

M. Fareed

and

M. M. Caldwell

Department of Range Science and the Ecology Center
Utah State University
Logan, Utah

Phenological Patterns of Two Alpine Tundra Plant Populations on Niwot Ridge, Colorado

Abstract

Inclined point quadrats were used to quantify phenological development of plant populations growing in an alpine tundra *Kobresia* meadow and a *Deschampsia* meadow during the summer of 1971 on Niwot Ridge, Colorado. These measurements suggest that variations in phenological patterns in the two sites may be related to differences in the duration of snow cover and surface meltwater. Snow melted from the *Kobresia* site 20 days earlier than from the *Deschampsia* site. Signs of dormancy were noted earlier in the *Kobresia* site plants, and the duration of fruit development was generally shorter than that observed in the *Deschampsia* community. Many plants in both sites remained vegetative throughout the season, while others completed only a portion of the reproductive cycle. Harsh alpine environmental conditions of the current season and/or of the previous season may be related to this lack of reproductive development.

Introduction

Strategies for plant survival in the harsh alpine environment hinge critically on the timing and duration of phenological stages during the short growing season. This is complicated by microsite variability and the vicissitudes of weather in the alpine tundra. This study characterizes phenological development in two alpine tundra plant communities in a saddle area of Niwot Ridge, Colorado. These communities are representative of community types of mesic to xeric conditions in the alpine region of the Eastern Slope of the Rocky Mountains.

Accumulation of snow, time of snow melt, and persistence of meltwater were the primary physical factors which differed in the two communities. Phenological sampling was conducted on a population basis so as to represent adequately microsite variability within each community.

Description of Area

The two major alpine community types examined here are located on a gently sloping saddle of Niwot Ridge, Colorado (40°40'N, 105°36'W, 3476 m elevation).

The *Kobresia* site has a southwest aspect and a 5° slope and is typical of a well developed, mesic meadow which can be snow-free for up to 250 days per year. The dominant species, *Kobresia myosuroides* (Vill.) Fiori & Paol., is associated with *Geum rossii* (R. Br.) Ser., *Trifolium parryi* Gray, and *Polygonum bistortoides* Purch. A total of 15 species were contacted in the *Kobresia* site.

The *Deschampsia* site is characteristic of areas where snow cover may persist until late June and where meltwater runoff is heavy. This site has a southeast aspect and a 4° slope. Because of its location on the saddle, the *Deschampsia* site is some-

what less exposed to wind than the *Kobresia* site, and snow accumulates to greater depths. Only 67 snow-free days per year were observed in this site in 1970 to 1971 (Ebert, unpublished data). Here, *Deschampsia caespitosa* (L.) Beauv. is commonly found with *Artemisia scopulorum* Gray and *Geum rossii*. The *Deschampsia* meadow is characterized by only 16 species, 11 of which also occur in the *Kobresia* site.

Figure 1 shows daily radiation, precipitation, and temperature for the 1971 growing season measured at the D-1 experimental site on Niwot Ridge. Climatic data were provided by the Institute of Arctic and Alpine Research, University of Colorado, Boulder. The relationship of the D-1 and saddle area sites is described by Marr (1967). The two areas on the ridge are climatically very similar (Clark, unpublished data).

Methods

Modified inclined point quadrats as described by Warren Wilson (1960) were used to measure phenology of plants on a population basis throughout the 1971 growing season for each species in the two communities. In each of ten plots, 47 point quadrats were placed at horizontal intervals of 2 cm and were passed through the low growing vegetation at an inclination of 32.5°. Sampling occurred at ten-day intervals between late June and late August.

For every plant contacted by the inclined point frame, the most advanced phenological stage was recorded. For example, if a plant were breaking bud and flowering at the same time, then it was categorized as being in the flowering stage.

A voucher collection of all species is on file with the Intermountain Herbarium, Logan, Utah.

Results

Quantitative indices of the phenology status of dominant species in the two alpine sites are given in Figure 2. The duration of snow cover varied in the two sites. Snow melted from the *Kobresia* meadow between May 25 and June 1, 1971, but not until June 15-20 from the *Deschampsia* site. Most of the *Deschampsia* meadow was saturated by meltwater from snow at higher positions on the same slope until late June.

A range of 150 to 600 plants were sampled on each date in the *Kobresia* site. The *Deschampsia* site community sample consisted of 90 to 300 plants on each sampling date. In both sites, the sample size decreased towards the end of the growing season. Because *Kobresia myosuroides* often reproduces by tillering, differentiating individual plants was occasionally difficult. Most clumps of *Kobresia* were treated as separate plants.

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* All. and *C. scopulorum* Holm were in flower. In the *Deschampsia* site, *Artemisia scopulorum* and *Caltha leptosepalla* DC., a minor component of the community, 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. Fruiting began about June 25 and continued for 50 days. In the *Deschampsia* site, *Artemisia scopulorum* and

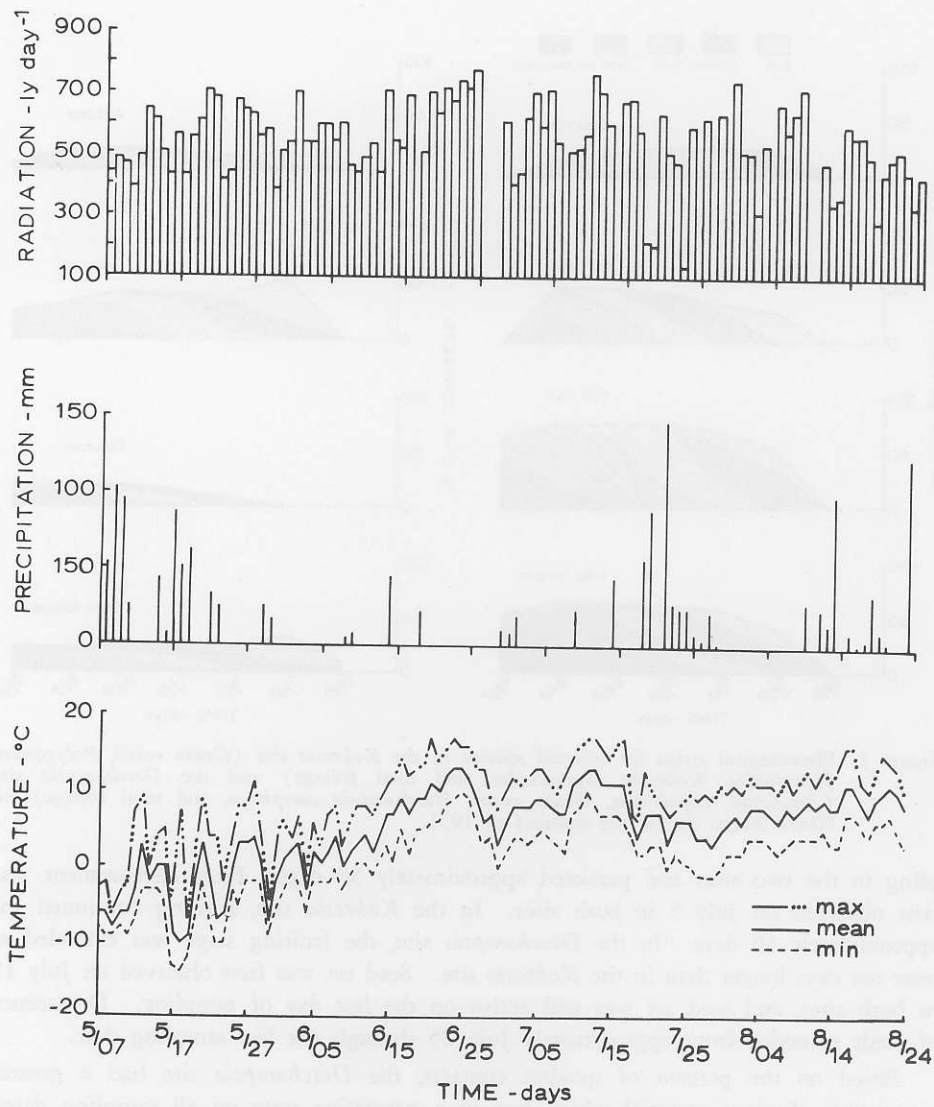


Figure 1. Daily radiation, precipitation, and temperature on Niwot Ridge (3727 m), Colorado from May through September, 1971. No radiation data were available for the following dates: 6/17, 6/26, 6/27, 6/28, 7/7, 8/9, and 8/10 (climatic data for Niwot Ridge D-1 station provided through the Institute of Arctic and Alpine Research, University of Colorado, Boulder).

Deschampsia caespitosa began fruit formation about July 15 and continued fruit production for 30 days. 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 the two communities are compared in terms of total foliage, the duration of phenological stages appears quite similar, although snow melted from the *Kobresia* meadow about 20 days before it did from the *Deschampsia* site. Bud stage began before sampling and continued for nearly 40 days. Flowering also began before sam-

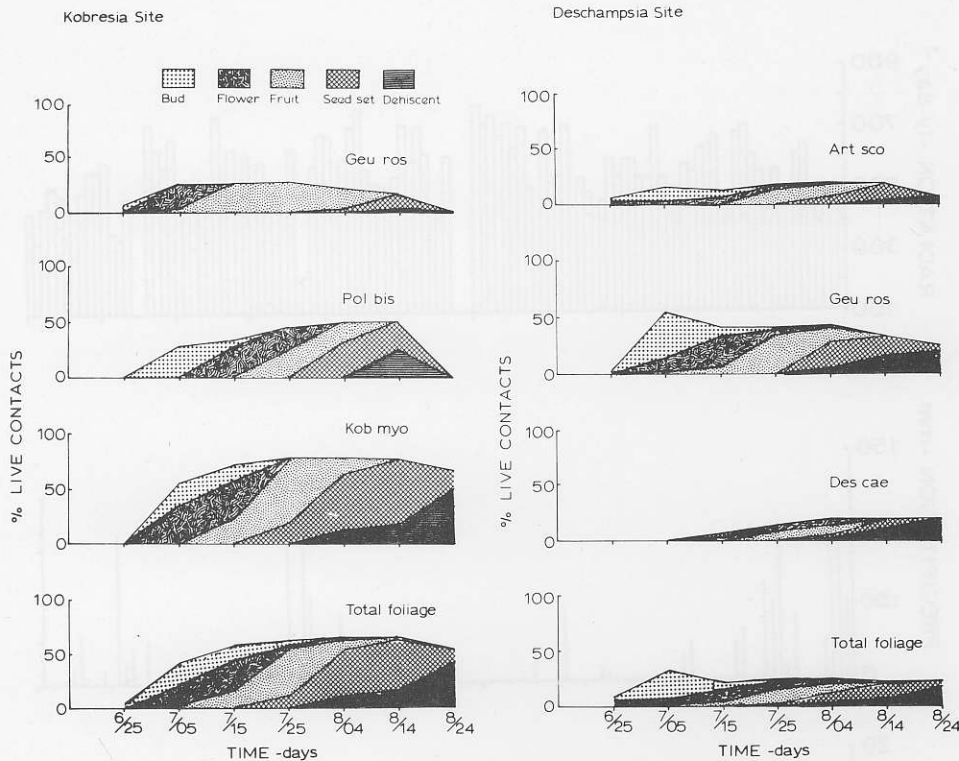


Figure 2. Phenological strips for selected species in the *Kobresia* site (*Geum rossii*, *Polygonum bistortoides*, *Kobresia myosuroides*, and total foliage) and the *Deschampsia* site (*Artemisia scopulorum*, *Geum rossii*, *Deschampsia caespitosa*, and total foliage) on Niwot Ridge during the summer of 1971.

pling 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 ten days longer than in the *Kobresia* site. Seed set was first observed on July 15 in both sites, and seed set was still active on the last day of sampling. Dehiscence of seeds extended from approximately July 25 through the last sampling date.

Based on the percent of quadrat contacts, the *Deschampsia* site had a greater proportion of plant material which was in a vegetative state on all sampling dates. On August 25, 75 percent of the *Deschampsia* site contacts, as compared to 41 percent in the *Kobresia* site, were vegetative.

Indications of dormancy were first observed in the *Kobresia* site in early August, when leaves of *Geum rossii* showed an increase in apparent anthocyanin content. In the *Deschampsia* site, signs of dormancy did not appear until late August, when *Artemisia scopulorum* and *Geum rossii* were the first species to show signs of senescence.

Discussion

The *Deschampsia* and *Kobresia* communities exhibited similar timing and duration of phenological stages. Yet, differences in phenological patterns appeared when species common to both communities were examined. *Deschampsia caespitosa* showed

variation in the initiation and duration of phenological phases at the two sites. Seed set began ten days earlier in the *Kobresia* site and lasted two weeks longer than the same stage in the *Deschampsia* site. There was at least a ten-day lag in the onset of the flower, fruit, seed set, and dehiscent stages of *Polygonum bistortoides* in the *Deschampsia* site, compared to the *Kobresia* site population. *Geum rossii* varied in the duration of bud and flower stages and in the time of initiation of dehiscence. Both bud and flower stages were completed earlier than the same stages in the *Deschampsia* site.

The observed variation in both the time of initiation and the duration of stages in a given species occurring in the two sites is in some contrast with the findings of Holway and Ward (1965). They found that, for a given species, the time of initiation for a phenological phase could vary considerably from site to site; yet, the duration of phases generally showed little variation within an alpine species.

Although plant phenology responds to an interacting complex of physical factors such as air temperature, precipitation, irradiation, soil temperature, and soil moisture content, as well as to community structure and competition, some abiotic factors appear to be particularly well correlated with phenological progression. Reproductive events of the phenological cycle are correlated to a greater extent with air temperature than with either precipitation or irradiation. The rise in air temperature during late May and early June paralleled the development of reproductive buds and flowering in both the *Kobresia* and the *Deschampsia* sites. Maximum mean daily air temperatures occurred between June 15 and July 17 when bud development, flowering, and fruit stages had all been initiated. A cooling trend, marked by occasional below-zero minimum temperatures, began on July 17, which was also the time of initiation of the seed set stage in both sites.

Soil temperature and moisture status may also be related to specific phenological events. Figure 3 shows average soil moisture and temperature data for the two Niwor Ridge study areas. In the *Deschampsia* site, a considerable increase in the fruit production of all species occurred approximately July 15, the date when average soil moisture began to decrease. Plants of *Geum rossii* in the *Kobresia* site (early snow release) exhibited changes in pigmentation approximately 20 days before plants of the same species in the *Deschampsia* site (late snow release). When dormancy was first observed in the *Kobresia* site in early August, the soil moisture was approximately 10 percent by weight lower than in the *Deschampsia* site.

In 1972, snow melt occurred approximately 18 days earlier in the *Kobresia* meadow than in the *Deschampsia* site, in a pattern similar to 1971. Leaf relative growth rate and photosynthetic capacity measurements of *Geum rossii* in the two sites indicated a much earlier curtailment of growth and photosynthesis in the *Kobresia* site (Johnson and Caldwell, 1974). This shift in photosynthetic capacity and growth rates between the two sites in 1972 is in some respects comparable to the shift in phenological progression based on reproductive organs; however, the shift between the two sites is not linear for all phenological stages. Instead, there is telescoping of the sequence of phenological stages of *Geum* in the *Deschampsia* site. This would seem to be beneficial in accommodating the less favorable weather patterns towards the termination of the growing season which would, of course, occur at about the same time for both sites.

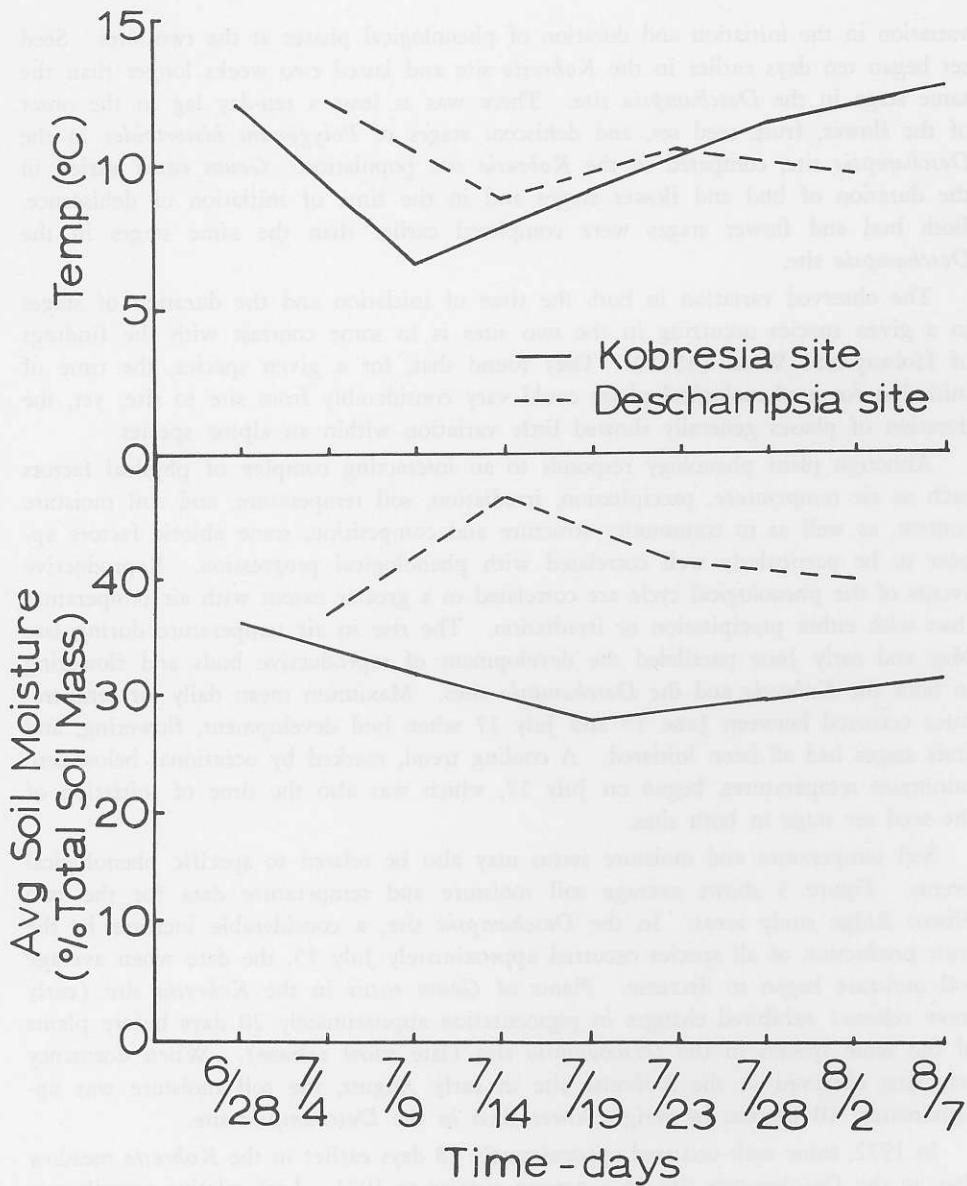


Figure 3. Soil temperature at a depth of 7.5 cm and average soil moisture for the *Kobresia* (solid line) and *Deschampsia* (dashed line) sites during 1971 (unpublished data, personal communication, Paul Gersper).

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 variable and unreliable, while vegetative reproduction in the form of apomixis, vivipary, and rhizomes is important for most tundra species (Billings and Mooney, 1968). Holch *et al.* (1941) noted that many alpine perennials reproduce vegetatively because the short alpine growing season is prohibitive to seed set. The greater proportion of plants which remained vegetative in the

Deschampsia site may be a reflection of the delayed timing of snow melt, resulting in a somewhat shorter growing season than occurred in the *Kobresia* site. Possibly, yearly variations in the severity of the alpine weather would also be reflected in the amount of vegetative reproduction.

The two communities depicted in this study appear to differ primarily in the length of time under snow, in the dates of snow melt in the spring, and in average soil moisture. These differences seem to be clearly reflected in the phenological progression of the principal species. For species common to both sites, telescoping of phenological events is apparent. In the *Deschampsia* site, where the duration of snow cover was greater and where snow melt occurred later in the spring, a greater number of plants remained vegetative throughout the growing season.

Acknowledgements

This work was financially supported by National Science Foundation Grant GU-29353X1 to M. M. Caldwell and L. L. Tieszen. Thomas Shoemaker, Roger Hanson, and Diane Hanson provided field assistance in this study. Support provided by the Institute of Arctic and Alpine Research, University of Colorado, and the I.B.P. Tundra Biome Center, University of Alaska is also gratefully acknowledged.

Literature Cited

- Billings, W. D., and H. A. Mooney. 1968. The ecology of arctic and alpine plants. *Biol. Rev.* 43: 481-529.
- Holch, A. E., E. W. Hertel, W. D. Oakes, and H. H. Whitwell. 1941. Root habits of certain alpine plants of the foothills and alpine belts of the Rocky Mountain National Park. *Ecol. Monog.* 11(2): 327-345.
- Holway, J. G., and R. T. Ward. 1965. Phenology of alpine plants in Northern Colorado. *Ecology* 46: 73-83.
- Johnson, D. A., and M. M. Caldwell. 1974. Field measurements of photosynthesis and leaf growth rates of three alpine plant species. *Arc. and Alp. Res.* 6: 245-251.
- Marr, J. W. 1967. Ecosystems of the East Slope of the Front Range in Colorado. Univ. Colo. Studies, Series No. 8, Univ. Colo. Press, Boulder, Colo. 134 pp.
- Warren Wilson, J. 1960. Inclined point quadrats. *New Phytol.* 59: 1-8.

Received March 4, 1974.

Accepted for publication November 19, 1974.