------|-----|------|-----|------|-----|------|-----|------|-----|------|-----|
| | 6/22 | | 7/05 | | 7/15 | | 7/25 | | 8/04 | | 8/14 | | 8.24 | |
| | LAI | SD | LAI | SD | LAI | SD | LAI | SD | LAI | SD | LAI | SD | LAI | SD |
| Kobresia site | | | | | | | | | | | | | | |
| <u>Carex rupestris</u> | .04 | .03 | .06 | .05 | .05 | .04 | .06 | .04 | .05 | .05 | .05 | .06 | .02 | .03 |
| <u>Geum rossii</u> | .08 | .08 | .08 | .07 | .09 | .07 | .09 | .07 | .07 | .09 | .06 | .07 | .01 | .02 |
| <u>Kobresia myosuroides</u> | 1.04 | .24 | 1.03 | .29 | 1.07 | .51 | 1.45 | .36 | 1.68 | .28 | 1.36 | .27 | .83 | .18 |
| Total Foliage | 1.45 | .35 | 1.54 | .71 | 1.57 | .50 | 2.03 | .49 | 2.16 | .33 | 1.73 | .32 | 1.09 | .24 |
| Deschampsia site | | | | | | | | | | | | | | |
| <u>Artemisia scopulorum</u> | .16 | .09 | .35 | .18 | .64 | .29 | .72 | .42 | .67 | .42 | .55 | .32 | .37 | .12 |
| <u>Deschampsia caespitosa</u> | .14 | .06 | .13 | .15 | .19 | .20 | .27 | .15 | .28 | .24 | .26 | .15 | .17 | .10 |
| <u>Geum rossii</u> | .13 | .06 | .39 | .16 | .59 | .15 | .60 | .30 | .55 | .32 | .46 | .25 | .25 | .22 |
| Total Foliage | .55 | .16 | 1.09 | .44 | 1.79 | .51 | 2.02 | .87 | 1.86 | .86 | 1.58 | .66 | .99 | .49 |

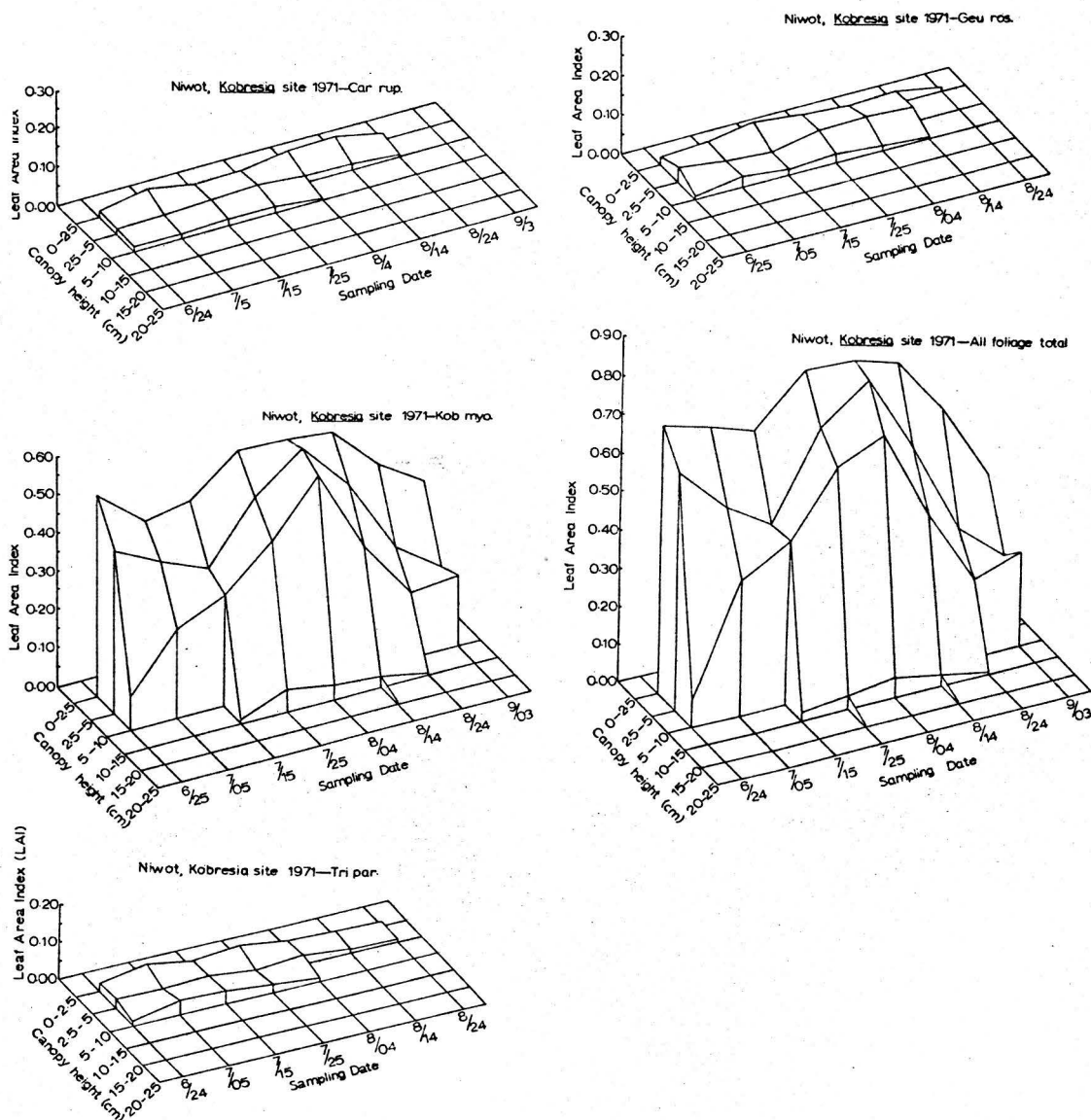


Figure 3. Distribution of leaf area at various heights in the Kobresia stand site for *Carex rupestris*, *Kobresia myosuroides*, *Trifolium parryi*, *Geum rossii*, and the total foliage on Niwot Ridge during the summer of 1971.

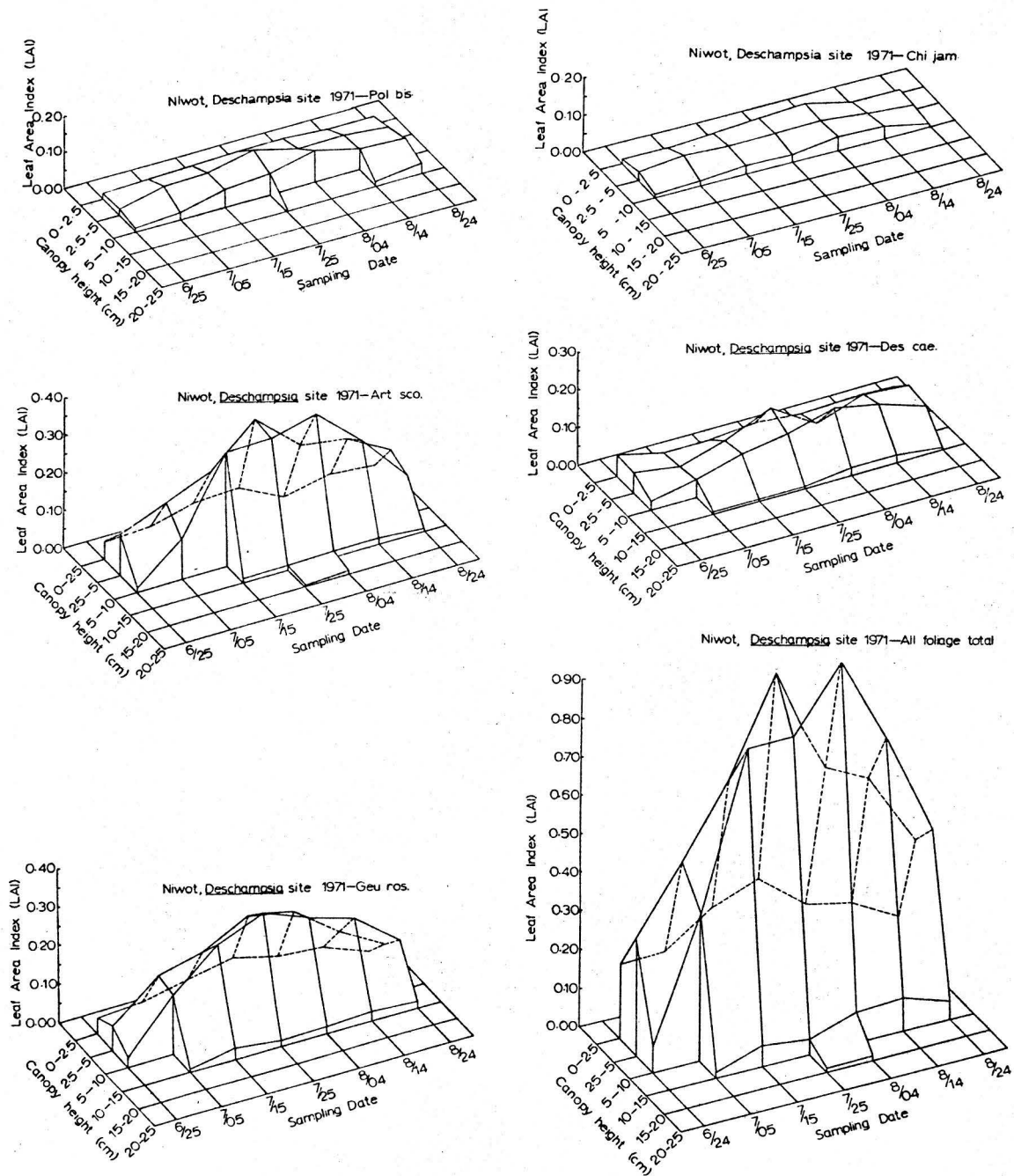


Figure 4. Distribution of leaf area at various heights in the Deschampsia meadow site for Polygonum bistortoides, Artemisia scopulorum, Geum rossii, Chianophilla jamesii, Deschampsia caespitosa, and the total foliage on Niwot Ridge during the summer of 1971.

were no live foliage contacts above 5 cm for Geum rossii, Trifolium parryi, or Carex rupestris.

In contrast to the Kobresia site, the Deschampsia meadow total foliage graph does not reflect a single dominant species. No contacts above 5 cm were made with the following four species: Luzula spicata, Festuca brachyphylla, Minuartia biflora, and Polygonum viviparum. Artemisia scopulorum, Geum rossii, Deschampsia caespitosa, Carex scopulorum, and Polygonum bistortoides were present in the 10-15 cm zone. Contacts in the 15-20 cm height zone were due to the stems and floral structures of Artemisia scopulorum.

Comparing the total foliage graphs for each site, initial LAI values were higher at all heights in the Kobresia site canopy. In the Deschampsia site, there was a four-fold increase in the total LAI from the beginning of the season to the date of maximum development. In contrast, the Kobresia site maximum LAI value is only 1 1/2 times greater than the initial LAI value.

The distribution of LAI with height varies within and between the two sites. In the Kobresia site, the greatest LAI values occurred in the 0-2.5 cm zone on every sampling date. Highest LAI values in the Deschampsia site were initially in the 2.5-5 cm zone; by early August, the region of maximum foliage had shifted to the 5-10 cm zone.

Senesced LAI

Figure 5 shows the progression of senescence within the two sites. In the Deschampsia site, contacts with senesced vegetation were first observed for Deschampsia caespitosa in late July. From August 14 to 26, Geum rossii and Artemisia scopulorum were responsible for 35 and 24% of the total foliage senesced LAI, respectively. Until late August,

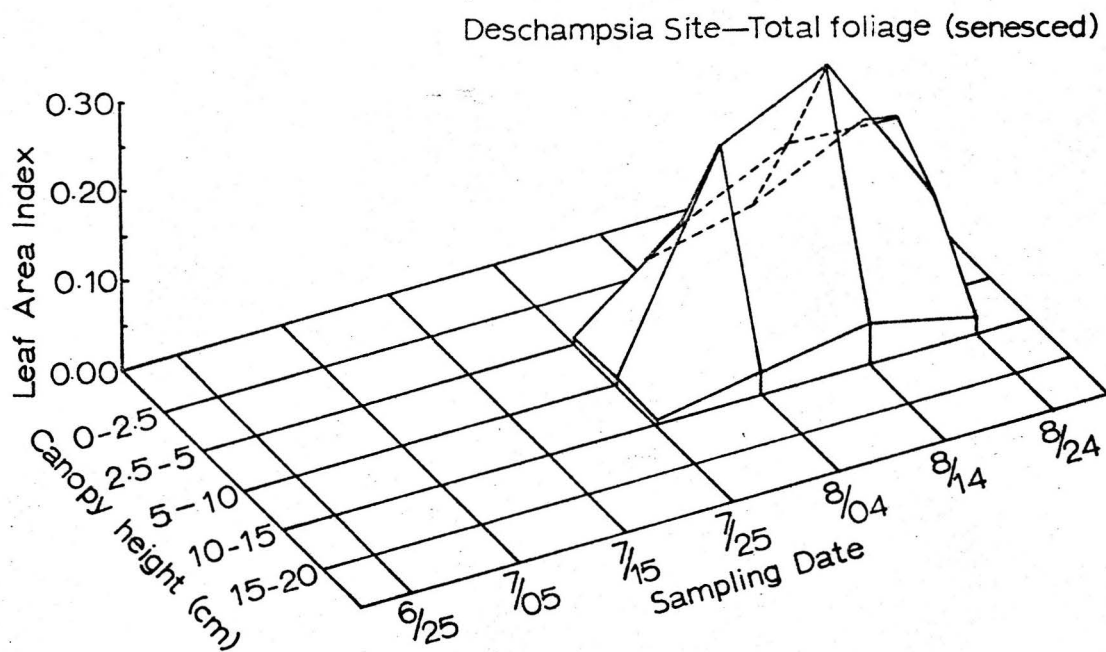
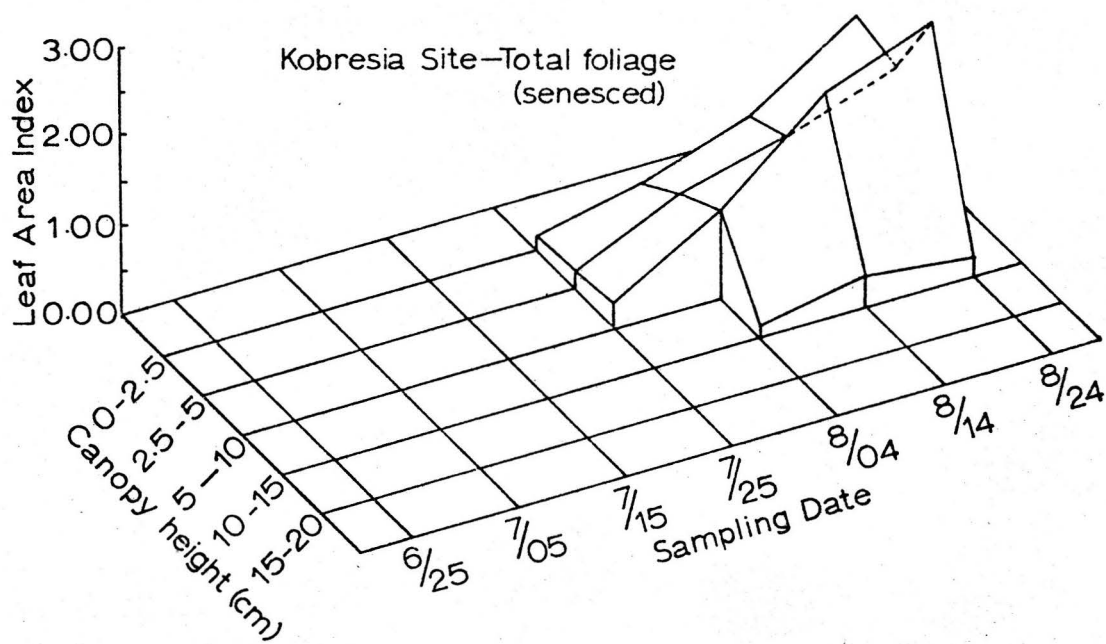


Figure 5. Distribution of senesced leaf area indices at various heights in the Kobresia and Deschampsia site canopies during 1971.

greatest senesced LAI values occurred in the zone with the greatest live leaf area (i.e., 5-10 cm). Maximum total foliage senesced LAI occurred around August 14. On the last sampling date, there was a reduction in senesced LAI at all heights above 2.5 cm.

The Kobresia site foliage also began senescing in late July. Kobresia myosuroides was responsible for more than 60% of the total foliage senesced LAI on all sampling dates. Unlike the Deschampsia site, Kobresia site senescent foliage continued to increase throughout August. Although the highest live foliage LAI values were in the 0-2.5 cm zone, the greatest senesced LAI values occurred between 5 and 10 cm.

Phenology

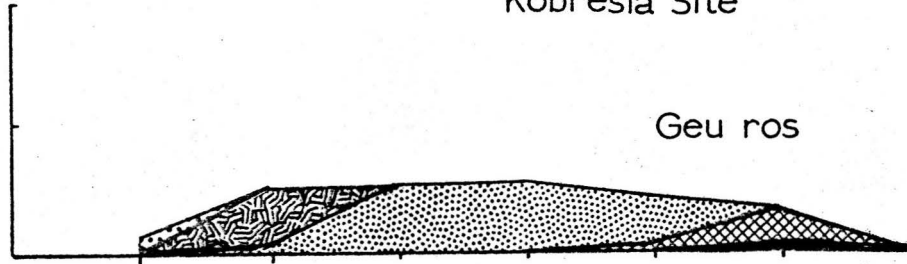
Based on the percent of contacts, the Deschampsia site showed a greater proportion of vegetative contacts on all sampling dates (Figures 6 and 7). On August 25, 75% of the Deschampsia site contacts, as compared to 41% in the Kobresia site, were vegetative.

A few species in each site had formed buds and flowers by the first sampling date. In both sites, Geum rossii was in bud and in the Kobresia site, Carex rupestris and C. scopulorum were in flower. In the Deschampsia site, Artemisia scopulorum and Caltha leptosepalla had reached the flower stage by the first sampling date.

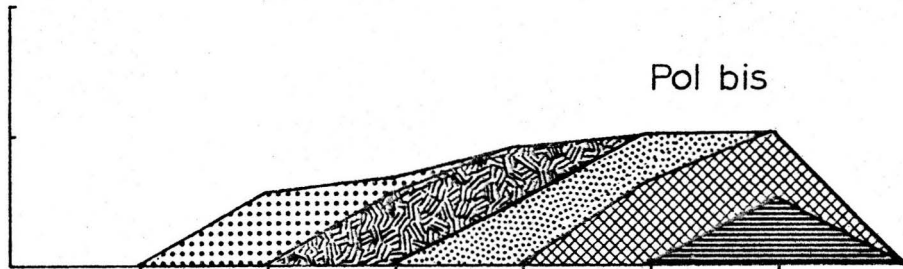
Within each site, species varied in the time of onset and the duration of phenological stages. Geum rossii plants in the Kobresia site tended to form buds, flowers, and fruits earlier than other species in this site. In both sites, G. rossii was the first species to form fruit. Fruiting began about June 25 and continued for 50 days. In the Deschampsia site, Artemisia scopulorum and Deschampsia caespitosa began fruit formation about July 15 and continued fruit production for 30 days.

Kobresia Site

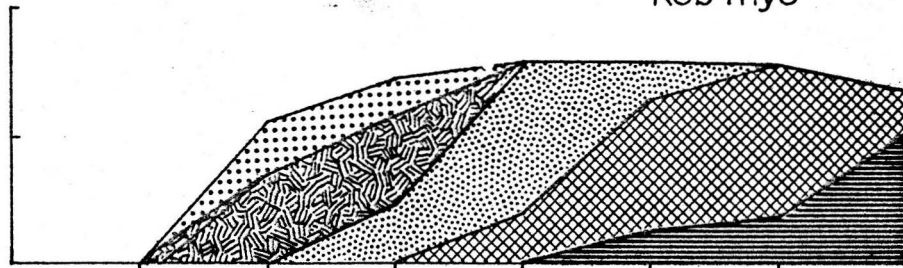
Geu ros



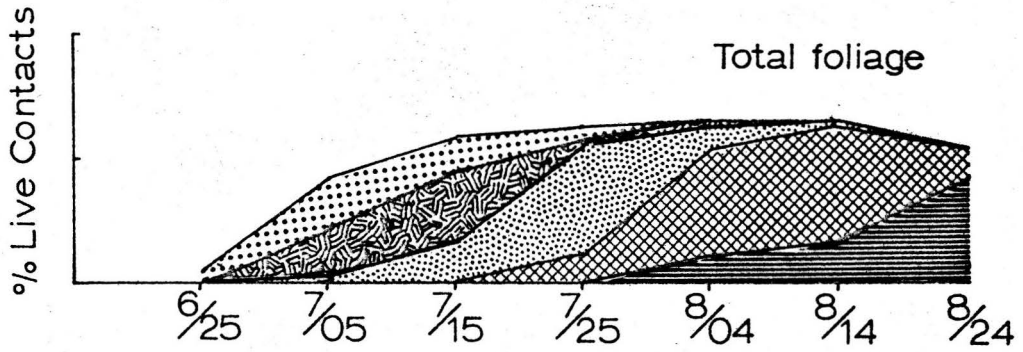
Pol bis



Kob myo

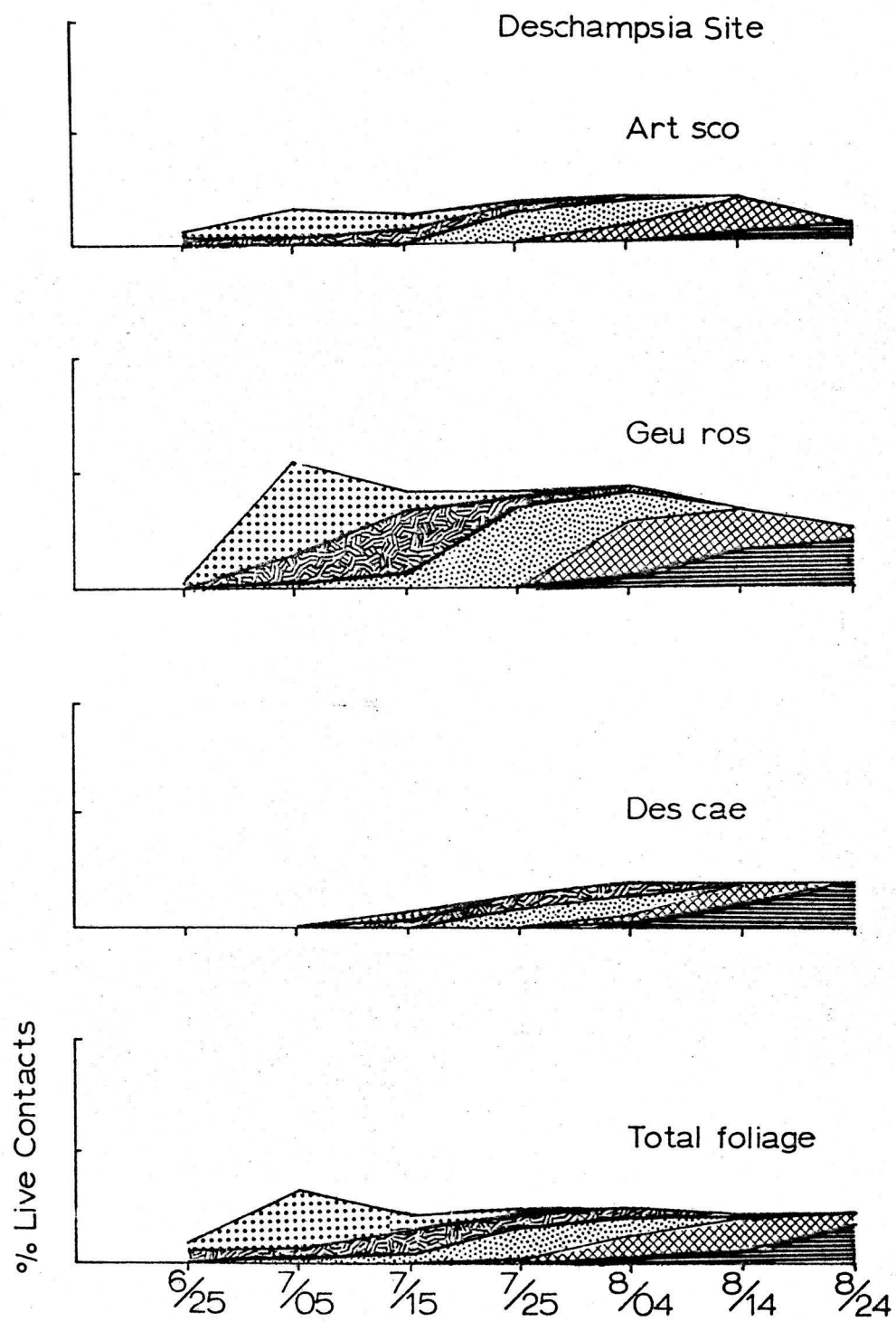


Total foliage



% Live Contacts

6/25 7/05 7/15 7/25 8/04 8/14 8/24



Similarly, in the Kobresia site, Polygonum bistortoides and Kobresia myosuroides first formed fruit on July 15. This stage persisted for 30 days in Polygonum and for 40 days in Kobresia.

When each community is considered as a unit, the duration of phenological stages appear quite similar. Bud stage began before sampling and continued for nearly 40 days. Flowering also began before sampling in the two sites and persisted approximately 50 days. Fruit development was first observed on July 5 in both sites. In the Kobresia site, fruiting continued for approximately 50 days. In the Deschampsia site, the fruiting stage was extended at least 10 days longer than in the Kobresia site. Seed set was first observed on July 15 in both sites. Seed set was still active on the last day of sampling. Dehiscence extended from approximately July 25 through the last sampling date.

Indications of dormancy were first observed in the Kobresia site in early August: leaves of Trifolium dasyphyllum began turning brown, while those of Geum rossii turned red. In the Deschampsia site, signs of dormancy did not appear until late August. Here Artemisia scopulorum and Geum rossii were the first species to change color.

DISCUSSION

Canopy Structure

Information on the structure and configuration of the photosynthetic portion of a plant community is requisite for an understanding of primary production. Leaf angle, area, shape, surface texture, and density at various heights largely determine the radiation profile of the canopy and the amount of chlorophyll exposed to radiation.

In the two alpine communities examined here, there is considerable variation in the leaf angles of associated species (Tieszen, unpublished data). In the Kobresia site the dominant species, Kobresia myosuroides, is characterized by an upper leaf inclination of 80 to 90° and the base of these leaves is only slightly less vertical. In contrast to the erectophilic nature of the Kobresia community, the Deschampsia meadow is dominated by species whose leaf angles are more horizontal at the base of the plant and tend toward the vertical at the top.

Leaf angle is an important factor in leaf energy receipt. The amount of light striking a leaf surface is proportional to the cosine of the angle of incidence (Kriedman, et al, 1964). Thus, as the inclination of a leaf approaches the vertical, the amount of light the leaf receives from the midday summer sun will decrease. This attenuation is particularly rapid as the leaf approaches a perpendicular orientation. Of the radiation striking a leaf, it is either absorbed, transmitted, or reflected. Absorption is largely determined by leaf morphology, structure and pigmentation.

Leaf angle can influence the amount of radiation received and, therefore, absorbed by a plant. This is important for both leaf temperature and photosynthetic reactions.

In the *Deschampsia* site, the distribution of vertical leaves at the top and more horizontally inclined leaves at the base of the canopy may be advantageous. The combination of vertically and horizontally oriented leaves would seem to optimize both the amount of sunlight absorbed by the canopy throughout the day and the total community photosynthesis. This would appear to be valid even though Bouger's law predicts a decrease in light with depth in a reasonably homogeneous medium. In contrast, a predominantly erectophillic canopy would expose a minimum amount of surface area to the midday sun, thus, minimizing its photosynthetic capacity.

However, in the drier *Kobresia* community, the erectophillic nature of the canopy could be important in reducing water loss by transpiration. During the warmest part of the day when the sun is close to the zenith, vertical leaves would intercept less radiation than horizontally-inclined leaves. This would minimize the amount of heat absorbed and help maintain leaf temperature close to air temperature, thus minimizing the vapor pressure deficit and transpiration.

Unlike the *Deschampsia* site, it does not seem that light penetrating the upper strata would be used as efficiently by the lower strata where leaves are also primarily vertical in orientation. However, verification with photocells and measurements of community photosynthesis is necessary. Duncan (1971) working with computer models of corn and soybean leaves, suggests that for communities of LAI less than 3.0, lowest rates of canopy photosynthesis resulted when all leaves were vertical. Yet, he concluded that at such low LAI values, leaf angles have little practical significance. For LAI values above 3.0, maximum photosynthesis could be attained when the canopy consisted of vertical leaf layers above horizontal leaf layers. Pendleton, et al, (1968), studied the effect of various leaf

inclinations on the yield of Zea maize. They found that when the upper leaves were tied in a vertical position, there was about a 15% increase in yield. Whether the lower leaves were horizontal or vertical had no effect on yield. However, at LAI values of 4.0, the more erect leaved plants produced 40% more grain than its counterpart with horizontal type leaves. These findings are in agreement with the models discussed by Anderson and Denmead (1969) and Loomis and Williams (1967).

Phenology

The Deschampsia and Kobresia communities have similar timing and duration of phenological stages. Yet, differences in phenological patterns appear when species common to both communities are examined. Geum rossii varied in the duration of bud and flower stages and in the time of initiation of dehiscence. The variation in the duration of stages may be due to the relatively small G. rossii population in the Kobresia site. Holway and Ward (1965) found that the time period required for the various phases generally showed little variation within an alpine species, while the time of initiation for a particular phase often varied considerably from site to site. Deschampsia caespitosa also showed variation in the initiation of phenological phases in the two sites. Seed set began 10 days earlier in the Kobresia site than in the Deschampsia site. There was at least a 10-day lag in the onset of the flower, fruit, seed set, and dehiscent stages in plants of Polygonum bistortoides in the Deschampsia site, compared to the Kobresia site population.

Micro-environmental differences in even a relatively limited area in the alpine tundra can be great. Yet, whether or not these microhabitat

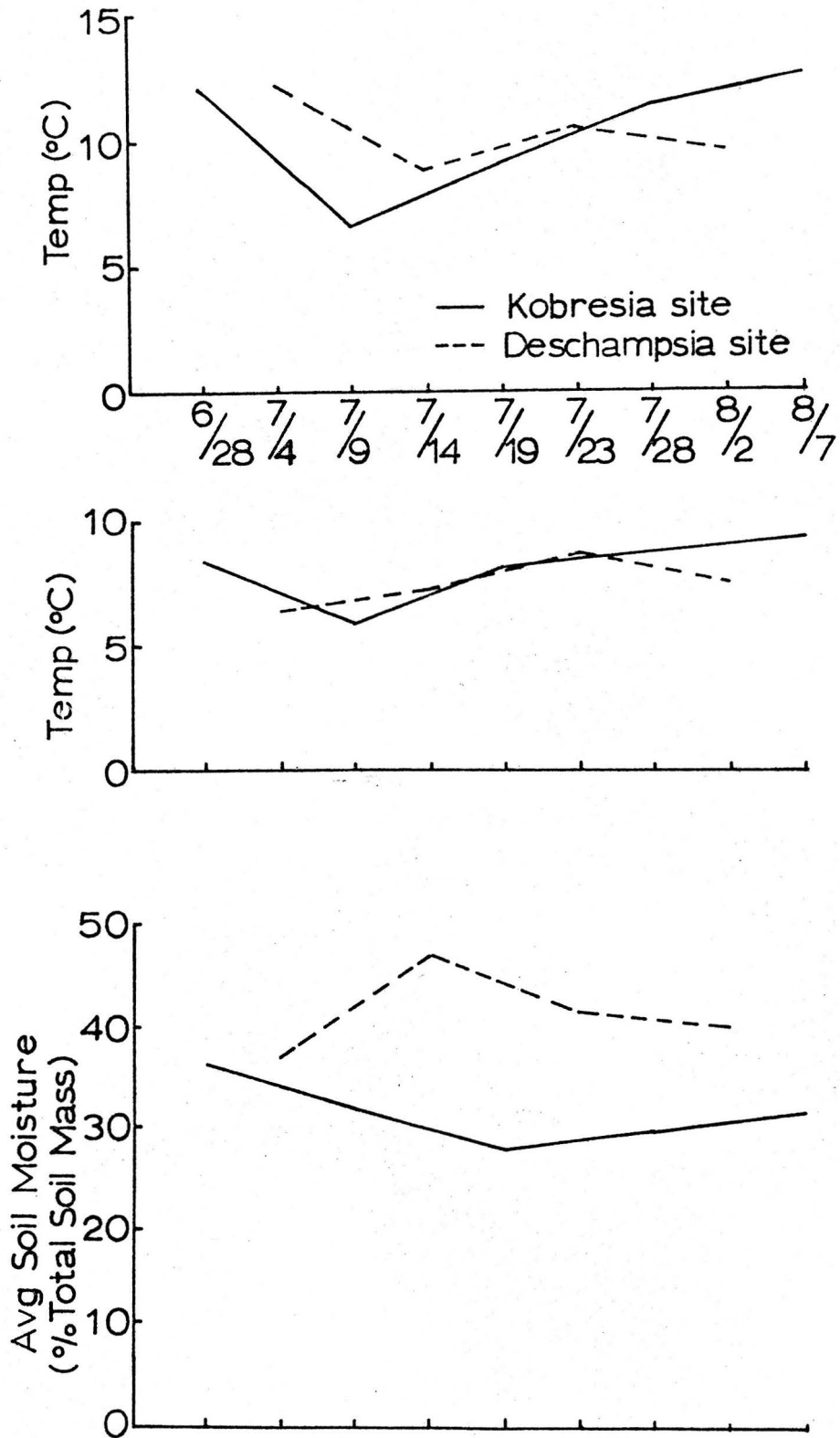


Figure 8. Soil temperature curves at 2.5 cm (top graph) and 7.5 cm (middle graph) and average soil moisture (bottom graph) in the Kobresia and Deschampsia sites during 1971 (based on data from Gersper, unpublished data).

differences produce ecotypic selection that may be related to variations in phenological patterns within a species needs to be studied.

Based on the conclusions of Holway and Ward (1963, 1965), the presence of snow cover and surface meltwater are correlated to some degree with species composition and the timing of phenological events. They suggest that the floristic similarity between snow-free and snow accumulation areas may be related to the correspondence in soil moisture and soil temperature at root depths (15 cm). Conversely, the delay in phenological stages and the differences in species composition in the snow accumulation sites may be related to the later beginning of the growing season, its consequent shortening, and to greater amounts of surface meltwater.

The primary effects of snowmelt runoff on the microclimate are to increase soil moisture and decrease soil temperature. Data on soil moisture and temperature are presented in figure 8. Surprisingly, though soil moisture is considerably higher in the *Deschampsia* site, soil temperature at 2.5 and 7.5 cm in the relatively snow free *Kobresia* site are quite comparable to those in the wet *Deschampsia* site. Perhaps, at these depths, the effect of water is to dampen the temperature variation usually observed in dry alpine soils. Because of the snowmelt, soil temperatures closer to the surface may be lower in the *Deschampsia* site and this could be influencing the timing of phenological events.

Phenological deviations from the complete reproductive cycle were observed in a number of species (Table 4). Thus, certain plants of *Geum rossii* in the *Deschampsia* site formed buds but no flowers, others formed flowers but no fruit, and still others developed mature fruit. According to Billings and Mooney (1968) and Hodgson (1966), the environmental condi-

Table 4. Species with incomplete phenological development

| Type of Development | Species | |
|---|-----------------------------------|--------------------------------|
| | Kobresia site | Deschampsia site |
| Vegetative growth, no floral development | <u>Artemisia scopulorum</u> | <u>Lewisia pygmaea</u> |
| | <u>Poa Glauca</u> | <u>Polygonum viviparum</u> |
| | <u>Lloydia serotina</u> | <u>Luzula spicata</u> |
| | <u>Calamagrostis purpurescens</u> | |
| | <u>Cerastium beeringianum</u> | |
| | <u>Heliotrichium mortonianum</u> | |
| | <u>Mertensia viridis</u> | |
| | <u>Phlox sibirica</u> | |
| | <u>Carex albonigra</u> | |
| | <u>Draba lanceolatum</u> | |
| | <u>Lewisia pygmaea</u> | |
| | <u>Poa alpina</u> | |
| | <u>Eretrichium aretoiodes</u> | |
| | <u>Poa arctica</u> | |
| <u>Sedum lanceolatum</u> | | |
| Buds but no floral expansion | <u>Minuartia biflora</u> | <u>Geum rossii*</u> |
| Failure of some flowers to develop mature fruit | <u>Kobresia myosuroides*</u> | <u>Castilleja occidentalis</u> |
| | <u>Trifolium dasyphyllum</u> | <u>Chianophilla jamesii</u> |
| | <u>Minuartia obtusiloba</u> | <u>Artemisia scopulorum*</u> |
| | <u>Campanula rotundifolia</u> | <u>Geum rossii*</u> |
| | <u>Polygonum bistortoides*</u> | |
| | <u>Trifolium parryi</u> | |

* Species showing both complete and incomplete phenological development.

tions of one season do not influence the flowering of that season as significantly as they influence the late season development of floral primordia and the subsequent flowering of the next season. Holway and Ward (1965) noted a reduction in flower production following a summer marked by intermittent drought periods and lower total precipitation.

Holway and Ward (1965) also suggest that low seed production in insect pollinated species may be directly related to the sparcity of pollinators in the alpine tundra. Conceivably, small numbers of bees could explain the failure of Trifolium dasyphyllum and T. parryi to develop mature seeds. Macior (1970) noted that the success of sexual reproduction in certain Colorado alpine species of Pedicularis may be limited by direct, interspecific competition of plants for pollinating insects.

The large number of species which remained vegetative can be explained, in part, by the severe alpine environment. In the most severe environments sexual reproduction decreases and becomes unreliable, while vegetative reproduction seems to increase (Billings and Mooney, 1968). Many tundra species reproduce by apomixis, vivipary, and rhizomes (Löve, 1959). Holch, et al. (1941) noted that many alpine perennials reproduce vegetatively because the short alpine growing season is prohibitive to seed set. Yet, Osburn (1958) found that under natural conditions many species do set seed and germinate. Possibly, yearly variations in the severity of the alpine climate would be reflected in the amount of vegetative reproduction.

In the Kobresia site, plants of Geum rossii exhibited changes in pigmentation 20 days before those in the Deschampsia meadow. When dormancy was first observed in the Kobresia site, the soil moisture was approximately

10% by weight lower than in the *Deschampsia* site. As Billings and Mooney (1968) noted, normally, dormancy is induced by a period of shortening day length, lowering temperatures, and, often, increasing drought. Dormancy response in *Geum turbinatum* has been correlated with soil moisture (Holway and Ward, 1965).

Productivity

For all dominant species in the two sites, maximum LAI occurred between late July and early August during flower and fruit production stages. Billings and Bliss (1959) observed a similar correlation between productivity and phenology in late July for alpine snowbank communities in the Medicine Bow Mountains of Wyoming.

The higher early summer total foliage LAI values in the *Kobresia* site as compared to the *Deschampsia* site, may be related to the greater number of snow-free days in the *Kobresia* site. Since the *Deschampsia* site received snowmelt runoff from a nearby slope until early July, perhaps low soil surface temperatures may partially explain the low total foliage LAI values in June. According to Mooney and Billings (1960), once dormancy is broken, there is rapid translocation of carbohydrates stored during the previous year in roots and rhizomes. This upward translocation in combination with the warming of the soil and air, the abundant soil moisture, and the exposure to full light intensity, cause rapid leaf expansion (Billings and Bliss, 1959). The *Deschampsia* community seems to exhibit this rapid growth pattern nicely. In less than 20 days, total foliage leaf area in the *Deschampsia* site was as great as that in the snow-free *Kobresia* site.

Both *Deschampsia caespitosa* and *Geum rossii* reached their maximum LAI in both sites in late July. However, the duration of the maximum

value varied between sites. In the *Deschampsia* site, *D. caespitosa* maintained a high LAI until late August (approximately 30 days after the maximum value was reached). In the *Kobresia* site, the drop off in LAI occurred within 10 days of the maximum value. *Polygonum bistortoides* was the only species in the *Deschampsia* site which reached a maximum LAI 20 days later than the same species in the *Kobresia* site.

As with dormancy, the early decrease in LAI in the *Kobresia* site species may be related to low soil moisture in the site since soil and air temperatures in late July and early August appeared to be adequate. Billings and Bliss (1959), working in the Snowy Range of the Medicine Bow Mountains, found that low temperatures during the growing season do not greatly reduce daily productivity of alpine plants as long as soil moisture is not limiting. Yet, even a short drought produced marked effects on productivity. Bliss (1956) also noted that the cessation of growth in both arctic species located near Umiat, Alaska and alpine species in the Medicine Bow Mountains of Wyoming was quite independent of prevailing temperatures.

Leaf area index data in arctic tundra vegetation at Barrow, Alaska (71° N, 157° W) has been collected by Tieszen (unpublished data) (Figure 9). The maximum total foliage LAI values for an arctic community dominated by *Eriophorum angustifolium*, *Dupontia fisheri*, and *Carex aquatilis* is 0.95. This value is less than half the maximum LAI reached in the alpine communities of the present study.

The lower arctic LAI value as compared to the alpine values is contrary to most standing crop studies. End of the growing season standing crop data in arctic *Dupontia* and *Carex-Eriophorum* communities at Point Barrow, Alaska are somewhat greater than those measured in alpine communities

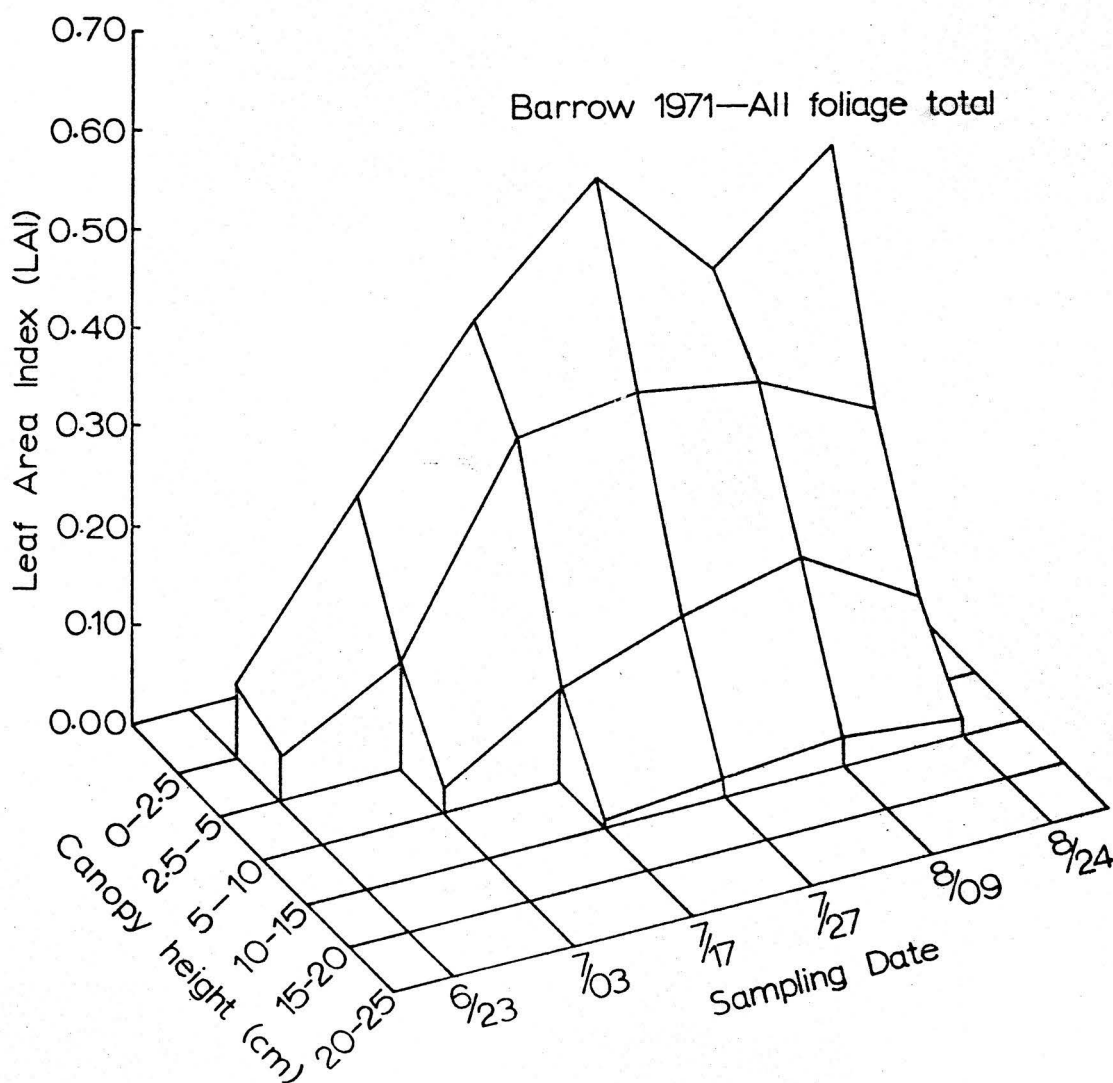


Figure 9. Total foliage leaf area indices at various heights in the canopy throughout the 1971 growing season at Barrow, Alaska (Tieszen, unpublished data).

in both the central Rocky Mountains and the Medicine Bow Mountains (Bliss, 1962a). However, a few standing crop values for alpine wet meadow communities do approximate arctic marsh and swale net productivity values.

A comparison of the arctic and alpine total foliage LAI graphs helps explain the low arctic LAI values. The alpine canopies are slightly taller than the arctic canopy and the two alpine canopies also appear to have more leaf area, both at the beginning of the season and at all heights above 2.5 cm for most of the growing season.

It should be noted that the presence of cushion plants was rare in either of the two alpine sites studied here. Many alpine standing crop studies have involved cushion plant communities. LAI values measured in ridge-top cushion plant communities tend to be lower than those measured in meadow-type vegetation.

The distribution of vegetation in the arctic canopy resembles that of the alpine *Kobresia* community: on every sampling date, highest LAI values are within 2.5 cm of the mean ground level. Unlike the alpine communities, the arctic vegetation shows two peaks in LAI in the lowest height increment. Also, the reduction in live LAI after the seasonal peak in late July is more gradual than in the alpine tundra. The timing of maximum leaf development in late July to early August appears similar in both arctic and alpine sites. Bliss (1956) found that maximum leaf expansion in plants growing at Umiat, Alaska (69° N 152° W) occurred somewhat earlier than in plants growing in the Medicine Bow Mountains of Wyoming. However, the High Arctic has a more severe environment than the Low Arctic.

SUMMARY

1. A comparative study was made of canopy structure and phenology in two alpine tundra plant communities on Niwot Ridge, Colorado. A modified inclined point frame was used to determine individual species and total community leaf area indices.
2. The Kobresia community, dominated by Kobresia myosuroides, was drier and had more snowfree days than the Deschampsia site. Slope and aspect of the two sites were comparable.
3. Although soil moisture was greater in the Deschampsia Meadow, soil temperatures at 2.5 and 7.5 cm were similar in both sites.
4. The Kobresia site had a maximum LAI of 2.2 and a predominance of vegetation lying below 10 cm. The Deschampsia site had a maximum LAI of 2.0 and vegetation reaching 20 cm in height.
5. Initial leaf growth was more rapid in the Deschampsia site where a four-fold increase in LAI occurred between the end of June and the end of August. The Kobresia stand showed a 1 1/2 fold increase in LAI between the end of June and the period of maximum LAI (early August).
6. Senescence began in both sites in late July. By the end of August, a large amount of the Deschampsia site plant material lying above 2.5 cm had senesced and fallen. In the Kobresia site, senescent contacts in the upper height zones continued to increase through the last sampling date.
7. Individual species phenological patterns tended to vary within and between sites. Geum rossii varied in the duration of bud and flower stages, while Deschampsia caespitosa and Polygonum bistortoides varied in the time of onset of specific stages in the two sites. Greater snow cover and surface melt water runoff may be related to the delay in phenological stages in certain Deschampsia site species.

8. Dormancy response appears to be related to increasing drought. First signs of dormancy occurred in the Kobresia site when the soil moisture was 10% lower than in the Deschampsia site.
9. Dominant species in the two sites showed maximum leaf production when flower and fruit production overlapped. As with phenological patterns, shared species varied in the duration of their maximum LAI.
10. Although alpine tundra standing crop values tend to be lower than those in the arctic tundra, the alpine leaf area indices measured on Niwot Ridge, Colorado were greater than those measured at Point Barrow, Alaska. The alpine tundra was slightly taller than the arctic vegetation and had more leaf area at all heights except the lowest.

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