START

Seasonal Development and Yield of NATIVE PLANTS

on the upper SNAKE RIVER plains and their relation to certain CLIMATIC FACTORS

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ACKNOWLEDGMENTS

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Seasonal Development and Yield of Native Plants on the Upper Snake River Plains and Their Relation to Certain Climatic Factors[1]

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INTRODUCTION

THE UPPER SNAKE RIVER PLAINS

As described by Russell (*72*),[2] the Snake River Plains consist of a roughly crescent-shaped belt along the Snake River extending entirely across southern Idaho. This belt is about 350 miles long and from 50 to 75 miles wide. The general appearance of this area is that of a vast, stream-eroded valley; however, it is actually a plateau formed principally of lava sheets, and does not owe its major surface features to erosion.

The eastern part of the Snake River Plains (about one-fifth of the total) is mostly above 5,000 feet elevation and is commonly known as the Upper Snake River Plains. This area is roughly circular and has a diameter of approximately 60 miles; its center is in the vicinity of 112° west longitude and 44° north latitude. It is bordered on the east by the Teton Range, on the north by the Centennial Mountains, and on the west by the Lemhi and Lost River Ranges. All of these are fairly high mountains, and many peaks are higher than 10,000 feet.

Topography and Soils

The lava of the Upper Snake River Plains is approximately 4,000 feet in depth and occurs in generally horizontal sheets from 10 to 200 feet thick (*72, 21*). The surface layers that overlie the Pliocene acid lavas are mostly Pleistocene basalt. Since basaltic lavas were very fluid, individual flows sometimes extended for miles, and formed a fairly level surface broken only by ridges forced upwards by pressures at the time of cooling. Low basaltic mounds that mark points of extrusion and a few well-formed craters provide the major relief.

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[2] Italic numbers in parentheses refer to Literature Cited, p. 64.

Although total relief in the areas where flows originated may be several hundred feet, variations in the general surface of the Upper Snake River Plains are slight (fig. 1). The Snake River and its main branches have not cut deep channels in this area, but flow on the plateau surface. Farther downstream, however, the river has cut a gorge that eventually reaches a depth of more than a thousand feet.

Even though there are numerous lava outcrops on which no soil has developed (fig. 1), most of the Upper Snake River Plains is covered by a soil mantle varying in depth from a few inches to several feet. Much of the soil is residual from the underlying basalt, but aeolian materials from alluvial deposits, ancient lacustrine beds, and cinder cones are also important components in certain areas. The texture is normally sandy loam at the surface and sandy clay loam beneath.

These soils are relatively low in nitrogen and organic matter, but as a result of the low precipitation, they have undergone little leaching and are consequently rich in mineral fertility, particularly calcium (51). Near the mountain borders and along the streams is a local covering of alluvium. Often this is coarse or gravelly, but along the Snake River and some of its larger tributaries, the alluvial soils are deep and fertile, and provide the bulk of the arable land.

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FIGURE 1.—A typical part of the Upper Snake River Plains near headquarters of the U. S. Sheep Experiment Station. The Centennial Mountains are in the background.

Climate

The continental climate of the Upper Snake River Plains is characterized by scanty precipitation, cold winters, and hot summers. This is typical of regions that have mild relief, are remote from tempering influences of the ocean, and are deprived of their full share of precipitation by the presence of high mountains in the path of the prevailing winds.

Precipitation averages about 10 inches annually and except for a slight concentration during May and June is rather evenly distributed throughout the year. Snow usually covers the ground from about mid-December to the end of March and attains a depth of from 1 to 3 feet. Snowmelt usually occurs gradually and most of the water sinks directly into the ground, providing abundant moisture at the beginning of the growing season. Summer precipitation comes largely as showers, usually of short duration, and provides little effective moisture. Soil moisture of the surface 18 inches usually falls below the wilting coefficient during late June or early July. Humidity is generally low, particularly during the summer and early fall.

Temperatures may reach a maximum of about 100° F. in summer and a minimum of −30° in winter. Despite low winter temperatures, the blanket of snow ordinarily prevents soil freezing below the depth of a few inches. The frost-free period is about 4 months long; the last spring frost occurs in May or June, and the first fall frost in September or October. In the summer, nights are cool and days are warm. Rapid temperature changes are characteristic.

Winds are common during all seasons, in the summertime usually blowing from the northeast at night and the southwest in daytime. High winds in winter, particularly from the north, cause considerable drifting and therefore a somewhat unequal distribution of the snow blanket. Summer winds combine with high temperatures to cause high water loss from both soil and vegetation.

Vegetation and Its Relation to Certain Environmental Factors

The native vegetation of the Upper Snake River Plains is predominantly shrubs with an understory of perennial grasses and forbs (nongrasslike herbaceous plants); however, vegetal cover is not continuous, and numerous patches of bare ground are exposed (fig. 2). A mulch of litter is present only under the larger shrubs.

Artemisia tridentata [3] is the dominant shrub that gives the

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[3] Authorities for plant names and the common names of species are listed on p. 63. For the most part, nomenclature of grasses follows Hitchcock (*31*) and that of shrubs and forbs, Davis (*15*). Specimens of most plants mentioned have been deposited in the herbarium of the Upper Snake River Experimental Range, Dubois, Idaho, and in the herbarium of the U. S. Forest Service, Washington, D. C.

F—46998

FIGURE 2.—A closeup of the vegetation near headquarters of the U. S. Sheep Experiment Station showing the three dominants: *Agropyron spicatum, Balsamorhiza sagittata*, and *Artemisia tripartita*.

characteristic gray appearance to most of the area. *A. tripartita,* a closely related species, is dominant on a number of areas, including the location of the present study. Except for occasional sprouting from the roots (*64, 80*), this species is ecologically very similar to *A. tridentata.* Other associated shrubs, often present in considerable quantities, are *Purshia tridentata, Tetradymia canescens* var. *inermis, Chrysothamnus puberulus,* and *Gutierrezia sarothrae.*

On a few small areas of saline soils, *Sarcobatus vermiculatus* or *Atriplex nuttallii* are found as dominants. On the slopes of old craters and buttes, *Juniperus osteosperma, J. scopulorum, Pseudotsuga menziesii,* and *Pinus flexilis* comprise part of the woody vegetation, and along the streams *Salix* spp. and *Populus* spp. occur.

The most abundant grasses of the typical Artemisia-herb community are *Agropyron spicatum, A. dasystachyum, Koeleria cristata, Oryzopsis hymenoides, Poa nevadensis, P. secunda,* and *Stipa comata.* *Agropyron spicatum* and *Poa secunda* are rather uniformly distributed throughout the entire Upper Snake River Plains, and *Stipa comata* and *Oryzopsis hymenoides* are particularly prominent on the most sandy soils. In the relatively moist areas of swales and at the uppermost elevations, *Festuca idahoensis, Calamagrostis montanensis,* and *Stipa columbiana* are present in considerable quantity. With the exception of the rhizomatous species, *Agropyron dasystachyum* and *Calamagrostis montanensis,* all these are perennial bunchgrasses.

Forbs are present in much greater variety than grasses, and their distribution is much less uniform. It is difficult, therefore, to list species that are abundant over the entire area. *Balsamorhiza sagittata* and *Lupinus caudatus*, for example, are very abundant on some areas but elsewhere very scarce. Other forbs present in varying quantities are as follows:

Achillea millefolium	*Eriogonum ovalifolium*
Antennaria dimorpha	*Lomatium macdougali*
A. parvifolia	*L. macrocarpum*
Arnica fulgens	*Lupinus leucophyllus*
Astragalus convallarius	*Penstemon deustus*
A. stenophyllus	*P. radicosus*
Comandra pallida	*Phlox hoodii*
Crepis acuminata	*P. longifolia*
Erigeron corymbosus	*Senecio integerrimus*
Eriogonum caespitosum	*Viola beckwithii*
E. heracleoides	*V. nuttallii*

These forbs are highly variable in character, ranging from low mat formers such as *Phlox hoodii* and *Eriogonum caespitosum* to tall, coarse plants like *Lupinus leucophyllus* and *Balsamorhiza sagittata*. Root systems vary from stout, deep taproots in Balsamorhiza and Lupinus to spreading, rhizomatous systems in *Arnica fulgens* and *Erigeron corymbosus*.

It is difficult to know how this Artemisia-grass-forb vegetation might appear if man-caused fires and grazing by domestic livestock were eliminated. Weaver and Clements (*83*) have pictured the climax vegetation as a grassland similar to the Palouse Prairie of Washington; but reports of early explorers indicate that sagebrush was always a dominant and that grasses and forbs were minor components of the original vegetation (*22, 24, 53, 75*).

Since then several ecologists have presented what is believed to be a more accurate conception of the original vegetation (*14, 18, 60, 66*). Although there may have been considerable local variation from heavy stands of Artemisia to almost pure grassland, the major part of the present Artemisia-grass-forb community was probably an open stand of Artemisia intermixed with a vigorous stand of perennial grasses and forbs. Recent investigations have substantiated the latter concept (*5*).

Grazing studies by Craddock and Forsling (*12*) and Pechanec and Stewart (*63*) have shown that conservative grazing is the key to preventing destruction of the climax vegetation. Additional information, indicating the importance of season at which grazing occurs, has been provided by Blaisdell and Pechanec (*6*) who carried out clipping studies at various times in the spring to simulate grazing, and by Mueggler (*52*) who compared effects of spring with fall grazing by sheep. Herbage removal is apparently most injurious to grasses and forbs during the middle part of their growth period—after the date when substantial regrowth is prevented by inadequate moisture, but before maturity. Grazing during the fall and winter usually causes little damage to herbaceous species, but may be very injurious to shrubs.

Effects of fire on the vegetation of the Upper Snake River Plains have been studied in considerable detail during the past

25 years (*5, 64*). All plants are damaged by fire, but if given complete protection from grazing for one season, most soon recover. Rapidity of recovery is much greater among shrubs with a strong sprouting habit and rhizomatous herbs than among shrubs such as *Artemisia tridentata* that are unable to sprout, the suffrutescent forbs, and the fine-leaved bunchgrasses like *Festuca idahoensis.*

Fire has an indirect effect on vegetation through its effect on soil; organic matter, total nitrogen, and moisture-holding capacity are temporarily reduced in the surface soil, and soluble mineral nutrients are apparently increased. Other than the reduction of Artemisia, most of the changes in vegetation and soil produced by single, planned burns are minor and rather short lived. Repeated burning, particularly at close intervals, upsets the ecological balance and causes a shift to a more fire-resistant type of vegetation as well as serious soil deterioration.

Despite the recognized importance of climatic factors, their effects on the vegetation of the area here considered have received but little attention. In studying effects of the 1934 drought on native vegetation, Pechanec, Pickford, and Stewart (*62*) found that annual precipitation 2.52 inches below normal accompanied by temperatures 5.7° F. above average caused decreases in cover amounting to 62 percent in perennial grasses, 75 percent in perennial forbs, and 47 percent in shrubs. Other studies have shown that annual fluctuations in weather caused important changes in amount of forage produced and in the time at which plant growth occurred (*12*).

Vegetation of the Upper Snake River Plains, then, has been described and studied to ascertain the effects of certain environmental factors, particularly grazing and fire. However, little is known about how and when plants grow in this locality, their year-to-year variations, and to what extent these variations are related to weather. The present investigation provides some information of this nature through a study of seasonal development and yield of native plants on the Upper Snake River Plains and their relation to climatic factors, especially precipitation and temperature. It involves an analysis of both vegetal and climatic records at the U. S. Sheep Experiment Station near Dubois, Idaho, over the 23-year period, 1932-54.

SEASONAL DEVELOPMENT AND YIELD OF NATIVE PLANTS

METHODS OF STUDY

Studies described herein were conducted near headquarters of the U. S. Sheep Experiment Station about 6 miles north of Dubois, Idaho, at an elevation of approximately 5,500 feet. In conjunction with grazing trials, 6 areas of 1½, 2, 3, 10, 10, and 80 acres were fenced to exclude livestock. Repeated observations of the vegetation within these exclosures over the 23-year period, 1932-54, have provided the fundamental vegetal data that form the basis of the present study.

Requirements of the over-all research program of the experiment station necessitated several revisions in type of records, and personnel shortages prevented collection of data in some years, so that a continuous, uniform set of records is not available for the entire period 1932–54. Although these changes and omissions cause considerable inconvenience in analysis, it is thought that they do not seriously impair the utility of the data.

Seasonal Development

The study of development consists of periodic observations of the vegetation to determine dates at which various phases (stages) were reached and to record growth (in height or weight) throughout the season.

For the 9-year period, 1932–40, observations of phasic development were made on the following species:

Grasses	Forbs
Agropyron spicatum	*Balsamorhiza sagittata*
Oryzopsis hymenoides	*Crepis acuminata*
Poa nevadensis	*Lupinus caudatus*
P. secunda	
Stipa comata	

Records throughout the growing season were maintained on 20 staked plants of each species, 10 in each of 2 exclosures. For the next 7 years, 1941–47, observations were continued on these and the following species:

Grasses	Forbs
Agropyron dasystachyum	*Antennaria dimorpha*
Koeleria cristata	*Arnica fulgens*
	Erigeron corymbosus
	Lomatium macdougali
Shrubs	*L. macrocarpum*
Artemisia tripartita	*Penstemon radicosus*
Chrysothamnus puberulus	*Senecio integerrimus*
Purshia tridentata	*Viola beckwithii*
Tetradymia canescens var. *inermis*	*V. nuttallii*

The use of staked plants was discontinued during the period 1941–47; instead, records were maintained on numerous plants of each species on four ½-acre blocks in each of two exclosures. In order to make accurate field observations, it was necessary to select slightly different developmental phases for grasses, forbs, and shrubs. The period from inception of growth through dissemination was covered in each group.

Measurements of leaf and flower stalk height throughout the growing season were made for the 1932–40 period on the same 8 species and the same 20 staked plants used for phasic development observations. After 1940, height measurements were discontinued for all except two species, *Agropyron spicatum* and *Balsamorhiza sagittata*. From 1941 to 1947 height measurements were made of these 2 species on 10 small plots in each of eight ½-acre blocks (4 blocks in each of 2 exclosures). The use of permanently staked plants was abandoned during this latter

period because frequent handling during measurement resulted in deterioration of these plants.

Herbage production data at intervals during the growing season were collected for *Agropyron spicatum* and *Balsamorhiza sagittata* for the 12-year period, 1936–47. Since yield was measured by clipping and weighing, a separate series of plants was required for each date at which the measurements were made. For the first 5 years, 100 plants of each species were selected along each of 6 belt transects located at random within an 80-acre exclosure. At 5 dates spaced at 15-day intervals, 20 plants in each transect were clipped at ground level, placed in paper sacks, and air dried. Thus at each clipping date, yield of each species was based on a series of 120 plants. New transects were established every year so that results would not be influenced by previous treatment.

For the last 7 years, instead of individual plants, small circular plots with a radius of 1.32 feet were used, and all plants of each species occurring on the plots were clipped. Seventy of these plots were located each year in each of eight ½-acre blocks previously described, and 10 were clipped at each of 7 dates spaced at 10-day intervals throughout the growing season.

Annual Yield

Yield, as used herein, refers to total production at the end of the growing season. It includes weight of herbage, area covered by herbage, height of both leaves and flower stalks, and number of flower stalks.

Although data on herbage weight for Agropyron and Balsamorhiza were provided by the last clipping each year in the seasonal development studies, more complete data on annual weight of herbage were supplied by estimates on 125 permanent 50-square-foot plots in 3 ungrazed exclosures (61). Estimates were also made of percentage utilized by insects and rodents so that herbage weight could be corrected to include this amount. This herbage inventory was made for each species at the completion of plant growth in 13 years of the period 1936–54. A complete record for the entire period was prevented by personnel shortages, especially during World War II.

Area of individual species was charted on 22 meter-square quadrats in 5 ungrazed exclosures in all but 4 years between 1932 and 1954. Crown spread of shrubs and basal area of grasses and forbs were mapped with a pantograph (59). This method of mapping vegetal area is shown in figure 3.

Total annual height of leaves and flower stalks was provided by the last measurements of the season in the seasonal development studies previously described. A 16-year record (1932–47) is available for *Agropyron spicatum* and *Balsamorhiza sagittata*, but only a 9-year record (1932–40) for *Oryzopsis hymenoides*, *Poa nevadensis*, *P. secunda*, *Stipa comata*, *Crepis acuminata*, and *Lupinus caudatus*.

FIGURE 3.— A two-man crew using a pantograph to chart vegetation on a meter-square quadrat.

Flower stalks were counted on the eight species listed in the preceding paragraph each year for the 1932–40 period, and number per plant was ascertained. Counts were continued on Agropyron and Balsamorhiza for the following 7 years, but these numbers are on a plot basis and are not directly comparable with the earlier records.

RESULTS

Seasonal Development

Phases

Systematic records of dates at which various developmental phases occurred during the 7-year period 1941–47 for 7 grasses, 12 forbs, and 4 shrubs make it possible to describe variations in development of these 3 groups and to compare individual species within groups. Averages for the 7-year period show that although grasses began growth first in the spring, other phases of development were attained earliest by the forbs, at intermediate dates by grasses, and latest by shrubs (fig. 4). Differences between groups generally increased as the season progressed; grasses completed dissemination about a month later than forbs, and shrubs an additional month later than grasses.

It should be noted, however, that group averages are not entirely adequate for describing phasic development inasmuch as a grass (*Poa secunda*), two forbs (*Crepis acuminata* and *Erigeron corymbosus*), and a shrub (*Purshia tridentata*) differed markedly from their respective groups (table 1). Development of Poa and
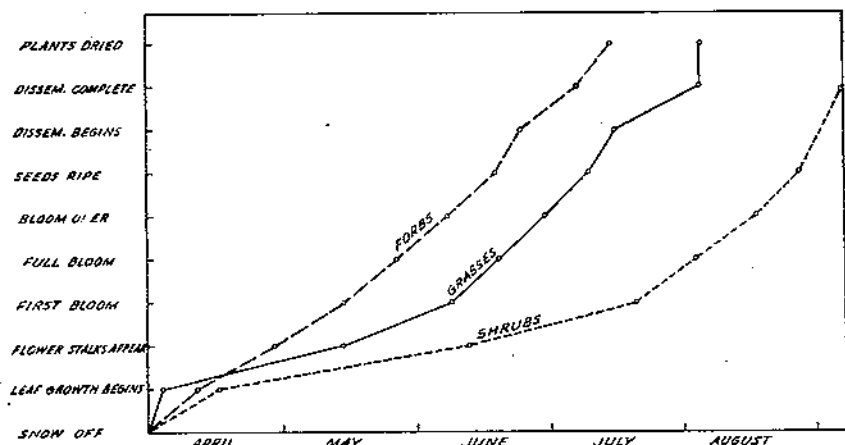
FIGURE 4.—Average phasic development of grasses, forbs, and shrubs at the U. S. Sheep Experiment Station, 1941–47.

Purshia was earlier than that of the other grasses and shrubs, respectively, whereas Crepis and Erigeron reached most of their developmental phases at a considerably later date than the other forbs.

GRASSES.—*Poa secunda* started to grow as soon as snow disappeared, and reached maturity considerably earlier than the other grasses. *Poa nevadensis* and *Koeleria cristata* were a few days later in starting and were usually 10 to 15 days later in reaching the other developmental phases. Development of *Agropyron spicatum* and *A. dasystachyum* followed these species at about the same interval. *Stipa comata* and *Oryzopsis hymenoides* also started late, and their development paralleled the Agropyrons during the early stages; however, after the heads were fully out, development was greatly accelerated and dissemination was completed at approximately the same time as for *Poa secunda*.

FORBS.—*Antennaria dimorpha* and *Viola beckwithii* developed rapidly after snow disappeared and had completed dissemination by early June. Corresponding phases in *Balsamorhiza sagittata, Lupinus caudatus*, and *Senecio integerrimus* were generally attained about 20 days later. *Erigeron corymbosus, Crepis acuminata*, and *Penstemon radicosus* were very slow in developing. These species did not bloom until mid-June and did not complete dissemination until early August. For these three groups, a fairly constant interval in time of reaching the various developmental phases was maintained.

In other species, however, the pattern was less distinct. *Lomatium macdougali* and *L. macrocarpum* bloomed at an early date, but were relatively slow in ripening and disseminating seed. *Arnica fulgens*, on the other hand, bloomed late but ripened and disseminated its seed soon afterwards. Similarly, *Viola nuttallii* was intermediate in reaching the first stages, but it finished blooming fairly early and completed dissemination as early as any of the forbs.

TABLE 1.—*Average dates at which individual species reached the various developmental phases, 1941–47* [1]

GRASSES

Species	Growth starts	Flower stalks appear	Heads fully out	Flowers in bloom	Seed ripe	Dissemination starts	Dissemination over	Plant drying	Plant dried
Agropyron dasystachyum..	4/1	5/21	6/16	6/27	7/27	8/8	8/20	7/12	8/11
A. spicatum	4/5	5/22	6/14	6/25	7/19	7/24	8/8	7/8	8/15
Koeleria cristata	4/2	5/7	6/1	6/17	7/10	7/15	8/11	7/4	8/7
Oryzopsis hymenoides	4/8	5/22	6/17	6/20	7/3	7/6	7/29	7/3	8/6
Poa nevadensis	3/30	5/6	6/3	6/18	7/9	7/15	8/8	6/30	8/9
P. secunda	3/30	4/27	5/15	6/5	6/26	6/30	7/25	5/23	7/9
Stipa comata	4/4	5/21	6/18	6/22	7/1	7/4	7/20	7/3	8/1
Average	4/3	5/14	6/8	6/19	7/9	7/15	8/4	6/29	8/4

FORBS

Species	Growth starts	Flower stalks appear	First-bloom	Full bloom	Bloom over	Seed ripe	Dissemination starts	Dissemination over	Plant drying	Plant dried
Antennaria dimorpha	4/4	4/18	4/26	5/3	5/14	5/24	5/28	6/6	6/23	7/10
Arnica fulgens	4/11	5/10	6/4	6/12	6/15	6/16	6/24	7/1	5/30	7/7
Balsamorhiza sagittata	4/19	4/26	5/9	5/25	6/4	6/14	6/18	7/9	6/22	7/31
Crepis acuminata	4/12	5/11	6/18	7/1	7/14	7/14	7/16	8/9	7/1	8/3
Erigeron corymbosus	4/15	5/21	6/18	7/2	7/14	7/17	7/18	7/29	7/3	7/29
Lomatium macdougali	4/8	4/13	4/18	4/29	5/20	6/6	6/13	6/24	6/8	6/29
L. macrocarpum	4/11	4/19	4/26	5/7	5/22	6/29	6/25	7/20	6/15	7/10
Lupinus caudatus	4/13	4/28	5/9	5/24	6/7	6/17	6/17	6/28	6/27	8/1
Penstemon radicosus	4/8	5/5	5/29	6/12	6/21	7/16	7/22	8/4	7/4	8/4
Senecio integerrimus	4/7	4/26	5/15	5/30	6/11	6/17	6/20	7/2	6/4	7/4
Viola beckwithii	4/10	4/16	4/20	4/29	5/12	5/22	6/1	6/14	5/30	6/6
V. nuttallii	4/13	4/28	5/4	5/11	5/20	5/22	....	6/10	6/2	6/27
Average	4/11	4/29	5/14	5/26	6/7	6/18	6/24	7/6	6/16	7/14

SHRUBS

Species	Leaf growth starts	Twig growth starts	Flower buds visible	First bloom	Full bloom	Bloom over	Seed ripe	Dissemination over	Leaves drying	Leaves drop
Artemisia tripartita	4/20	6/25	6/17	9/5	9/18	9/30	10/14	....	7/30	....
Chrysothamnus puberulus	4/13	5/24	6/30	7/27	8/18	9/8	9/2	⁻9/10	....	....
Purshia tridentata	4/16	6/9	5/12	5/28	6/11	6/23	7/17	?	8/6	....
Tetradymia canescens	4/17	5/27	6/18	7/17	7/25	8/7	8/15	/7	8/11	10/6
Average	4/16	6/6	6/12	7/20	8/3	8/17	8/27	9/6	8/5	....

[1] Average date of snow melt for this period was 3/30.

SHRUBS.—*Purshia tridentata* was intermediate in time of beginning leaf and twig growth, but it was much earlier than the other shrubs in reaching the other reproductive stages. It is perhaps significant that flower buds of Purshia develop directly on the old wood whereas those for the three other shrubs are produced on the current year's twigs. Although *Chrysothamnus puberulus*,

Tetradymia canescens var. *inermis*, and *Artemisia tripartita* reached the initial stages of development at approximately the same date, Tetradymia attained the later stages about 1 month before Chrysothamnus and 2 months before Artemisia.

Further examination of table 1 indicates that differences between species were greatest among the shrubs and least among the grasses. This is well illustrated by the following chronology for "first bloom" ("heads fully out" for grasses):

Mid-April.—*Lomatium macdougali, Viola beckwithii*
Late April.—*Antennaria dimorpha, Lomatium macrocarpum*
Early May.—*Viola nuttallii, Lupinus caudatus, Balsamorhiza sagittata*
Mid-May.—*Senecio integerrimus, Poa secunda*
Late May.—*Purshia tridentata, Penstemon radicosus*
Early June.—*Koeleria cristata, Poa nevadensis, Arnica fulgens*
Mid-June.—*Agropyron spicatum, A. dasystachyum, Oryzopsis hymenoides, Stipa comata, Crepis acuminata, Erigeron corymbosus*
Mid-July.—*Tetradymia canescens* var. *inermis*
Late July.—*Chrysothamnus puberulus*
Early Sept.—*Artemisia tripartita*

There was more than a month between average dates at which this phase occurred for the grasses *Poa secunda* and *Stipa comata*, 2 months between the forbs *Lomatium macdougali* and *Erigeron corymbosus*, and more than 3 months between the shrubs *Purshia tridentata* and *Artemisia tripartita*.

It is also interesting to note the spacing of this developmental stage over a 5-month period. From mid-April to early June only two or three species began blooming during each 10-day period, 6 species reached this stage during mid-June, and the remaining 3 shrubs bloomed in mid-July, late July, and early September, respectively.

As shown by ranges and standard deviations, dates at which individual species reached particular stages of development in the various years also differed widely (table 2). Species for which a 16-year record was available had a range of at least 20 days and a standard deviation of at least 6. There was less variation among some of the species whose record was for only 7 years, but in no instance was the smaller amount of variation consistent for all developmental stages of a particular species.

Height growth

Records of leaf and flower stalk height over the 9-year period 1932–40 are available for the 5 grasses and 3 forbs previously mentioned. Since individual species varied widely in actual height growth, comparisons are best made by expressing height throughout the growing season as percentages of total height attained and plotting these over the various dates.

GRASSES.—Average growth curves of 5 grasses for the 9-year period are shown in figure 5. In general, height growth followed the common sigmoid pattern, being slow at the beginning and end of the season but rapid during the intermediate period. The

TABLE 2.—*Seasonal variation in date at which individual species attained a particular stage of development as measured by the range and standard deviation*

[Based on the 7-year period, 1941–47, except as otherwise noted]

Species	Flower stalks appear [1]		First bloom [2]		Full bloom		Plant drying		Seed ripe	
	Range	Standard deviation	Range	Standard deviation	Range	Standard deviation	Range	Standard deviation	Range	Standard deviation
	Days	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*
Grasses:										
Agropyron dasystachyum	13	5.8	13	5.8	18	8.0	31	12.9	21	8.4
A. spicatum [3]	29	9.4	31	9.1	20	6.1	57	18.8	35	12.6
Koeleria cristata	17	5.9	18	5.5	15	6.0	52	16.9	22	7.8
Oryzopsis hymenoides [3]	27	7.9	26	8.6	20	6.5	48	17.8	21	7.3
Poa nevadensis [3]	33	8.8	40	11.6	33	8.2	58	20.6	21	8.1
P. secunda [3]	42	11.0	39	9.1	31	9.3	50	13.7	22	7.0
Stipa comata [3]	44	10.6	40	10.7	18	6.2	49	19.1	22	6.9
Forbs:										
Antennaria dimorpha	14	5.8	16	6.3	17	6.1	17	7.5	23	8.6
Arnica fulgens	14	4.9	20	9.8	26	11.1	35	14.9	7	5.0
Balsamorhiza sagittata [3]	24	7.3	35	9.0	35	9.4	32	8.4	17	6.6
Crepis acuminata [3]	42	9.3	40	11.0	43	11.1	53	15.0	20	6.2
Erigeron corymbosus	21	7.2	25	8.7	21	7.3	25	8.8	14	8.8
Lomatium macdougali	21	6.6	18	6.0	39	13.1	61	20.5	55	21.8
L. macrocarpum	17	8.4	15	6.7	13	4.8	47	19.5	17	8.5
Lupinus caudatus [3]	29	9.8	45	10.4	45	10.8	47	12.6	25	10.0
Penstemon radicosus	11	5.0	27	9.7	29	10.2	21	7.5	25	11.8
Senecio integerrimus	9	3.0	39	7.2	23	7.7	32	12.0	23	9.0
Viola beckwithii	12	4.3	13	5.1	17	5.9	32	17.0	26	11.8
V. nuttallii	9	4.1	11	4.0	21	7.3	21	11.2		
Shrubs:										
Artemisia tripartita	36	14.7	12	5.9	6	3.1	32	22.6	17	8.5
Chrysothamnus puberulus	57	18.5	26	11.7	22	9.2	53	32.3	17	9.3
Purshia tridentata	5	2.9	21	7.3	28	10.0	46	21.6	14	5.5
Tetradymia canescens var. inermis	42	12.0	15	5.9	6	2.5	53	19.2	32	12.0

[1] Flower buds visible for shrubs.
[2] Heads fully out for grasses.
[3] Based on a 16-year period, 1932–47.

period of most rapid leaf growth, excluding *Poa secunda*, was between April 10 and May 25, whereas flower stalks grew most rapidly during a shorter period, May 20 to June 15. Early leaf growth of a particular species was usually followed by a similarly early flower stalk growth.

Poa secunda was far ahead of the other grasses in making its seasonal height growth. *P. nevadensis*, *Agropyron spicatum*, *Oryzopsis hymenoides*, and *Stipa comata* followed in that order. Height growth of both leaves and flower stalks roughly paralleled reproductive development, as those species that made early height growth also completed their reproductive processes at a relatively early date. Although growth curves in individual years had similar form, there was considerable variation in time at which most of the growth occurred. For example, on the average *Agropyron spicatum* completed about 58 percent of its leaf height growth by May 5, but it varied from only 19 percent of its total leaf growth on this date in 1933 to 95 percent in 1934.
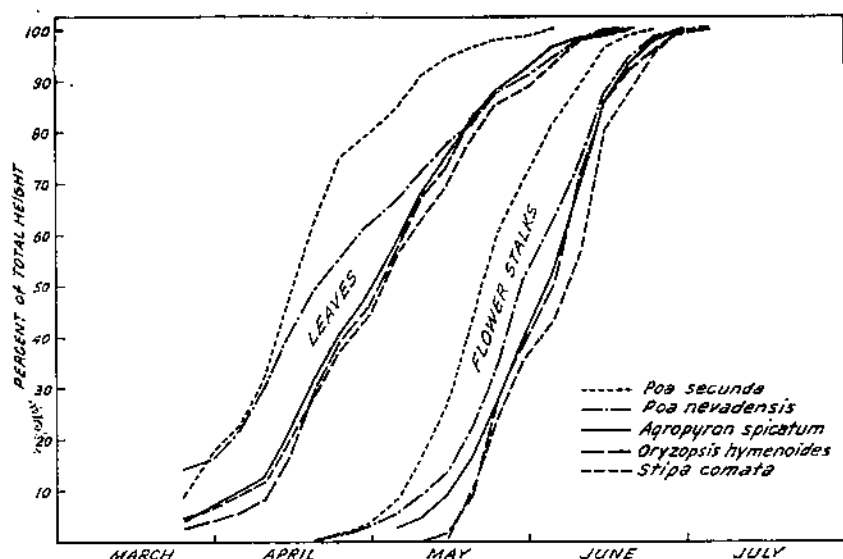
FIGURE 5.—Average height growth of five grasses expressed as a percentage of the total, 1932–40.

FORBS.—Average height growth curves of the three forbs were also of the familiar sigmoid type (fig. 6). Leaf growth of all three species was similar, but flower stalk growth of *Crepis acuminata* was approximately 2 weeks later than the others. The lateness of Crepis flower stalk growth is especially noticeable because leaf growth of this species was the earliest of the three
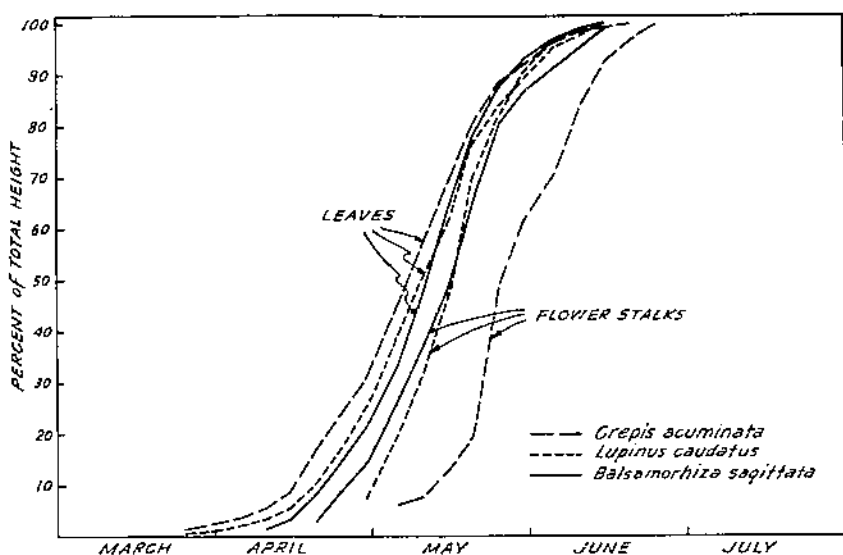
FIGURE 6.—Average height growth of three forbs expressed as a percentage of the total, 1932–40.

forbs. Growth of leaves was most rapid during the first 3 weeks of May, and most rapid growth of flower stalks, excluding Crepis, occurred during a period of similar length but slightly later. As with the grasses, there was considerable variation between years in time of growth. *Balsamorhiza sagittata,* which averaged about 33 percent of its total leaf height growth by May 5, had completed only 10 percent at this date in 1933, but 96 percent in 1934.

A comparison of height growth of the 5 grasses and 3 forbs shows a number of differences. Height growth of grass leaves was considerably ahead of that for forbs during all but the latter part of the growing season. For example, grass leaves completed 50 percent of their height growth by about April 25 whereas forb leaves did not complete half of their growth until May 10. On the other hand, flower stalk growth of forbs was generally ahead of grasses, the halfway point for height being reached on about May 20 and June 1, respectively.

As with individual grass species, then, height growth of grasses and forbs agreed well with reproductive development (fig. 4) ; grass leaves began growth earlier than forbs, but forbs reached the various developmental stages first. Further comparison of figures 5 and 6 also indicates that growth rates of grass and forb flower stalks were similar, but that leaves of forbs grew proportionately faster than those of the grasses. The difference in rate of leaf growth is illustrated by the fact that it required only about 20 days for forbs to increase from 30 to 80 percent (half) of their total height growth whereas a similar increase in grasses required approximately 30 days.

Weight growth

Records of herbage weight at various times throughout the growing season are available over the 12-year period 1936–47 for *Agropyron spicatum* and *Balsamorhiza sagittata.* These are fairly typical of grasses and forbs, respectively, and since they are two of the most abundant species on the study area, they give a good picture of herbage increases through the growing season. A direct comparison with height is possible as data on leaf height growth for these species are available over the same 12-year period.

Average air-dry herbage yield of both Agropyron and Balsamorhiza followed the familiar sigmoid pattern (fig. 7). During the early part of the season Agropyron was slightly ahead of Balsamorhiza in reaching a specified percentage of total weight yield, but about June 1 Balsamorhiza gained the lead. Examination of figures 5 and 6 suggests that this was the result of the more advanced growth of Balsamorhiza flower stalks at this date.

Herbage yield of both Agropyron and Balsamorhiza closely paralleled leaf height. During most of the season, date of reaching a specific percentage of the total was considerably later for weight than for height. The lag of herbage weight behind leaf height was approximately 12 and 9 days in Agropyron and Balsamorhiza, respectively.

It is interesting to examine the relation of growth of these two species to reproductive development. This can be done by a comparison of figure 7 with table 1, even though slightly different periods are involved. On the average, *Agropyron spicatum* flower stalks appeared at the time it had completed 66 percent of its weight and 83 percent of its leaf height growth; by the time heads were fully out, it had completed about 90 and 97 percent of its weight and leaf height growth, respectively; and by the time flowers were in bloom nearly all (97 percent) of its weight and all of its height growth were completed. On the other hand, *Balsamorhiza sagittata* flower stalks appeared when only about 5 percent of its weight and 15 percent of its leaf height growth were completed, and it was in full bloom when only 63 and 85 percent, respectively, of its weight and leaf height growth were completed.
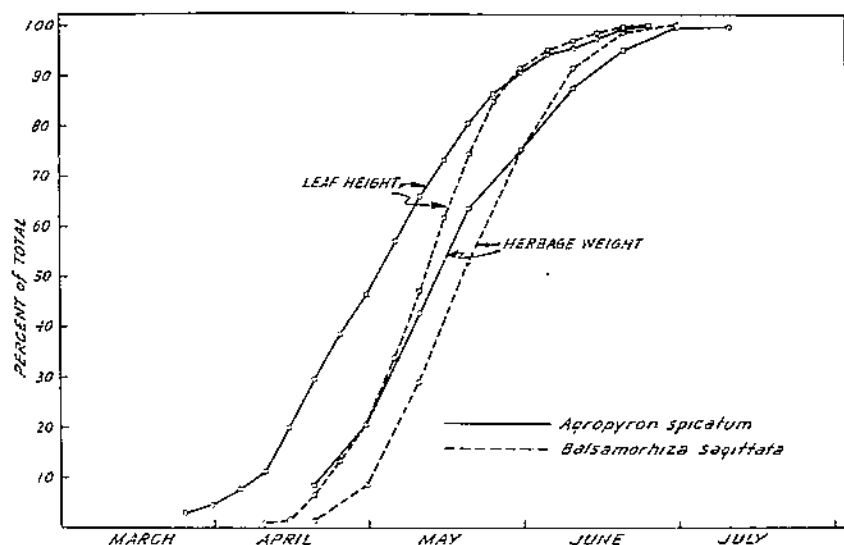
FIGURE 7.—Average height and weight growth curves for Agropyron and Balsamorhiza expressed as percentages of the totals, 1936–47.

Annual Yield

Weight

Herbage weight of grasses, forbs, and shrubs for 13 years of the period 1936-54 are shown in table 3. Although certain cyclic trends in weight are evident, there is no indication of progressive changes in yield of the three groups. During these years herbage production fluctuated considerably; total of the highest year was more than double that of the lowest. Range in production between the highest and lowest years within the grass and forb groups was even greater.

Overall variability was similar to that indicated by the ranges as coefficients of variation were 29, 23, 20, and 20 percent for grasses, forbs, shrubs, and total, respectively. In general, high or

low weights of one group in particular years were associated with similar yields of the other two; but there were a few notable exceptions. In relation to forbs and shrubs, weight of grasses was high in 1938 and 1939; forb weights were relatively high in 1952 and 1953 but low in 1937; and shrubs were high in 1942 but low in 1941.

TABLE 3.—*Air-dry herbage production per acre in ungrazed exclosures at the U. S. Sheep Experiment Station for 13 years of the period 1936–54*

Year	Grasses	Forbs	Shrubs	Total
	Pounds	*Pounds*	*Pounds*	*Pounds*
1936	120. 2	183. 8	238. 6	542. 6
1937	198. 3	179. 8	431. 2	809. 3
1938	297. 0	252. 5	515. 9	1, 065. 4
1939	234. 3	232. 2	397. 0	863. 5
1940	210. 3	237. 0	468. 5	915. 8
1941	259. 9	296. 0	412. 9	968. 8
1942	175. 2	247. 9	519. 0	942. 1
1947	128. 5	198. 0	385. 9	712. 4
1949	153. 3	194. 5	403. 7	751. 5
1950	195. 0	224. 4	392. 7	812. 1
1952	201. 1	331. 2	420. 2	952. 5
1953	194. 2	281. 7	379. 0	854. 9
1954	102. 0	133. 3	253. 5	488. 8
Average	189. 9	230. 2	401. 4	821. 5

Similar data are available for individual species within groups; however, consideration of a single group, grasses, appears sufficient to demonstrate the variability among species. Coefficients of variation for species were considerably higher than those for the groups, being 39, 59, and 44 percent for production of *Agropyron spicatum*, *Koeleria cristata*, and *Stipa comata*, respectively. Also weights of some grasses were high in years when others were low (table 4); in this respect individual species were even less consistent than the three groups. For example, weight of *Agropyron spicatum* was relatively high in 1936 and 1938 but low in 1950 and 1952; weight of *Stipa comata* was relatively low in 1939 and 1940 but high in 1949 and 1953; and weight of *Koeleria cristata* was relatively low in 1937 and 1954. Similar differences were apparent among species within the forb and shrub groups.

Area

Area of vegetation on 22 permanent meter-square quadrats mapped in most years during the study is given in table 5. Area exhibited about the same degree of variation as herbage weight. However, in contrast to weight, forb area was more variable than that of grasses or shrubs. Coefficients of variation were 23, 29, and 24 percent for grasses, forbs, and shrubs, respectively.

TABLE 4.—*Herbage production per acre of three grasses included in the group totals of table 3*

Year	Agropyron spicatum	Koeleria cristata	Stipa comata
	Pounds	Pounds	Pounds
1936	87. 4	3. 0	9. 2
1937	129. 5	4. 7	22. 6
1938	209. 9	10. 4	19. 0
1939	150. 7	11. 3	15. 5
1940	115. 6	13. 6	15. 2
1941	117. 4	12. 5	20. 2
1942	82. 6	5. 2	14. 0
1947	61. 3	9. 7	17. 0
1949	69. 6	9. 5	28. 3
1950	80. 0	24. 8	41. 4
1952	97. 5	15. 4	38. 5
1953	110. 8	8. 5	34. 4
1954	62. 1	2. 7	19. 4
Average	105. 7	10. 1	22. 7

TABLE 5.—*Area of vegetation on 22 meter-square quadrats in ungrazed exclosures at the U. S. Sheep Experiment Station, 1932–54* [1]

Year	Grasses	Forbs	Shrubs	Total
	cm.²	cm.²	cm.²	cm.²
1932	11, 349	2, 268	16, 769	30, 386
1933	11, 984	2, 705	24, 652	39, 341
1934	6, 894	1, 499	14, 733	23, 126
1935	6, 878	2, 331	21, 966	31, 175
1936	6, 274	1, 894	18, 775	26, 943
1937	7, 386	2, 787	24, 119	34, 292
1938	7, 780	1, 900	26, 738	36, 418
1939	9, 374	2, 092	24, 570	36, 036
1940	8, 442	2, 632	25, 772	36, 846
1941	6, 594	2, 338	26, 643	35, 575
1942	5, 660	2, 332	20, 662	28, 654
1945	8, 623	2, 040	41, 937	52, 600
1946	10, 267	3, 825	24, 269	38, 361
1947	11, 487	3, 697	21, 436	36, 620
1949	8, 538	2, 447	19, 405	30, 390
1950	10, 327	2, 271	22, 205	34, 803
1951	10, 160	2, 983	20, 852	33, 995
1952	12, 322	4, 156	24, 156	40, 634
1954	10, 831	3, 986	28, 354	43, 171
Average	9, 009	2, 641	23, 580	35, 230

[1] Measurements represent basal area of grasses and forbs but crown area of shrubs.

As with weight, the areas of all groups behaved similarly in some years; but in others, area responses were quite different. In 1934, for example, area of all three groups was low. In 1940 it was intermediate in all groups, and in 1954 it was fairly high. In 1945, however, shrub area was extremely high, area of forbs was low, and grass area was about average; and in 1952 grass and forb areas were high, but area of shrubs was close to average. It should be recognized that numerous personnel changes occurred during the study and that despite the attempted precision in mapping vegetation with a pantograph, subjective errors have arisen, particularly in connection with crown area of shrubs. The extremely high value shown for shrubs in 1945, for example, may be partially a result of such error.

The wide variation of individual species is indicated by a comparison of basal areas of four grasses (table 6). Areas in the lowest years were only 34, 14, 17, and 22 percent of the highest for *Agropyron spicatum, Koeleria cristata, Poa secunda,* and *Stipa comata,* respectively; and coefficients of variation were 30, 53, 57, and 44 percent. Behavior of individual grasses was not uniform, relatively large areas of one species often being associated with small areas of another.

In 1932 and 1933, area of Agropyron was relatively large; but areas of the other species were only moderate or small. Conversely, Agropyron had but a small area in 1945, whereas area of Poa was relatively large and that of the other two species, intermediate.

TABLE 6.—*Basal areas on 22 meter-square quadrats of four of the grasses included in the group totals of table 5*

Year	Agropyron spicatum	Koeleria cristata	Poa secunda	Stipa comata
	cm.²	cm.²	cm.²	cm.²
1932	6, 290	601	920	2, 326
1933	6, 943	750	790	2, 431
1934	3, 857	358	510	1, 512
1935	3, 712	381	687	1, 366
1936	3, 668	266	560	1, 138
1937	4, 074	367	660	1, 548
1938	4, 386	435	670	1, 459
1939	4, 878	1, 032	724	1, 701
1940	4, 578	511	778	1, 498
1941	3, 175	396	794	1, 332
1942	2, 370	355	981	994
1945	2, 558	682	1, 884	1, 978
1946	2, 813	1, 195	1, 752	2, 841
1947	3, 099	1, 175	2, 419	3, 158
1949	2, 967	958	589	2, 998
1950	3, 520	1, 140	784	3, 694
1951	3, 474	1, 309	931	3, 159
1952	4, 231	1, 676	631	4, 145
1954	4, 616	862	411	3, 960
Average	3, 958	760	920	2, 276

Relatively large areas of Koeleria and Stipa in 1952 were associated with a small area of Poa and a moderate area of Agropyron. The smallest area of Poa occurred in the same year, 1954, that area of Stipa was large and areas of Agropyron and Koeleria were intermediate.

A comparison of tables 3 and 5 indicates that weight of the vegetation was not closely related to area covered. This observation was substantiated by the small correlation coefficients between weight on plots and area on quadrats: −.235, .009, and .115 for grasses, forbs, and shrubs, respectively.

The periodic maps of the meter-square quadrats have a unique value in that they provide a record of spatial relations of the plants throughout the period of study. Although the vegetation is apparently stable, close inspection of the quadrat charts indicates continual changes that are not discernible in most other records. On a part of one quadrat (fig. 8), the charts for a 20-year period
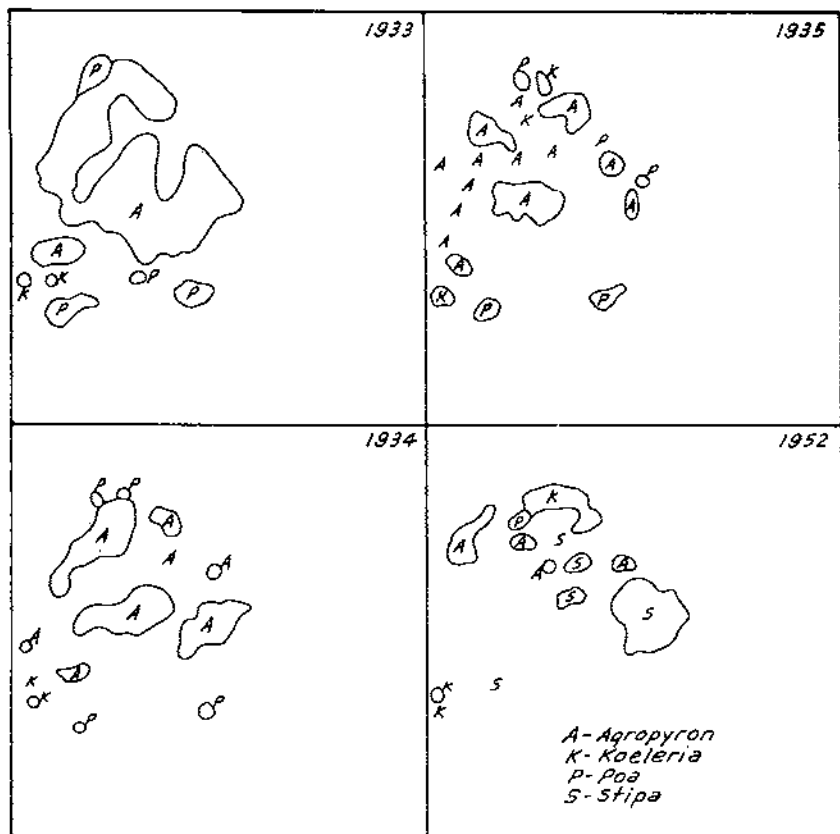
FIGURE 8.—A part of a meter-square quadrat (P10E1–Q1) in four different years. A letter symbol with no area shown indicates that the plant covers less than half of a square centimeter.

show the deterioration of a large clump of *Agropyron spicatum* and almost complete replacement by *Stipa comata* and *Koeleria cristata*. During the same period on another part of this quadrat, grass (chiefly Stipa) became established on an area that was previously barren (fig. 9).
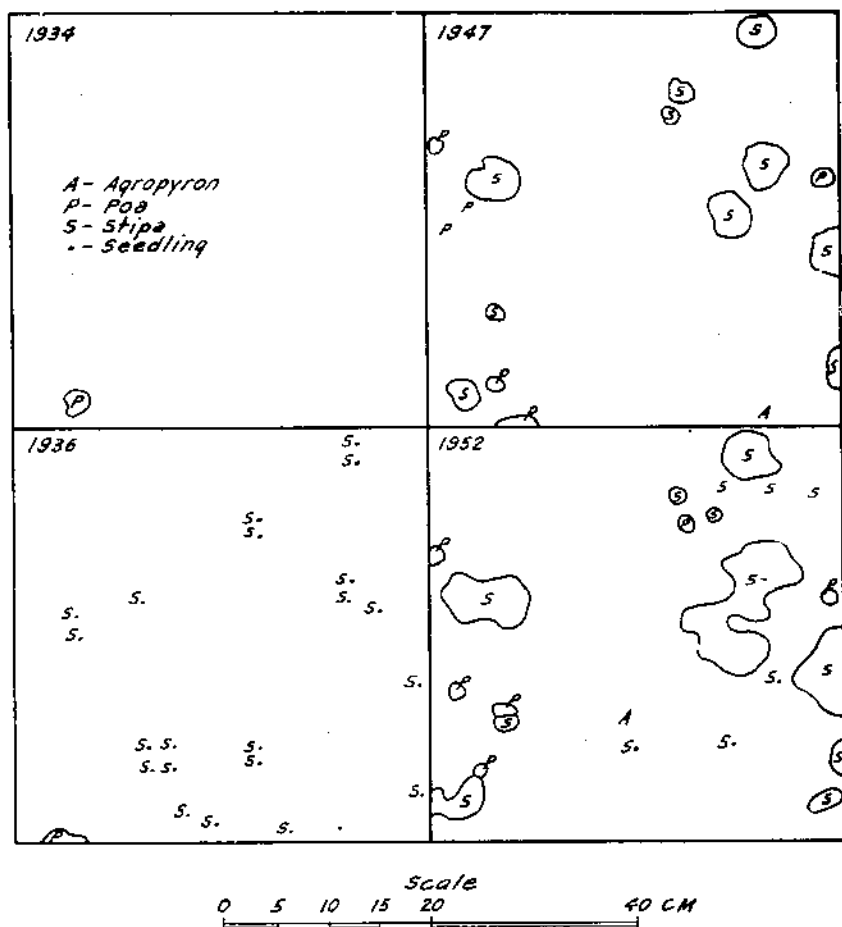
FIGURE 9.—Another part of P10E1–Q1 showing establishment of grass on a barren area. A letter symbol with no area mapped indicates that the plant covers less than half of a square centimeter.

Changes on parts of the quadrat shown in figures 8 and 9 are indicative of the changes on the entire quadrat between 1932 and 1954. During this period, coverage of Agropyron decreased from 445 to 157 square centimeters while Stipa increased from 35 to 266. On other quadrats, however, opposite changes were evident. For example, on P1E1–Q1, Agropyron increased from 265 square centimeters in 1932 to 588 in 1954 while Stipa remained about constant. A part of this quadrat is shown in figure 10. In contrast to figure 8, the upper left corner shows replacement of a large
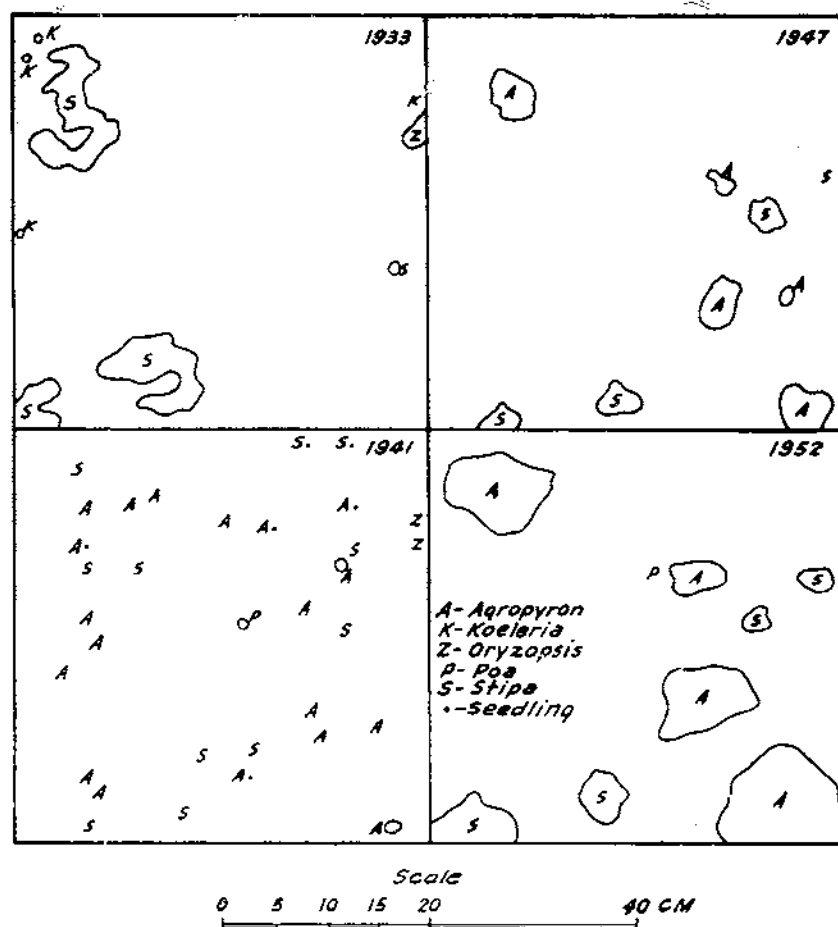
FIGURE 10.—A part of P1E1–Q1 showing replacement of a large clump of Stipa with Agropyron (upper left) and grass establishment in barren areas. A letter symbol with no area mapped indicates that the plant covers less than half of a square centimeter.

bunch of Stipa by Agropyron. Despite such changes in certain species on individual quadrats, total grass area in 1954 was almost the same as in 1932 (table 5).

The quadrats are also useful in providing a record of annuals and seedlings of perennial species. In the 19 years that the 22 meter-square quadrats were charted, the total number of annuals varied from 0 to 5,351, and the number of seedlings from 0 to 3,664 (table 7). In general, seedling numbers of grasses, forbs, and shrubs varied consistently and high total numbers were associated with high numbers of annuals. There was a positive relation between seedling occurrence and the previous year's flower stalk production, but none of the correlations were strong.

Despite numerous seedlings in many years, actual establishment was very low. This is well illustrated by a few specific examples,

In 1936 there were 202 *Agropyron spicatum* seedlings on P7E1–Quadrat 1, but fewer than 10 of these were still living in 1937. On another quadrat (P1E1–Q1), there were 245 *Crepis acuminata* seedlings in 1936, but apparently all were dead in 1937. In 1952 there were 154 *Artemisia tripartita* seedlings on P1–Q2, but only 3 were alive in 1954. In spite of these high mortalities during the first year of growth, a few seedlings continually became established both in barren areas and in others where previous occupants had deteriorated (figs. 8, 9, 10).

TABLE 7.—*Seedlings and annuals on 22 meter-square quadrats in ungrazed exclosures at the U. S. Sheep Experiment Station, 1932–54*

Year	Seedlings				Annuals	Total
	Grasses	Forbs	Shrubs	All		
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
1932	2,436	138	803	3,377	1,401	4,778
1933	151	20	178	349	260	609
1934	0	0	0	0	0	0
1935	0	2	153	155	2,525	2,680
1936	1,921	1,383	360	3,664	5,351	9,015
1937	115	400	64	579	743	1,322
1938	151	106	265	522	1,060	1,582
1939	18	25	82	125	305	430
1940	46	65	44	155	427	582
1941	646	165	110	921	1,155	2,076
1942	845	393	314	1,552	4,585	6,137
1945	136	390	98	624	4,326	4,950
1946	24	180	30	234	414	648
1947	18	46	7	71	379	450
1949	9	81	3	93	0	93
1950	70	45	1	116	315	431
1951	29	53	9	91	614	705
1952	242	62	438	742	645	1,387
1954	0	0	4	4	84	88

Height

Leaf and flower stalk heights of *Agropyron spicatum* and *Balsamorhiza sagittata* showed considerable variation during the 16-year period 1932-47 (table 8). Average height in the highest year was 2 or 2½ times that in the lowest. Leaf heights were less variable than flower stalk heights. Coefficients of variation for Agropyron and Balsamorhiza leaves were 18 and 15 percent, respectively, whereas the coefficient of variation for flower stalks of both species was 23 percent. Both leaf and flower stalk heights, then, were considerably less variable than herbage weight and area of individual species.

As with weight and area, in some years height of both species behaved similarly, but in others heights were quite different. For example, leaves of both species were short in 1934, 1936, 1937, and

1943, but Agropyron leaves were tallest in 1933, 1935, 1945, and 1946, whereas leaves of Balsamorhiza were tallest in 1932, 1940, 1942, and 1945. Flower stalk heights of these two species were even less similar. Despite these differences, the correlation between leaf heights of Agropyron and Balsamorhiza was highly significant ($r = .731$).

Height was poorly correlated with herbage weight. For the 12-year period 1936–47, weight of the same plants used in the height studies was determined by clipping at the end of the growing season. Correlation coefficients between average leaf height and herbage weight were $-.369$ and $-.024$ for Agropyron and Balsamorhiza, respectively.

TABLE 8.—*Average leaf and flower stalk height of Agropyron spicatum and Balsamorhiza sagittata at the end of the growing season, 1932–47*

Year	Agropyron		Balsamorhiza	
	Leaves	Flower stalks	Leaves	Flower stalks
	Centimeters	*Centimeters*	*Centimeters*	*Centimeters*
1932	17.6	37.3	28.6	42.8
1933	21.0	37.0	24.9	
1934	11.4	18.0	14.8	24.2
1935	19.2	39.3	24.4	44.6
1936	12.2		20.8	34.0
1937	13.8	34.0	18.4	41.8
1938	18.6	34.9	23.6	30.3
1939	16.0	33.3	23.6	
1940	18.6	38.0	26.4	25.8
1941	13.4	43.6	23.9	35.9
1942	15.4	24.6	25.3	23.6
1943	12.5		20.1	35.6
1944	16.3	45.5	24.5	32.5
1945	19.7	43.2	28.9	35.0
1946	19.2	42.6	23.3	27.0
1947	18.2	30.0	24.2	43.5

Flower stalk numbers

Flower stalk production of 5 grasses and 3 forbs is summarized in table 9. Numbers were highly variable, some species ranging from zero in some years to nearly 30 per plant in others. To obtain an indication of the relative degree of variability, a few coefficients of variation were computed. These coefficients for the 1932–40 period were 90, 74, 132, and 110 percent for *Agropyron spicatum,* all grasses, *Balsamorhiza sagittata,* and all forbs, respectively.

As a group, grasses were more consistent flower producers than forbs. In 6 of the 8 years, 1933–40, grasses produced more than 6 flower stalks per plant whereas forbs produced comparable numbers in only 3 years. There were also great differences between individual species. For example, in 1933 *Poa nevadensis* produced more than 18 flower stalks per plant whereas *P. secunda* produced

less than 1; in 1939 Agropyron produced more than 28 flower stalks per plant and Oryzopsis, less than 1.

TABLE 9.—*Flower stalk production per plant in ungrazed exclosures at the U. S. Sheep Experiment Station, 1932–40*

GRASSES

Year	Agropyron spicatum	Oryzopsis hymenoides	Poa nevadensis	Poa secunda	Stipa comata	Average
	Number	Number	Number	Number	Number	Number
1933	4. 4	6. 9	18. 6	0. 7	---------	7. 6
1934	. 1	0	. 6	0	0. 1	. 2
1935	20. 3	19. 7	8. 0	7. 4	15. 4	14. 2
1936	0	. 8	2. 4	1. 5	. 1	1. 0
1937	5. 8	12. 8	4. 8	. 2	8. 9	6. 5
1938	11. 8	27. 6	7. 6	. 2	8. 2	11. 1
1939	28. 3	. 4	24. 0	13. 2	4. 6	14. 1
1940	13. 4	26. 4	7. 8	8. 8	6. 4	12. 6

FORBS

Year	Balsamorhiza sagittata	Crepis acuminata	Lupinus caudatus	Average
1932	3. 0	3. 9	---------	3. 4
1933	0	. 3	0. 9	. 4
1934	1. 2	. 4	. 6	. 7
1935	12. 8	4. 8	8. 6	8. 7
1936	. 1	1. 3	2. 4	1. 2
1937	. 6	1. 8	. 1	. 8
1938	12. 6	5. 4	11. 8	9. 9
1939	0	. 6	1. 2	. 6
1940	5. 4	3. 4	7. 4	5. 4

It is interesting to examine the year-to-year differences in flower stalk production. In 1934 and 1936 production was generally poor for grasses and forbs, whereas in 1935 and 1938, it was good for both groups. In 1933 and 1937, production of flower stalks was fair for grasses but poor for forbs. Grass flower stalk production was good in 1939 and 1940, but forb production was poor and fair, respectively. Although records for the 1941-47 period are not directly comparable, they further indicate the high variability between years and between species:

	Flower stalks per plot [1]	
	Agropyron spicatum (number)	Balsamorhiza sagittata (number)
1941	30. 1	2. 2
1942	4. 9	. 3
1943	. 1	5. 5
1944	. 2	4. 9
1945	----	. 2
1946	9. 9	. 1
1947	3. 7	. 9

[1] Circular plots 5.5 and 8.5 square feet for Agropyron and Balsamorhiza, respectively.

DISCUSSION

Although there is considerable variation in development among individual species, forbs in this locality generally complete their reproductive processes at a relatively early date; development of grasses follows at a fairly close interval, but the 4 dominant shrubs are approximately 2 months later. As a result of these differences, certain advantages and disadvantages are evident for each group.

Early reproductive development of forbs allows them to escape effects of summer drought, but at the same time makes them vulnerable to late spring frosts. Most of the shrubs escape damage from spring frosts, but occasionally some species may be damaged by early fall frosts. Although they must sometimes endure summer drought, their deep root systems ordinarily supply sufficient moisture for normal development even though moisture in the topsoil is reduced below the wilting coefficient. Intermediate development of grasses exposes them to late spring frosts and early summer droughts, but normally they escape both. The fact that a shrub, *Artemisia tripartita*, a forb, *Balsamorhiza sagittata*, and a grass, *Agropyron spicatum*, are the most abundant species indicates that no group has a superior pattern of development.

The three groups, then, are able to grow together in a single community and make efficient use of available materials. As an example, it has been demonstrated that mixtures of sagebrush and herbaceous species produce a higher herbage yield than either grown alone (*4, 5*). Apparently each is able to use some moisture or nutrients which are not available to the other.

The wide variations between individual species in average time of development are also of interest. Although growing in essentially the same environment, they may have widely different phenological adaptations. For the most part, reasons for these differences are not apparent; but inherently different temperature, day-length, or moisture requirements probably are responsible. There are, however, certain obvious differences in plant structure which influence development, e.g., type of root system. Relatively shallow-rooted species such as Viola and *Poa secunda* must complete their development before exhaustion of moisture from the surface layers of the soil, whereas deep-rooted shrubs such as Artemisia and Tetradymia have a fairly permanent source of moisture in the subsoil. At any rate it is apparent that many mechanisms allow widely different plants to live successfully in a given environment.

Growth curves for leaf and flower stalk heights and herbage weights of species reported herein appear to be of the logistic (*58*) or autocatalytic (*70*) type resulting from an accelerating component at the beginning of plant growth and a decelerating component as the plant matures. However, many mathematical curves of the sigmoid type probably would fit the data equally well. Because of the limited value of such curve fitting (*36, 76*) and the lack of precision in the field measurements and estimates, no attempt has been made to fit mathematical equations to growth data

of these species. Comparisons herein are made on the basis of unsmoothed growth curves.

As might be expected, growth patterns of grasses and forbs vary in much the same fashion as their phasic development. Grass leaves begin growth earlier than forbs, and the growth curves indicate that this lead is maintained until leaf growth is practically completed. On the other hand, forbs produce flower stalks first, and their relative height growth is generally ahead of the grasses throughout. Flower stalk growth is well correlated with phasic development of individual forb species, but there are certain discrepancies among the grasses. *Agropyron spicatum* is intermediate in time of flower stalk growth but is late in completing its developmental stages, and flower stalk growth of Oryzopsis and Stipa is late but reproductive processes are completed relatively early.

Growth curves for most of the species studied have similar form, but there is considerable variation in time at which most rapid growth occurs and in length of this rapid-growth period. A similar situation was observed by Jackson (*35*) who found a wide variation in time at which radial growth of several forest trees was most rapid and in the length of this period. Undoubtedly, optimum environmental conditions for growth are not the same for all species.

Since examination of various measures of annual yield indicates no cumulative changes of consequence during the study, it appears that the vegetation is in general equilibruim with its environment. Such overall stability, however, does not indicate a static condition. Year-to-year comparisons of maps of plant cover on permanent quadrats show continual changes: one perennial species is replaced by another; areas covered by vegetation become barren, and barren areas become occupied; annuals and seedlings of perennials appear and disappear. Two parts of the same community may be undergoing similar changes at the time, or what seem to be directly opposite changes may be occurring.

Since such changes in individual species or groups may balance out on a large area or even on small plots, much of this dynamic aspect of the plant community might pass unnoticed were it not for quadrat charts that provide a record of year-to-year spatial relations. Not only do these charts show that changes continually occur, but they also show something about the manner of change.

Since environmental factors of the Upper Snake River Plains do not allow a full vegetal cover, there are always some areas that are barren. Although some colonization of the bare areas occurs from time to time, the tendency is for bare areas to remain bare and for areas covered by vegetation to remain covered. Similar observations were made by Ellison (*19*) on the Wasatch Plateau in Utah. As clumps of vegetation deteriorate, new plants (often different species) become established in them and may eventually replace the former occupants. Despite competition in such areas, soil moisture and fertility are probably more favorable than in areas that have remained barren for a long time.

Another aspect of community dynamics is the variation in response of individual species to the same environmental factors. Since yield of one species may be high at the same time yield of a similar species is low, it is readily apparent that specific conditions can be favorable for one species and unfavorable for another. This agrees with results of Arnold (*3*), who found that certain grasses in Arizona attained maximum leaf heights during the same season that heights of others were at a minimum. Seasons sufficiently extreme to be unfavorable to all species, then, should be rare. As a matter of fact, in only one year during the study, 1934, were all available measures of yield fairly low for all species. In no single year were all yields high for all species.

Undoubtedly, variation and change are inherent elements of the apparently stable vegetation. With the existing maze of environmental factors, certain species on the area as a whole or all species on certain micro-areas can be greatly changed without materially affecting the overall structure of the community. Functioning of the plant community, then, cannot be adequately described by response of individual species or by changes on individual microsites. The various components constantly supplement each other, and proper characterization of the community must consider all of them.

In this respect, it is interesting to consider the tendency for compensation in herbage production among individual species. As shown by coefficients of variation, production from year to year is highly variable for individual grasses, intermediate for the groups of species, and low for the total. Apparently the increased yield of one species compensates for decreased yield of another, thereby dampening the oscillations in total production.

Absence of a close correlation between basal area and herbage weight of grasses and forbs indicates that variations in weight must be caused by variations in height or in density of individual stems within a specified basal area. Since correlations between height and weight of the two most abundant herbaceous species, *Agropyron spicatum* and *Balsamorhiza sagittata*, were poor, it appears that density of both leaves and flower stalks within the clump area is the factor that largely determines herbage weight. The various measures of yield (weight, area, height, flower stalk numbers) tend to be similar, but it is apparent that any one measure is inadequate for describing vegetal response. Furthermore, the differences indicate that the various measures of yield cannot be directly compared.

Because of the temporary nature of annuals and most seedlings of perennial species, they are, for the most part, treated in a separate category. The positive correlation between occurrence of annuals and seedlings indicates that both are favored by the same environmental conditions. Apparently variations in number of seedlings of both annuals and perennials are caused by both seed supply and weather of the current season. The failure of most seedlings to become permanently established, however, is probably less attributable to unfavorable weather than to a fully stocked community that is closed to mass invasion of new plants.

CLIMATIC FACTORS

METHODS OF STUDY

Daily records of precipitation, temperature, wind, and cloudiness were maintained at the cooperative weather station on the study area (fig. 11). Since the weather station is centrally located with respect to the ungrazed exclosures where vegetal observations were made and is within a mile of the most remote, its records are considered reasonably representative.

Two standard rain gages were used to collect precipitation, and maximum and minimum thermometers were exposed in a standard Weather Bureau shelter 5½ feet above the soil surface to measure temperature extremes. Wind movement was measured by a 3-cup Friez anemometer mounted about 5 feet above the ground. Cloudiness was assigned a numerical rating between 0 (no clouds) and 10 (completely overcast). Observations were made daily at 5:00 p.m. Records of precipitation and temperature are available for the entire 23-year period July 1931 through June 1954. Records of cloudiness, however, did not begin until January 1932, and records of wind until July 1935.

In order to overcome obvious difficulties in relating vegetal response to weather of the calendar year, weather records have been arranged to correspond as nearly as possible with the "growth" or "crop" year of the vegetation, July 1 to June 30. Since the various species differ in time of growth and phasic development,
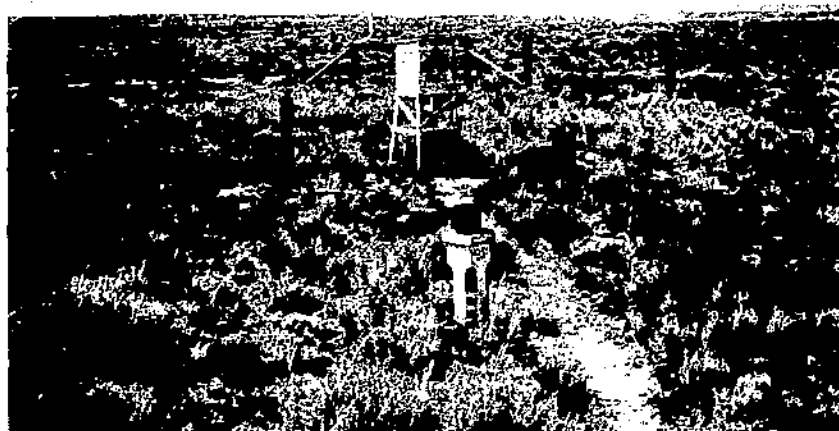
FIGURE 11.—The weather station at the U. S. Sheep Experiment Station. This installation is more than 200 yards from the nearest building.

choice of a suitable growth year must be rather arbitrary. However, examination of the vegetal records indicates that height and weight increments of grasses and forbs have ceased each year by the end of June and that their reproductive development has been completed, with the exception of seed ripening and dissemination in some species. Although it probably would be preferable to start the growth year for shrubs about a month later, this would be less satisfactory for herbs. The growth year here adopted is also most suitable for relating weather to herbage yield, as weight estimates were made each year in late June or early July.

RESULTS

Precipitation

For the 23-year study period, 1932-54, average annual precipitation was 11.06 inches (table 10). More than one-third of this amount fell in the spring, and the remainder was rather evenly distributed throughout the other seasons. However, there was considerable variation throughout in monthly, seasonal, and annual amounts. For example, June precipitation varied from 0.06 inch in 1935 to 8.26 inches in 1944; summer (July–September) precipitation varied from 0.47 inch in 1934 to 5.69 inches in 1940; and total, from 7.23 inches in 1933–34 to 16.13 in 1943-44. The coefficient of variation for total annual precipation was 20 percent of the mean. The general distribution pattern was erratic, but there was a tendency toward like amounts of precipitation in several successive years.

Temperature

Mean temperatures for the same period as precipitation are shown in table 11. In most years, mean temperatures were above 40° F. for the 7-month period April–October, inclusive. Mean temperatures for the coldest month, January, averaged 17.6°, and of the warmest month, July, 69.3°. Temperatures were much less variable than precipitation, but there was a range of 24° in January mean temperatures, about 13° in fall and winter averages, 11° in spring, but only 6° in summer. The 1933–34 year was the warmest of the period with a mean temperature of 49.0°, and the 1951–52 year was the coldest with a mean temperature of 40.5°. The average annual mean temperature was 43.0° and coefficient of variation was 4 percent.

The highest temperature recorded during the 23-year period was 102° F. in July 1931, and the lowest was -- 28° in January 1937. The frost-free season varied from 77 to 152 days, averaging 120. The last spring frost normally occurred in late May or early June, and the first fall frost in September or occasionally October.

Wind

During the 19-year period for which records are available, average hourly wind movement was 6.6 miles (table 12). Average

TABLE 10.—*Precipitation at the U. S. Sheep Experiment Station near Dubois, Idaho, July 1931 through June 1954*

Year	Summer				Fall and winter							Total, July-Mar.	Spring					Total, July-June
	July	Aug.	Sept.	Total, July-Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total, Oct.-Mar.		Apr.	May	June	Total, Apr.-June	Total, Oct.-June	
	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches
1931-32	0.67	0.68	0.82	2.17	0.14	0.69	2.46	0.78	0.49	0.23	4.79	6.96	0.87	0.74	2.04	3.65	8.44	10.61
1932-33	2.52	1.29	.02	3.83	.27	.36	.47	1.91	.41	.31	3.73	7.56	.92	2.10	.26	3.28	7.01	10.84
1933-34	.06	1.04	.52	1.62	.36	.34	.86	.55	.36	.15	2.62	4.24	.34	.42	2.23	2.99	5.61	7.23
1934-35	.00	.06	.41	.47	1.49	1.51	.70	1.23	.29	.87	6.09	6.56	1.80	.78	.06	2.64	8.73	9.20
1935-36	.74	.32	.24	1.30	1.45	.45	.91	1.16	.17	.04	4.18	5.48	.64	.79	1.92	3.35	7.53	8.83
1936-37	.90	1.31	.61	2.82	.20	.06	1.00	.92	.84	.72	3.74	6.56	.71	.41	1.48	2.60	6.34	9.16
1937-38	1.26	.23	.43	1.92	.46	.51	1.36	.68	1.43	2.61	7.05	8.97	.58	1.07	1.35	3.00	10.05	11.97
1938-39	2.23	.71	.06	3.00	3.67	.45	.06	.91	.90	.42	6.41	9.41	.70	.57	.78	2.05	8.46	11.46
1939-40	.63	.15	1.16	1.94	1.18	.00	.42	.99	1.47	1.33	5.39	7.33	1.46	.30	1.21	2.97	8.36	10.30
1940-41	1.01	.77	3.91	5.69	1.31	.91	1.07	1.48	.32	.52	5.61	11.30	1.74	.97	1.85	4.56	10.17	15.86
1941-42	.89	1.77	.91	3.57	.97	.37	1.66	1.44	.57	.34	5.35	8.92	.81	1.96	.94	3.71	9.06	12.63
1942-43	.26	.02	.38	.66	.54	.96	1.32	1.59	.83	.16	5.40	6.06	.65	1.50	1.63	3.78	9.18	9.84
1943-44	.28	.27	.12	.67	1.59	.39	.44	.42	.83	.57	4.24	4.91	1.11	1.85	8.26	11.22	15.46	16.13
1944-45	.58	.08	.66	1.32	.51	2.10	.34	.52	1.42	.54	5.43	6.75	.43	2.59	3.38	6.40	11.83	13.15
1945-46	.09	3.53	1.40	5.02	.04	.86	1.02	.37	.73	1.63	4.65	9.67	.15	2.22	.90	3.27	7.92	12.94
1946-47	.48	.20	.47	1.15	1.08	2.38	1.09	.29	.22	.36	5.42	6.57	1.17	1.07	2.31	4.55	9.97	11.12
1947-48	.62	.19	1.59	2.40	.71	.86	.29	.13	.42	1.13	3.54	5.94	.63	1.80	2.95	5.38	8.92	11.32
1948-49	.22	.86	.90	1.98	.25	.58	1.01	.90	1.02	.22	3.98	5.96	.37	2.97	1.74	5.08	9.06	11.04
1949-50	.78	.36	.51	1.65	1.19	.78	.71	.93	.74	1.16	5.51	7.16	.55	.56	2.09	3.20	8.71	10.36
1950-51	.43	.70	2.15	3.28	.69	.10	.98	.42	.46	.22	2.87	6.15	.66	1.20	.36	2.22	5.09	8.37
1951-52	1.27	2.17	.00	3.44	1.30	.30	1.45	1.25	1.52	1.24	7.06	10.50	.22	.79	1.80	2.81	9.87	13.31
1952-53	.55	1.38	.07	2.00	.00	.02	1.19	.55	.59	.34	3.50	5.59	1.06	2.00	2.16	5.22	8.81	10.81
1953-54	.33	.14	.06	.53	.22	.27	.73	.25	.57	1.19	3.23	3.76	.90	.85	2.39	4.14	7.37	7.90
Average	.73	.79	.76	2.28	.85	.70	.94	.86	.72	.71	4.78	7.06	.80	1.28	1.92	4.00	8.78	11.06

TABLE 11.—Mean temperature at the U. S. Sheep Experiment Station near Dubois, Idaho, July 1931 through June 1954

Year	Summer				Fall and winter							Spring			
	July	Aug.	Sept.	Average	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Average	Apr.	May	June	Average
	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.
1931–32	73.3	68.8	57.9	66.7	46.8	27.8	22.0	11.8	18.7	24.0	25.2	40.2	52.0	59.0	50.4
1932–33	66.6	66.8	59.2	64.2	41.7	33.5	13.4	17.0	9.6	28.8	24.0	40.3	47.0	65.4	50.9
1933–34	72.8	67.0	56.6	65.5	49.8	34.0	28.1	26.6	34.2	44.8	36.2	52.2	60.8	60.8	57.9
1934–35	72.5	71.6	53.9	66.0	50.0	36.8	22.9	22.4	24.1	27.7	30.6	39.9	49.2	61.6	50.2
1935–36	70.0	68.3	61.2	66.5	45.9	25.0	23.7	18.5	17.7	27.2	26.3	42.9	57.6	62.8	54.4
1936–37	71.8	67.4	56.4	65.2	47.0	31.4	23.6	3.0	16.6	27.7	24.9	39.0	55.4	58.0	50.8
1937–38	69.8	67.2	59.8	65.6	48.2	32.5	24.4	20.6	23.4	28.4	29.5	40.8	49.2	60.6	50.2
1938–39	65.5	65.2	63.2	64.6	46.1	21.6	23.9	18.8	13.2	31.0	26.3	45.0	54.3	56.2	51.8
1939–40	69.8	68.2	57.6	65.2	44.4	38.0	28.3	20.3	24.8	33.0	31.5	43.2	55.6	64.4	54.4
1940–41	70.2	70.6	57.3	66.0	47.6	27.8	25.2	22.5	26.0	33.0	30.4	42.4	51.8	57.8	50.7
1941–42	68.3	64.6	50.2	61.0	43.5	33.2	25.6	18.6	16.3	25.2	27.1	43.9	46.6	56.8	49.1
1942–43	71.0	68.6	57.8	65.8	45.6	30.3	21.0	16.2	22.3	22.9	26.4	47.8	48.6	55.2	50.5
1943–44	68.9	67.2	61.2	65.8	48.2	34.4	26.4	17.5	21.8	23.4	28.6	41.0	52.4	54.7	49.4
1944–45	61.8	64.6	57.4	62.3	51.0	27.4	20.0	20.3	23.6	26.2	28.1	36.4	50.4	53.4	46.7
1945–46	69.0	66.3	52.8	62.7	48.2	28.0	18.5	16.4	18.6	30.2	26.6	46.2	50.4	60.4	52.3
1946–47	70.1	69.2	56.9	65.4	38.0	30.8	27.0	13.9	25.2	35.8	28.4	41.3	55.4	55.6	50.8
1947–48	70.4	67.0	58.2	65.2	49.0	25.9	22.0	19.2	22.6	25.4	27.4	41.4	51.8	62.0	51.7
1948–49	67.8	66.8	59.2	64.6	47.6	25.5	15.2	7.0	16.5	32.5	24.0	48.0	54.1	59.0	53.7
1949–50	69.1	70.2	59.8	66.4	39.2	38.1	19.5	12.6	23.4	27.3	26.7	40.6	48.0	58.2	48.9
1950–51	66.1	66.1	56.0	62.7	48.5	33.8	27.5	16.1	23.0	24.0	28.8	43.7	52.6	55.2	50.5
1951–52	69.2	64.0	57.4	63.5	42.0	29.1	15.4	15.2	16.1	22.3	23.4	40.9	53.3	60.7	51.6
1952–53	66.0	67.3	66.1	66.5	50.2	25.7	22.4	27.2	22.1	31.0	29.8	38.4	46.4	56.9	47.2
1953–54	71.6	67.9	61.4	67.0	49.4	37.3	19.9	22.4	30.2	28.8	31.3	44.4	54.0	56.6	51.7
Average	69.3	67.4	58.2	65.0	46.4	30.9	22.4	17.6	21.3	28.7	27.9	42.6	52.0	58.8	51.1

wind velocities were low during November and December; uniformly high during the 6-month season, March through August; and intermediate during the other 4 months.

In contrast to average velocities, maximum velocities occurred mostly in the winter months. During the 19-year period, 31 days had a velocity greater than 20 miles per hour for the entire 24 hours. Of these 31 days, 12 occurred in January, 10 in February, 3 in March, 2 in December, 2 in October, and 1 each in April and May. Often high winds persisted for two or three consecutive days.

There was considerable variation between years in average velocity in individual months. For example, average January velocity varied from 3.7 miles per hour in 1952 to 10.5 in 1949. However, variations in average annual velocity were slight, ranging from 6.0 miles per hour in 1947–48 to 7.2 in 1936–37 and in 1942–43. Coefficient of variation for average annual velocity was 6 percent.

TABLE 12.—Average wind velocity at the U. S. Sheep Experiment Station, July 1935 through June 1954

Year	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Average
	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.	m.p.h.
1935–36	9.3	9.1	9.0	7.1	4.7	4.5	6.0	6.8	7.4	6.8	7.4	7.3	7.1
1936–37	6.8	9.1	7.1	6.6	5.8	4.8	7.8	7.3	9.0	7.4	7.7	7.6	7.2
1937–38	7.0	7.9	6.7	5.4	1.7	5.8	5.4	8.2	7.6	7.3	6.3	6.6	6.6
1938–39	5.9	7.0	6.0	6.5	5.2	3.8	3.9	7.1	6.4	6.2	7.3	7.6	6.1
1939–40	7.4	6.8	6.2	5.2	4.9	4.1	6.5	6.2	7.1	7.0	6.7	6.5	6.2
1940–41	7.0	6.8	5.3	4.7	4.8	5.5	5.9	6.1	7.4	7.4	7.4	6.4	6.2
1941–42	6.6	6.9	7.5	6.1	5.6	8.8	5.2	7.0	6.3	7.3	7.2	7.6	6.7
1942–43	8.3	7.7	6.9	6.8	5.9	4.3	7.7	7.8	7.9	7.7	7.3	8.0	7.2
1943–44	7.4	7.4	7.2	6.2	4.9	4.9	5.1	7.0	9.3	6.8	7.1	6.2	6.6
1944–45	6.5	7.8	7.0	6.3	4.3	5.8	5.1	7.2	7.6	8.5	7.0	5.7	6.6
1945–46	5.6	6.0	6.5	5.7	5.4	4.5	5.8	6.3	8.5	7.1	7.5	7.8	6.4
1946–47	7.0	7.2	6.6	7.1	5.5	4.5	4.6	8.1	5.7	7.2	7.4	7.4	6.5
1947–48	7.5	7.1	6.5	5.7	3.6	3.7	4.2	6.7	6.3	7.8	6.5	6.8	6.0
1948–49	7.9	7.7	7.0	6.2	4.4	5.1	10.5	7.7	6.6	7.2	7.2	7.7	7.1
1949–50	7.7	7.1	7.2	7.0	5.1	6.5	7.2	5.7	6.9	7.2	7.5	7.1	6.8
1950–51	7.3	8.7	6.4	6.1	4.7	2.7	6.0	5.6	7.2	7.9	6.9	6.2	6.1
1951–52	7.1	6.6	7.0	5.5	4.1	5.0	3.7	4.8	7.7	7.8	7.5	7.5	6.2
1952–53	6.8	6.5	6.4	5.5	7.1	5.2	6.1	9.0	7.5	7.5	6.5	7.3	6.8
1953–54	6.9	6.9	6.3	6.4	4.1	1.5	6.7	5.2	7.7	7.?	7.6	6.7	6.4
Average	7.2	7.3	6.8	6.1	5.0	4.8	6.0	6.8	7.4	7.4	7.2	7.1	6.6

Cloudiness

Visual estimates over the 23-year period indicate that the average degree of cloudiness was 4.9, or about half overcast (table 13). Skies were most clear during the summer months. Cloudiness gradually increased during the fall to a maximum in December and January and then diminished during late winter and spring to a

minimum in midsummer. Although there was considerable variation between years in average cloudiness of individual months, variations in average annual cloudiness were relatively small. Cloudiness rating varied from 4.0 in 1933–34 to 5.4 in three different years, and coefficient of variation was 8 percent.

TABLE 13.—*Average degree of cloudiness at the U. S. Sheep Experiment Station expressed as a numerical rating from 0 (no clouds) to 10 (completely overcast), January 1932 through June 1954*

Year	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Average
1931–32							7.8	6.5	7.1	6.6	7.2	6.2	
1932–33	4.1	3.7	3.0	4.8	6.0	5.1	7.1	5.3	4.4	4.1	6.0	2.8	4.7
1933–34	2.9	4.0	3.0	3.2	3.4	6.0	5.3	4.0	4.2	4.6	3.0	4.1	4.0
1934–35	2.0	2.6	3.8	4.7	5.5	4.6	5.2	3.7	5.0	5.5	6.4	4.4	4.4
1935–36	2.1	2.8	3.7	5.0	6.5	5.9	6.4	6.6	5.9	4.5	4.0	3.7	4.8
1936–37	5.5	4.0	3.0	3.5	3.2	7.5	5.9	6.3	3.9	5.7	4.2	5.4	4.9
1937–38	4.4	3.4	4.4	3.5	6.1	6.4	6.5	6.4	7.1	4.5	6.2	4.8	5.3
1938–39	5.0	3.8	3.7	5.1	5.6	6.9	7.7	6.1	5.8	4.8	4.9	5.6	5.4
1939–40	4.0	3.7	4.0	5.1	3.4	7.1	6.8	7.8	5.5	5.2	4.0	4.6	5.1
1940–41	3.5	3.4	6.1	4.3	6.1	5.6	6.0	6.1	4.7	5.8	6.2	5.2	5.2
1941–42	4.8	4.4	5.1	4.6	4.8	7.1	5.9	6.2	5.7	5.6	5.6	4.7	5.4
1942–43	2.4	3.5	4.0	4.8	6.2	7.3	6.5	5.2	4.3	4.7	5.6	4.3	4.9
1943–44	2.7	2.8	3.1	5.4	5.0	4.6	5.6	7.1	5.8	7.0	5.6	5.7	5.0
1944–45	4.6	2.8	3.5	3.1	7.3	6.7	7.3	5.5	5.2	5.8	6.0	6.6	5.4
1945–46	3.7	3.7	3.4	3.1	6.4	7.4	5.8	5.6	5.2	5.5	6.1	4.9	5.1
1946–47	5.1	4.3	3.9	6.8	6.0	7.1	5.5	4.2	5.0	4.9	4.1	5.9	5.2
1947–48	2.5	2.6	3.3	4.1	6.2	7.0	4.8	5.6	6.3	5.3	5.3	5.6	4.9
1948–49	3.5	3.9	3.0	2.9	7.0	7.0	4.4	5.5	5.0	2.9	5.5	3.2	4.5
1949–50	2.4	3.2	2.8	4.3	2.7	6.0	7.1	5.4	6.2	3.8	5.0	5.3	4.5
1950–51	5.1	4.7	4.0	4.3	5.7	6.7	5.3	6.3	6.6	4.9	4.5	4.7	5.2
1951–52	2.9	5.0	3.6	5.4	5.9	7.2	6.7	4.4	5.6	3.5	4.0	4.6	4.9
1952–53	3.5	2.9	2.2	3.1	5.6	7.0	7.2	5.1	5.1	5.1	5.7	3.7	4.8
1953–54	2.1	2.5	2.2	2.7	4.3	5.4	7.2	4.4	4.6	3.8	4.6	5.7	4.1
Average	3.6	3.5	3.6	4.3	5.4	6.5	6.3	5.6	5.4	5.0	5.2	4.9	4.9

COMPARISON OF FACTORS

For ease in comparing trends in climatic factors throughout the growth year, the various measures for individual months have been expressed as percentages of the highest month and plotted (fig. 12). With the exception of a peak in May and June, precipitation is fairly evenly distributed through the year. Its distribution is therefore different from the other factors, which show either a maximum or minimum in winter. As might be expected at this latitude, mean temperature is highest in July, and gradually diminishes to a minimum in January, and then increases to the July maximum.

Wind velocities follow a pattern similar to that of temperature, but they reach their minimum a month earlier and then rise to
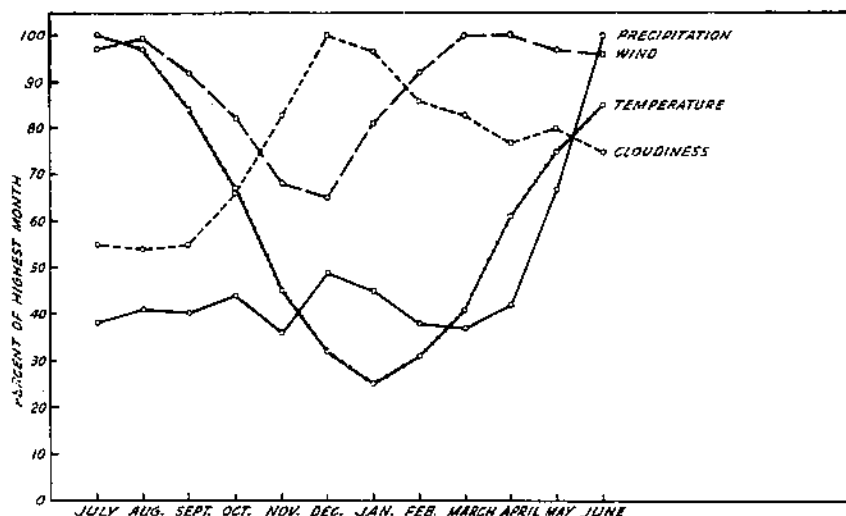
FIGURE 12.—Average precipitation, wind, mean temperature, and cloudiness during the study, expressed as percentages of the highest month.

their maximum in March and remain near this level through August. Degree of cloudiness follows a pattern directly opposite to that of wind velocity, being low in summer and high in winter. In general, then, cloudiest skies occur during the season when wind and temperature are at the minima, and clearest skies occur during the months when wind velocities and temperatures are high.

Examination of the annual values for the various climatic factors indicates that year-to-year variation was greatest in precipitation and least in mean temperature. This observation is substantiated by the coefficients of variation for the annual values: 20 percent for precipitation, 4 percent for temperature, 6 percent for wind, and 8 percent for cloudiness. With the exception of precipitation, there is much less variation between annual values than between averages of individual months.

Further examination of these data indicates a lack of close correlation between any of the factors; however, there is a tendency for precipitation to vary directly with cloudiness, and for both precipitation and cloudiness to vary inversely with temperature. Simple correlation coefficients between annual measures of the various factors substantiate this observation:

Precipitation—Cloudiness__	.581**	Wind—Cloudiness _ _____	—.315
Temperature—Cloudiness__	—.482*	Temperature—Wind _____	—.274
Precipitation—		Precipitation—Wind _____	—.260
Temperature_____	—.381		

*Significant at the 5-percent level.
**Significant at the 1-percent level.

These coefficients also suggest that wind is less closely related to the other factors than they are to each other.

DEVELOPMENT AND YIELD IN RELATION TO CLIMATIC FACTORS

The relation between seasonal development of plants and climatic factors has received considerable attention, but mostly in connection with cultivated crops. Early investigations, particularly those of European workers concerned with temperature effects and the development of thermal constants, were summarized by Abbe (1). Although numerous hypotheses were formulated and tested, it was not possible to establish reliable thermal constants for the various stages of plant development.

Bradford (7) also reviewed early work in connection with his study of the relation of temperature to blossoming in the apple and peach in Missouri. He found that quantity of heat above a specified base received from January 1 to the time of blossoming varied with both season and locality, and concluded that temperature is not always a limiting factor. Thompson (78) made an extensive review of temperature in relation to development of cultivated plants but was unable to arrive at definite conclusions because of difference in methods of measuring response and failure to consider other factors.

Grainger (27) found from his studies in England that flowering in some species was hastened by temperatures higher than normal prior to flower bud formation, but in others by temperatures lower than normal. Flower emergence in 13 wild plants, however, was hastened by a temperature higher than normal for a period just before the time of opening. Working with cereals and cotton, Lysenko (85) found that the time required for completion of the various developmental stages was inversely related to temperature.

Sampson (73) grew potted plants of field peas and wheat at three elevations in the Wasatch Mountains of Utah and found that rate of maturation decreased directly with decrease in temperature from the lowest to the highest elevation. Maclagan (48) found that in Scotland low temperatures during certain narrow belts of time delayed opening of flower buds of three shrubs, whereas high temperatures during the same periods induced early flowering. Using soy beans in Maryland, McLean (49) concluded that temperature was the limiting factor for plant growth during the first two weeks following planting, after which moisture conditions were limiting.

Early phenological studies reviewed by Thornthwaite [1] as well as recent studies in New Jersey indicate the importance of temperature, photoperiodism, and moisture to plant development. Laude (39) investigated the nature of summer dormancy in 20 perennial grasses in California and found that dormancy of 13 species was caused by drought; but in the other 7, high temperatures and long day-lengths caused dormancy even though adequate water was supplied. Working with florist crops in New York, Post (67)

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[1] Thornthwaite, C. W. *Temperature relations to time of maturity of vegetable crops.* Paper presented at 78th Ann. Meeting New Jersey Hort. Soc. 18 pp. 1952. (Typewritten.)

found that some plants did not respond to either increased or reduced day-length unless temperature was within a certain range, and concluded that temperature control for bud formation is equal to day-length.

Studies of forest vegetation have shown the importance of light quantity, particularly in seedling establishment of southern pines in the Piedmont region (57, 38). In this case, increase in light intensity allowed extensive root development so that the pine seedlings could compete successfully for the limited soil moisture. Light-vegetation relation in other plant communites have received much less emphasis; however, Daubenmire (13) cites studies indicating that maximum photosynthesis in many smaller plants occurs at light intensities of 30 percent or less of full sunlight, and that full sunlight is often supraoptimal.

Wind has been studied mostly in connection with desiccation, dwarfing, and deformation of trees. Dry winds, particularly during cold weather when water-supplying power of the soil is low, can kill leaves, twigs, and buds (68, 13). Although strong winds from a constant direction often result in dwarfing, they may allow near normal height growth but cause asymmetrical crowns with branches only on the leeward side. Such deformation is caused by death of twigs and buds on the windward side or by the wind-training of branches that emerge on the windward side until they point permanently in the leeward direction (40).

The effect of wind on seasonal development and yield has received only limited attention; however, Finnell (23) found that a continuous wind of 15 miles per hour supplied by an electric fan reduced rate of height growth of marigolds, increased time required for maturity by about 10 days, and reduced herbage weight by approximately 50 percent as compared to similar plants not subjected to wind. Since wind-caused low herbage production does not result in a corresponding decrease in water consumption, transpiration efficiency is greatly reduced (50).

The effect of annual variations in precipitation and temperature on plant growth has also received considerable attention in connection with radial growth of trees. However, since the present research deals mainly with production of herbage, the literature on radial increment of stems is treated briefly. Douglass (17) made extensive studies of the relation of climate to annual rings of trees in several Western States and found fairly strong correlations between precipitation and ring width.

In similar studies in the Great Basin, Antevs (2) found that tree growth corresponded to water supply available during the growing season in about 75 percent of the years. Diller (16), investigating the relation of temperature and precipitation to growth of beech in northern Indiana, found inverse correlations between annual ring width and growing season temperatures, but direct correlations with precipitation. He concluded that temperature and precipitation during the period of most active growth (May, June, July) are particularly important in determining ring width.

In New England, Lyon (46, 47) found significant positive corre-

lations between mean ring width of several species and precipitation during certain periods of the year, but some species showed no consistent agreement. There was little correlation between growth increments and temperatures of the growing season. Lyon emphasized the importance of rainfall during the growing season and concluded that water supply is the controlling factor in growth rate. However, Hustich (*33*) concluded that in general the temperature influence on tree growth is dominant at the higher latitudes, whereas precipitation is dominant at the lower latitudes. In an extensive review of the literature, Glock (*26*) pointed out the importance of precipitation and temperature to tree growth but cautioned against extending interpretation beyond the samples included in the correlation calculations.

Investigations of relations between herbage production and weather are less numerous, but some work has been done on both native and cultivated plants. The effect of precipitation has received by far the most study, especially during drought periods. Sarvis (*74*) reported that the 1934 drought weakened or killed much of the herbaceous vegetation in experimental pastures in North Dakota. Ellison and Woolfolk (*20*), studying effects of this drought in Montana, reported that a summer rainfall only 38 percent of normal accompanied by exceptionally high temperatures caused a 50-percent reduction in top growth of shrubs the following year and a reduction by approximately 70 percent in basal area of grasses and sedges. In Nebraska, Robertson (*69*) found that the hot, dry summer of 1936 continued the destruction started by the 1934 drought and considerably modified the native prairie vegetation, reducing yield of perennial grasses by 22 percent and of perennial forbs by 10 percent.

Weaver (*82*) concluded that grass yield is determined by water relations of soil and air and that other factors are merely contributory. Nelson (*54*) investigated the influence of precipitation on *Bouteloua eriopoda* and concluded that the change in area covered from one fall to the next is influenced mainly by the vigor of the plants at the start of the current growing season as reflected by the previous year's precipitation and that current summer rainfall has no significant effect on the current change in plant cover. In the same study, however, he concluded that rainfall during the summer season largely determines height growth. Similarly, Turner and Klipple (*79*) found that volume of *B. gracilis* herbage varied widely from year to year, depending largely upon the amount and distribution of rainfall during the growing season.

In a study of the relation between native forage production and precipitation on the northern Great Plains, Rogler and Haas (*71*) found highly significant correlations between yield and the April–July precipitation of the same year and between yield and soil moisture in the surface 3 feet the previous fall. Also, Hutchings and Stewart (*34*) found a close correlation ($r = .944$) between herbage production on winter range in Utah and precipitation for the preceding 12 months (Oct. 1 to Sept. 30). Studies in Arizona demonstrated that variations in rainfall significantly influenced

cover and height growth of three native grasses (44). Although individual species differed considerably in their response to rainfall distribution, increased rainfall was generally more effective in fall or spring than in other seasons.

From studies on the Great Plains, Chilcott (9) concluded that annual precipitation is important in determining grain yield but is seldom if ever the dominant factor. However, in a 30-year study also on the Great Plains, Cole (10) reported significant correlations between yield of spring wheat and annual precipitation for the year ending July 31. In studies of the effect of precipitation on crop yield in South Dakota, Pengra (65) divided precipitation into a preseasonal period of August 1 to March 31 and a seasonal period of April 1 to July 31. With small grains, correlation coefficients for preseasonal precipitation and yields were larger than corresponding correlations of yield and seasonal precipitation. Seasonal precipitation was rarely great enough to overcome a marked deficiency in soil moisture at planting time.

Kezer and Robertson (37) concluded that time of applying water is an important factor in spring wheat production. Water applied at "jointing" increased the yield of straw and grain, but irrigation as late as "blossoming" and "filling" had very little effect. Results of soil-moisture experiments carried out in potometers did not agree with those from similar experiments under field conditions. In England, Hooker (32) computed a large number of correlation coefficients between grain and hay yield and precipitation and temperature, and generally found positive correlations with precipitation of the growing season, but negative correlations with temperature. Furthermore, the calculation of partial coefficients indicated that the negative relation between yield and temperature existed irrespective of precipitation.

Although some of these results are conflicting and many may not be directly applicable to the Upper Snake River Plains, they indicate in a general way some of the effects of climatic factors on plant development and yield. High temperatures hasten phasic development and growth, but reduce yield. Although there is considerable disagreement about period during which precipitation is most effective, yield generally varies directly with precipitation. Day-length and temperature are important factors in the initiation of flowering. Light quantity is probably less important in herbaceous communities than it is in forest stands. Wind usually is deleterious: it retards phasic development and growth rate and reduces yield.

METHOD OF STUDY

As previously indicated, the method of studying vegetal-climatic relations has been to eliminate as many as possible of the environmental factors known to influence plant development and yield while observing the correlation between these phenomena and natural variations in the climatic factors. Fires, and grazing by domestic livestock or big-game animals, were completely excluded from the study areas. Although insects and rodents were

not excluded, a record was made of all observable effects on the vegetation. For the most part, populations were not large enough to cause unusual damage, but in some cases it was necessary to estimate the extent of herbage removal and apply corrections to the appropriate yield data.

Topography has been eliminated as a causal agent because plant observations were made on exactly the same site each year. For this same reason, soil can be largely eliminated as a cause of variations in plant development and yield. Although sizable year-to-year variations in soil fertility may occur under conditions of cropping, burning, grazing, severe erosion, etc., in the present study it is believed that the protected areas supporting a stable vegetation have a fairly constant soil composition. For example, as measured by the standard Kjeldahl method, total nitrogen in the top half inch of soil on a nearby area showed almost no variation in three different years: 1932, 0.15 percent; 1934, 0.16 percent; and 1948, 0.16 percent.

In using correlation analysis (77) throughout this study to relate climatic factors to each other and to plant growth, it has been assumed that the data possess the proper characteristics for such analysis, i.e., normality, linear relationship of variables to each other, and homoscedasticity. No exact statistical tests were possible for these assumptions, but the various distributions were examined and enough of them plotted to indicate that the correlation coefficient is at least a fairly appropriate measure of association of the variables concerned.

Although correlation is certainly not proof of causal relations between two variables, it does suggest that causality may be involved. This is particularly true in the present study because it has already been well established that climate strongly influences vegetation. Furthermore, the elimination in this study of many other factors that are known to influence plant growth makes it even more plausible that much of the variation in development and yield is caused by variations in climatic factors. For these reasons, close correlations between weather and plant response are mostly interpreted herein as cause-effect relations.

Seasonal Development

Phases

Data for the 16-year period 1932–47 were used to ascertain the relation between phasic development of plants and the climatic factors, temperature, precipitation, and degree of cloudiness. Although plant development records for these years were available for only eight species (*Agropyron spicatum*, *Oryzopsis hymenoides*, *Poa nevadensis*, *P. secunda*, *Stipa comata*, *Balsamorhiza sagittata*, *Crepis acuminata*, and *Lupinus caudatus*), it was thought that the 16-year period would provide a more reliable correlation than the 7-year period, 1941–47, with a greater number of species. Since wind-velocity data were not available prior to 1936, phasic development-wind correlations are

based on a period of only 12 years, 1936–47. In order to obtain an expression of earliness or lateness of plant development for each year, the species were combined and the average date at which they reached each stage was computed.

In every year, plant development earlier than average was associated with mean temperature higher than average; similarly, development later than average was always associated with lower than average temperature. The correlation coefficient between average date of the stage "flower stalks appear" for the eight species and March–April mean temperature was −.619*, and the correlation coefficient between "full bloom" and March–May mean temperature was −.927**.[5]

Probably a more reliable expression of earliness or lateness of plant development is provided by an average of several stages. Average date at which the combined stages, "flower stalks appear" through "full bloom" occurred, and mean temperature of the 3-month period, March–May, were also fairly well correlated ($r = -.880$**). Grasses and forbs were much alike in their relation to temperature; correlation coefficients for the combined developmental stages with March–May mean temperatures were −.840** and −.877**, respectively.

Development during the latter part of the growing season was apparently more closely related to precipitation than temperature. Date of "plant drying" was positively correlated with April–May precipitation ($r = .812$**). In other words, late drying of the plants was associated with above-average precipitation. This stage was also negatively correlated with the April–May mean temperature, but the coefficient was lower ($r = -.635$*). There was a positive correlation ($r = .718$**) between date of "seed ripe" and April–May precipitation, but correlation with temperature of the same period was negative and much weaker ($r = -.332$).

Phasic development was also related to cloudiness. The correlation coefficient between cloudiness during April–May and date at which the combined developmental stages occurred in grasses and forbs was .531* and between degree of April–May cloudiness and "full bloom" was .694**. As a matter of fact, all of the correlation coefficients between degree of cloudiness and date of reaching the various developmental stages were positive, indicating that higher-than-average cloudiness was often associated with later-than-average plant development.

Phasic development showed no consistent relation to wind movement. Correlation coefficients between April–May and April–June wind and date of reaching the various phases of development were all small, varying between −.106 and .315.

In general, then, early phasic development of grasses and forbs was associated with high temperatures, low precipitation, and relatively clear skies. Conversely, late development was associated with low temperatures, high precipitation, and cloudy skies. There was no apparent relation between plant development and wind.

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*Significant at the 5-percent level (significant); **significant at the 1-percent level (highly significant).

Growth

Correlation analysis was also used to show relations between plant growth (height and weight increments through the growing season) and climatic factors. Since leaf height records of two species, *Agropyron spicatum* and *Balsamorhiza sagittata*, were available from 1932 through 1947, it was possible to relate height growth to temperature, precipitation, and degree of cloudiness during this 16-year period. Records of herbage weight and wind, however, were not available prior to 1936, so correlations involving either of these variables cover a period of only 12 years.

Correlation coefficients were computed between percent of total annual leaf height growth on May 5 and March–April mean temperature ($r = .822^{**}$), between height on May 15 and March–May temperature ($r = .726^{**}$), and between percent of total annual weight on May 20 and April–May mean temperature ($r = .640^{*}$). In other words, there was a direct relation between growth achieved at a particular date and temperature, high percentages of total annual growth being associated with high mean temperatures, just as early phasic development was associated with high temperature.

Growth correlations involving precipitation were generally weaker than those between growth and temperature, and the coefficients were negative, high precipitation tending to be associated with low percentage growth attained at a particular date. Correlation coefficients between growth and precipitation were: $-.219$ between May 5 leaf height and March–April precipitation, $-.629^{**}$ between May 15 height and April–May precipitation, and $-.668^{*}$ between May 20 weight and April–May precipitation.

There was also an inverse relation between degree of cloudiness and growth and between wind and growth, but most of the correlation coefficients were small. The strongest correlations were between March–May cloudiness and herbage weight on May 20 ($r = -.619^{*}$) and between March–April wind and leaf height on May 5 ($r = -.666^{*}$). It is perhaps worthy of note that all 12 of the correlation coefficients between growth and cloudiness or wind were negative.

As with phasic development of grasses and forbs, then, early attainment of a particular height or weight for Agropyron and Balsamorhiza was associated with high temperatures, low precipitation, and relatively clear skies. In addition early growth was associated with low wind movement. However, the relation between growth and cloudiness or wind were generally very weak.

Discussion

One of the early theories to explain timing of phenological events was that a particular stage of development depends upon receipt of a certain quantity of heat above a specified base, but according to Daubenmire (*13*) "no method of calculating such

heat units has yielded satisfactory correlations with plant development." Furthermore, Went (84) stated that because of the numerous climatic factors and the interaction in plant response between these factors, "the effect of climate on a plant cannot possibly be expressed in a simple formula, like a heat sum."

Nuttonson (55), however, found that date of maturity of winter wheat in both Czechoslovakia and the Pacific Northwest was rather closely related to day-degree summations (above a 40° F. base) beginning on the date of seedling emergence in the fall and on March 1. Since March 1 proved to be as satisfactory a starting point for the summations as emergence date, he concluded that fall and winter temperatures could be ignored when predicting date of heading or ripening of winter wheat.

Brown (8) grew several grasses in thermoregulated growth chambers and found that optimum temperatures for growth varied from 70° for some species to over 100° for others. Also, Livingston (45) concluded that elongation of maize shoots was most rapid at temperatures of about 90°. Since temperatures on the Upper Snake River Plains are relatively low during April and May, much of the plant growth must occur at temperatures below optimum. Apparently temperatures during these months seldom rise above the optimum for plant growth. For example, during the spring of 1934, the warmest on record, the maximum daily temperatures recorded at the weather station on the study area were 81°, 88°, and 83° in April, May, and June, respectively.

Although the effect of spring temperature on the Upper Snake River Plains is perhaps modified by other factors, it is undoubtedly of major importance, particuarly during the early stages of plant development. During the early part of the growing season, soil moisture is usually abundant and plant development at this time is controlled chiefly by temperature. Later in the season, rate of development is hastened by reduced soil moisture and retarded by an abundance. Actually, precipitation and temperature are inversely related so that rapid phasic development may often be caused by a combination of high temperatures and inadequate moisture.

Plant growth apparently is regulated in much the same manner as phasic development; and rapid growth and consequently early attainment of a certain height or weight are caused mainly by high temperature. In spite of the inverse correlations between seasonal growth and precipitation, high precipitation is not believed to have a deleterious effect on growth rate in this arid climate. This conclusion is supported by results of Haynes (28), who found that herbage growth of corn increased markedly with increased soil moisture within the range from near permanent wilting percentage to near saturation. Lewis, Work, and Aldrich (43) also found that comparatively small increases in soil moisture caused growth rate of pear fruits to increase, even when moisture content was well above the wilting point. The apparent effect of high precipitation in this study, then, is probably a result of the lower temperatures associated with rainy weather.

Since cloudiness is associated with both low temperature and high precipitation, it is quite probable that the slower rate of phasic development and growth associated with cloudiness is caused by these other factors, particularly temperature. This appears especially plausible since the sky is relatively clear during spring and summer on the Upper Snake River Plains, and since other studies (13) indicate that optimum light intensity for plant growth is often considerably less than full sunlight. Futhermore, Oosting (56) states that reduced light actually favors elongation and vegetative growth.

Although correlations between wind movement and phasic development of plants were poor, wind undoubtedly has at least an indirect effect through its influence on water losses from transpiration and evaporation. As suggested by Finnell (23), wind may actually retard rate of growth, since all 6 correlation coefficients between wind and growth were negative and 1 was statistically significant. The poor correlation between wind and the other climatic factors indicate that growth-wind correlations are not merely the result of wind being closely correlated with another factor that was actually causing the variation in plant growth.

On the basis of deviations of only 3 or 4 days from average date of first bloom, Leopold and Jones (42) have suggested that development of certain species is governed primarily by day-length. Inspection of individual plant development records on the Upper Snake River Plains reveals a wide range in dates at which the various developmental stages occurred; range of variation in average date of first bloom during a 7-year period was 11 days for the least variable species, and the average range for the 23 species was more than 3 weeks.

Although day-length is undoubtedly important in determining general time of reproductive development of some species, individual developmental stages can occur over a fairly wide range in day-length, varying with temperature and other environmental conditions. This is in agreement with Garner and Allard (25), who concluded that "under field conditions variations from year to year in date of flowering of both early and late varieties of soybeans are due chiefly to differences in temperature, while day-length is the primary external factor responsible for the fact that one variety is always relatively early and another late in attaining the reproductive stage."

Costello and Price (11) report that date of snowmelt can be used to predict date of developmental stages of herbaceous plants in the mountains of Utah. On the Upper Snake River Plains, snowmelt is related to phasic development, but the correlations are not strong enough to allow reliable predictions. For example, the correlation coefficient between dates of "snow off" and "flower stalks appear" for the combined grasses and forbs was only .533*.

Experience has shown that ranges in this locality are ready to graze each spring when *Agropyron spicatum* reaches a height of 2½ inches, and attempts were made to relate the date this height

was attained to snowmelt and temperature. Although this date, which averaged April 25 during the 16-year period, was highly correlated with snowmelt ($r = .710^{**}$), the correlation coefficients with mean temperature of March ($-.813^{**}$) and with March–April mean temperature ($-.909^{**}$) were even stronger.

Annual Yield

Correlation analysis was again used to show the relation of yield to precipitation, temperature, cloudiness, and wind. In order to minimize the possibility of overlooking significant relations, numerous correlation coefficients were computed between annual yield of the different plant groups and weather of the various seasons.

Weight

Correlations involving herbage weight of grasses, forbs, and shrubs were based on data for the 13 years shown in table 3, p. 17. Precipitation of the 9-month period immediately preceding the growing season was fairly well correlated with herbage weight (table 14). Although correlation coefficients were generally highest between weight and precipitation of the July–March period, exclusion of July and August or inclusion of April made little difference. Correlation coefficients between weight and annual precipitation for the period July 1 to June 30 were mostly lower, undoubtedly because of the negative correlation between spring (April–June) precipitation and weight.

Further analysis of the inverse relation between spring precipitation and herbage production indicated that precipitation during June was primarily responsible, as all correlation coefficients between weight of the various vegetal groups and June precipitation were negative and considerably higher than those for the entire spring period. Precipitation during the 3-month period preceding June was positively correlated with weight, but none of the correlation coefficients were statistically significant. Precipitation during a 3-month period the previous fall was also positively correlated with herbage production, but again, none of the coefficients were significant.

TABLE 14.—*Correlation coefficients between precipitation of various periods and herbage weight the following summer for 13 years of the period 1930–54*

Plant group	July–March	Sept.–March	July–April	July–June	Oct.–May	March–May	April–June	June	Sept.–Nov.
Grasses	**.745	**.717	**.713	*.617	*.604	.348	.354	−.525	.306
Forbs	**.787	*.676	**.774	**.815	**.712	.229	.037	220	.311
Shrubs	*.612	*.502	*.598	.516	*.608	.477	.210	*.536	.103
Grasses and forbs	**.815	**.758	**.887	**.758	**.725	.320	219	−.414	.340
All	**.808	**.732	**.796	**.741	**.765	.428	−.235	**−.563	.251

*Significant.
**Highly significant.

A better picture of weight-precipitation relations is probably provided in figure 13. Here only herbage weight of the combined grasses and forbs is considered; but many more seasonal precipitation periods are presented than in table 14. In addition to the points already mentioned, this figure indicates that correlations between weight and precipitation during short periods are generally poor. It further indicates that precipitation during long periods ending in March or April is better correlated with herbage
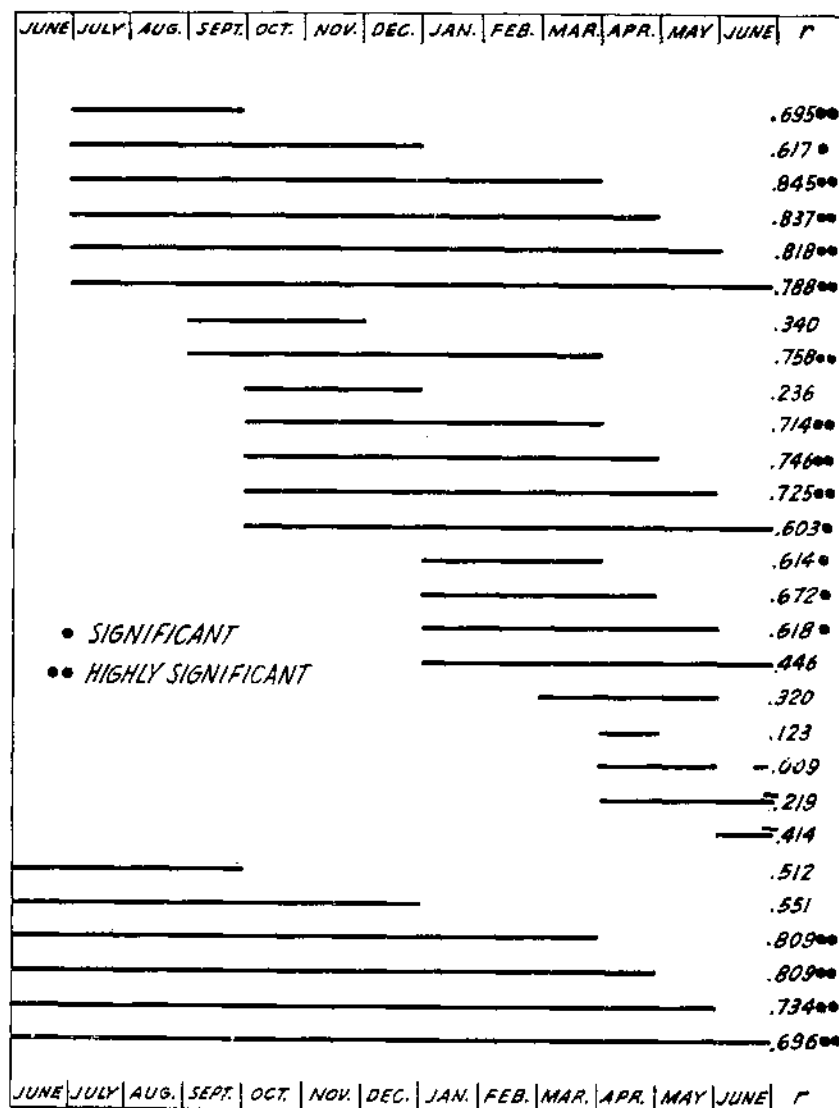

FIGURE 13.—Correlation coefficients between annual herbage weight of the combined grasses and forbs and precipitation of the season indicated for 13 years of the period 1936–54.

weight of the growing season immediately following than is precipitation of periods ending prior to or after March and April. Since June precipitation was apparently not effective in increasing current herbage production, an attempt was made to relate it to production of the following year. Correlation coefficients between herbage weight and precipitation of periods beginning in June, however, were not as high as those for periods beginning in July.

Although precipitation during certain seasons was rather closely related to herbage weight of vegetation as a whole or of groups of species, in only a few instances was it closely related to weight of individual species. For example, correlation coefficients between July–March precipitation and herbage production were: *Agropyron spicatum*, .460; *Stipa comata*, .059; *Balsamorhiza sagittata*, .711**; *Crepis acuminata*, .452; *Artemisia tripartita*, .633*; and *Purshia tridentata*, .061. It is especially noticeable that poorest correlations were with the least abundant species.

Although correlation coefficients between mean temperature and weight were generally not statistically significant (table 15), a number of relations may be inferred. The fact that all but one of the correlations between weight and mean temperature were negative indicates that low production was often associated with high temperature, particularly during the spring. The correlation between mean annual (July–June) temperature and weight was consistently negative but rather weak, and for the October to March period, scarcely any correlation was indicated.

TABLE 15.—*Correlation coefficients between mean temperature of certain seasons and subsequent herbage weight for 13 years of the period 1936–54*

Plant group	July–Sept.[1]	July–June	Oct.–March	March–May	April–May	April–June
Grasses	−.107	−.022	.117	−.310	−.406	−.268
Forbs	−.339	−.257	−.071	−.472	−.494	−.345
Shrubs	*−.630	−.289	−.037	−.316	−.397	−.299
Grasses and forbs	−.244	−.151	−.027	−.429	−.496	−.338
All	−.459	−.234	−.002	−.413	−.493	−.350

[1] Temperature of this period correlated with weight the following summer.
*Significant.

Since weight was best correlated with July–March precipitation and April–May mean temperature, multiple correlation coefficients were computed between weight and these two factors (table 16). Comparison with the simple correlation coefficients between herbage production and precipitation indicates that only a little was gained by the inclusion of the temperature factor. Partial correlation coefficients were also computed in these cases to allow examination of precipitation and temperature effects independently of each other.

TABLE 16.—*Simple, multiple, and partial correlation coefficients of herbage weight with July–March precipitation and April–May mean temperature for 13 years of the period 1936–54*

Plant group	Simple		Multiple	Partial	
	Precipitation	Temperature		Precipitation (temperature effect removed)	Temperature (precipitation effect removed)
Grasses	**.745	−.406	**.792	**.745	−.403
Forbs	**.787	−.494	**.861	**.811	−.568
Shrubs	*.612	−.397	*.675	*.596	−.362
Grasses and forbs	**.845	−.496	**.911	**.880	*−.638
All	**.808	−.493	**.878	**.836	*−.587

*Significant.
**Highly significant.

Elimination of the effects of one factor generally resulted in a slightly higher correlation between weight and the other, but the relations were otherwise unaffected. In other words, July–March precipitation was still positively correlated with herbage production after the effect of April–May temperature was eliminated, and April–May temperature was negatively correlated with production after elimination of the July–March precipitation effect. Furthermore, there was an inverse relation between April–May temperature and herbage weight after elimination of the influence of April–May precipitation.

To further clarify the weight-moisture-temperature relations, correlations were made between herbage weight and April–May soil moisture during 8 years of the period 1936–47. Correlation coefficients between average soil moisture of the surface 18 inches during these 2 months and herbage production are shown in table 17. These correlation coefficients are similar to those between weight and July–March precipitation (table 14).

Correlation coefficients were also computed between weight and April–May mean temperature during the same 8 years (table 17) so that partial correlations could be made of weight with April–May temperature and soil moisture. Elimination of the temperature effect caused only slightly lower positive correlations between weight and soil moisture, but elimination of the soil moisture effect resulted in a change from negative to positive correlations of weight of grasses and forbs with April–May temperature.

Herbage weight was positively correlated with cloudiness, but negatively correlated with wind (table 18). In other words there was a tendency for high production to be associated with cloudy skies and, to a lesser extent, with low wind movement. It is readily

apparent that correlation coefficients between cloudiness or wind prior to the start of the season (about April 1) and herbage weight were as high as or higher than coefficients involving these factors during the actual season of growth.

TABLE 17.—*Simple and partial correlation coefficients of herbage weight with April–May soil moisture and mean temperature for 8 years of the period 1936–47*

| Plant group | April–May soil moisture | | April–May mean temperature | |
	Simple	Partial (temperature effect removed)	Simple	Partial (moisture effect removed)
Grasses	**. 893	**. 877	—. 475	. 347
Forbs	*. 707	. 618	—. 439	. 057
Shrubs	. 683	. 364	*—. 766	—. 572
Grasses and forbs	**. 885	**. 854	—. 497	. 258
All	**. 876	*. 770	—. 701	—. 332

*Significant.
**Highly significant.

TABLE 18.—*Correlation coefficients between cloudiness or wind of certain seasons and subsequent herbage weight during 18 years of the period 1936–54*

CLOUDINESS

Plant group	July–March	July–June	March–May	April–May	April–June
Grasses and forbs	*. 574	*. 596	*. 629	. 500	. 379
Shrubs	*. 617	*. 652	*. 561	. 481	. 411

WIND

Plant group	July–March	July–June	March–May	April–May	April–June
Grasses and forbs	—. 421	—. 433	—. 073	—. 285	—. 212
Shrubs	—. 178	—. 166	—. 213	—. 272	—. 196

*Significant.

Area

All correlations involving vegetal area and precipitation, temperature, and cloudiness were based on data for the 19 years indicated in table 5, p. 18. Wind-area correlations, however, were based on only a 15-year period because wind records were not available prior to 1936. Although the sudden drop in vegetal area in 1934 apparently was caused by the severe drought of that year, the overall correlation between precipitation and area of vegetation was poor (table 19). Crown area of shrubs exhibited a slight

positive relation to precipitation, but there was no apparent relation between grass and forb basal area and precipitation.

Correlation of temperature with area, as with weight, was generally negative (table 20). Although most of the correlation coefficients were small, the inverse correlation of spring temperature with crown area of shrubs was significant.

Correlation coefficients between vegetal area and cloudiness or wind were also small (table 21). No trends were apparent in behavior of the three plant groups or between relations of pregrowing season and growing season weather.

TABLE 19.—*Correlation coefficients between vegetal area [1] and seasonal precipitation for 19 years of the period 1932–54*

Plant group	July–March	July–June	Sept.–May	March–May	April–June
Grasses	.033	.019	−.169	−.010	−.024
Forbs	.123	.108	−.020	.191	−.012
Shrubs	.202	.433	.376	*.515	*.499
All	.202	.398	.273	*.474	.428

[1] Basal area of grasses and forbs, crown area of shrubs.
*Significant.

TABLE 20.—*Correlation coefficients between vegetal area [1] and seasonal temperature for 19 years of the period 1932–54*

Plant group	July–Sept.[2]	Oct.–March	April–May	April–June
Grasses	.019	−.397	−.186	−.172
Forbs	−.150	−.254	−.070	−.100
Shrubs	−.271	−.002	*−.499	**−.576
All	−.249	−.173	*−.505	*−.570

[1] Basal area of grasses and forbs, crown area of shrubs.
[2] Temperature of this period correlated with weight the following spring.
*Significant.
**Highly significant.

TABLE 21.—*Correlation coefficients between vegetal area and cloudiness or wind of certain seasons during the period 1932–54*

Plant group	Cloudiness [1]		Wind [2]	
	July–March	April–June	July–March	April–June
Grasses	.108	−.034	−.468	.171
Forbs	−.028	−.105	−.445	.512
Shrubs	.096	.360	−.216	−.225

[1] Based on 19 years.
[2] Based on 15 years.

Height

Records of leaf and flower stalk height of *Agropyron spicatum* and *Balsamorhiza sagittata* for the 16-year period 1932–47 (table 8, p. 24) were used to relate total height to variations in precipitation, temperature, and cloudiness. Correlations involving wind are based on only 12 years, since records of this factor were not available prior to 1936. Although records of several species were available for the 1932–40 period, it was thought that the use of only two species for a longer period would allow a more reliable expression of the relations.

In general the relation of height to precipitation was not as close as that between herbage weight and precipitation; however, with the exception of Balsamorhiza flower stalks, correlation coefficients between height and March–May precipitation were fairly high (table 22). Mean temperatures of the April–May period were also well correlated with height of these two species, but the correlations were negative. Apparently June temperatures had little effect on height growth as their inclusion resulted in lower correlations between height and mean temperature. A comparison of tables 15, 20, and 22 shows that height was more closely related to mean temperature than was weight or area.

TABLE 22.—*Correlation coefficients between height at the end of the growing season and seasonal precipitation and mean temperature, 1932–47*

Species	Precipitation			Temperature			
	July–March	July–June	March–May	April	April–May	April–June	May–June
Agropyron spicatum:							
Leaves ...	.290	.270	**.667	*—.559	**—.611	—.495	—.236
Flower stalks [1]	.259	*.615	**.638	*—.603	*—.571	*—.535	—.375
Balsamorhiza sagittata:							
Leaves.	.373	*.533	*.547	**—.657	**—.698	*—.594	—.449
Flower stalks [1]	—.168	—.035	—.124	*—.578	—.400	—.398	—.162

[1] Data available for only 14 years.
*Significant.
**Highly significant.

Although leaf and flower stalk heights tended to be correlated positively with cloudiness and negatively correlated with wind, most of the coefficients were small (table 23). Cloudiness during the growing season was more strongly correlated with height than was pregrowing season cloudiness, but correlations involving wind during April through June were very similar to those during the July–March period.

Flower Stalk Numbers

Comparable records of flower stalk numbers were available for the eight species in table 9 during the period 1933–40; these were used to ascertain the relation of flower stalk production to pre-

TABLE 23.—*Correlation coefficients between height at the end of the growing season and cloudiness or wind of certain seasons during the period 1932–47*

Species	Cloudiness [1]		Wind [2]	
	July–March	April–June	July–March	April–June
Agropyron spicatum:				
Leaves	.213	.334	−.531	−.483
Flower stalks	.131	*.629	−.153	−.259
Balsamorhiza sagittata:				
Leaves	*.570	**.660	*−.613	−.536
Flower stalks	−.020	.372	.391	.359

[1] Based on 16 years for leaves and 14 years for flower stalks.
[2] Based on 12 years for leaves and 10 years for flower stalks.
*Significant.
**Highly significant.

cipitation, mean temperature, and cloudiness. Correlations involving wind were not attempted because of the limited number of years in which both flower stalk and wind records were available.

Flower stalk numbers in both grasses and forbs were positively correlated with precipitation and cloudiness, and for the most part, negatively correlated with temperature (table 24). Flower stalk production was more strongly correlated with weather of the early part of the growing season than with weather of the preceding period. Correlation coefficients between numbers and precipitation or temperature of the previous fall were very small.

Discussion

Examination of the various correlation coefficients between precipitation and herbage weight indicates that precipitation prior to the beginning of the growing season influences herbage production more than precipitation during the growing season. This is in essential agreement with results of studies on yield of spring grain by Pengra (65), who found that precipitation during the growing season was rarely great enough to overcome a marked deficiency in soil moisture at planting time, and by Kezer and Robertson (37), who found that early application of water increased yield of straw and grain whereas later irrigation had little effect. The chief effect of precipitation prior to the growing season, however, is probably not its influence on the vegetation at that time, but merely assurance of soil moisture during the period of active growth.

As might be expected, annual herbage production is apparently influenced rather strongly by overall precipitation, but not by that of any short period. It is evident that June (and perhaps late May) rainfall is primarily responsible for the inverse rela-

TABLE 24.—*Correlation coefficients between number of flower stalks and precipitation mean temperature, or cloudiness of certain seasons during the 8-year period 1933–40*

PRECIPITATION

Plant group	July–March	Sept.–Oct.	March–April	April–May
Grasses	*. 783	. 531	*. 726	. 425
Forbs	. 309	. 008	**. 915	. 302

MEAN TEMPERATURE

	July–March	Sept.–Oct.	March–April	April–May
Grasses	—. 157	—. 060	—. 583	—. 567
Forbs	. 349	. 043	—. 424	—. 437

CLOUDINESS

	July–March	Sept.–Oct.	March–April	April–May
Grasses	. 395	. 582	. 551	*. 755
Forbs	. 059	. 329	*. 713	. 650

*Significant.
**Highly significant.

tion between herbage weight and spring precipitation. Most of the plant growth in this locality is completed prior to June, and the normally abundant precipitation in June has little effect on current production. The negative and fairly high correlation coefficients between June precipitation and weight do not indicate an inhibiting effect of this precipitation on herbage production, but are merely a result of a negative correlation between June precipitation and that of the preceding months (July–March) during the 13 years under consideration.

The generally strong correlations of precipitation with herbage production of vegetation as a whole and the weak correlations with production of individual species illustrate the kind of equilibrium existing between vegetation and the environment. Such factors as high insect or rodent populations, disease, and late frosts may severely damage individual species; but when this happens, others are often able to utilize the moisture made available, increase their yield, and thus compensate for the decreased yield of the injured species. Various factors, then, can disrupt performance of individual species without seriously affecting overall community-environmental relations.

On the Upper Snake River Plains, highest herbage weights are associated with a cool growing season, April through June. The effect of mean temperature, however, is much less than that of precipitation. Since an inverse relation exists between precipitation and temperature, it might be expected that the apparent effect of a cool growing season is actually due to increased rainfall, but this factor must be discounted because precipitation during the growing season was not closely correlated with herbage

weight and because partial correlations indicate that the inverse effect of temperature on weight is independent of precipitation.

A possible explanation of the inverse relation between herbage production and temperature has been suggested by two early investigations. In studies of *Bacillus ramosus*, Ward (*81*) concluded that "at the optimum it metabolizes, grows, and respires at its best; but at higher temperatures removed from that it may grow for a short time more rapidly, but soon exhausts itself and so produces a poorer crop in the end." Lehenbauer (*41*) found that for a 12-hour period optimum temperatures for growth of corn shoots was 32° C., but at such high temperatures initial growth rate was not maintained; whereas at temperatures near the minimum (12°–14°) for shoot growth, no decrease in rate was evident during rather prolonged periods of exposure.

Furthermore, it has been emphasized by Hildreth, Magness, and Mitchell (*30*) that "the optimum temperature that produces the highest growth rate is not necessarily the most favorable for the general welfare of the plant. Too-rapid growth may delay or entirely prevent fruiting; it may produce plants that are structurally weak, susceptible to disease or insect attacks, and subject to damage by wind, hail, or other climatic influences." It is quite possible, then, that lower than average temperatures actually favor growth of native plants during the growing season as a whole, causing a relatively high production of herbage. At any rate, negative correlations (independent of precipitation effect) have also been reported between temperature and yield of numerous cultivated crops (*32*).

The inverse effect of temperature on herbage weight may be at least partly due to increased moisture available to the vegetation as a result of lowered rates of evaporation and transpiration during cool weather, for partial correlations indicate that when the influence of soil moisture is removed there is a slight positive relation between April–May temperature and weight of grasses and forbs. Since correlations of weight with temperature are generally poor, and since partial correlation coefficients are not consistently positive or negative, further study will be necessary to establish the true relation of temperature to herbage production.

Although variations in herbage production of native plants on the Upper Snake River Plains were more closely related to precipitation than to temperature, this situation is not universal. Heady (*29*) reported that at high altitudes changes in temperature affected yearly growth of *Agropyron spicatum* more than moisture, but the reverse was observed at low altitudes. Also, Hustich (*33*) concluded that in the northern part of the temperate zone temperature is more strongly correlated with crop yield than precipitation is.

Since there was a fairly high correlation between cloudiness and precipitation, it seems very probable that the cause-effect relations are between precipitation and herbage weight, not between cloudiness and weight. Also, the fact that correlations between cloudiness prior to the growing season and herbage weight

were as good as or better than those involving cloudiness during the growing season indicates that plant growth and consequently herbage production is not directly benefited by cloudy weather. Cloudiness, of course, could have a beneficial effect on moisture relations through reduction in evaporation and transpiration.

Correlations between wind and herbage production, like those between wind and height, were consistently negative, but there is no evidence that wind has a direct effect on plant growth. In the first place, all correlation coefficients were small; secondly, those between wind prior to the growing season and herbage weight or height were as large as or larger than growing season wind-weight correlations. It is very probable, then, that the apparent wind effect is actually an indirect one associated with reduced moisture.

Variations in basal area of grasses and forbs apparently are not closely related to any of the climatic factors under consideration. The absence of close correlation of area with temperature, cloudiness, and wind is to be expected in view of the generally poor correlation between weight and these factors; but the poor correlation between basal area and precipitation is at first surprising. However, it is difficult to imagine that normal fluctuations in precipitation in this locality would result in immediate increases or decreases in underground parts of the plants, a prerequisite for fluctuations in basal area of grasses and forbs.

The fact that several investigators (20, 62), demonstrated distinct decreases in vegetal area in 1934 as a result of the severe drought of that year does not necessarily indicate a good correlation between annual variations in area and precipitation. In the first place, many of these decreases still persisted after 1 or 2 favorable years; and, secondly, the effects of severe moisture deficiencies probably are not comparable to the usual fluctuations.

Crown area of shrubs differs in most respects from basal area of grasses and forbs, and its relation to precipitation and temperature is somewhat similar to that of herbage weight. Crown area, however, is apparently only slightly affected by annual variations in cloudiness and wind.

Examination of height-precipitation and weight-precipitation correlations indicates that herbage weight is most closely related to precipitation prior to the growing season, whereas height is most closely related to precipitation during the growing period. Although these differences may not be real, they are perhaps logical. Since weight seems chiefly dependent upon number of shoots, conditions during the period of shoot initiation should be more related to weight than conditions during the active period of growth.

Height growth is apparently favored by low light intensities associated with cloudy weather; however, this apparent effect could be at least partly caused by increased precipitation and lower temperature, or merely improved moisture relations resulting from a combination of these conditions. It is noticeable that although height and weight were both positively correlated with

cloudiness, height was correlated best with cloudiness of the growing season whereas weight was best correlated with cloudiness prior to the growing season.

As with weight, height is inversely related to mean temperature of the active growing period, but the relation is much stronger. In view of the differences in precipitation and cloudiness relationships discussed above, it appears that height growth actually reacts differently from herbage yield to a given set of conditions. A similar situation was reported by McLean (*49*) who found "that the rate of elongation of plant stems is influenced by external conditions differently from the rates of development of leaf surface and of dry weight for the same plants."

Frost, rather than other aspects of weather, may explain the generally poor flower stalk production of forbs, the earliest of the three groups to exsert them. It was observed that early spring frosts following the appearance of Balsamorhiza flower heads killed 85, 70, 73, and 66 percent of the flower stalks in 1940, 1942, 1943, and 1944, respectively. Since these flower stalks soon dried up and became inconspicuous, it is possible that such losses were unnoticed in some other years.

Although individual species apparently have widely varying requirements for optimum flower stalk production, the tendency is for high numbers to be associated with high precipitation and cool, cloudy weather, particularly during the early part of the growing season. In this respect, then, flower stalk production is related to climatic factors in more or less the same manner as height and herbage weight.

PRACTICAL CONSIDERATIONS

Although many results of studies reported herein are not directly applicable to range management at present, they add to the store of ecological information that serves as the foundation for development of improved practices. Certain results, however, can be put to immediate use; e.g., the relation of early plant growth and development to temperature and the relation of herbage yield to precipitation.

Ordinarily, experience has provided the range manager with certain criteria that indicate the time a range may be safely opened to grazing each season. These criteria may be based on soil condition but more often on a particular height or stage of development of certain species. Since it is important that the grazier know the date of range readiness a few weeks in advance, reliable methods for predicting this date are desirable.

On the Upper Snake River Plains, date at which *Agropyron spicatum* reaches a height of 2½ inches has been found to be a usable criterion for opening the grazing season, and this date can be predicted with suitable accuracy from the mean temperature of March. The regression equation for estimating date of range readiness from temperature is:

$$Y = 65.86 - 1.39X$$

in which Y is the number of days after March 31 and X is March mean temperature. This relation is shown graphically in figure 14. The standard error of estimate is 5.66 indicating that in about 2 out of 3 years the actual date at which the range is ready for grazing will be within about 6 days of the date predicted.
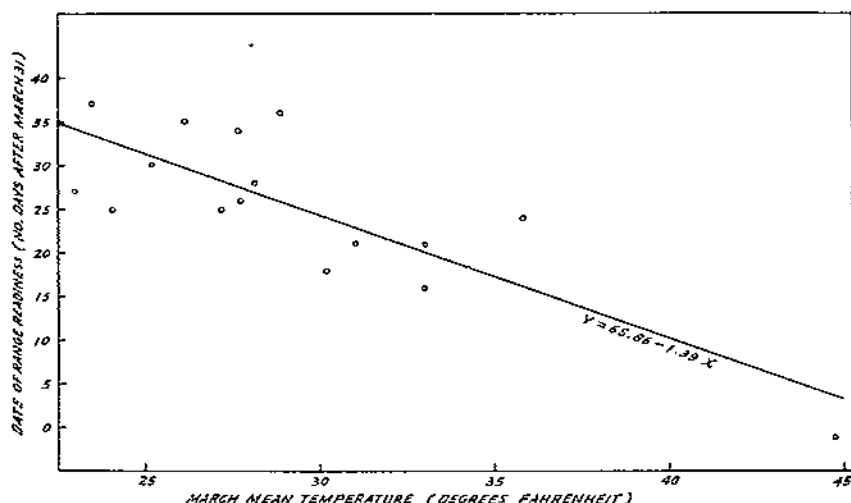

FIGURE 14.—Regression of date of range readiness (*Agropyron spicatum* 2½ inches high) on March mean temperature for the 16-year period 1932–47.

Range forage production is known to fluctuate widely from year to year, and despite safety measures that base rates of stocking on average or even below average forage production, severe overgrazing can occur in certain subnormal years. The close correlation between herbage weight and precipitation of the July to March period preceding the growing season offers a method for predicting herbage yield on the Upper Snake River Plains and an opportunity to adjust livestock numbers prior to the opening of the grazing season. Correlations between precipitation and herbage production of shrubs were not especially high, but shrubs can be ignored when predicting spring forage production because they are not grazed to any appreciable extent in the spring.

The regression equation for estimating combined grass and forb yield from the preceding July–March precipitation is:

$$Y = 133.40 + 38.23X$$

in which Y is air-dry herbage yield in pounds per acre and X is precipitation in inches. This relation is graphically shown in figure 15. The standard error of estimate is 55.2 indicating that in about 2 out of 3 years the actual herbage yield per acre will be within about 50 pounds of the predicted yield.

It is interesting to explore possible reasons for the wide divergence of one point (5.59, 475.9) from the regression line

(fig. 15). In this year (1953) precipitation of the July–March period was only 5.59 inches, but inspection of the records shows that an additional 2.31 inches fell during the last 10 days of June preceding this period and the first 7 days of April immediately following. If precipitation for this additional 17-day period is included for that year, the total is 7.90 inches, and the plotted point then falls well inside 1 standard error of the regression line.
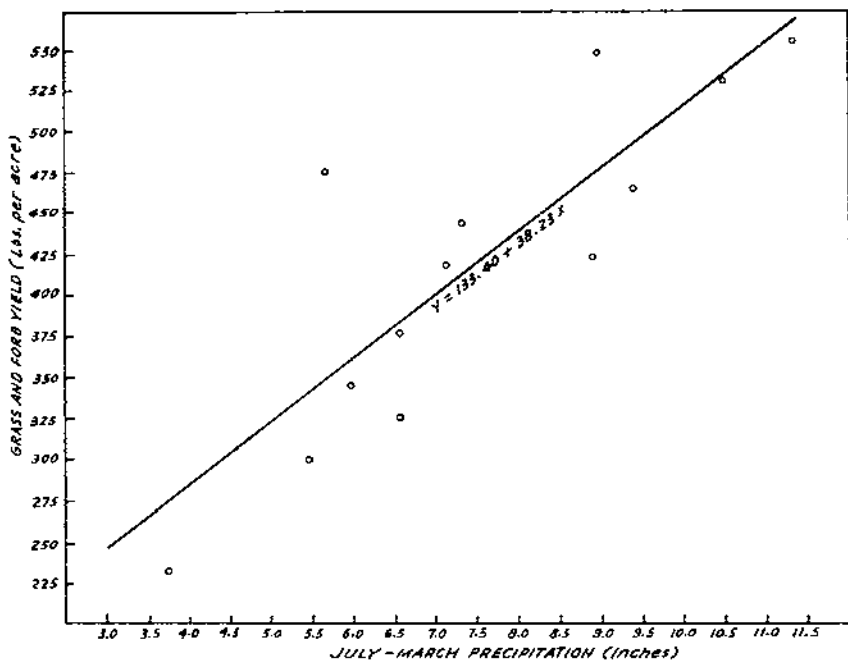

FIGURE 15.—Regression of grass and for herbage production on July–March precipitation, 13 years of the period 1936–54.

Records of phasic development for native range plants have certain practical values in respect to seed collection for artificial seeding of depleted ranges. By knowing when seed of the desired species is ripe and how long it remains on the plant before dissemination, it is possible to prepare time schedules for collection of required seed.

Knowledge of plant development and yield in relation to climatic factors is helpful in interpretation of change in range condition. Since management is often based on trend in condition under a certain degree of use, changes can be wrongly attributed to grazing unless effects of climate on vegetation are recognized and properly evaluated.

Results of these studies also indicate a need for a careful study of ecological methods—especially the various quantitative measurements of vegetation and their relation to each other. Certain investigators have measured plant response in terms of area whereas others have used height or weight, and the three measure-

ments have been directly compared. Although some of the results reported herein are based on estimates and may be subject to sizable errors, they indicate that vegetal area, height, and weight are not related to environment in exactly the same way and should not be directly compared.

SUMMARY AND CONCLUSIONS

Studies were made of seasonal development and yield of native plants and their relation to climatic factors, particularly precipitation and temperature, on the Upper Snake River Plains of eastern Idaho over a 23-year period, 1932–54. The study area is near the headquarters of the U. S. Sheep Experiment Station, Dubois, Idaho, at an elevation of 5,500 feet. As measured by herbage production, vegetation is composed roughly of 50 percent shrubs, and 25 percent each of grasses and forbs. The most abundant species are *Artemisia tripartita, Agropyron spicatum,* and *Balsamorhiza sagittata.*

In conjunction with grazing studies at the Sheep Station, several ungrazed exclosures were maintained as control areas. Repeated observations of seasonal development and yield of the vegetation within these exclosures over a 23-year period have provided the vegetal data that form the basis of the present investigation. Seasonal development studies consisted of periodic observations to determine dates at which various phases (stages) were reached and to record growth (increases in height or weight) throughout the season.

Phasic development was generally early in forbs, intermediate in grasses, and late in shrubs; however, development of individual species within a particular group was variable. Differences between species were greatest among the shrubs and least among the grasses.

In general, height growth of both grasses and forbs followed the common sigmoid pattern, being relatively slow at the beginning and end of the season, and rapid during the intermediate period. Growth rates of grass and forb flower stalks were similar, but leaves of forbs grew proportionately faster than leaves of grasses.

Herbage weight of grasses, forbs, and shrubs was highly variable between years, but there was no evidence of progressive changes during the 19-year period for which weight data were available. With a few exceptions, high or low weights of one group were associated with similar yields of the other two. Weight was not closely related to either area or height.

Vegetal area exhibited about the same variations as weight. In some years all groups behaved similarly, but in others areal variations were quite different. Continual changes in this apparently stable community were indicated by quadrat charts that provided a record of spatial relations of the plants. Seedling mortality on the quadrats was very high.

Leaf and flower stalk heights of *Agropyron* and *Balsamorhiza* showed about the same variation as weight and area. In some

years their height variations were parallel, but in others they were very divergent.

Flower stalk production was very erratic, numbers ranging from zero in some years to nearly 30 per plant in others. As a group, grasses were more consistent flower producers than forbs.

Daily records of precipitation, temperature, wind, and cloudiness were maintained at the weather station on the study area. Average annual precipitation was approximately 11 inches, rather evenly distributed throughout the year. Mean temperatures were normally above 40° F. for a 7-month period, and the frost-free period averaged 120 days. Average hourly wind movement was 6.6 miles. Skies were clearest during the summer and cloudiest in winter; average cloudiness was about 50 percent. Year-to-year variations were greatest in precipitation and least in mean temperature. Although the various factors were not closely correlated, precipitation tended to vary directly with cloudiness, and both precipitation and cloudiness tended to vary inversely with temperature.

Correlation analysis was used to relate plant development and yield to climatic factors. In general, early phasic development of grasses and forbs was associated with high temperatures, low precipitation, and clear skies. Conversely, late development was associated with low temperatures, high precipitation, and cloudy skies. There was no apparent relation between phasic development and wind.

As with phasic development of grasses and forbs, early attainment of a particular height or weight for Agropyron and Balsamorhiza was associated with high temperatures, low precipitation, clear skies, and low wind movement. However, correlations between growth rate and cloudiness or wind were generally very weak.

Precipitation prior to the growing season was fairly well correlated with herbage weight of the grass, forb, and shrub groups, but not with weight of individual species. High herbage weight tended to be associated with low temperature, particularly during April and May, but correlations were weak. Herbage weight was positively correlated with cloudiness and negatively correlated with wind, but coefficients were rather low.

Basal area of grasses and forbs was poorly correlated with all four of the climatic factors. Crown area of shrubs, however, was positively correlated with spring precipitation and negatively correlated with spring temperatures.

With the exception of Balsamorhiza flower stalks, height was positively correlated with precipitation, especially that of the March–May period. Correlations of height with mean temperature of the growing season were negative. Height was not closely related to cloudiness or wind.

Although most of the correlation coefficients were not large, flower stalk numbers in both grasses and forbs were positively correlated with precipitation and cloudiness, and for the most part, negatively correlated with temperature. Flower stalk produc-

tion was more strongly correlated with weather of the early part of the growing season than with weather of the preceding period.

From the results of these studies, the following conclusions are drawn with respect to plant growth on the Upper Snake River Plains:

1. Although grasses, forbs, and shrubs differ widely in time of phasic development, none appears to have a distinctly superior developmental pattern.

2. Height or weight growth curves of most species have similar form, but the time at which most rapid growth occurs and the length of this rapid-growth period vary considerably.

3. Continual changes occur in the vegetation of various microsites, even on protected areas where the plant cover is apparently stable.

4. Since individual species may vary greatly in their response to the same environmental factors, specific conditions appear to be favorable for one species but unfavorable for another. Increased yield of one species can compensate for decreased yield of another, and thereby dampen oscillations in total production.

5. Of the observed climatic factors, annual precipitation is the most and mean temperature the least variable. As might be expected, precipitation tends to vary directly with cloudiness, and both precipitation and cloudiness tend to vary inversely with temperature.

6. Early in the spring, phasic development of plants is controlled chiefly by temperature, but later in the season temperature becomes less important and development is hastened by a shortage and retarded by an abundance of moisture.

7. Plant growth is apparently regulated by weather, particularly temperature, in much the same manner as phasic development, early growth being caused mainly by high temperature.

8. Both phasic development and growth are related to date of snowmelt, but correlations with mean temperature are stronger.

9. Precipitation is the dominant climatic factor affecting herbage production.

10. Precipitation prior to the beginning of the growing season influences herbage weight more than precipitation during the growing season. The chief effect of precipitation prior to the growing season, however, is probably not its influence on the vegetation at that time, but merely assurance of soil moisture during the period of active growth.

11. Precipitation is more closely related to total weight of the vegetation or weights of the various groups than it is to weight of individual species. Apparently it is the community, not the individual, that is in equilibrium with moisture supply.

12. Although temperature has only a slight influence on herbage weight, highest yields are apparently associated with cool growing seasons.

13. The slight beneficial effect of cloudiness on herbage production and the adverse effect of wind are apparently indirect and are associated with moisture relations.

14. Variations in basal area of grasses and forbs are not closely related to any of the climatic factors under consideration. Crown area of shrubs is related to precipitation and temperature in somewhat the same manner as herbage weight.

15. Height is directly related to precipitation and inversely related to mean temperature of the growing season.

16. Although individual species apparently have widely varying requirements for optimum flower stalk production, large numbers of flower stalks tend to be associated with high precipitation and cool cloudy weather, particularly during the early part of the growing season.

17. Date for opening the range to grazing each year can be estimated from temperature using the equation: $Y = 65.86 - 1.39X$ in which Y is the number of days after March 31 and X is March mean temperature.

18. Yield of grasses and forbs can be estimated from the preceding July–March precipitation by using the equation: $Y = 133.40 + 38.23X$ in which Y is air-dry herbage weight in pounds per acre and X is precipitation in inches.

19. Area, height, and weight are not equivalent measures of plant response to particular environmental conditions and should not be directly compared.

COMMON AND SCIENTIFIC NAMES OF SPECIES MENTIONED

GRASSES AND GRASSLIKE PLANTS

Agropyron dasystachyum (Hook.) Scribn. .... thickspike wheatgrass
A. spicatum (Pursh) Scribn. & Smith .. . .. bluebunch wheatgrass
Calamagrostis montanensis Scribn.. . ... .. plains reedgrass
Festuca idahoensis Elmer...... . ... Idaho fescue
Koeleria cristata (L.) Pers......... ... . prairie Junegrass
Oryzopsis hymenoides (Roem. & Schult.) Ricker _ Indian ricegrass
Poa nevadensis Vasey....................... .. Nevada bluegrass
P. secunda Presl.......................... Sandberg bluegrass
Stipa columbiana Macoun .... Columbia needlegrass
S. comata Trin. & Rupr.................... needle-and-thread

FORBS

Achillea millefolium L.... .... common yarrow
Antennaria dimorpha (Nutt.) Torr. & Gray... . low pussytoes
A. parvifolia Nutt... .. .. littleleaf pussytoes
Arnica fulgens Pursh ... . orange arnica
Astragalus convallarius Greene .... timber poisonvetch
A. stenophyllus Torr. & Gray.. . ... narrowleaf milkvetch
Balsamorhiza sagittata (Pursh) Nutt .... arrowleaf balsam-root
Comandra pallida A. DC..... ... . common comandra
Crepis acuminata Nutt.................... .. tapertip hawksbeard
Erigeron corymbosus Nutt. .... purple-daisy fleabane
Eriogonum caespitosum Nutt.................. .. mat eriogonum
E. heracleoides Nutt. ... . Wyeth eriogonum
E. ovalifolium Nutt.. .. .. cushion eriogonum
Lomatium macdougali C. & R............ ... MacDougal lomatium
L. macrocarpum (H. & A.) & F.. .. .. bigseed lomatium
Lupinus caudatus Kell. ... . tailcup lupine
L. leucophyllus Dougl .. .. velvet lupine
Penstemon deustus Dougl... .. .. scabland penstemon
P. radicosus A. Nels .... matroot penstemon
Phlox hoodii Richn.. . ... Hoods phlox
P. longifolia Nutt .... longleaf phlox
Senecio integerrimus Nutt.................. lambstongue groundsel
Viola beckwithii T. & G................... Beckwith violet
V. nuttallii Pursh...................... .... Nuttall violet

SHRUBS

Artemisia tridentata Nutt. .. ... . big sagebrush
A. tripartita Rybd. ... . threetip sagebrush
Atriplex nuttallii S. Wats ... Nuttall saltbush
Chrysothamnus puberulus (D. C. Eat.) Greene. . downy rabbitbrush
Gutierrezia sarothrae (Pursh) Britt. & Rusby broom snakeweed
Purshia tridentata (Pursh) DC. ... bitterbrush
Sarcobatus vermiculatus (Hook.) Torr. _ black greasewood
Tetradymia canescens var. *inermis* (Nutt.) A. Gray. spineless gray horsebrush

TREES

Juniperus osteosperma (Torr.) Little_____ Utah juniper
J. scopulorum Sarg_____ Rocky Mountain juniper
Pinus flexilis James_____ limber pine
Populus spp_____ cottonwoods; poplars
Pseudotsuga menziesii (Mirb.) Franco_____ Douglas-fir
Salix spp_____ willows

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