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Phenology of Steppe Plants in Wet and Dry Years

Abstract

In the arid *Artemisia tridentata-Agropyron spicatum* plant community of south-central Washington, precipitation in the 1973-74 season (October 1 to September 30) was 2.78 times that in the 1972-73 season. Nine of 12 plant species flowered later and longer in the 1973-74 season than in the 1972-73 season, even though temperatures during the flowering period of the two years were similar. These data suggest that the greater soil water content of the 1973-74 season caused the prolonged and delayed phenological development. The species not responding to the added precipitation and soil moisture in 1973-74 had growth restricted to the cool, wet months of late winter and early spring. It appears that early growing species, although unable to take advantage of added precipitation, have a stable habitat. In contrast, warm-season species can use the additional water of a wet year, but risk drought in years of low precipitation.

Introduction

In general, phenology is the study of the relationship between developmental state and environment. Ecosystem dynamics, both within and between trophic levels, depend in large part on the timing of plant developmental stages. For example, reproductive success in pronghorn is directly related to the developmental state of the food plants (Ellis, 1970).

The undisturbed Arid Lands Ecology (ALE) Reserve on the Energy Research and Development Administration's Hanford Reservation in south-central Washington offers the opportunity to study steppe plants in an environment not grazed by livestock. The drought of the 1972-73 season (October 1 to September 30) and abundant precipitation of the 1973-74 season presented the opportunity to compare the phenological response of native species on the ALE Reserve to these contrasting weather conditions. The purpose of this paper is to show the phenological response of 12 native species to the contrasting water availability of the 1972-73 and 1973-74 seasons. The effect of temperature on phenological change is also considered, but a detailed analysis of the effect of temperature on phenological change is not the purpose of this paper.

Phenological change has been correlated with insolation and average daily air temperature (Caprio, 1971), cumulative sums of degree hours (Lindsey and Newman, 1956; Jackson, 1966), moving averages of maximum and mean temperatures (Sauer, 1975), increasing air temperatures and insolation in spring (Ratcliff, 1961), photoperiod and rainfall pattern (Tothill, 1966), period of heaviest precipitation (Burk, 1966), soil temperature (Holway and Ward, 1965) and patterns of temperature and rainfall (Mueggler, 1972; Blaisdel, 1958).

Methods

All observations were made on the US/IBP Grasslands Biome ungrazed study area (elevation 365 m) on the ALE Reserve in south-central Washington. This area is of uniform slope, exposure, vegetation, and soil (Rickard *et al.,* 1975) and is in the *Artemisia tridentata-Agropyron spicatum* association of Daubenmire (1970).

Ten plots each 15 m x 15 m were set out in March 1973. In each plot one individual of all plant species present was marked with a small flag. Periodically the phenological stage (Table 1) of each flagged individual was recorded. Length of time between observations varied from one week, when plants were rapidly changing in spring and summer, to monthly during fall and winter.

TABLE 1. The six phenophases used to describe developmental state.

1.	Begin Growth
2.	Begin Reproduction (floral buds appear)
3.	Begin Flowering
4.	End Flowering
5.	End Reproduction (all seeds ready for dispersal)
6.	End Growth

In August 1973, a wildfire burned the phenology plots. To continue the observations on comparable vegetation, another 10 plots were established approximately 200 m away in a very similar unburned area with the same experimental design and procedures.

Plant nomenclature is that of Hitchcock and Cronquist (1973).

Soil water content was gravimetrically sampled at 10 cm depth increments within 25 m of the phenology plots. Air temperatures, at 1 m height, were taken approximately 20 meters in 1972-73 and 100 meters in 1973-74 from the phenology plots, and reduced to monthly averages of maximum and minimum. The abiotic data were taken from the meteorological network located on ALE. Soil water data were collected in connection with the US/IBP Grasslands Biome study.

These data are presented for the period October 1 to September 30 for each year. In this region, growth starts with the first soaking rains in fall, then stops with low winter temperatures. In spring, rising temperatures accompany a burst of growth, which ceases with summer drought and heat.

Results and Discussion

Precipitation in the wet 1973-74 growing season was 37.5 cm, considerably more than the 13.5 cm that fell during the dry 1972-73 growing season. Nearly all precipitation fell in the fall and winter months (October to March). Clearly, higher soil water contents and deeper percolation occurred during the 1973-4 season (Table 2). In 1972-73 precipitation percolated to approximately 60 cm, but in 1973-74 the soil was wetted to a depth of 180 cm. During July, 1973, soil water content was below 6 percent, the approximate soil water content for –15 bars soil water potential, at all soil depths, but in July, 1974, all strata but two were above 6 percent soil water content. Deep rooted species or species with the capacity to grow roots deep into the soil therefore had a reservoir of soil water well into summer. It should be noted that biomass continued to accumulate after soil water content decreased below 6 percent indicating that the –15 bar value is not the lower limit of soil water potential for water uptake (Cline *et al.,* 1975).

TABLE 2. Percent soil water at two dates in the growing season to illustrate the greater soil water content in the 1973-74 season. Soil water content at –15 bars soil water potential is approximately 6 percent.

Depth dm	Feb. 16, 1973	Feb. 6, 1974	July 27, 1973	July 31, 1974
0-1	18.1	13.4	1.7	3.0
1-2	14.6	14.6	2.8	4.8
2-3	12.9	16.2	4.2	6.1
3-4	12.7	18.6	5.0	6.6
4-5	12.1	19.1	5.4	6.9
5-6	9.1	19.3	5.2	7.1
6-7	7.6	17.7	4.4	6.2
7-8	5.0	17.6	4.0	6.0
8-9	4.4	16.3	4.0	6.0
9-10	4.2	14.8	4.0	6.0
10-11		12.0		6.5
11-12		9.5		7.0
12-13		6.2		7.5
13-14		4.2		8.0
14-15		4.5		8.1
15-16				8.1
16-17				7.2
17-18				6.3

Maximum air temperatures (Table 3) in March and April and minimum winter temperatures were slightly higher in 1973-74 than the previous season.

TABLE 3. Monthly average temperatures (C°) illustrating the slightly warmer 1973-74 season.

	Maximum Air Temperatures		Minimum Air Temperatures	
	1972-73	1973-74	1972-73	1973-74
October	22.2	27.8*	10.0	14.5*
November	18.4	*	7.6	*
December	6.4	15.6	1.4	8.2
January	2.8	*	–1.7	*
February	2.3	11.1*	–4.3	4.9*
March	6.3	10.0	–.4	3.4
April	12.3	14.4*	2.4	4.9*
May	17.4	17.2	4.5	7.2
June	23.7	21.6	9.4	9.4
July	26.7	32.1	12.1	15.8
August	33.5	33.3	17.3	16.9
September	30.6	34.0	15.0	18.9

* Indicates more than 10 days of data missing from that month due to instrument failure.

Phenological progression through the 1972-73 and 1973-74 seasons for 12 prominent species in shown in Figure 1. These species vary in growth form from a woody shrub (*Artemisia tridentata* Nutt.) to small shrubs less than 30 cm in height (*Erigeron filifolius* Nutt. and *Phlox longifolia* Nutt.) to a decumbent, semi-woody perennial in direct contact with the soil surface (*Antennaria dimorpha* (Nutt.) T. & G.) to perennial bunchgrasses (*Agropyron spicatum* (Pursh) Scribn. and Smith, *Poa sandbergii* Vasey, *P. cusickii* Vasey, *Stipa thurberiana* Piper) to suffrutescent perennials (*Lupinus laxiflorus* Dougl. *Lomatium macrocarpum* (Nutt.) Coult. and Rose, *Crepis atrabarba* Heller ex Lindl., to a bulb (*Calochortus macrocarpus* Dougl.). A phenophase is indicated on Figure 1 when one or more of the tagged individuals were in that phenophase, except in the case of dead or dormant leaves which were recorded when all individuals were in that state.

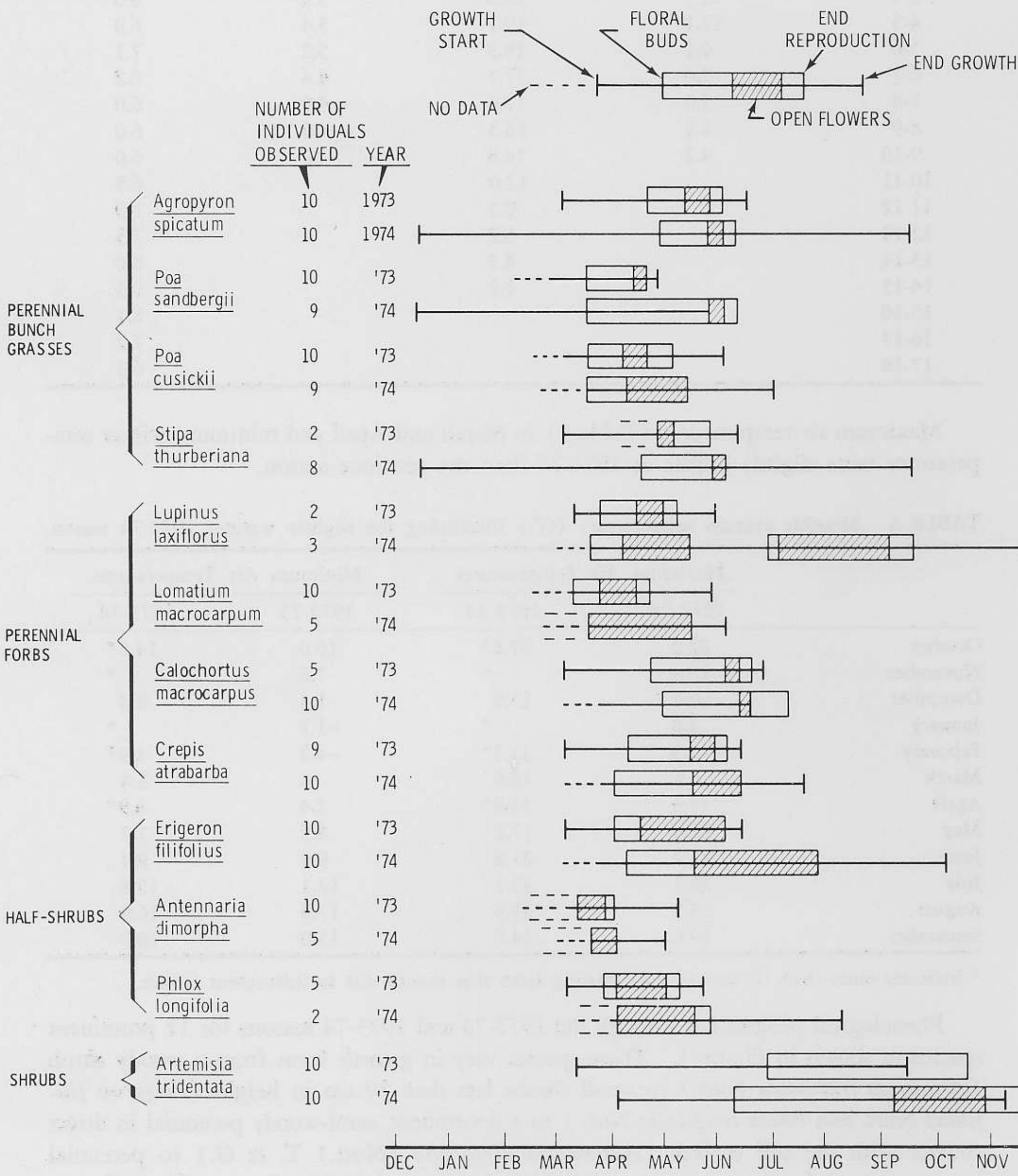

Figure 1. Phenological state of 12 species through the 1972-73 and 1973-74 growing seasons, and the number of individuals of each species observed.

These twelve species differed in phenophase development betwen the two years, but to different degrees. The least different was *Antennaria dimorpha,* one of the first species to flower in the spring and complete its growth cycle. Most differences occurred for species which normally continue growth during the warm and dry weather. The additional soil water available in 1974 apparently permitted many of the later growing species to continue to grow and even flower through the summer. *Agropyron spicatum* and *Stipa thurberiana* remained green, at least to a limited degree, through the 1974 summer, but were dormant by mid-summer in 1973. All individuals of *Erigeron filifolius* continued to grow vegetatively and in some cases flower and set seed through the 1974 summer in sharp contrast to the early summer onset of dormancy in 1973. *Lupinus laxiflorus* grew through the 1974 summer and had two flowering and growth periods. The first period was associated with larger individuals, presumably older plants, and the second period was associated with smaller individuals, possibly plants that germinated during the fall of 1973.

Several species (*Poa sandbergii, P. cusickii, Erigeron filifolius, Stipa thurberiana, Calochortus macrocarpus, Artemisia tridentata, Lomatium macrocarpum, Crepis atrabarba,* and *Phlox longifolia*) flowered later and longer in 1973-74 than in 1972-73. Later flowering has been associated with lower temperatures (Sauer, 1975; Harris and Scott, 1969; Stanfield, Ormrod, and Fletcher, 1966; Blaisdel, 1958). However, 1974 was slightly warmer than 1973, suggesting that soil water content also regulates phenological change and that the extended period of phenological progression is a result of the extended period of available soil water in 1974. Perhaps these air temperature data are not adequate to describe the temperature environment of these plants. The temperature of the soil surface, particularly on a clear day, would be higher than the air temperature at 1 m, and those plants on or near the soil surface would experience higher temperatures than those above the soil surface. The first species to flower, *Antennaria dimorpha,* is a low growing plant that remains in contact with the soil surface.

Agropyron spicatum and *Stipa thurberiana* resumed growth earlier in 1973-74 than in 1972-73. The January-March period of 1973 was colder than the same period of 1974, suggesting that the earlier growth of these two bunchgrasses in 1974 was a result of the warmer winter temperatures. In 1962, *Agropyron spicatum* had initiated growth by October 6 in many plant communities of eastern Washington, including the *Artemisia tridentata-Agropyron spicatum* community type on the ALE Reserve (Daubenmire, 1970). The nearly 2.5 month difference in growth initiation between 1974 and 1962 can be traced to the presence of soil water at greater than −15 bars soil water potential, a minimum of 2.5 months earlier in Daubenmire's 1962 study area (Daubenmire, 1972) than on the ALE 1973-74 study sites. An additional response in some species to the increased soil water reserves of 1973-74 was abundant flowering and seed set, particularly in *Artemisia tridentata* and *Calochortus macrocarpus.*

A problem encountered in this study was delimiting in time the beginning and end of each phenophase. The initiation of growth in the bunchgrasses was obscured by dead stems. Those species with leaves present year around presented particular problems. *Artemisia tridentata* and *Erigerion filifolius* displayed no clear start and stop of growth, as by bud burst or leaf drop. Perhaps these species only stopped growing and remained capable of growing at any time of the year when temperature and water conditions were simultaneously adequate for growth. Summer temperatures may stop growth, even when water is available. Growth then would be resumed in the fall with the return of moderate temperatures and continue until low winter temperatures again stopped growth. These hypotheses should be tested experimentally.

It is tempting to speculate that the early growing species have a different evolutionary strategy than late growing species. In late winter and early spring, the upper soil layers (top 30 cm, for example) are usually wet and soil water content nonlimiting to growth. While air temperatures are low, soil surface temperatures are higher and adequate for growth of those species adjacent to the soil surface. These early growing species have evolved an early growth to avoid drought even in years of low rainfall when only the top soil layers are wetted. For this dependability of habitat, these species pay the price of being unable to take advantage of above average rainfall. Those species that grow later in the season risk the possibility of poor growth and seed production, but have the capacity to take advantage of above average rainfall. Further speculating, if there should be a period of several years of above average rainfall, the late growing species would increase at the expense of the early growing species. On the other hand, a long series of dry years would favor the early growing species.

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