A PHENOLOGICAL COMPARISON OF MOWED AND UNMOWED TALLGRASS PRAIRIE SITES IN NORTH-CENTRAL OKLAHOMA

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CHAPTER I

INTRODUCTION

The study of phenology is a relatively young science and thorough phenological studies are few in number. During the past fifty years several reports have given detailed descriptions of the phenology of individual plants, while others have provided data on aspects which result from the overall adjustment of plants to seasonal changes (Weaver and Fitzpatrick, 1934; Dyksterhuis, 1948; Weaver and Rowland, 1952; Weaver, 1954).

A study of the cyclic changes of plants might include periods of photosynthesis, growth, pollination, flowering, ripening of seeds and fruits, leaf formation, shoot elongation, duration of foliage, leaf fall and seed dissemination (Braun-Blanquet, 1932; Hanson, 1950).

The study of phenology has been found to be of importance in weed control work (Stevens, 1956); in managing of pastures in regards to grazing, burning, reseeding and seed harvesting; in diagnosing gains or losses in weight or death of livestock from plant poisoning; in aiding field recognition of plants; and in various other ways (Dyksterhuis, 1948).

In this study the differences between the phenologies of two prairie sites were measured and recorded. The effect of past treatment was observed, along with the effects of variation in temperature and soil moisture.

It was hoped that this study would provide a record of variations in plant composition of the two areas and a resultant relationship of any variation to temperature and soil moisture. A developmental comparison of many species, as well as a description of the overall seasonal changes, was undertaken.

CHAPTER II

DESCRIPTIONS OF STUDY SITES

Location

The areas selected for this study were located nine miles west and one mile north of Stillwater on Highway 51, Payne County, Oklahoma, and adjacent to Lake Carl Blackwell. The study areas, about 500 yards apart, each occupied approximately three acres.

The geographic location is 36°08" latitude and 97°05" longitude and the elevation if 910 feet, according to U.S. Weather Bureau statistics.

History

Histories of these areas revealed that one area had been undisturbed for twelve years, and the other had been mowed annually for, at least, the past eight years. On the latter area the foliage was cut and removed, leaving little mulch, while on the former old foliage accumulated and formed a thick mulch (Figures 1, 2).

Climate

The climate of this locality is considered temperate with pronounced seasonal variation in temperature and precipitation. The annual monthly mean temperature for Stillwater over the past 30 years is 60.8°F. The average range is from 48.9°F to 72.6°F. The mean

Figure 1. Unmowed Prairie Site. Showing the extent of accumulated mulch.

Figure 2. Mowed Prairie Site. After one year without removal of vegetation.

precipitation based on a 56-year period (1898-1954), according to U.S.D.A. Outdoor Hydraulic Laboratory, Lake Carl Blackwell, is 33.3 inches. The air temperatures during the study period, April through October, 1963, averaged slightly above normal, with the exception of August. Total precipitation for the year at the lake area was 26.7 inches, 80% of the average yearly mean of 33.3 inches (Table I).

The growing season extended 238 days. This was based on the period from the last 32°F day in the spring to the first 32°F day in the fall or from March 9th to November 2nd. Weather Bureau data over the past 30 years indicate the average growing season to be 207 days, extending on the average from the 4th of April to the 28th of October. The growing season, as determined by climatological data, exceeded the average during 1963 by 31 days.

Topography

These study sites are included in Bruner's (1931) classification as part of the redbed plains. The local topography of both areas was that of a gradual slope toward the near-by lake. The undisturbed site had a slope of about two to three degrees toward the west and the mowed area about five degrees in the same direction.

Soil

The soil of the unmowed area consisted primarily of Kirkland silt-loam with Renfrow silt-loam on the upper slope and intermittent areas of Kirkland slick-spots on the lower slope. Percentages of each soil type were estimated to be approximately 70%, 25% and 5%, respectively. The soil of the mowed area was more consistent throughout--

approximately 90-95% Zaneis loam and 5-10% inclusion of Renfrow silt-loam.*

Vegetation

In general it was assumed that the microenvironments of these areas, as influenced by climate, varied little due to their similarity in topography and closeness in proximity, and hence any variations in the vegetations would be due to the treatment. The dominant vegetation type was that of the tallgrass prairie. Dominant species encountered are listed on Table II. Broad-leaved herbs were evenly dispersed throughout the mowed site, while they were most prominent on small claypan localities within the unmowed area. Composition varied more in the different species which were present per area than in total number on each area. These study areas are considered part of the tallgrass prairie, although mapped as postoak-blackjack forest type by Duck and Fletcher (1945). The land adjacent to the lake is actually intermittent postoak-blackjack forest and tallgrass prairie.

At the beginning of the study the mowed area was nearly void of old culms, foliage and seed stalks and little loose litter was apparent on the soil surface (Figures 3, 4). Remnants of previous year's growth was apparent on the unmowed site (Figure 5).

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*Soil classification is that of James R. Culver, Soil Scientist, Soil Conservation Service, and Jon G. Bockus, 1964.

TABLE I

PRECIPITATION DATA. MONTHLY ACCUMULATIVE TOTAL FOR 1963, AVERAGE MONTHLY ACCUMULATIVE TOTALS FOR 1898 THROUGH 1954 AND THE 1963 DEFICIT FROM THE AVERAGE TOTALS.

MONTH	1963 ACCUMULATIVE TOTAL	1898-1954 ACCUMULATED AVG.	1963 ACCUMULATED MONTHLY DEFICIT
March	3.62 inches	4.59 inches	0.97 inches
April	6.92	8.4	1.43
May	9.68	13.17	3.49
June	11.72	17.26	5.54
July	15.62	19.94	4.32
August	18.35	23.14	4.79
September	22.49	26.66	4.17
October	24.45	29.64	5.19
December	26.68	33.32	6.64

TABLE II

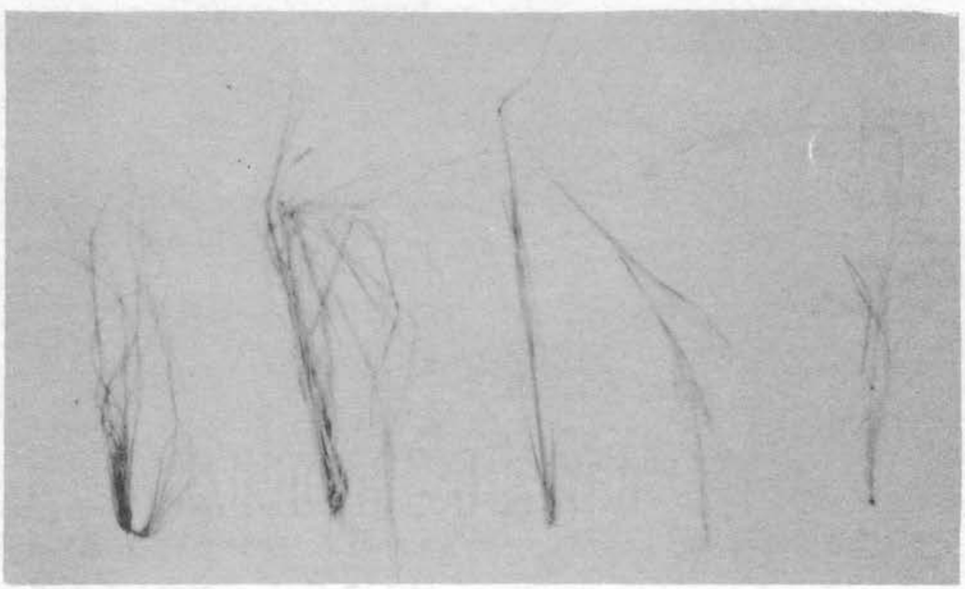
IMPORTANCE OF DOMINANT SPECIES. DETERMINED BY BASAL COVER (BC) AND RELATIVE FREQUENCY (RF).

	UNMOWED		MOWED	
SPECIES	BC	RF	BC	RF
Andropogon scoparius	7.20%	71.8%	8.70%	58.5%
Sorghastrum nutans	0.35	3.8	2.05	17.5
Andropogon Gerardi	- --	- -	0.85	7.5
A. saccharoides	0.50	6.9	- --	- -
Leptoloma cognatum	0.30	4.6	0.55	5.5
Bouteloua curtipendula	- --	- -	0.40	3.5
Chloris verticillata	0.20	3.1	- --	- -
Panicum virgatum	0.20	2.3	0.05	0.5
P. oligosanthes	0.10	1.5	0.20	2.0
Bouteloua hirsuta	- --	- -	0.15	1.5
Ambrosia psilostachya	0.15	2.3	- --	- -
Aristida oligantha	0.10	1.5	- --	- -
Carex species	0.05	0.8	0.20	2.0
Other species	0.10	1.6	0.15	1.5
TOTAL	9.25%	100.2%	13.30%	100.0%

Figure 3. Mowed Prairie Site, April 1963. Before initiation of study.

Figure 4. Preverval Aspect of Mowed Prairie Site. After one year without removal of vegetation.

Figure 5. Prevernal Aspect of Unmowed Prairie Site. Height of vegetation remaining after the winter season.



A B C D

Figure 6. Developmental Stages of Andropogon ternarius. A, vegetative; B, elongation of culm with sheath; C, anthesis; D, in seed.

CHAPTER III

METHODS AND MATERIALS

Basal Contact Method

A comparison of the vegetations of these two prairie sites was made by using a slight modification of the Levy-Madden (1933) point transect method of vegetational analysis. A ten-point frame was placed down at intervals of three paces along sampling lines transecting each area. One hundred samples were taken along each of these two lines for a total of 2,000 points on each area. Plants were recorded only if in contact with a point at ground level. Points not coming in contact with plants were recorded as bare ground. From these data were calculated the basal cover, relative composition, frequency and relative frequency of species encountered.

Soil Temperature

Surface temperatures of the soil were taken in duplicate each week on both areas with a standard thermometer. A soil thermograph recorded the temperature six inches below the surface continuously during the seven-month period of study. From these data comparisons of average temperatures were made. The continuous recording thermograph provided maxima-minima data, as well as average daily temperatures.

Soil Moisture

Weekly soil moisture data were obtained in duplicate on each study area at levels from zero to six inches, six to twelve inches, one to two feet and from two to three feet. Samples were taken at these levels using a tubular soil sampler or geotome and were transferred to seamless metal cans. Wet weights were taken, then the samples were placed in a drying oven at 105° C and later re-weighed to obtain dry weights. Percentage soil moisture was then calculated. These figures were analyzed for similarities and differences at the various levels and between study sites on a weekly basis.

Observation Method

Weekly phenological observations of the vegetations were made utilizing a tenth-meter square quadrat. The quadrat was placed down every three paces along perpendicular lines transecting each of the areas. These sampling lines were chosen arbitrarily, and they transected the sites in the directions of northwest-southeast and northeast-southwest. Fifty quadrats were sampled in each direction, making a total of 100 quadrats per area each week with which to compare the various stages of development of the plants between the areas. Each species occurring within the quadrat was recorded, along with its particular stage of development.

Limitation of phenological observations of individual plants to the more obvious changes in development resulted in eight readily observable stages for grasses and seven for forbs. Grasses, depending upon whether annual or perennial, were first recorded as being in either the stage of germination or perennating, respectively; the criterion for the former being a germinating plant of less than an inch in height. Perennating sprouts were sprouts above the soil level. Annual grasses over an inch in height were considered vegetative, as well as perennial grasses with actively growing shoots. The next stage recorded in order of a maturing grass plant was that of elongation of culm with sheath. The next successive stage was that of exertion of the inflorescence from the sheath, followed by anthesis. The grass was recorded as being at anthesis as long as pollen was deposited on fingers lightly passing over the inflorescence or if the floral parts were open for receiving pollen. When these characters were no longer evident it was assumed pollination had occurred with subsequent formation of fruit. This stage of being "in fruit" continued until it was apparent that the fruit had matured and had begun to disseminate; hence the stage " in seed," which was the last recorded stage. No further observations were noted of plants past the seed production stage unless they remained in one of the developmental stages as, for example, Andropogon saccharoides,* which continued to vegetate, produce new culms, etc., throughout an extended period after having produced seed early in the growing season (Figure 6).

Observed developmental stages of forbs were germinating, perennating, vegetating, production of reproductive buds, anthesis, fruit formation and dissemination of fruits and seeds. A plant was considered germinating if it retained its cotyledons--with some reservation for those species with cotyledons which remained functional. It was considered at anthesis when the corolla opened, when the stamens were releasing pollen, or when the pistil was ready for receiving pollen and had begun to enlarge. Dissemination of fruits

*Scientific nomenclature will follow that of U. T. Waterfall (1962).

and seeds was conspicuous with the voluntary detachment of either from the mature plants.

CHAPTER IV

OBSERVATIONS AND DISCUSSION

Basal Cover and Relative Frequency

True to the characteristics of a prairie vegetation (Steiger, 1930; Weaver and Fitzpatrick, 1934), these study areas had perennial grasses and forbs as their dominant and subdominant species.

The major portion of the basal cover on both of these sites was provided by *Andropogon scoparius*. *A. saccharoides*, *Sorghastrum nutans* and *Leptoloma cognatum* were of secondary importance on the unmowed site. Dominant species on the mowed site were *Andropogon Gerardi*, *Sorghastrum nutans*, *Leptoloma cognatum* and *Bouteloua curtipendula*, in order of abundance. The basal cover and relative frequency data of these and other plants are tabulated on Table II. The basal cover of vegetation on the mowed area was 13.3%, in comparison with 9.3% for the unmowed area. Basal cover data obtained in this study are comparable with those obtained by Weaver and Fitzpatrick (1934) on areas also dominated by *Andropogon scoparius*.

Numbers of Species

The number of species encountered in this study on the unmowed site was 110 with 107 on the mowed site. Others have recorded 165 and 155 species in grassland studies (Weaver, 1958; Ahashapanek, 1962). A number of plants were found on one site and not on the other. Each site had approximately the same number of plants peculiar to it. (Table III.) Other plants were observed but did not occur in the quadrats.

The most important plant families making up prairie vegetation are: Compositae, Gramineae, Leguminosae and Rosaceae (Weaver and Fitzpatrick, 1934; Weaver 1958; Whitford, 1958). Of the total number of plants encountered 55.3% belonged to either the Gramineae, Leguminosae or Compositae (Table IV).

Aspects

Seasonal changes in vegetation are determined primarily by vegetative growth, flowering and fruiting (Weaver and Fitzpatrick, 1934; Hanson, 1950). Denotation of the extent of the gross changes seems dependent not only upon these natural phenomena, but also upon the connotations of the observer. Whether definite limitations can be set depends on the geographic location, as well as definition (Kurz, 1928). Comparisons of phenological data have shown that specific responses may vary as much as a month from year to year (Ahlgren, 1957). It is due to these variables that hesitation arises when trying to delineate when one aspect ends and another begins. The ensuing paragraphs show a month-by-month description of the vegetations of these prairie sites.

April, 1963

Prevernal and vernal aspects are characterized by early growth of plants of rather low stature (Weaver and Fitzpatrick, 1934). Often these plants are ephemeral (Weaver, 1954). Among plants commonly listed as being signs of the prevernal aspect are species of *Carex*, *Antennaria* and *Anemone* (Weaver and Fitzpatrick, 1934). When this study began during the first of April the plants which had begun active growth were relatively

TABLE III

SPECIES PECULIAR TO AREAS

MOWED AREA

Amorpha canescens
Ascelepias viridiflora, var. viridiflora
Aster oblongifolius
Callirhoe involucrata, var. involucrata
Crotalaria sagittalis
Desmodium sessilifolium
Draba brachycarpa
Eriogonium longifolium
Festuca octoflora
Hypericum Drummondii
Lactuca Scariola
Lepidium virginianum
Lesquerella auriculata
Manisuris cylindrica
Monarda citriodora
Plantago virginica
P. Purshii, var. Purshii
Polygala incarnata
Polytaenia Nuttallii, var. Nuttallii
Psoralea esculenta
Ptilimnium Nuttallii
Ruellia humilis
Salvia azurea, var. grandiflora
Senecio plattensis
Specularia biflora
S. lamprosperma
Stillingia sylvatica

UNMOWED AREA

Acacia angustissima
Agrostis hyemalis
Ammoselinum Popei
Andropogon saccharoides
Aristida purpurea
Bouteloua gracilis
Claytonia virginica
Cyperus ovularis
Dalea candida
Desmanthus illinoensis
Erechtites hieracifolia, var. intermedia
Euphorbia serpyllifolia
Helianthus annuus
Linaria canadensis, var. texana
Lotus americanus
Myosotis verna
Oenothera laciniata
Opuntia species
Physalis angulata
Plantago Purshii, var. spinulosa
Rhus glabra
Rumex crispus
Solanum carolinense
S. eleagnifolium
Solidago canadensis, var. gilvocanescens
S. rigida
Sorghum halepense
Strosphostyles helvola
Tridens flavus

TABLE IV

IMPORTANT PLANT FAMILIES.

FAMILY	MOWED AREA No. Species	MOWED AREA % Total	UNMOWED AREA No. Species	UNMOWED AREA % Total
Gramineae	21	19.6	26	23.6
Leguminosae	15	14.1	16	14.5
Compositae	21	19.6	21	19.1
All Others	50	46.7	47	42.8
Total	107	100	110	100

few in number. Perennial grasses were represented by small shoots at the bases of the old stems. In contrast, the annual grass, Bromus japonicus, was common and appeared in up to 40% of the quadrats on both sites in the vegetative stage. Other winter annuals and perennating rosettes of certain perennial plants were found.

An obvious perennial forb of importance on the undisturbed site during April was Achillea lanulosa. During the month this plant, along with Erigeron strigosus, Artemisia ludoviciana, Ambrosia psilostachya, Aster ericoides, Andropogon scoparius, A. saccharoides, Sorghastrum nutans, Chloris verticillata, Leptoloma cognatum and Schedonnardus paniculatus, began to revive from winter dormancy. Oxalis stricta, Cassia fasciculata and Baptisia leucophaea were observed to be germinating. Lepidium densiflorum and Lithospermum incisum began to flower, while Krigia oppositifolia came into bud. Panicum oligosanthes, var. scribnerianum, was recorded to have been elongating and Nothoscordum bivalve and Hedeoma hispida flowered and proceded to go into seed.

On the disturbed site prevernal growth was more evident with such species as Plantago Purshii, Anemone caroliniana, Hedyotis crassifolia, Nothoscordum bivalve and Lepidium densiflorum already at anthesis when the study began. Evidences of growth were apparent in such plants as Aster ericoides, Andropogon scoparius, Bouteloua curtipendula, Panicum oligosanthes, Sorghastrum nutans, Linum sulcatum, Achillea lanulosa and Leptoloma cognatum. During the month Lithospernum incisum, Sisyrinchium angustifolium and Oxalis stricta came into bud.

The vegetations of these sites began to show considerable change during the first month of observation despite the spring drouth conditions. Temperatures were above normal, while precipitation was mostly sub-normal.

What was the dull coloration of the dead remains of last year's vegetation began to lighten with bright flowers of the low-growing, normally quite inconspicuous, plants enumerated above. These superficial changes were noticeable particularly on the mowed site where the numbers of these plants were greater and where last year's vegetation had been removed making the site more suited for this lower layer of vegetation. Hanson (1950) noted a many-fold increase in numbers of plants of the lower stratum when taller plants were mowed or removed.

May, 1963

The ensuing weeks brought even more obvious changes to both prairie sites with the verdant grasses beginning to show. Weaver (1954) associates the vernal aspect with the replacing of the drab appearance of the prairie with the new green growth as numerous plants become vegetative. He states that, as the season progresses, the struggle for light becomes increasingly severe for the low-growing plants which typify the vernal and prevernal aspects. The vernal aspect is dominated by the green of the new growth, i.e., growth of the species which will be of greater importance as the seasonal cycle continues. Numerous plants appeared in the quadrats in the vegetative stage on the disturbed site. Along with these plants, which characterized the lushness of new growth, were the many flowering-plants most often associated with the coming of spring, such as the conspicuous blue flowers of Sisyrinchium angustifolium, the yellow and blue of Oxalis stricta and O. violacea, and the white flowers of Nothoscordum bivalve, which appeared along with Cerastium brachyopodum and the earlier-mentioned Plantago virginica, P. Purshii, Lepidium densiflorum and Hedeoma hispida. As the numbers of these plants in flower began to dwindle, others appeared to take over the sequential role of being "most conspicuous." The comparatively large plants of Baptisia leucophaea and B. australis, var. minor were outstanding with heavy inflorescences of white and blue; the white corymbs of Achillea lanulosa, forma lanulosa, were present, although in lesser number than on the undisturbed area; the purple flowers of Psoralea tenuiflora, though small, were produced profusely on plants dispersed over the site; Linum sulcatum appeared for the first time, initiating a long period of flowering; the spring-flowering composites, Krigia oppositifolia and Erigeron strigosus contributed with their flowers of yellow and white; infrequent displays of color were furnished by Tradescantia occidentalis, Gaura sinuata, Oenothera serrulata, Schrankia uncinata and Callirhoe alcaeoides; and Panicum oligosanthes was recorded to have begun anthesis.

On the unmowed site also during the month of May were changes in the aspect; however, less salient amid the tall stalks of Andropogon scoparius, which remained erect in clumps from the year before. Plants characteristic of this lower layer of the vernal and prevernal aspects were frequently found in abundance on the disturbed, clay pan localities and in lesser abundance amid the tallgrasses. Continuing to flower on into the month of May were: Plantago Purshii, var., spinulosa and Hedeoma hispida. Cerastium brachyopodum began to flower along with Achillea lanulosa, which had developed buds several weeks before, Psoralea tenuiflora, Geranium carolinianum, Oenothera serrulata and Polygala verticillata. At this time Bromus japonicus, which was found not only on disturbed localities, but also throughout the site between clumps of tallgrasses, began to appear at anthesis. Panicum oligosanthes, found in less abundance than Bromus and in less abundance than on the unmowed area, also began anthesis at this time.

Through the month of May the aspect changed from one of a few small spring-flowering plants, found in communities primarily on clay pan localities on the unmowed site and scattered throughout the mowed prairie, to the prolific new growth of species which were to play more important roles later. Interspersed with these were the late spring-flowering plants which furnished a continued dominance of flowering plants comprising the vernal aspect.

June, 1963

As *Geranium carolinianum*, *Lepidium densiflorum*, *Plantago Purshii*, var. *spinulosa* and *Psoralea tenuiflora* completed their life cycles with seed production and dominant grasses continued vegetative growth, *Leptoloma cognatum* and *Andropogon saccharoides* began to elongate and exert their inflorescences. During the month the following forbs were recorded to have come into or continued to bloom on the undisturbed site: *Erigeron strigosus*, *Geranium carolinianum*, *Polygala verticillata*, var. *isocycla*, *Achillea lanulosa*, *Linum sulcatum*, *Apocynum cannabinum*, *Acacia angustissima*, var., *hirta* and *Physalis angulata*. Grasses at anthesis included: *Chloris verticillata*, *Schedonnardus paniculatus*, *Elymus virginicus*, var. *jejunus*, *Aristida purpurea*, *Eragrostis spectabolis*, *Panicum capillare*, *P. oligosanthes* and *Bromus japonicus*. Coming into bud were *Cassia fasciculata*, *Rudbeckia hirta* and *Sabatia campestris*.

This same period on the mowed site was characterized by multitudes of plants at their height of physiological activity, i.e., during the period of anthesis (Weaver and Fitzpatrick, 1934). Plants characterizing the vernal and prevernal aspects such as *Lithospermum*, *Nothoscordum*, *Plantago*, *Hedeoma*, *Sisyrinchium*, *Lepidium* and *Oxalis* were noted in the stage of seed dispersal. *Schrankia uncinata*, *Sabatia campestris*, *Monarda* citriodora, Linum sulcatum and Tragia ramosa came into bud and flowered. Psoralea tenuiflora and Rudbeckia hirta were obvious parts of the aspect at this time. Bromus japonicus was at its peak of development while grasses of lesser importance to the aspect, also at anthesis or in seed during this time, were Panicum oligosanthes, Eragrostis spectabilis, Panicum capillare and Bouteloua curtipendula. The flower stalks of Hieracium longipilum began to elongate. Other forbs primarily in flower were: Achillea lanulosa, Polygala verticillata, P. incarnata, Erigeron strigosus, Amorpha canescens and Oenothera serrulata.

July, 1963

Through the beginning weeks in July numerous species which had been previously recorded as vegetative were noted to have come into bud and flower. The aspect at this time would safely fall within the aestival aspect delineated by Ahashapanek (1962) in studies at Norman, Oklahoma, as occurring between June 5th and July 31st. On the unmowed prairie Acalypha gracilens and Strophostyles leiosperma, quite unnoticeable in the aspect, were recorded as being in flower, in bud and in seed during July. Grasses began to play a more important role, and during the last weeks in July the culms of the dominant grasses began to elongate. The new foliage of Andropogon scoparius and A. Gerardi began to hide the old culms. Culms from the clumped basal leaves of Sporobolus asper became evident. The omnipresent Bromus japonicus produced and disseminated its seed. Achillea, Psoralea, Schedonnardus, Plantago and Linum were also found to be in the stage of seed dispersal. The late maturing Leptoloma cognatum continued to elongate, and as was invariably the case, Andropogon saccharoides was recorded at various stages of development throughout the month from vegetative to seed production. Earlier-flowering plants such as Polygala verticillata, Acacia angustissima and Lithospermum incisum produced seed. The more gaudy blossoms of Cassia fasciculata, Dalea candida, Solanum eleagnifolium, Physalis pumila, and Polygala incarnata were evident. Lespedeza virginica and Liatris punctata came into bud; a scarce plant or two of Elymus virginicus produced a flowering culm, flowered and went into seed; and the gaudy Sabatia continued to flower and to produce seed capsules.

Much of the same periodicity was evident in the flora of the mowed site at this time, i.e., the grasses began to dominate, but the salient forbs at anthesis appeared different in composition, but no less in number, than in earlier aspects. Sorghastrum nutans, Andropogon scoparius and Bouteloua curtipendula began culm formation. The latter was soon found with inflorescences exerted, at anthesis, in seed and dispersing seeds. Plants which reached maturity and began to disperse their disseminules were: Bromus japonicus, Erigeron strigosus, Psoralea tenuiflora, P. esculenta, Carex spp., and Lithospermum incisum. Linum sulcatum might well be included in this category; however cessation of bloom did not occur until later. Linum continued to be found in all stages from vegetative to seed dispersal. During this time Hieracium longipilum came into bud, flowered and produced seed; Rudbeckia hirta, Strophostyles leiosperma, Polygala incarnata, Tragia ramosa and Solidago missouriensis were first recorded in bud; Croton Lindheimerianus, Achillea lanulosa and Amorpha canescens were recorded in seed; Sabatia campestris was found in flower and in seed.

August, 1963

The advent of August on the unmowed prairie brought only a few scattered flowers of Cassia, a few early flowers of Gutierrezia dracunculoides and the downy mature inflorescences of Andropogon ternarius. The general aspect was dominated by grasses. The ephemeral Bromus japonicus continued to disperse seed, however, quite inconspicuously amid the culms of the Andropogons which had begun to elongate. During August culms of Andropogon scoparius began to show the inflorescences and began anthesis, quickly followed by Panicum virgatum and Sorghastrum nutans. Achillea lanulosa and Psoralea tenuiflora were found to be dispersing seeds, while Liatris punctata and Solidago missouriensis were first recorded to be in bud. The monotony was broken only by an occasional flower of Solanum eleagnifolium, Solidago missouriensis and Physalis angulata. Plants with blossoms somewhat less conspicuous included: Euphorbia serpyllifolia, Acalypha gracilens, Croton Lindheimerianus, C. glandulosus, Ambrosia psilostachya and Aristida oligantha were recorded in flower by the end of August.

In addition to Linum and Cassia, Gnaphalium obtusifolium, Solidago missouriensis and Salvia azurea gave some variety to the aspect dominanted by grasses on the mowed prairie. Andropogon Gerardi, A. scoparius and Sorghastrum nutans began to mature, but only the tallgrass Panicum virgatum advanced to anthesis on this area during the month of August. Most of the previously mentioned aestival-flowering species were found to be completing their life cycles with the production and dispersal of seed. Foremost among these were: Bouteloua curtipendula, Bromus japonicus, Rudbeckia hirta and Sabatia campestris.

September, 1963

Dispersed within the unmowed prairie study site were Liatris punctata, Gutierrezia dracunculoides and Euphorbia marginata, which played a small role in September's aspect with flowers, along with Cassia fasciculata, Solidago rigida and S. missouriensis. The perennial grasses, Andropogon Gerardi, A. scoparius, Sorghastrum nutans, reached their peak and were recorded as being in seed during the latter weeks in September. Leptoloma cognatum reached its height of activity and quickly went into seed.

Somewhat later than on the unmowed site the tallgrasses, Andropogon Gerardi, Panicum virgatum and Sorghastrum nutans reached anthesis and, along with Andropogon scoparius, were recorded in seed on the mowed prairie. Leptoloma cognatum reached its peak of development. Obvious on the area were the seed stalks of the current year's mature plants such as Achillea, Salvia and Gnaphalium which often still held their seeds. Such autumnal-flowering plants as Ambrosia psilostachya and Aster ericoides were noted to be in bud, while an occasional flower of Chrysopsis pilosa, Solidago missouriensis, Lespedeza virginica, Linum and Cassia could be seen.

October, 1963

With October a gradually changing picture of the vegetation on both study sites continued to characterize an autumnal aspect. Precipitation was sub-normal for the month and temperatures were above normal. Weaver (1954) noted in Nebraska studies that beginning in July there is a tapering-off of growth and the death of aerial parts of many of the grasses and forbs indicating the beginning of the autumnal aspect. The cessation of growth and maturation of many of the aestival species, the preponderance of fall-flowering composites, the renewal of growth with resulting winter rosettes of several species and the germinating of winter annuals was indicative of an autumnal aspect.

On both sites Andropogon Gerardi, A. scoparius, Sorghastrum nutans, and Panicum virgatum were found to have come into flower and have completed their annual cycle with dispersal of seed later during the month of October. Giving a somewhat lighter touch with flowers to the rather dull aspect of the prairies were Aster ericoides, Gutierrezia dracunculoides and Liatris punctata, with an occasional late bloom from such species as Linum sulcatum. Of less obvious character, but at the peak of development, was Ambrosia psilostachya. Erigeron strigosus, Plantago spp., Anemone caroliniana and Bromus japonicus were found germinating on the mowed site late in October and just preceding the first killing frost--marking the end of the growing season and the beginning of what might well be called the hiemal aspect. The hiemal season has been characterized by the maturation of the vegetation due to frosts. Criteria of the hiemal aspect include: dried flowers and fruits; deterioration of foliage; bare stems; loss of green; and the appearance of winter rosettes (Weaver, 1954).

In summary, delineation of the duration of aspects during this period of study might be made in the following manner. When observations began some plants had initiated growth, thus designation of the beginning of the prevernal aspect is not possible. Records of the numbers of species becoming important in the aspect around the first of May (April 29) indicate the end of the prevernal and beginning of the vernal aspect. The maturation of these early-flowering plants and the rapid succession of vegetative and floral development was indicative of the aestival aspect evident May 29th through August 21st. The advancing growing season led to the cessation of active summer growth; seed-production of the aestival plants; and initiation of bloom of a few plants, bringing with it the autumnal aspect which continued with little noticeable change until a light frost October 29th followed by a hard frost November 2nd. This terminated the autumnal aspect and began the hiemal aspect.

Comparison of Species

Andropogon scoparius was the dominant species of both study areas, occurring on from 80-100% of the 0.1 meter quadrats each week. On the mowed prairie the individual plants were evenly dispersed with annual and perennial grasses and forbs, all being present in large numbers. In sharp contrast, however, A. scoparius was found on the unmowed prairie to occur in clumps and other plants occurred primarily between these dense clumps (See Figures I, II).

Because of the abundance of A. scoparius on both sites, a good comparison of the developmental changes of this species was made. Frequencies of 47% on the unmowed site and 58.5% on the mowed site were obtained for this species using the point transect method of vegetational sampling. On April 3rd, A. scoparius appeared in the vegetative stage in 32 quadrats on the unmowed site and in 14 on the mowed. The dates that A. scoparius was first recorded in the stages of elongation of culm with sheath, exertion of inflorescence from the sheath, and anthesis were earlier on the unmowed site. In general the same held true for A. Gerardi; however this species occurred with considerably less frequency on both study sites, particularly so on the unmowed prairie.

Bromus japonicus was found on both areas in about the same frequencies. On April 29th this annual grass occurred on the mowed area in 41 quadrats and was first noted to be starting to elongate. Two weeks later it was found to be in the stage of culm elongation on the unmowed area, and by coincidence, it appeared in 41% of the quadrats. All stages of development were first recorded approximately one week in advance on the former area for this ephemeral species.

Leptoloma cognatum and Panicum oligosanthes, var. scribnerianum, completed their life cycles on the mowed prairie shortly before the same species on the unmowed. L. cognatum had a frequency value of

17.4% on the unmowed area and 27.3% on the mowed; P. oligosanthes, 14.3% and 52.8%, respectfully, on these areas.

Linum sulcatum, which was relatively abundant on the mowed site, i.e., appearing in about 40% of the frame quadrats, and relatively infrequent on the other area, i.e., appearing on only about 3% of the quadrats, was observed to begin flowering, to go into seed and to disperse seed earlier on the former area.

Other early-flowering plants, for example, Hedyotis, Erigeron and Polygala, were likewise found to mature more quickly on the mowed site. Hedyotis crassifolia was found in flower when the study began. It was recorded in seed and dispersing its seed first on the mowed site where it occurred in greater numbers. Erigeron strigosus was found to visibly initiate flower buds on the mowed prairie two weeks in advance of the unmowed and proceded to flower a month earlier on the same area. By a margin of somewhat less, Polygala verticillata came into bud and proceded to develop to seed dispersal first on the mowed prairie.

Rudbeckia hirta, with approximately the same frequency as Linum, was recorded to have come into bud and completed its life cycle at earlier dates on the mowed site; while Sabatia campestris, of about equal rank in numbers on both areas, like the above, proceded to come into each of the stages about a week earlier on this same area.

Aster ericoides occurred in an average of 30.0% and 40.9% of the weekly quadrats on the mowed and unmowed prairies, respectively. This perennial species was noted in flower and in seed on the unmowed prairie first. Achillea lanulosa, forma lanulosa, along with Ambrosia psilostachya, was one of the few forbs occurring on the unmowed prairie in a greater number of the weekly quadrats. Average frequencies for occurrence of Achillea were 8.6% and 25.2% on the mowed and unmowed areas, respectively. At the beginning of the study Achillea was found and recorded as vegetative with 37 occurrences on the unmowed site and 14 on the mowed. In all stages it proceded plants of the same species on the mowed site with the exception of the stage of flowering. A single plant was recorded within a quadrat to be in flower on the unmowed prairie.

It appeared that many of the earlier-flowering species, which occurred on both study areas in sufficient numbers adequate for comparison, were better able to grow and develop to maturity at a faster rate (Table V) on the mowed prairie, while Ambrosia psilostachya, Andropogon scoparius and Aster ericoides, for example, came into flower and matured sooner on the unmowed prairie.

Temperature and Moisture Variation Between Areas

In April, when the studies began, there was a slight difference in the surface temperatures--the mowed area averaging 1.6°F warmer for the month than the unmowed area. As observations continued, this difference increased to a maximum of 7.6°F and 7.4°F during the months of June and July, respectively. During October a minimum difference, that of only 0.1°F, was noted (Figure 7). This variation in soil temperature might well account for the difference in numbers of low-growing, ephemeral species which were found on these areas during the first months of plant growth (Table VI). The mowed site was apparently favored in number of species due, at least partially, to the higher surface temperatures. With lesser amounts of basal cover, retardation of smaller, early-maturing plants is lessened because of higher temperature (Weaver and Rowland, 1952). The effects of temperature on the vegetation are greater in the spring months. Differences between the highs and lows later in

TABLE V

FIRST DATES OF CYCLIC CHANGES. G, GERMINATING; P, PERENNATING; V, VEGETATING; E, ELONGATION OF SHEATH; I, EXERTION OF SHEATH; B, BLOOMING; F, FLOWERING; S, IN SEED; D, DISSEMINATING SEED.

	UNMOWED AREA								MOWED AREA							
SPECIES	G-P	V	E	I	B	F	S	D	G-P	V	E	I	B	F	S	D
Acacia angustissima	4-12	4-19	---	---	5-18	6-15	6-29	---	---	---	---	---	---	---	---	---
Acalypha gracilens	5-3	4-26	---	---	6-22	6-29	7-13	8-23	---	---	---	---	---	---	---	---
Achillea lanulosa	---	4-3	---	---	4-26	5-10	6-22	6-22	---	4-3	---	---	4-29	5-14	7-12	7-19
Ambrosia psilotachya	---	4-3	---	---	8-17	8-30	9-12	10-10	---	4-10	---	---	9-19	9-26	9-26	---
Andropogon Gerardi	---	---	---	---	---	---	---	---	---	4-3	8-22	8-29	---	9-12	9-19	10-17
A. saccharoides	---	4-12	5-25	6-1	---	6-8	6-8	6-29	---	---	---	---	---	---	---	---
A. scoparius	4-12	4-3	7-13	8-17	---	8-17	9-6	10-3	4-10	4-3	7-19	9-6	---	9-12	9-12	10-3
Anemone caroliniana	---	---	---	---	---	---	---	---	10-24	4-3	---	---	---	4-3	---	---
Aristida oligantha	---	6-28	7-20	8-9	---	8-9	8-23	9-26	---	---	---	---	---	---	---	---
Aster ericoides	---	4-3	---	---	9-19	9-26	10-10	---	---	4-3	---	---	9-19	10-3	10-17	10-24
Bouteloua curtipendula	---	---	---	---	---	---	---	---	---	4-3	6-14	5-23	---	6-14	7-5	7-5
Bromus japonicus	---	4-3	5-10	5-10	---	5-25	5-25	6-15	4-3	4-3	4-29	4-29	---	5-23	5-23	6-6
Erigeron strigosus	---	4-3	---	---	5-18	5-25	---	---	---	4-3	---	---	4-29	5-8	6-21	6-21
Geranium carolinianum	---	4-3	---	---	5-10	5-10	5-10	---	---	---	---	---	---	---	---	---
Hedeoma hispida	---	---	---	---	---	---	---	---	---	4-3	---	---	4-24	4-24	4-29	5-23
Hedyotis crassifolia	---	4-3	---	---	---	4-3	4-12	5-3	---	4-3	---	---	3-29	4-3	4-3	4-29
Hypericum Drummondii	---	---	---	---	---	---	---	---	---	4-3	---	---	5-23	5-29	6-14	10-17
Leptoloma cognatum	---	4-3	6-1	5-25	---	6-22	9-12	9-19	---	4-3	5-29	6-21	---	6-14	6-14	8-29
Linum sulcatum	---	4-12	---	---	5-10	6-1	6-15	7-6	---	4-3	---	---	5-14	5-23	5-29	6-14
Nothoscordum bivalve	---	---	---	---	---	---	---	---	---	4-3	---	---	4-3	4-3	4-17	5-14
Oxalis stricta	4-3	4-3	---	---	5-3	4-19	5-10	---	4-24	4-3	---	---	4-17	4-24	5-8	---
Panicum capillare	---	---	---	---	---	---	---	---	---	4-3	5-23	5-14	---	5-14	5-14	6-6
P. oligosanthes	---	4-3	4-26	4-26	---	5-3	5-18	6-8	4-10	4-3	4-24	4-24	---	5-8	4-29	6-6
Polygala verticillata	---	6-1	---	---	5-25	5-25	6-15	7-28	---	5-23	---	---	5-23	5-23	5-29	7-19
Psoralea tenuiflora	4-26	4-19	---	---	6-22	5-3	6-8	6-22	4-17	4-17	---	---	5-8	5-8	5-29	7-6
Rudbeckia hirta	---	---	---	---	---	---	---	---	---	4-24	---	---	5-23	5-29	6-21	7-5
Sabatia campestris	---	---	---	---	---	---	---	---	---	4-3	---	---	5-29	5-29	6-28	8-8
Schrankia uncinata	---	---	---	---	---	---	---	---	---	4-17	---	---	5-8	5-23	5-29	---
Sisyrinchium angustifolium	---	---	---	---	---	---	---	---	---	4-10	---	---	4-17	4-17	4-24	5-23
Sorghastrum nutans	---	---	---	---	---	---	---	---	4-3	4-3	7-19	9-6	---	9-12	9-19	10-3
Strophostyles leiosperma	5-10	5-10	---	---	6-15	6-22	6-22	---	---	---	---	---	---	---	---	---
Tragia ramosa	---	---	---	---	---	---	---	---	---	4-3	---	---	5-23	5-23	6-14	---

later in the growing season have little influence (Steiger, 1930).

In a study by Weaver and Rowland (1952) on a prairie undisturbed for 15 years and where mulch had been allowed to accumulate, the soil temperatures were 22-28°F lower than on a mowed prairie in the spring. This caused a delay in growth of about three weeks, delayed production of flower stalks and reduced yields. The temperature difference of the areas in this study where not as great as in this work by Weaver and Rowland; however a general lag in early growth of many species was noted on the unmowed area.

Data indicate little variation in the differences on a monthly basis between the maximum and minimum soil temperatures six inches below the soil surface (Table VII). The peak of maximum temperatures was reached during the month of July. The lowest soil temperature recorded between April 20th and November 1st was 47°F. This latter reading was recorded in May and again in October. During the period of maximum ground temperatures in July the number of plants at anthesis was at a mid-season low (Figure 8).

A close parallelism between phenology and temperature summation based on meteorological records has been made (Lindsay and Newman, 1956). Others report the importance of temperature on aquatic vegetation (Penfound, et.al., 1945), on germination (Juhren, et.al. 1956), on certain native grasses (Benedict, 1940) and on prairie vegetation verses a corn field (Weaver, 1954). Braun-Blanquet (1932) emphasized the importance of phenologic data when compared with climate and, in particular, with temperature. The importance of temperature in this work was illustrated primarily in the numbers of early-growing plants on the area with warmer surface temperatures. Also of significance was the earlier initiation of growth on this area.

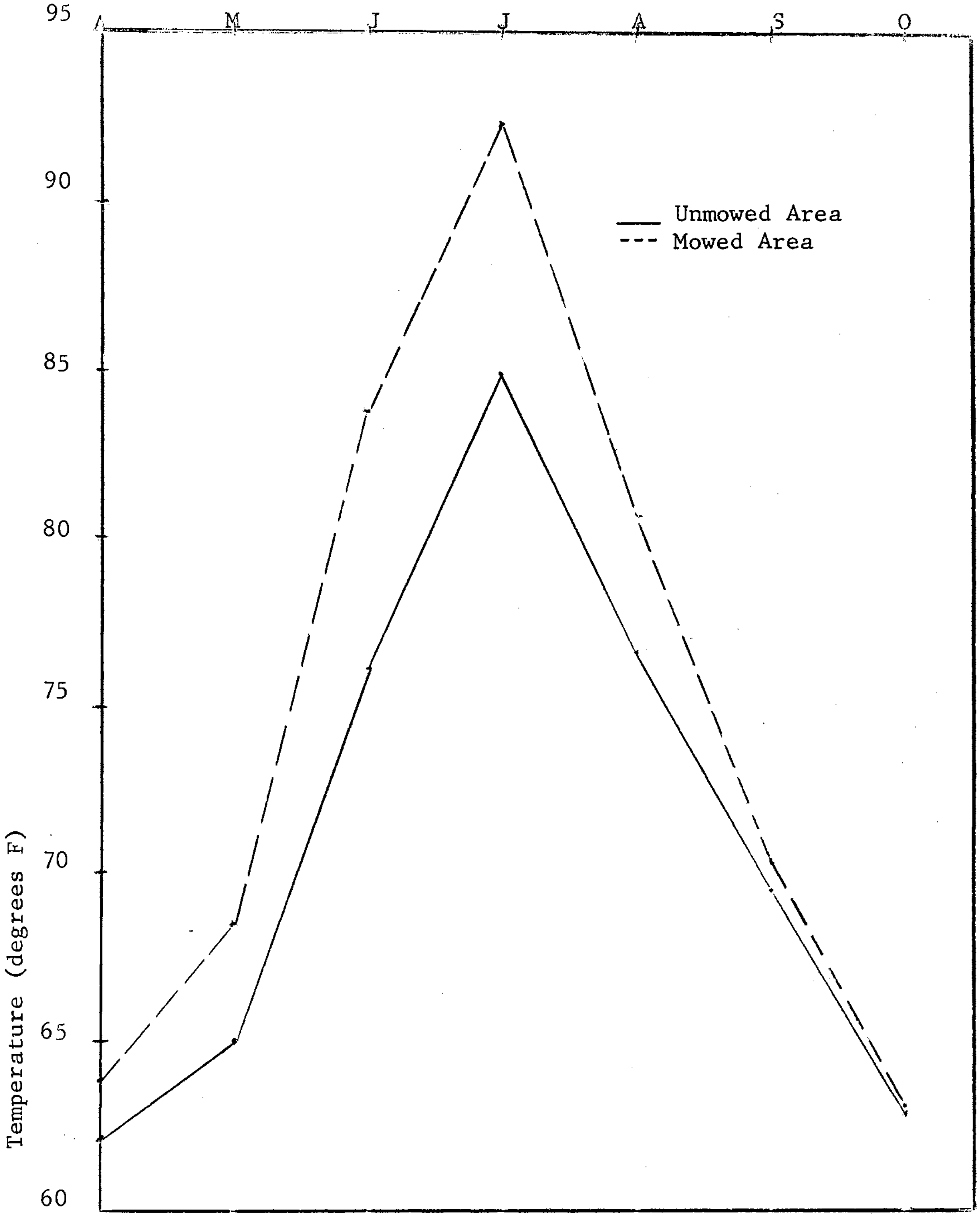


Figure 7. Average Monthly Surface Temperatures.

TABLE VI

NUMBERS OF GRASSES AND FORBS COMPARED.

MONTH	UNMOWED AREA				MOWED AREA			
	FORBS		GRASSES		FORBS		GRASSES	
	Number	%	Number	%	Number	%	Number	%
April	39	70.9	16	29.1	47	83.9	9	16.1
June	41	66.2	21	33.8	49	75.4	16	24.6
August	38	64.5	21	35.5	38	77.6	11	22.4
October	31	67.4	15	32.6	37	71.2	15	28.8
Average % of Total		67.3		32.8		77.1		23.0

TABLE VII

MAXIMUM-MINIMUM TEMPERATURES. AVERAGE WEEKLY TEMPERATURES PER MONTH SIX INCHES BELOW THE SURFACE ON THE UNMOWED SITE.

MONTH	MINIMUM	MAXIMUM	DIFFERENCE
May	57.2 degrees	72.2 degrees	15.0 degrees
June	66.0	81.8	14.8
July	73.5	88.5	15.0
August	70.6	89.0	18.4
September	67.5	80.5	13.0
October	53.8	69.8	16.0

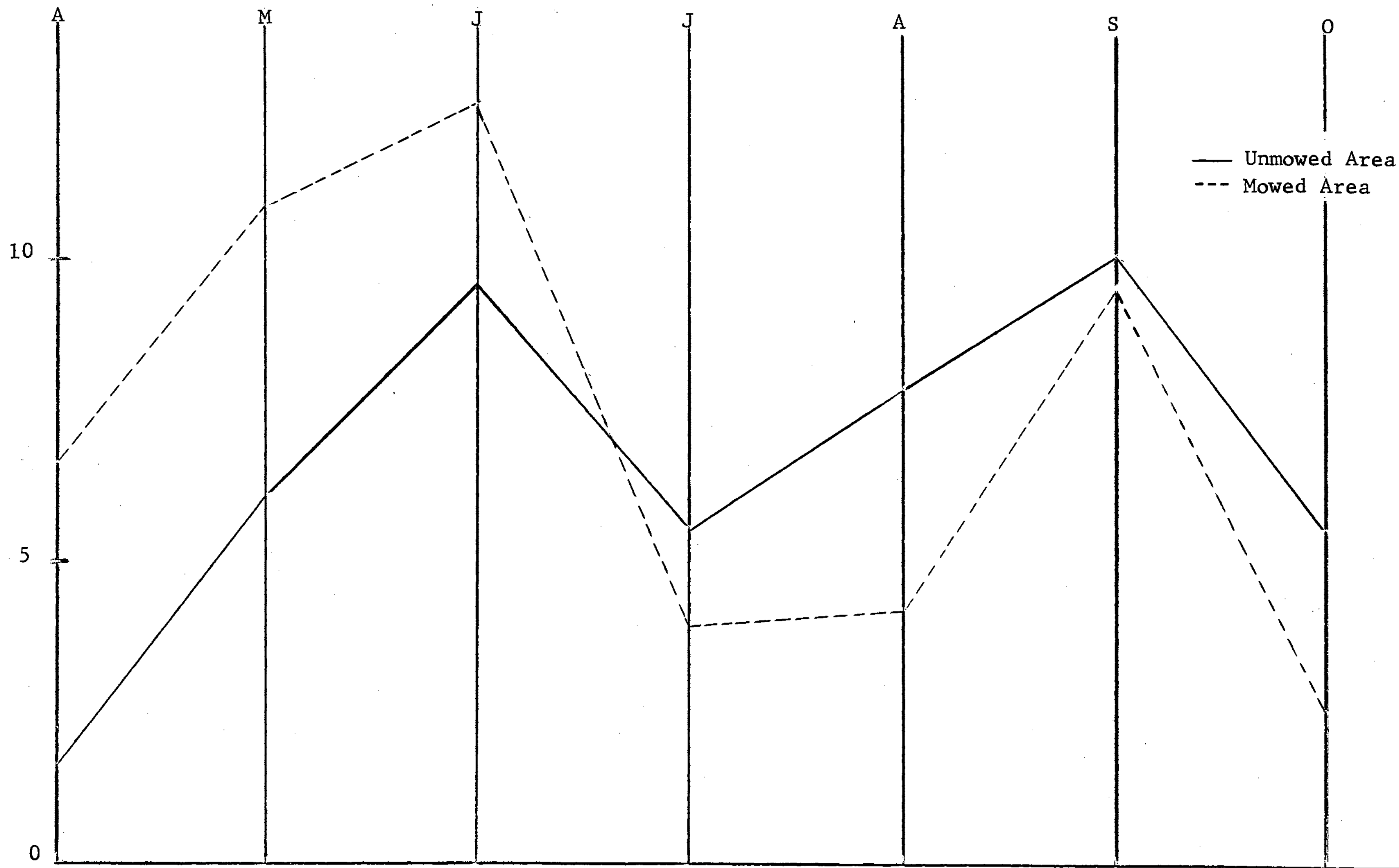


Figure 8. Comparison of Average Number of Plants at Anthesis per Area per Month.

The percentage moisture content of the soil from the surface to six inches below the surface showed greater fluctuation when compared with data at other depths than between areas at the same depth. This variation compares favorably with the amount and duration of periods of precipitation (Figure 9). The peaks (about on the 20% moisture level) occurred during July and again in September. This correlation, however, is not so obvious at lower depths in the soil. At these lower depths weekly recordings of soil moisture content did not show the fluctuations that occurred at the surface, but rather a gradual change from between 20-25% in April through May to low percentages of between 10-15% during August, September and October. This showed the effect of the sub-normal lows in amount of precipitation during 1963.

Higher moisture levels, with the exception of the 2-3 foot depth, were consistently maintained on the unmowed site. This is doubtless indicative of the heavy accumulation of mulch on the unmowed prairie which, according to Weaver and Rowland (1952), helps to intercept more moisture and retard evaporation. Mowing promotes water loss from upper layers of soil (Steiger, 1930). Comparing a grazed with an undisturbed prairie, Kelting (1954) found that the top six inches of soil on the grazed prairie had slightly lower percentages of water content.

There was no evidence of increased number of species at anthesis during July which might be correlated with the high precipitation received on the areas during this time. This would indicate a diminishing development due to other factors, including temperature. However the total number of species at anthesis on the unmowed site began to exceed that of the mowed site in July and continued to do so through the growing season. This was possibly due to higher moisture levels which were maintained on the unmowed area. There is a peak in need for moisture

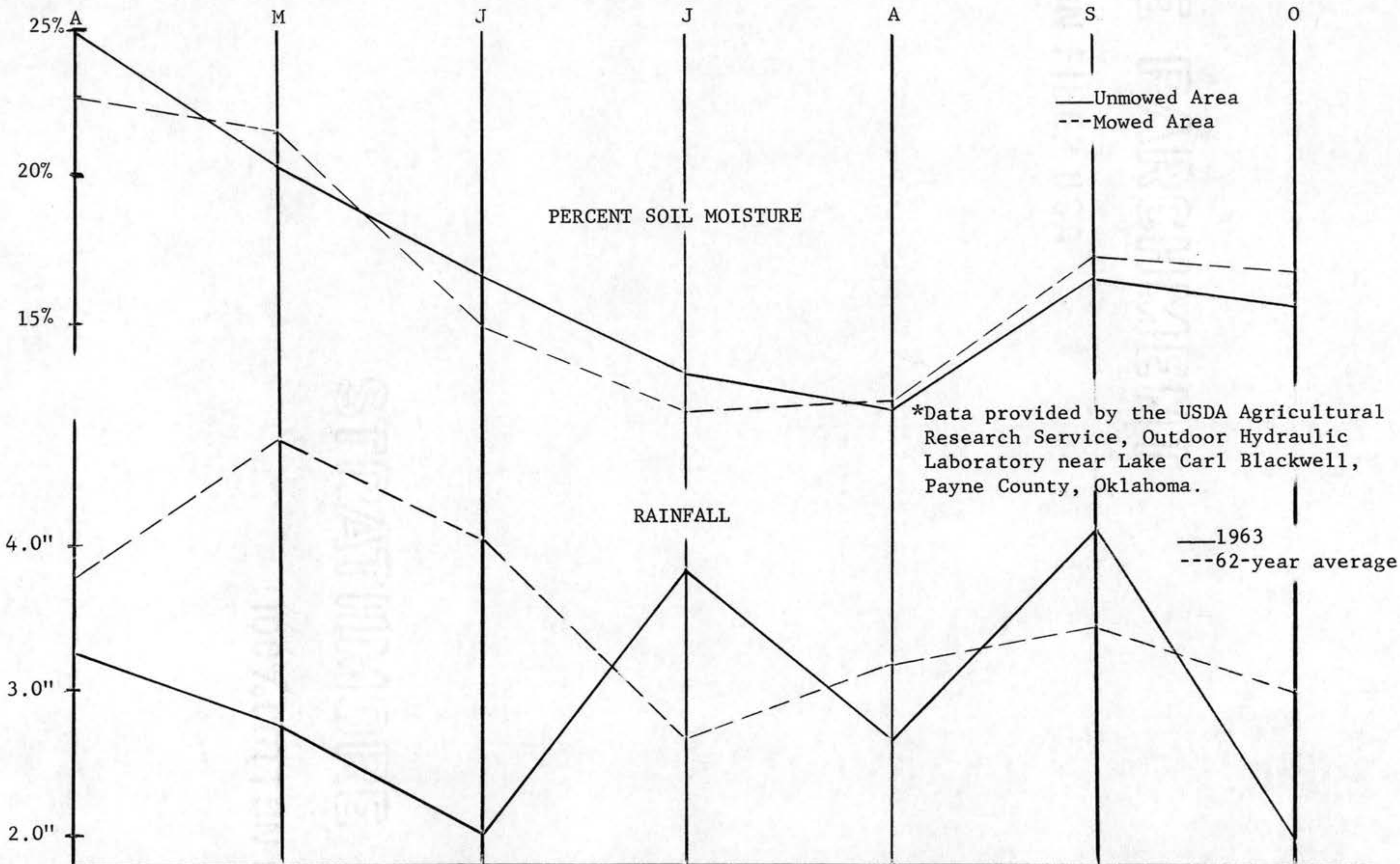


Figure 9. Comparison of Soil Moisture and Precipitation. Average monthly percent soil moisture, 0-6 inches and 1963 monthly deviation of rainfall from normal amounts received.

because of higher transpiration rates in July (Weaver, 1954), however this may not be the sole limiting factor of anthesis as indicated by this data.

The influence of temperature and moisture upon the phenology of plants is of unquestioned significance in shortening or prolonging initiation and duration of each change; however, other factors play important roles. Stevens (1956) has observed that certain plants will vary, particularly in the flowering dates, for no apparent reason. He cites the example of a few giant ragweeds which may flower a week or more before any others. The effect of light on these changes (photoperiodism) is recognized (Benedict, 1940; Leopold and Jones, 1947; Larsen, 1947; and Rice, 1950). Correlations between these external factors have been made in various studies, but internal factors, as influenced by environment, are significant as well. Genetic differences within species may cause varied responses in periodicity (Hanson, 1950; Leopold and Jones, 1947; McMillan, 1956, 1958).

The significance of the environmental factors studied in this work is somewhat limited without a measurement of other external, as well as internal, factors affecting plant growth. Further studies should correlate more of these factors to attain an adequate explanation of the periodic responses of vegetation.

CHAPTER V

SUMMARY

Both the mowed and unmowed tallgrass prairie sites were dominated by a plant cover of perennial grasses and numerous forbs. The basal cover of the mowed prairie was 13.3%, while the basal cover of the unmowed prairie was 9.3%. One hundred seven and one hundred ten species were encountered on the mowed and unmowed prairies, respectively; the majority of these species belong to one of three families; Compositae, Gramineae and Leguminosae.

Arbitrary dates delineate the length of the aspects as 30 days (April 29th-May 5th) for the vernal aspect; 53 days (May 5th-July 21st) for the aestival aspect; and 104 days for the autumnal aspect.

Surface temperatures on the mowed prairie sites were always slightly warmer. The greatest difference was noted at mid-season. There were insignificant differences in the ranges between maximum-minimum temperatures over the seven-month period.

The amount of soil moisture was found to be greater through the period on the unmowed site with the one exception, at the two- to three-foot level.

Differences in composition and development might well have been partially attributed to the higher temperatures on the mowed prairie and the higher moisture levels maintained on the unmowed prairie. Both factors are doubtless interrelated.

The above mentioned physical factors (temperature and moisture)

and biotic factors (density and species composition) were influenced by the amount of mulch which, due to the treatment, varied drastically in the amount of accumulation.

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