DEVELOPMENTAL GROWTH OF FOUR SPECIES OF RANGE GRASSES IN NORTH-CENTRAL OKLAHOMA

By

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H. L. H.

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CHAPTER I

INTRODUCTION

Several workers have reported on the phenological aspects of native grasses (Rice, 1950, Ashapanek, 1962, Larsen, 1947, McMillan, 1956 and 1959, and Benedict, 1940), but there has been a decided lack of work on growth rates of native grasses.

Work has been published correlating growth, particularly height, with root depth (Weaver and Darland, 1947), forage production (Klages, 1942), and general vigor of grass (Weaver and Darland, 1947). It was felt that information concerning the relative rates of growth in native grasses and the environmental factors affecting them would be an aid to further research in this area.

In this study, the rate of growth of little bluestem[1] (Andropogon scoparius Michx.), big bluestem (Andropogon gerardi Vitmin), indiangrass (Sorghastrum nutans [L.] Nash.), and switchgrass (Panicum virgatum L.) was studied. These species were selected on the basis of their wide range throughout the prairie region (Cooper, et al., 1957) and because of their dominant position in the prairie (Duck and Fletcher, 1945, Bruner, 1931, and Harlan, no date). The area in which this study was conducted is considered to be within the area of major distribution for each of the four species (Cooper, et al., 1957).

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[1]Common names used will follow Anderson (1961).

An attempt was made to correlate the rate of growth for each of the four species with the amount of soil moisture present and with the temperature of the soil. In addition, phenological notes were made throughout the study. To provide information on the study area, the relative composition, basal cover, forage production, and mulch production were determined.

CHAPTER II

DESCRIPTION OF STUDY AREA

The site used for the study was part of a relict area adjacent to the east side of Lakeside Memorial Park Golf Course, two miles north and one-half mile east of Stillwater, Payne County, Oklahoma, in the north-central part of the state.

Topography

The elevation of this area is about 880 feet above sea level. The topography is characterized by a gentle slope of about two percent toward the southwest. The plot occasionally receives some runoff from the overflow of a pond in a nearby pasture.

Climate

Records from the United States Weather Bureau for Stillwater, Oklahoma, for the years 1893-1960 inclusive show a mean annual precipitation of 30.83 inches. Eighty-one percent (24.95 inches) falls during the months March through October, the period covered in the study. During this eight month period in 1961, 31.65 inches were recorded, which was 6.7 inches above the long term mean for these months, and 1.2 inches above the long term annual mean.

A mean annual temperature of 60.9° F was recorded for the sixty-seven years. The temperature averaged 68.1° F during the eight months this study was conducted, 1.85° below the long term mean of 70.0° for this period.

The average frost free period is slightly over 200 days, extending from mid-April through late October. During 1961 the frost free period was 192 days long, and extended from April 17 to October 26.

Vegetation

The vegetation was vigorous and healthy. The site was dominated by tall and mid-grasses. Broad leaved plants were present but comprised less than five percent of the total vegetation. The predominant grasses in the area were: little bluestem, big bluestem, indiangrass, switchgrass, tall dropseed (Sporobolus asper [Michx.] Kunth), sideoats grama (Bouteloua curtipendula [Michx.] Torr.), and scribner panicum (Panicum scribnerianum Nash).

The area is included in the tall grass prairie of Duck and Fletcher (1945), or the mixed prairie of Harlan (no date). Claypan areas characterized by short grasses were found in the area, but were not present in the study plot.

The area has occasionally been mowed but was undisturbed for the three years preceeding the study. Accidental burning has occurred in the past, but not for the last five years. There was a great accumulation of mulch and standing organic material in the area. The standing material consisted largely of little bluestem and seed stalks and leafy material of other species.

Soil

The soil in the area is a deep reddish prairie soil. The texture of the soil is a sandy clay loam (U. S. D. A. Guide for Textural Classification, 1947). The soil contains 2.5% organic matter and is slightly to moderately acid. The soil has been classified as Vernon Loam by the Soil Conservation Service.

CHAPTER III

METHODS

Relative Composition and Basal Cover

The relative composition of the grasses was determined by the point quadrat method of analysis adapted from Levy and Madden (1933). The sampling apparatus consisted of an aluminum frame carrying ten metal pins spaced three inches apart and inserted at a 30 degree angle.

Only contact of the pin with the base of a plant was recorded as a "hit". Pins coming in contact with the soil were recorded as bare ground. Samples were taken 10 paces apart along equally spaced transects running the length of the study area. A total of 1, 100 points were recorded.

The basal cover was determined by dividing the number of hits by the total number of points recorded, and multiplying by 100.

$$\frac{\text{total hits}}{\text{total no. of points}} \times 100 = \text{basal cover}$$

The relative composition was determined by dividing the number of times a species was hit by the total hits for all species and multiplying by 100.

$$\frac{\text{hits per species}}{\text{total hits}} \times 100 = \text{relative composition}$$

Forage Production

The forage production values were based on 25 quadrats eleven and one-half inches by twenty-four inches in size. The quadrats were clipped at ground level and the vegetation was separated into the following components: Andropogon scoparius, Andropogon gerardi, Sorghastrum nutans, Panicum virgatum, other grasses, and forbs. The samples were air dried and the forage weight converted to pounds per acre.

Mulch

The amount of mulch present was determined by 15 quadrats spaced at random throughout the plot. The quadrats measured 3.1 feet square. The depth of mulch, measured at 10 random points within each quadrat, was recorded. In addition all of the unattached, non-living plant material was collected from each quadrat and oven dried. The weight of each sample was converted to pounds per acre.

Soil Moisture

Soil moisture determinations were made at intervals of approximately one week, beginning the 10th of April and extending through October 28. Samples were taken with a soil tube or geotome at four levels; 0 to 6 inches, 6 to 12 inches, 12 to 24 inches and 24 to 36 inches.

Duplicate samples were taken for each level, placed in seamless metal cans, and the weight recorded to the nearest tenth of a gram. The samples were dried at 100° C for one week and reweighed. The water content for each level was expressed in percentage of the dry weight of the soil (Weaver, 1938).

Soil Temperature

Temperature readings were made weekly with a standardized thermometer, usually at 3 p.m. on Friday on each week. Readings were taken at three levels; beneath the mulch on the soil surface, at a depth of one half inch, and at the six inch level. Two readings were taken at each depth and the average of the two recorded.

A recording soil thermograph was kept in continuous operation at the one-half inch level during the study period. The bulb was placed in a typical location and the overlying vegetation was undisturbed. The readings were checked weekly with a standardized thermometer and adjustments were made at that time. The information obtained from the thermograph was used to compute the weekly maximum and minimum temperatures as well as serving as a comparison or check for the other weekly readings.

Average weekly figures for air temperature and precipitation were based on the monthly records of the U. S. Weather Bureau station at Stillwater.

Plant Measurements

Observations and measurements were made on four species of grass: little bluestem, big bluestem, switchgrass, and indiangrass, from March 6 to October 28. The end of the study coincided with the date of the first frost on October 26. The plants were measured specifically for height, leaf length, leaf width, and stem diameter.

At the outset of the study four plants of each species were collected from the field plot, potted, and placed in the greenhouse. Measurements were made on these plants for the entire study period. Due to the loss of one clone of big bluestem at the outset of the study, the measurements for that species represent three plants.

On March 6, visual observations of growth initiation were begun in the greenhouse and by March 20, all of the plants had attained sufficient size to be measureable. The height of the plants was measured weekly from March 20 to October 27. The other measurements were made weekly from March 20 to June 22 and then biweekly for the remainder of the study.

During the second week in March ten plants of each species were selected in the field for study. On June 16 the number of plants per species was increased to twenty. Four tall stakes were driven along the south side of the plot, each about 20 feet apart. One tall stake was used for each species and the specimens studied were located along a line extending northward from the stake. This was done to facilitate the location of the plants for measurements. In addition a small numbered stake was placed next to each sample plant for identification purposes.

The little bluestem measurements were made from separate clumps, while in the case of switchgrass and indiangrass a group of clumps occupying an area of 50 to 100 square centimeters, and which obviously came from the same rootstock were selected. Both methods were used in the case of big bluestem, which was found in both tufted and rhizomatous forms. In all specimens it was necessary to remove a certain amount of mulch from the base of the plant in order to obtain accurate measurements. It is felt that this may have had some effect upon the early growth of the plants.

Observations in the field were begun on March 11, and by April 16 the specimens had attained sufficient growth for measurements to begin. Only the height of the plants was measured until June 16. At this time measurements of the leaf length, leaf width, and stem diameter were begun. These measurements were made approximately biweekly until September 1, and from then on until the end of the study on October 28, the plants were measured monthly. The height was measured approximately every seven days for the duration of the period. In addition they were measured a year later on September 15, 1962, when the height was obtained.

In measuring the average height of little bluestem, big bluestem and indiangrass, only the living vegetative portion was considered. The maximum height measurements, however, did include the seed stalks. In the case of switchgrass where each culm is capable of bearing an inflorescence, the total height of the culm exclusive of the inflorescence was measured to determine the average height.

The height of ten random culms in each clone was measured and the mean height recorded. After all twenty plants had been measured the twenty mean heights were averaged. In addition the tallest stalk in each clump was measured and recorded. This measurement included the seed stalk and inflorescence.

Measurements were made from the ground level and recorded in centimeters.

In measuring the length of leaves, only living tissue was considered. The total length of the blade, from collar to tip was measured in centimeters. Five random leaves per plant were measured and the mean length recorded, along with the length of the longest leaf on each plant.

The width of five random living leaves per plant was measured at their widest point and the average width recorded in millimeters. The width of the widest blade on each plant was recorded in millimeters.

In measuring stem diameter only living stems were considered. Seed-bearing stalks were excluded in all species except switchgrass. The diameter of five random stems was measured with a vernier caliper and the mean diameter recorded in centimeters. The diameter of the largest stem of each plant was also recorded. Measurements of each stem were made in the middle of the thickest internode, except in the case of little bluestem where the thickness of the flattened stem was measured at the base.

Measurements were made the following year (1962) on September 15 of the average and maximum height of all plants which could be located. These were intended to serve as a comparison between the two years.

Observations of the general condition of the vegetation in the area were made. Records were also kept of the developmental stages of the plants each time they were measured. The stages recorded were; bud formation, shoot formation, seed stalk formation, seed head formation, and anthesis.

CHAPTER IV

RESULTS AND DISCUSSION

Vegetational Analyses

The results of 110 samples with a point transect showed that the vegetation provided a basal cover of 12.2% (Table I). Five grasses (little bluestem, big bluestem, indiangrass, tall dropseed, and switchgrass) comprised over 94% of this vegetation. Of these five, little bluestem was by far the most prevalent species, comprising one-half of the vegetative cover. Big bluestem and indiangrass were secondarily important species, comprising 18.7 and 16.4 percent respectively.

Analysis of 25 clipped quadrats indicated that the area produced slightly over 4,000 pounds of air dry forage per acre (Table II). The four dominants produced by far the largest percentage (90%) of this forage. Again little bluestem was the most important species contributing 38.8% of the total production, followed by indiangrass with 27.7%, big bluestem with 19.7% and switchgrass, 4.8%. Forbs comprised only 3.3% of total forage production.

A study of the unattached dead material (mulch) showed 4,375 oven-dry pounds per acre to be present. This was more than the total poundage of living material present, and would have been much higher had the standing dead material been included. The average depth of this mulch was 5.4 cm.

TABLE I

Basal cover and percentage of composition of the grass species comprising 1.0 percent or more of the natural vegetation.

Species	Basal Cover	Relative Composition
Andropogon scoparius	6.1%	50.0%
Andropogon gerardi	2.3%	18.9%
Sorghastrum nutans	2.0%	16.4%
Sporobolus asper	0.6%	4.9%
panicum virgatum	0.5%	4.1%
Bouteloua curtipendula	0.2%	1.6%
Panicum scribnerianum	0.2%	1.6%
Carex sp.	0.1%	0.8%
Others	0.2%	1.6%
Total	12.2%	99.9%

TABLE II

Forage production of dominant species in pounds per acre.

Species	Pounds of forage per acre	Percent of total
Andropogon scoparius	1, 587. 0	38. 8%
Sorghastrum nutans	1, 131. 0	27. 7%
Andropogon gerardi	797. 5	19. 7%
Panicum virgatum	195. 5	4. 8%
Other grasses	230. 5	5. 7%
Forbs	135. 5	3. 3%
Total	4, 077. 0	100. 0%

Phenological Data

The main objective of this phase of the study was to measure the rate of growth of the grasses. The following observations were made in the course of measuring the plants and were considered more or less incidental. This should be borne in mind when evaluating these data. The dates reported are the dates when the phenomena were first observed. The actual occurrence could have been at any time during the preceeding week.

Little bluestem

When field investigations were begun on March 11, 80% of the little bluestem plants examined showed the presence of buds, and by the eighteenth every clone showed signs of rejuvenation. Also at this time many of the old stems were becoming green from the base upward. On April 3, 70% of the plants had new shoots showing above the ground. The soil temperature at the one-half inch level at 3 p.m. on this day was 62° F. By April 7, all clones exhibited new shoots.

In Cleveland County, Oklahoma, Ashapanek (1962) noted spring activity on April 4 and Rice (1950) listed March 30 as the date of the first visible signs of growth. The earlier development of the plants in this study might be explained by the removal of much of the surrounding litter to facilitate measurements. Weaver and Rowland (1952) showed that in May, unmulched soil was 22 to 28° F warmer than mulched soil. In addition the average temperature for February and March was 2.4° warmer than the long term mean (U. S. Weather Bureau). McMillan (1959), working with *Panicum virgatum* and the *Andropogon gerardi-halii* complex, stated that certain temperature phenomena apparently triggered spring activity. He mentioned that different thresholds for spring activity are indicated for the different species. Leaf expansion began during the first week of April and by the tenth, 30% of the plants had visible leaves.

All of the little bluestem clones in the greenhouse showed signs of rejuvenation on March 6, only 2 days after they were placed in the greenhouse. Two days later two of the four specimens had expanded leaves evident and one fourth of the shoots were over 1 cm in height. By March 20, the shoots had reached a measurable size and averaged 1.6 cm in height. This was about 10 days ahead of the field plants. By mid-April, however, the field specimens had "caught up" and from then on grew much more rapidly.

Seed stalk formation (culm elongation) in the field began in the latter part of July and by August 5, almost half of the plants had seed stalks in some stage of development. By September 15, seed stalk development had occurred in virtually all the clones. Two of the twenty little bluestem plants examined did not produce seed stalks.

Seed stalk formation in the greenhouse began in mid-July, about 2 weeks before the plants in the field. All of the greenhouse specimens formed seed stalks.

Noticeable seed head formation in the field (exertion of the inflorescence) began in late August, with 25% of the plants exhibiting inflorescences by the twenty-ninth. The soil temperature on this date was 82° F at the one-half inch level following a steady decline from late July's high of 86°. There was a much sharper decline in the weekly minimum temperature which dropped to 66° F during the last week in August. By the second week in September, seed head formation was complete. Only 16 of the 20 clones formed inflorescences during this study.

In the greenhouse, seed head formation began in all 4 little blue-stem clones during the first week of August. There was an interval of about one month between culm elongation and inflorescence exertion in the field, and a lapse of only 2 weeks in the greenhouse.

Anthesis (visible exertion of the anthers) began during the first week in September and had occurred in all 16 flowering clones by September 22. An interval of one week occurred between inflorescence exertion and anthesis.

In the greenhouse, anthesis began in late August, approximately 3 weeks after exertion of the seed heads, and slightly over one week before it occurred in the field.

Seed formation and dispersal had occurred in all 16 flowering plants by September 22, although it was not complete at that time.

Big bluestem

On March 11, 80% of the plants showed signs of rejuvenation and by March 18 all 20 clones showed some sign of regrowth. New shoots first appeared above the ground on April 3. The soil temperature at 3 p.m. on this date was 62° F at the one-half inch level. By April 16, eighteen of the twenty big bluestem clones had new shoots. Two clones did not resume growth throughout the season. Expansion of leaves began during the first week of April.

The big bluestem plants studied in the greenhouse all showed formation of new shoots on March 6. By March 20, all of the shoots had reached a measurable size averaging 1.4 cm in height. As in all four species studied this rapid growth after their inclusion in the greenhouse leveled off after about 4 weeks.

Seed stalk formation in big bluestem began in late July, following a 10° rise in temperature from July 14 to July 20. As in little bluestem, seed stalk formation varied widely among the specimens. Seven of the twenty clones had developed no seed stalks by the beginning of October, and three of these had not developed any at the end of the study in late October. This means that seed stalk formation began in the different clones over a period of three months.

Seed stalk formation began in the greenhouse during the second week in July, almost two weeks before the field specimens began.

Seed head formation began during the last week in August, but only 20% of the clones produced seed heads before October. The weekly maximum and minimum temperatures which had reached a peak of 87° F and 76° F, respectively, on August 7 were declining during this time. One month elapsed between the first culm elongation and the first inflorescence exertion. Four of the twenty big bluestem plants produced no inflorescence during this study. Rice (1950) cites evidence which suggests that shoots which do not initiate inflorescence before a certain date remain vegetative. The first appearance of inflorescence in the greenhouse was on August 5, almost a month before their appearance in the field.

Anthesis began in some clones in early September, but did not begin in the majority until October. By October 27, anthesis was complete in the 16 plants which had inflorescences. Anthesis followed inflorescence exertion by slightly over one week.

Anthesis began in the greenhouse in the latter part of August, and by August 31, all of the big bluestem specimens had flowered.

The first sign of seed formation was September 24. Seed formation and dispersal continued throughout September and October, and by the end of the study, all 16 of the plants which formed inflorescences had formed seed.

Indiangrass

When first observed on March 11, 2 of the clones had young shoots above the ground with leaves. No further shoots were observed until April 3. It was quite possible that the first shoots had been formed late in the previous growing season and were not killed during the winter. Assuming that these shoots did overwinter, we can make the qualified statement that shoot growth began in early April. This is much nearer the dates of April 4 and April 19, found by Rice (1950) and Ashapanek (1962). The soil temperature on April 3 was 62° F at the one-half inch level. Excluding the two clones which had shoots at the outset of the study, leaf expansion began on April 10.

Indiangrass was the only one of the four species in the greenhouse which did not have shoots on March 6. The first appearance of shoots in this species was on March 16, two weeks before shoot formation in the field. Shortly after these plants were placed in the greenhouse, an elongation of the stems remaining from the previous year occurred.

Culm elongation was first observed in the field on July 29. As in little bluestem and big bluestem, this followed a rise in the one-half inch temperature to 86° F by July 20. Seed stalk formation was first observed in the greenhouse on July 24, two weeks before the plants in the field.

Exertion of inflorescence began during the last week in August and continued until September 25, when all 20 of the indiangrass clones bore inflorescences. Thirty days elapsed between the first culm elongation and the first appearance of an inflorescence.

Anthesis was first observed on September 9, with approximately 10 days occurring between the beginning of inflorescence exertion and anthesis. Anthesis was first observed in the greenhouse on September 15, almost one week after it occurred in the field. In the other species anthesis occurred in the greenhouse before it occurred in the field.

Seed development began late in September, and by September 25th, 18 of the 20 plants produced seed. Two of the indiangrass clones formed no inflorescences and therefore did not produce seed.

Switchgrass

On March 11, 40% of the clones exhibited buds. By April 3, 90% of the specimens had new shoots showing above the ground and all clones showed some sign of rejuvenation. New leaves began expanding from the shoots on April 10 and by April 22, shoot formation had occurred in every clone.

Since the culms which bore the inflorescences also bore the vegetative leaves, no date was recorded for the initiation of reproductive structures. A period of rapid culm elongation occurred during the last week in May.

The switchgrass clones in the greenhouse had all developed shoots on March 6. These remained relatively small until the latter part of March.

Exertion of inflorescence was first noticed in the field on July 9, before the rapid rise in temperature which occurred between the thirteenth and the twentieth. On the thirteenth of July, four days after the first infloescence was noticed, over half of the clones had seed heads. Inflorescences were present in all 20 clones by August 30. In the greenhouse, exertion was evident on May 26 in one clone, over 2 months before exertion in the field. Not until July 14, however, did all 4 clones show seed heads.

Anthesis began in the middle part of August. Slightly over 4 weeks elapsed between the first exertion of an inflorescence and anthesis. Anthesis began in one plant in the greenhouse on June 16, two months before the plants in the field and occurred continuously in at least part of the plants until the end of August.

Seed formation began in the field shortly after anthesis, in August. By the end of August, over one half of the switchgrass clones had formed seed. By the end of September, all 20 clones had dispersed the greater part of their seeds. Seed formation did not begin in the greenhouse until September 15.

Comparison of the four species

Shoot formation was observed in all four species on the same date (Figure 1), indicating that the shoots presumably appeared during the preceeding week. Rice (1950) found little bluestem to be the first species to resume growth. He found it to be followed about 6 days later by indiangrass and switchgrass, with big bluestem starting approximately 12 days later. Even more variation was found by Ashapanek (1962), who also found little bluestem to be the first species to resume growth, but almost 3 weeks elapsed before the second species, indiangrass, began. Big bluestem and switchgrass followed, 25 days later than little bluestem. McMillan (1959) observed the same sequence as Ashapanek.

In the greenhouse, indiangrass appeared to be somewhat retarded. New shoots were not observed in it until 10 days after they were observed in the other 3 species. The old stems appeared to elongate during this period.

Culm elongation was noticed on the same date in little bluestem,

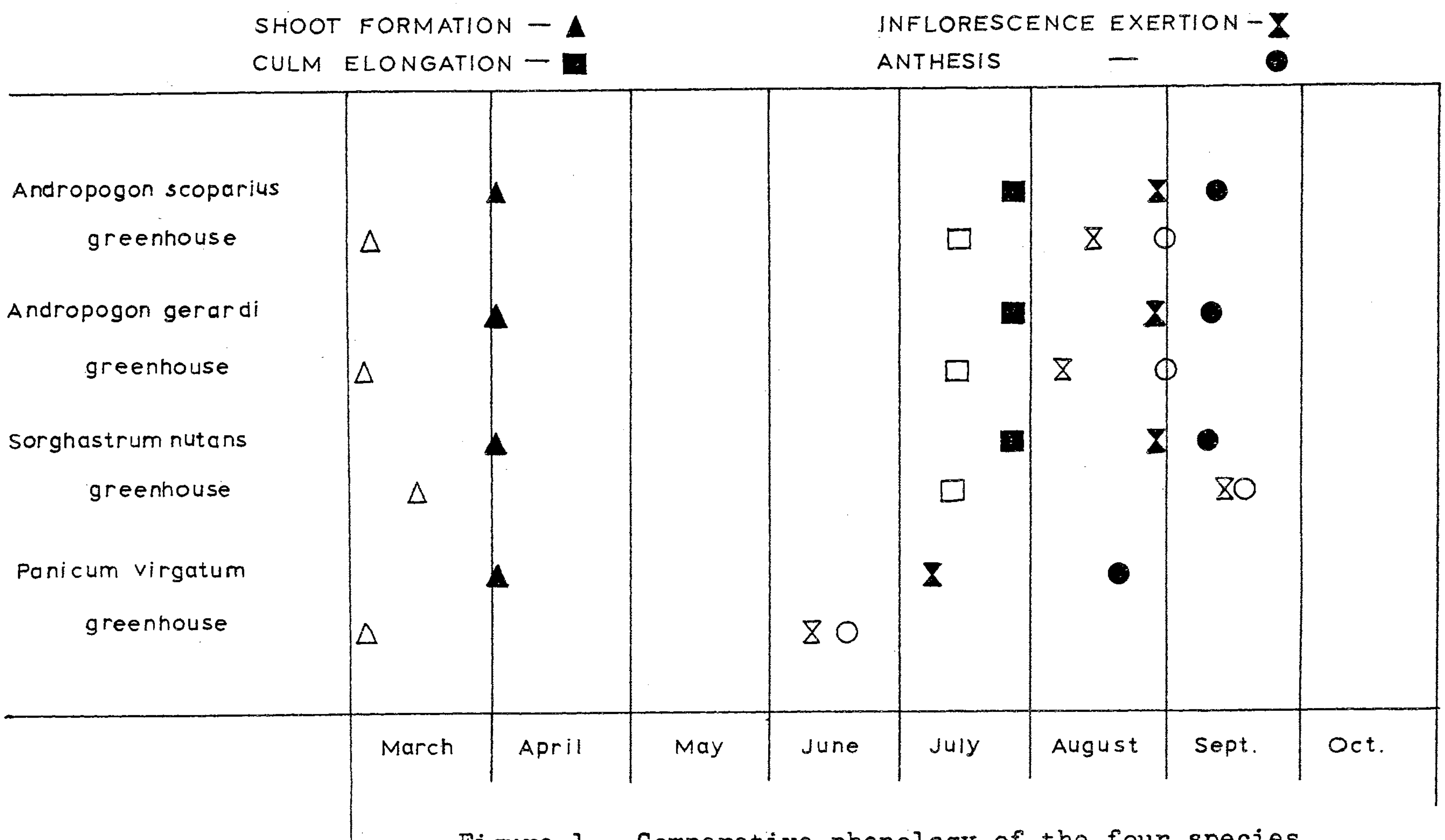

Figure 1. Comparative phenology of the four species.

big bluestem, and indiangrass, both in the field and in the greenhouse (Figure 1). Rice (1950) found switch grass to be the first to undergo culm elongation, followed by little bluestem and indiangrass, with big bluestem being the last to elongate. He found one month elapsing between culm elongation in switchgrass and big bluestem. Ashapanek (1962) also found switch to be the first to show culm elongation, but he found little bluestem and big bluestem to be next, and indiangrass to be the last of the four species. This was essentially the same sequence as reported by McMillan (1959).

Inflorescence exertion occurred first in switchgrass. Approximately 45 days later, inflorescences were observed in the other 3 species. In the greenhouse, switchgrass exerted first, then big bluestem, little bluestem, and finally indiangrass.

Anthesis in the field occurred in the same sequence as inflorescence exertion, but in the greenhouse, little bluestem showed anthesis on the same date as big bluestem (Figure 1). Anthesis followed inflorescence exertion by 12 days in all species except switchgrass. In the greenhouse, over 20 days elapsed between inflorescence exertion and anthesis in little bluestem and big bluestem, and less than 1 week in indiangrass and switchgrass.

Growth Measurements

The findings of growth measurements should not by any means be considered terminal. It is felt they might be useful as a means of comparison or as a point of reference until further research can be done on the subject. This is particularly true since no references to previous work on this particular subject were found. It should be noted that climatic conditions during this study were more favorable than the long term mean, and there were no apparent stresses on the vegetation.

Little Bluestem

Following growth resumption at the beginning of April the plants increased in height at a steady rate until mid-June (Figure 2). From June 13 until September 9, the height of the vegetative portion of the plants remained between 40 and 45 cm. This agrees with Flory (1936) who reported that vegetative growth of both little and big bluestem was 85% complete by June 30, and development thereafter is largely that of flower stalk production, flowering and fruiting. There was an increase in the maximum height, starting in the latter part of July, due to the appearance of seed stalks. This increase in growth rate lasted until August 29, when a maximum height of 70 cm was recorded. There was practically no change in the maximum height until the latter part of October, when there was a slight decline of 3-4 cm. This drop may have been due to the deterioration of some of the seed stalks. The greatest height of an individual seed stalk of little bluestem was 98 cm, recorded on September 9. At the time of maximum development, the average maximum height was 27 cm taller than the average height excluding the seed stalks. The vegetative portion of the plants showed a steady rate of decline which may be attributed to the death of many of the leaves. It is not thought that any of the living leaves or stems decreased appreciably in size.

On September 15, 1962, one year later, 15 of the original 20 clones were measured. The average height was 47 cm, as compared with an average of 42 cm for the same 15 clones in 1961. The average maximum height of 64 cm in 1961 was considerably less than the 92 cm

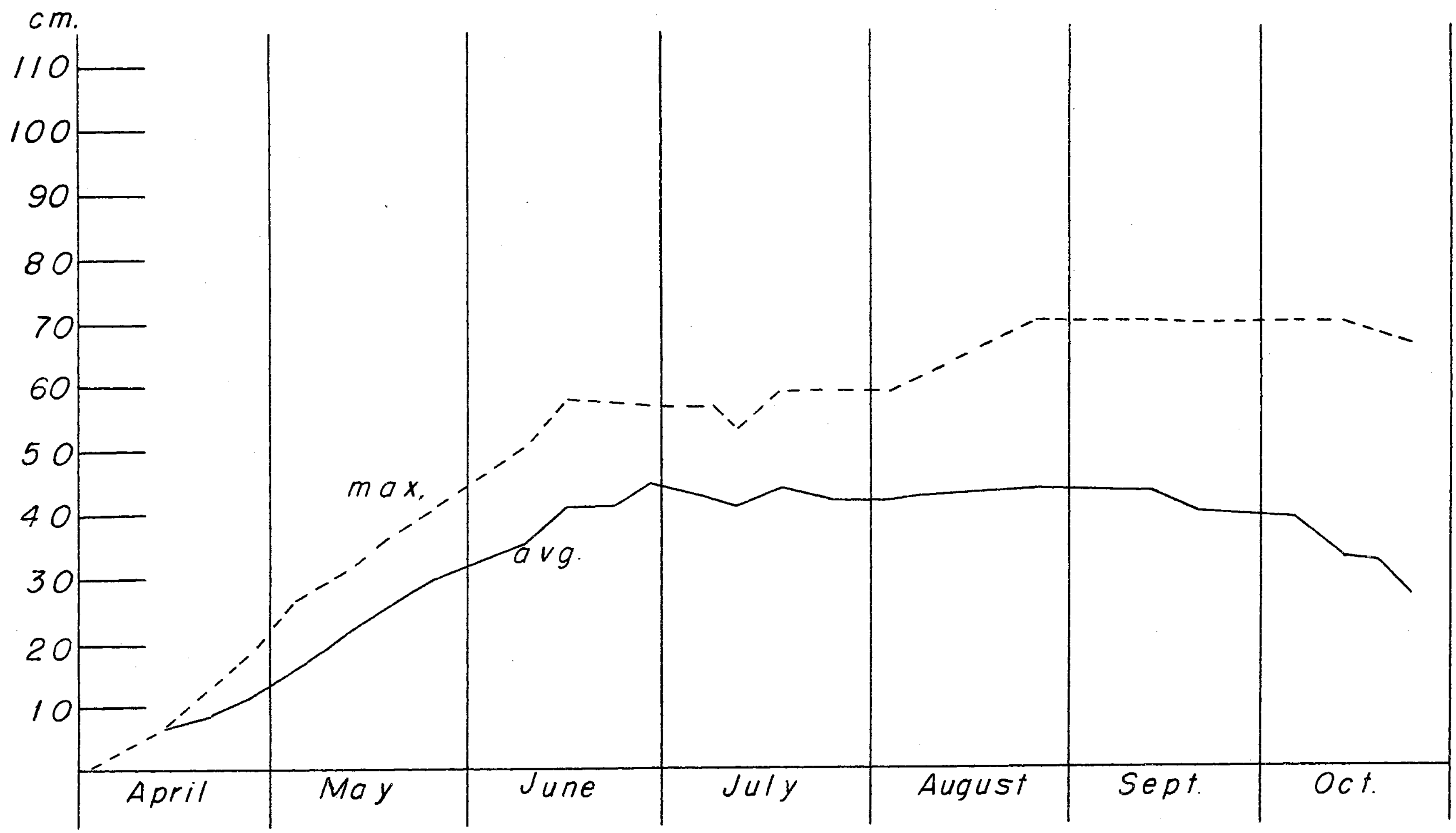

Figure 2. Average and average maximum height of little bluestem.

recorded in 1962. There appeared to be a better seed stalk development in 1962 than in 1961.

Weaver (1941), studying little bluestem in Nebraska, recorded an average foliage height of 45.7 cm on August 29, and an average flower stalk height of 55.9 cm. His maximum recorded for the vegetative portions is very close to the 44 cm recorded in this study.

After an initial "spurt", the height of the greenhouse specimens of little bluestem remained about 17 cm for over one and one-half months from April 4 to May 26 (Figure 3). From March 26 until September 15, there was a steady increase of about 5 cm per month in the vegetative height. From this peak of 29 cm on September 15, there was a gradual decline until the end of the study. There was no stable or "leveling off" period in the greenhouse as there was in the field. The maximum average height in the field was 14 cm more than in the greenhouse.

The maximum height (which included the seed stalks) underwent a much more rapid increase in the greenhouse. It reached a peak of 95 cm on September 9.

The soil temperature at the one-half inch depth at the time of maximum height was 74° F (Figure 4). The maximum temperature (87° F) at the half-inch depth occurred on July 30. The plant height had been relatively constant for several weeks preceeding this and continued to remain so for several more weeks. There was a sharp drop in the temperature to 74° F on September 15. The weekly minimum for the week was 62° F at the one-half inch level (Figure 5). The drop in temperature coincided closely with the start of the decline in plant height in all the species except switchgrass (Figure 5). Whether the drop in temperature actually initiated the decline in height could not be determined for certain, but the two coincide closely.

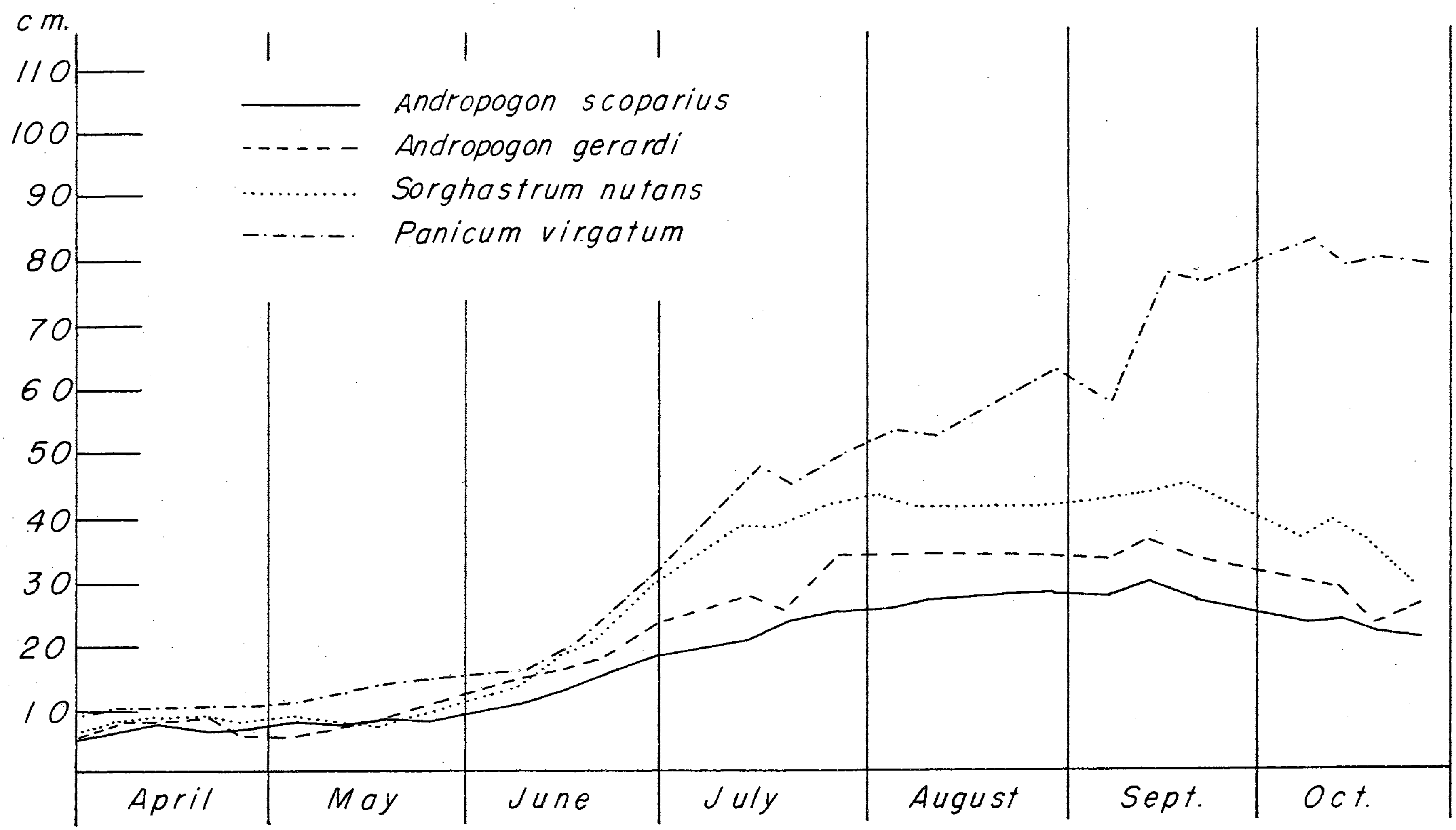

Figure 3. Average heights of the four species in the greenhouse.

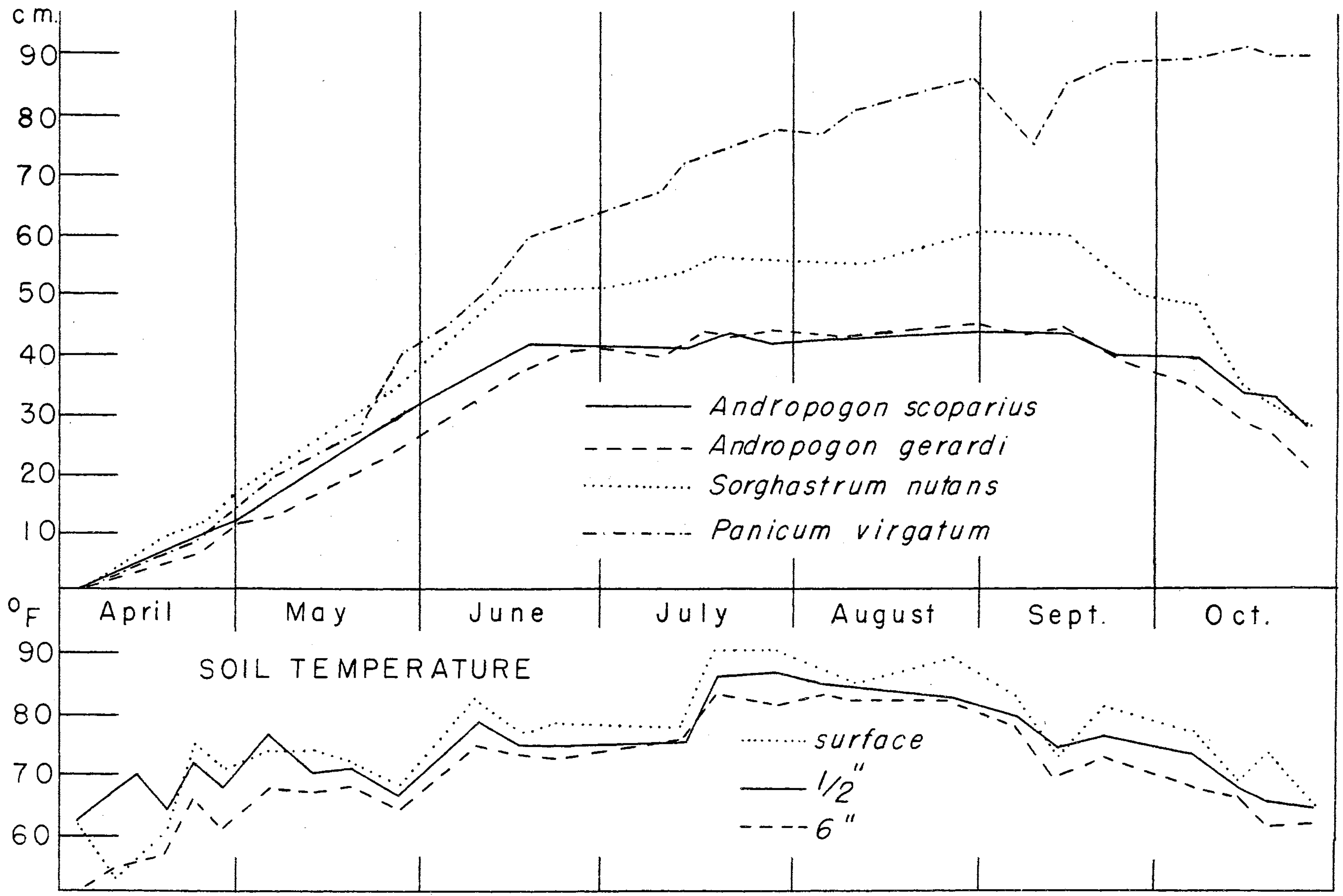

Figure 4. A comparison of plant heights with the weekly soil temperature.

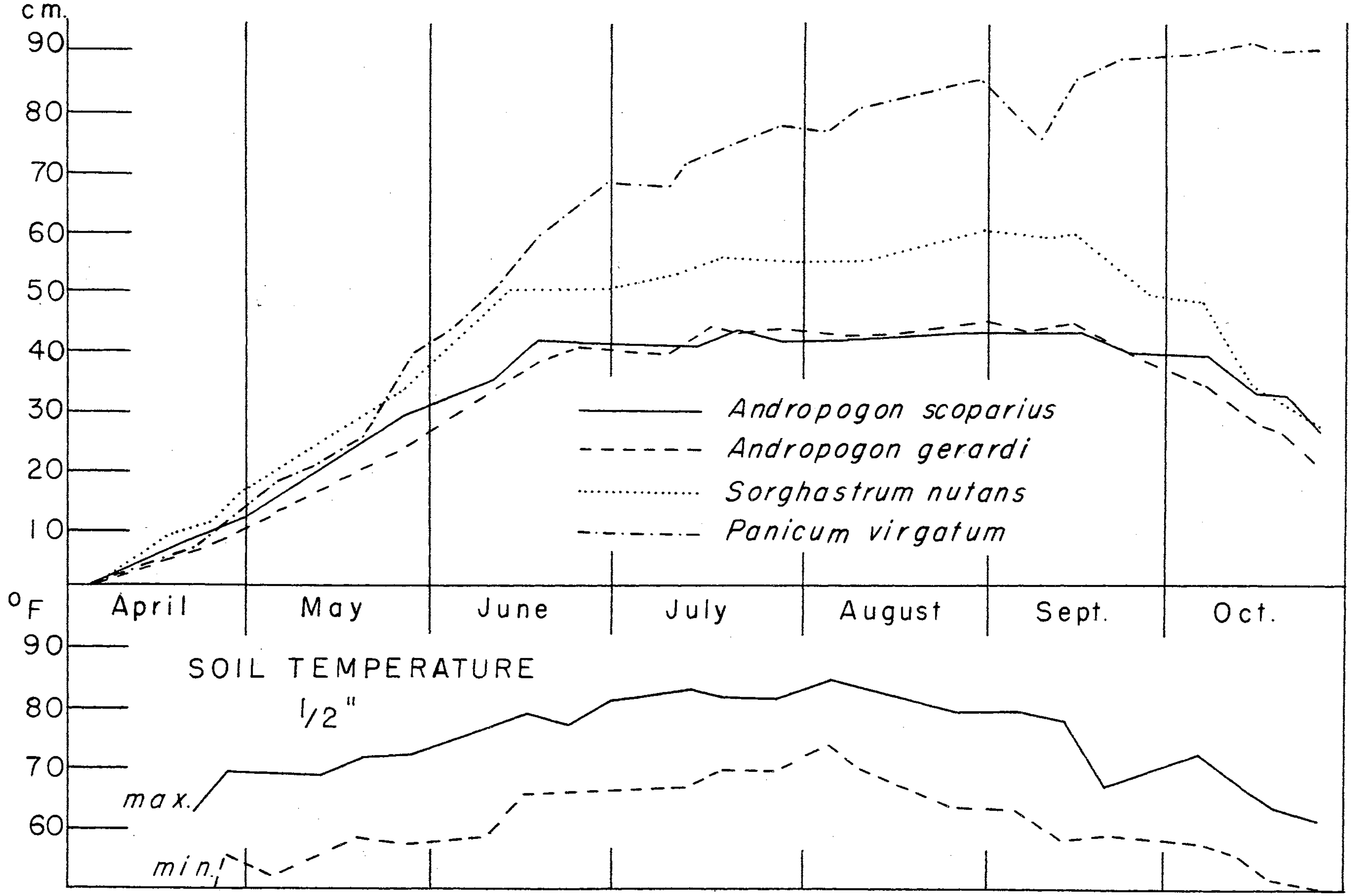

Figure 5. A comparison of plant heights with the weekly maximum and minimum soil temperature.

The soil moisture in the upper 6 inches declined from a maximum of 30% on May 20, to a minimum of 10% on August 28 (Figure 6). From then it steadily increased to 23% in the latter part of October. There was a brief rise in moisture in mid-July, due to an increase in precipitation. No apparent correlation could be found between the growth curves of all four species and the soil moisture curves. There appeared to be practically no moisture stress during this study. Only on one day did the leaves appear curled.

The average leaf length in little bluestem was 26 cm when first measured on June 11 (Figure 7). It increased to 31.0 cm by the August 8 measurement, the greatest length attained. From this point, the death of leaves caused a steady decline. The average maximum leaf length was 41.5 cm on June 11, and increased to a peak of 46.0 cm on August 8. The longest single leaf recorded was 55 cm.

In the greenhouse, the greatest average leaf length was 19.5 cm on August 10. The greatest average maximum was 29 cm and was recorded on the same date. There was very little decline in leaf length in the greenhouse, which would seem to indicate that a temperature factor was responsible for the death of leaves in the field.

When the decline in leaf length began in the field, it followed the peak weekly maximum and minimum one-half inch temperatures by only a few days. These occurred during the week preceeding August 6. The drop in temperature which occurred in mid-September was not reflected by any changes in leaf length. As in plant height, there was no apparent correlation between leaf length and soil moisture.

The average leaf width for little bluestem remained between 2.5 and 3.0 mm (Figure 8). This was by far the most consistent species of

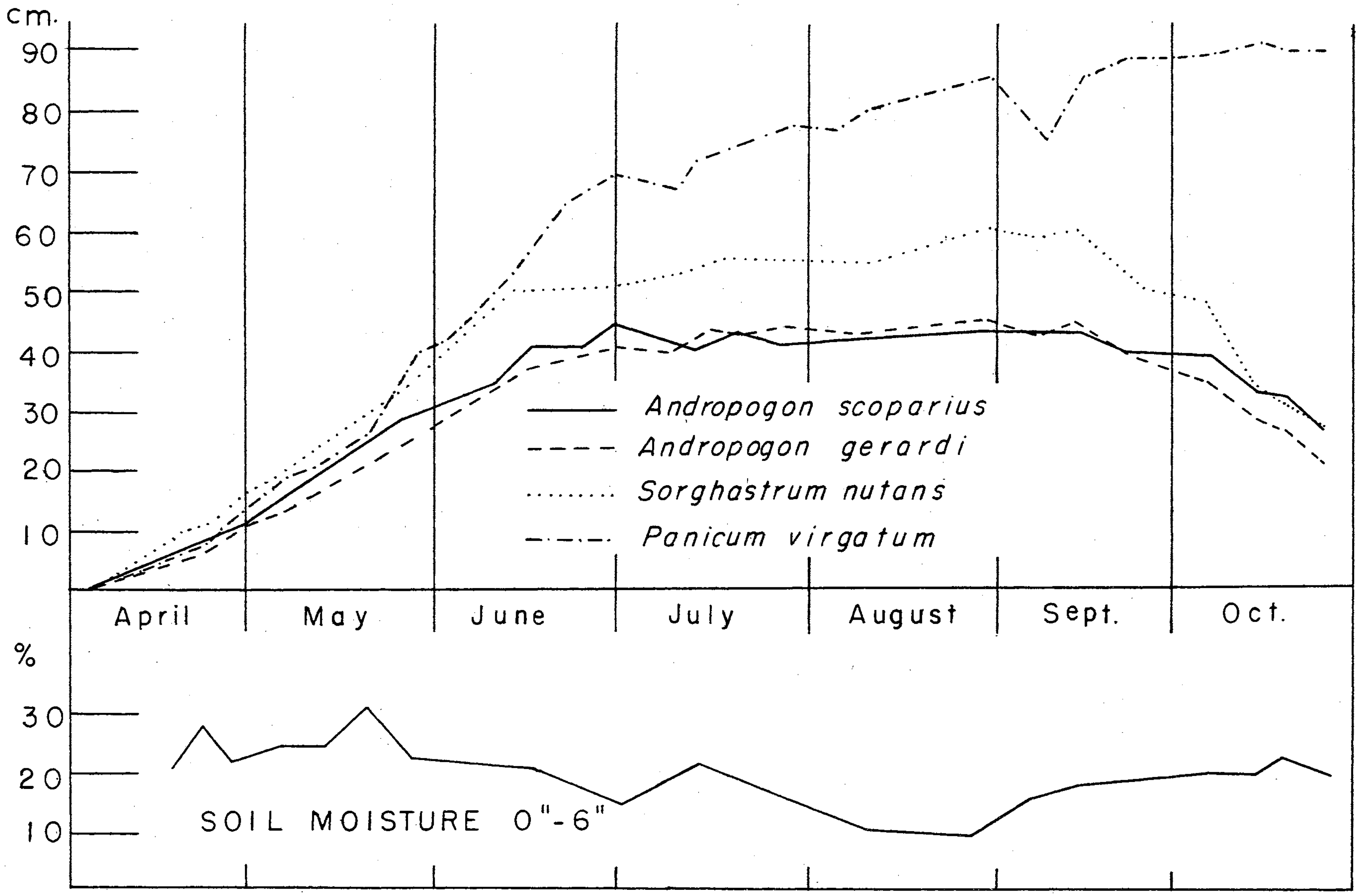

Figure 6. A comparison of plant heights with the soil moisture in the first six inches of soil.

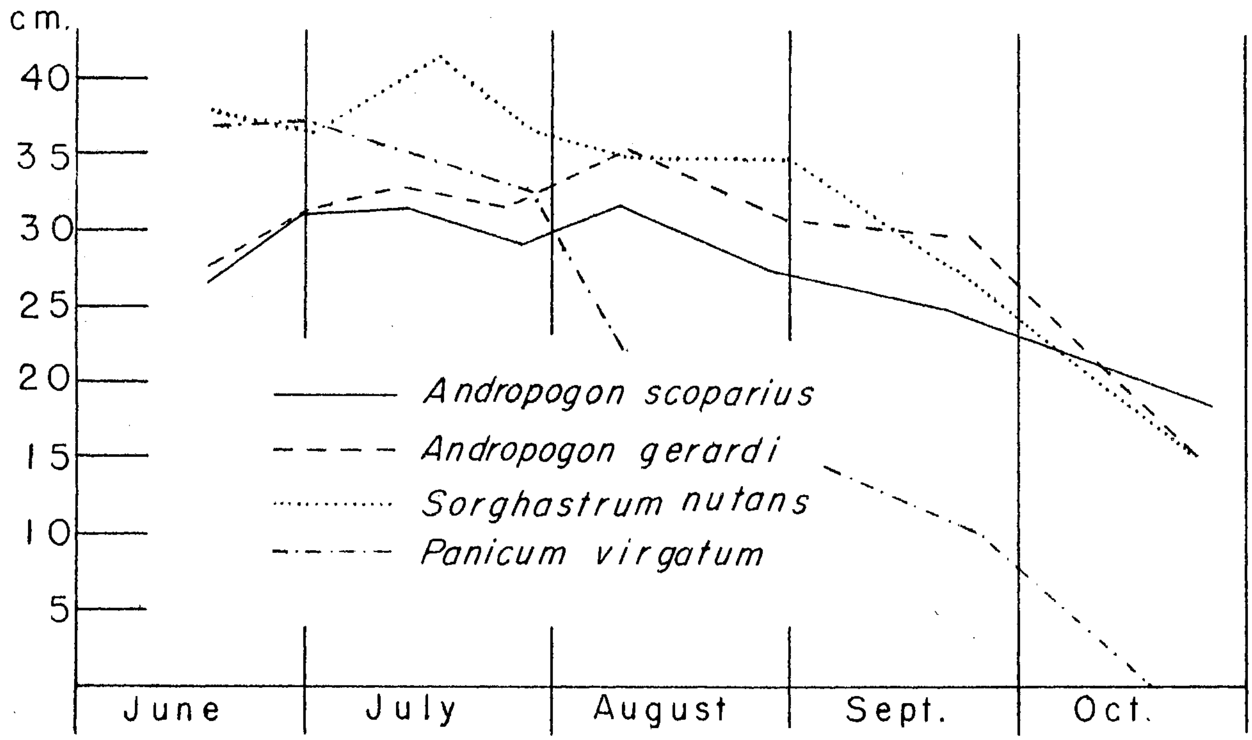

Figure 7. Average length of leaves of the four species.

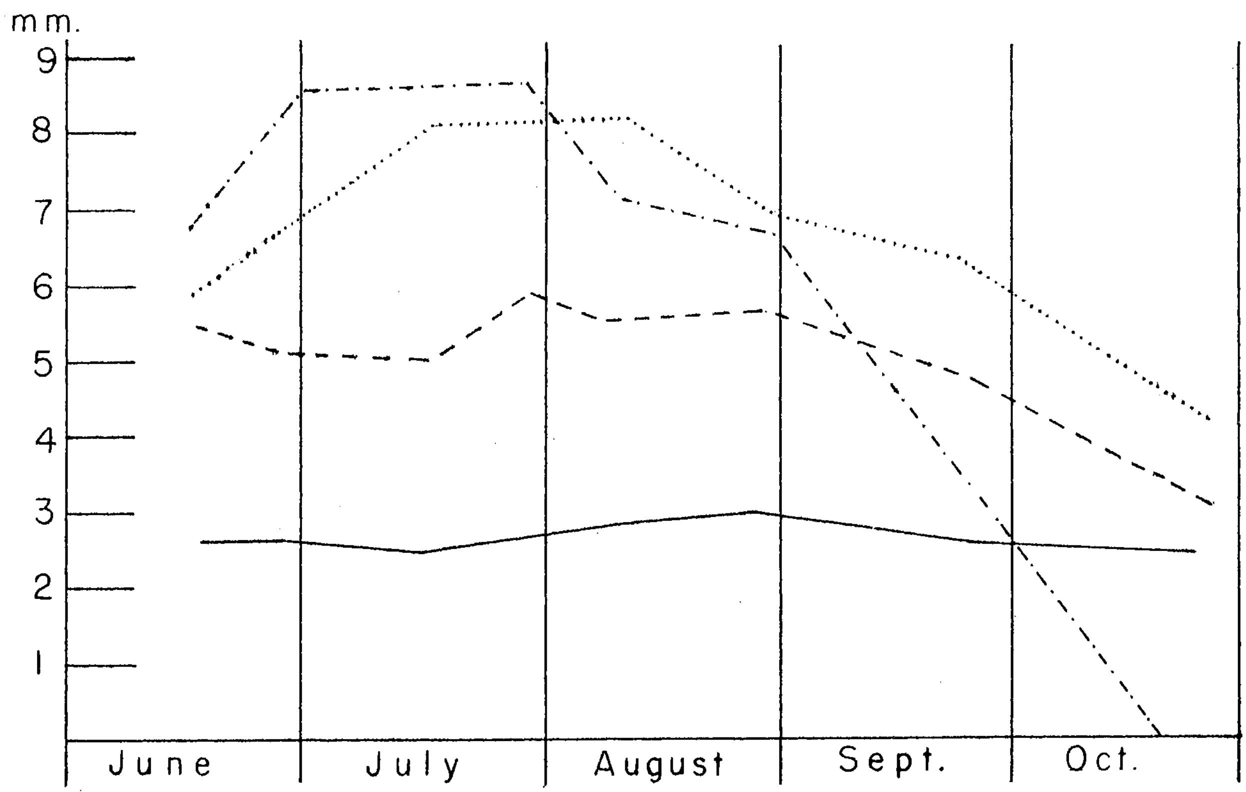

Figure 8. Average width of leaves of the four species.

the four studied. The average maximum leaf width reached a high of 3.9 mm on August 29.

There was much more variation in leaf width in the greenhouse. The average width ranged from 2 mm on April 14 to 3.8 mm on July 28. The average maximum width was less variable. It attained maximum width of 4 mm on July 29.

The average stem diameter in little bluestem was at its greatest (1.2 mm) when first measured on June 16 (Figure 9). After that it remained between 0.8 and 1.0 mm until the end of the study. The average maximum stem diameter reached a peak of 2.0 mm on August 28. The average diameter in the greenhouse reached a maximum of 1.1mm. The average maximum stem diameter was considerably more in the greenhouse than in the field.

Big bluestem

Growth in height in big bluestem closely paralleled that of little bluestem (Figure 4). It was somewhat slower in developing and did not level off until July 16. It remained about the same for two months, with the exception of a slight increase on August 31 to 45 cm which was the maximum reached. There was a decline in height beginning in mid-September which occurred slightly faster than the decline in little bluestem. One significant difference in big and little bluestem was that the average maximum height (seed stalks) decreased in big bluestem (Figure 10). This was probably due to the destruction of seed stalks by the wind, rodents, or other natural factors. Many of the seed stalks were cut near the ground. The greatest average maximum recorded was 66 cm on September 9. The tallest single culm recorded was 114 cm. Several of the culms were greater than 100 cm in height but

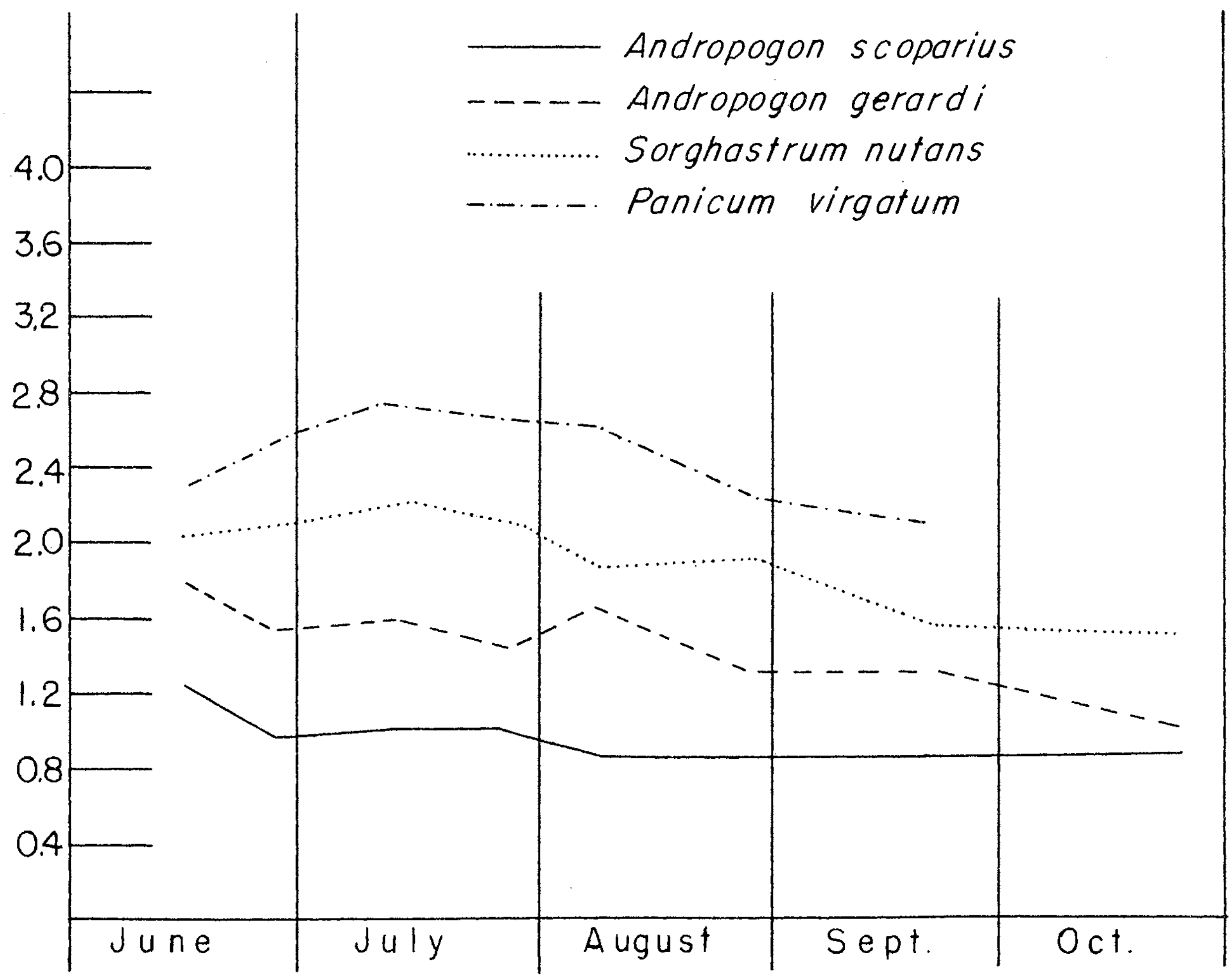

Figure 9. Average stem diameter of the four species.

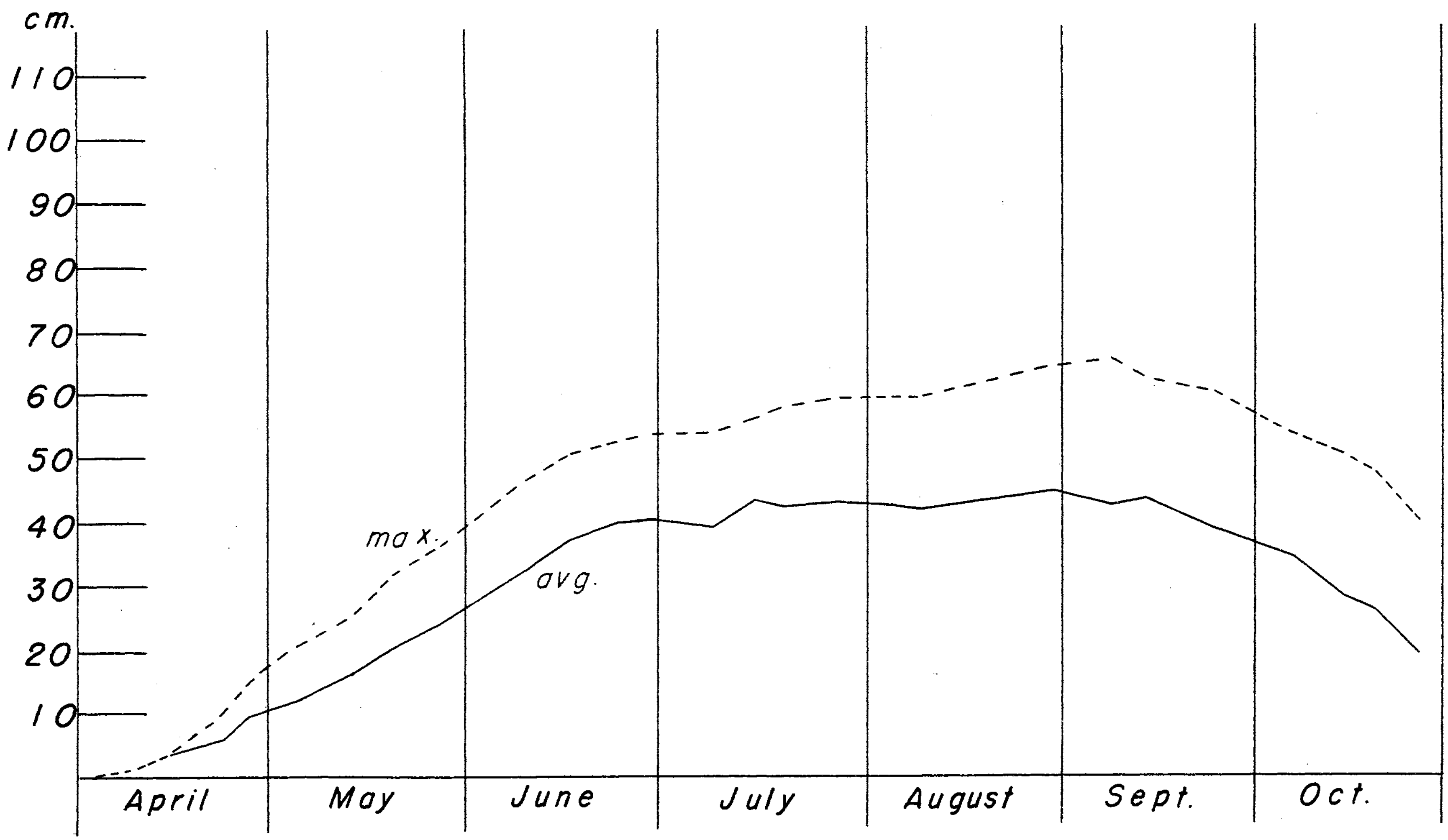

Figure 10. Average and average maximum height of big bluestem.

since many of the clones did not produce healthy seed stalks, the average maximum was lower than for little bluestem.

The height of the nine clones which were measured in 1962 was 44 cm, the same height as was recorded in 1961. The maximum heights was 64 cm in 1961 as compared with 65 cm in 1962.

Growth of the seed stalks in the greenhouse was striking. After seed stalk formation began in mid-July, elongation proceeded at the average rate of 1.8 cm per day. Rapid elongation ceased on September 15, when the average maximum height was 153 cm, more than twice the comparable height of the plants in the field. The tallest single clum recorded in the greenhouse measured 180 cm. The rate of growth of the vegatative portion closely paralleled that of the field plants. The greatest average height in the greenhouse was 36 cm on September 15 (Figure 3). At the point of maximum development, there was a difference of 117 cm in the maximum height and the average vegetative height.

The average height of big bluestem began declining in the field on September 15. As in little bluestem, this coincided with the drop in soil temperature which occurred on this date (Figures 4 and 5). There were no significant correlations between growth rate and soil moisture (Figure 6).

The leaf length in big bluestem was still increasing when measurements were begun on June 16 (Figure 7) and continued increasing until August 10, when the average length was 34 cm. The average maximum length reached a peak two weeks earlier with 51 cm being recorded. The longest single leaf measured was 65 cm.

In the greenhouse, the leaves elongated during the last half of March and the first half of April. Following this, both the average and the maximum length of the leaves decreased almost one-third of their former length. The leaves began lengthening again during the first week in May, and steadily increased until September 9, at which time they had an average length of 25 cm. Between September 9 and the last measurement on October 9, the average length decreased almost 5 cm. The decrease in length was much less pronounced in the greenhouse than in the field.

Following the decline in late April, the average maximum leaf length also increased steadily until September 9 when the length was 39 cm. There was no significant decrease in the average maximum length after this. The longest single leaf measured in the greenhouse was 44 cm. Leaf length was much shorter in the greenhouse than in the field.

As in little bluestem, the decline in leaf length in the field began during the same week as the decline in the weekly maximum and minimum temperatures. The drop in temperature which occurred in mid-September was followed by a slight increase in the rate of decline in leaf length.

The average leaf width remained between 5 and 6 mm from the first measurement of June 16 until the first week in September (Figure 3). Between the first of September and October 27, the average width decreased 3.1 mm. If this decrease were due to the death of leaves instead of an actual shrinking of individual leaves, and since the death of random leaves would theoretically leave the average unchanged, this decrease in width seems to indicate that the wider, and presumably older, leaves die first. The widest individual leaf measured was 9 mm.

After an erratic start in the greenhouse, the average width increased to a maximum of 7 mm on June 15. It then decreased steadily to 4. 8 mm on October 9. The average maximum width reached 8. 4 mm in late July. The average widths were greater in the greenhouse than in the field.

The average stem diameter was 1. 8 mm on June 17 (Figure 4). From this it declined more or less regularly throughout the summer to a width of 1. 0 mm on October 27. The average maximum stem diameter, which included the seed stalks, remained between 2. 4 and 2. 6 mm from June 17 to September 26. The thickest single culm measured had a diameter of 4. 7 mm.

In the greenhouse, the average stem diameter increased to 2. 2 mm on July 13, and then steadily decreased to 1. 3 mm on October 9. The average maximum stem diameter increased sharply when seed stalks began appearing and reached a peak of 4. 1 mm on July 28, considerably more than the 2. 6 mm recorded in the field. This was due to the fact that all big bluestem clones in the greenhouse produced relatively large seed stalks. As for individual seed stalks, there were several in the field which were as large as those in the greenhouse.

Indiangrass

From the resumption of growth in early April until the middle of June, the plants increased height at a relatively constant rate of 0. 74 cm per day (Figure 11). The average height at the end of this period was 50 cm. From June 13 until September 16, the average height increased from 50 to 60 cm. From September 16 until the end of the study, the average height declined steadily. The maximum height closely paralleled the average height until late July when seed stalks appeared. There was marked increase in the maximum height from August 11 to September 24, due to the rapid elongation of seed stalks.

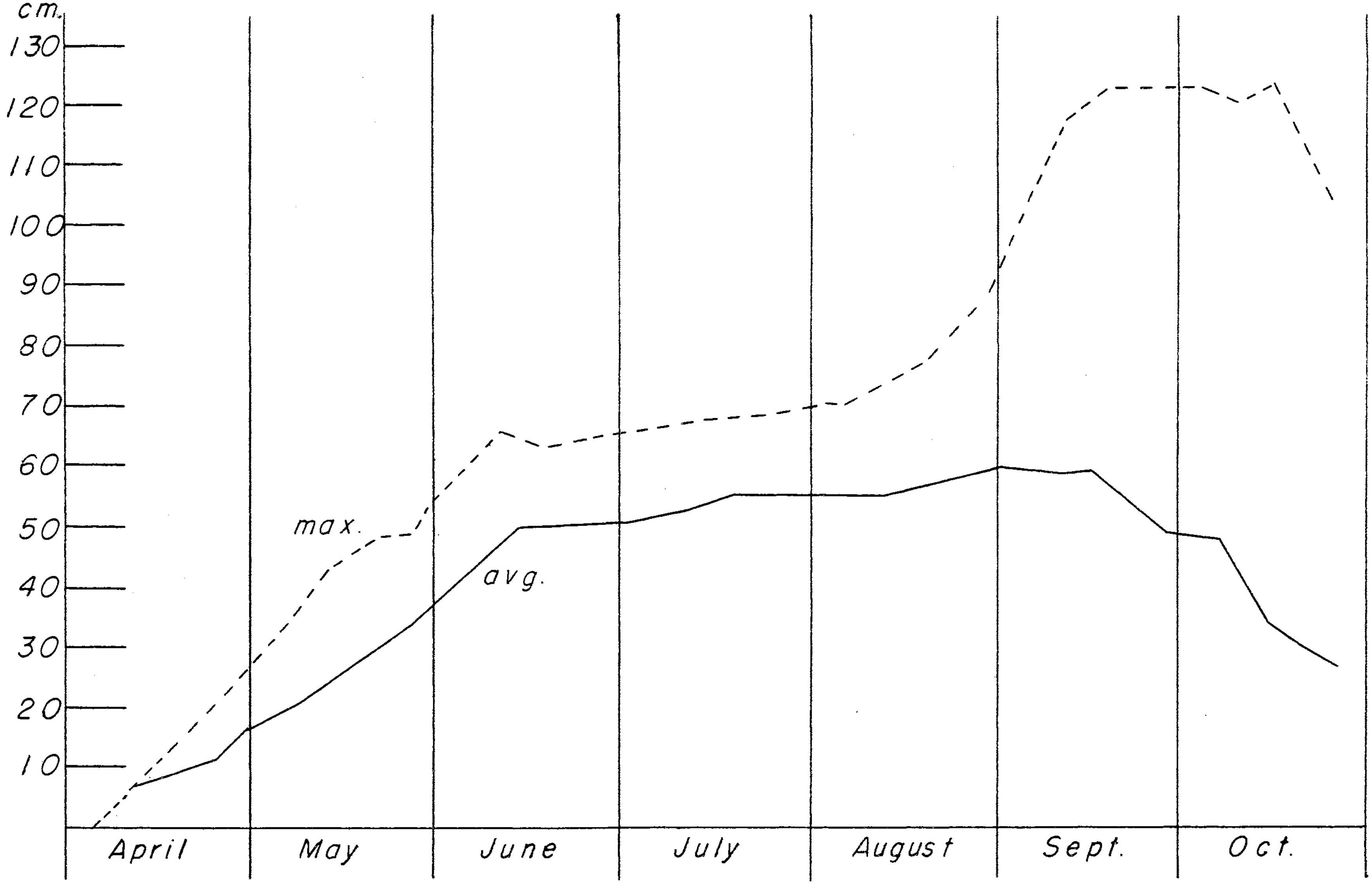

Figure 11. Average and average maximum height of indiangrass.

The rate of growth for this period averaged 1.3 cm per day, and the height on September 24 was 127 cm. There was difference of 84 cm between the maximum and average heights on this date. Rice (1950) reported an average maximum stem height of 156 cm. The tallest individual culm measured was 170 cm.

There appeared to be considerable rodent damage to the indiangrass seed stalks in October. Many of the seed stalks were severed near the base, and the seed from the felled stalks appeared to have been removed. There was considerable increase in the number of cotton rats observed in the area during the months of September and October.

On September 15, 1962, 14 of the original 20 clones were measured. The average height was 45.7 cm compared with an average of 57.6 cm for the same 14 clones on the same date in 1961. An even greated difference was found in the maximum height with 63.3 cm in 1962 compared with 111.6 cm in 1961. The difference could be due to a later development in 1962 and does not necessarily mean that the height was less.

The average height of the indiangrass plants in the greenhouse remained rather constant until August 30 (Figure 3). At that time a rapid elongation of the stalks was apparent. The greatest height (86 cm) was reached on September 22. The maximum height of 86 cm was considerably less than the 126 cm in the field. At the time of greatest development, the average maximum height was 42 cm more than the average height. The greatest individual height recorded in the greenhouse was 130 cm. Half of the plants in the greenhouse did not exceed a height of 60 cm.

The decline in the average height of indiangrass began on September 16. As in big and little bluestem, this coincided with the drop in soil temperature which occurred during the same week (Figure 4).

The average leaf length in indiangrass was 37 cm when measurements were begun in mid-June (Figure 7). One month later the length had increased to 41 cm which was the greatest average length recorded. The average maximum length also reached a peak on July 17 with 51 cm. There was only 10 cm difference in the average and the average maximum lengths at that time. The longest single leaf measured was 65 cm.

In the greenhouse, leaf elongation occurred during the last half of April. Following this, as in big bluestem, both the average and the maximum length of the leaves decreased. The leaves began lengthening relatively rapidly in late May, and by June 13 had reached a peak of 34 cm. The average maximum leaf length did not reach a peak until July 29, when it measured 51 cm. The longest leaf measured in the greenhouse was 62 cm.

The maximum leaf length in indiangrass was recorded on the same date as the maximum soil temperature. It did not, however, correspond with the greatest weekly maximum soil temperature.

The average leaf width was increasing when first measured, and continued to increase until the middle of July (Figure 8). The greatest average width was 8.2 mm recorded on August 11. From this time until the end of the study, the average width decreased. The greatest average maximum leaf width was 10.5 mm recorded on July 28. The widest individual indiangrass leaf measured was 15 mm.

Leaf width in the greenhouse increased gradually until July 28, when a maximum average width of 6.3 mm was recorded. From then until the end of the study the width decreased only 1 mm. The greatest average maximum width was 7.7 mm. The width in the greenhouse was less than the width in the field throughout the season.

As with leaf length, the greatest average leaf width was recorded on the same date as the greatest one-half inch soil temperature. The beginning of the decline in width also coincided with the decline in the weekly maximum and minimum soil temperatures.

The average stem diameter was 2.0 mm on June 18 and increased to a diameter of 2.2 mm on July 17 (Figure 9). The average maximum stem diameter increased from 3.0 mm on June 18 to 4.2 mm on August 11. The thickest single culm measured had a diameter of 6.3 mm.

In the greenhouse, the greatest average stem diameter recorded (1.8 mm) was in mid-April, shortly after measurements were begun. The average maximum diameter (2.7 mm) did not reach a peak until seed stalk formation was complete on September 7. The largest single culm measured had a diameter of 3.0 mm.

Again the greatest average diameter coincided with the greatest one-half inch soil temperature.

Switchgrass

Following the start of growth in early April, switchgrass continually increased in height throughout the study (Figure 12), because the culms were used as the basis of measurement instead of the leaves. This also accounts for the greater height shown for switchgrass than for the other three species. An unexplained decline in height was recorded in early September. A similar decline was recorded in the greenhouse the preceeding day. The greatest average height recorded was 90 cm on October 15. The average maximum height reached a peak of 117 cm on September 10. Rice (1950) reported an average maximum height of 124 cm for switchgrass. The tallest single culm measured in the

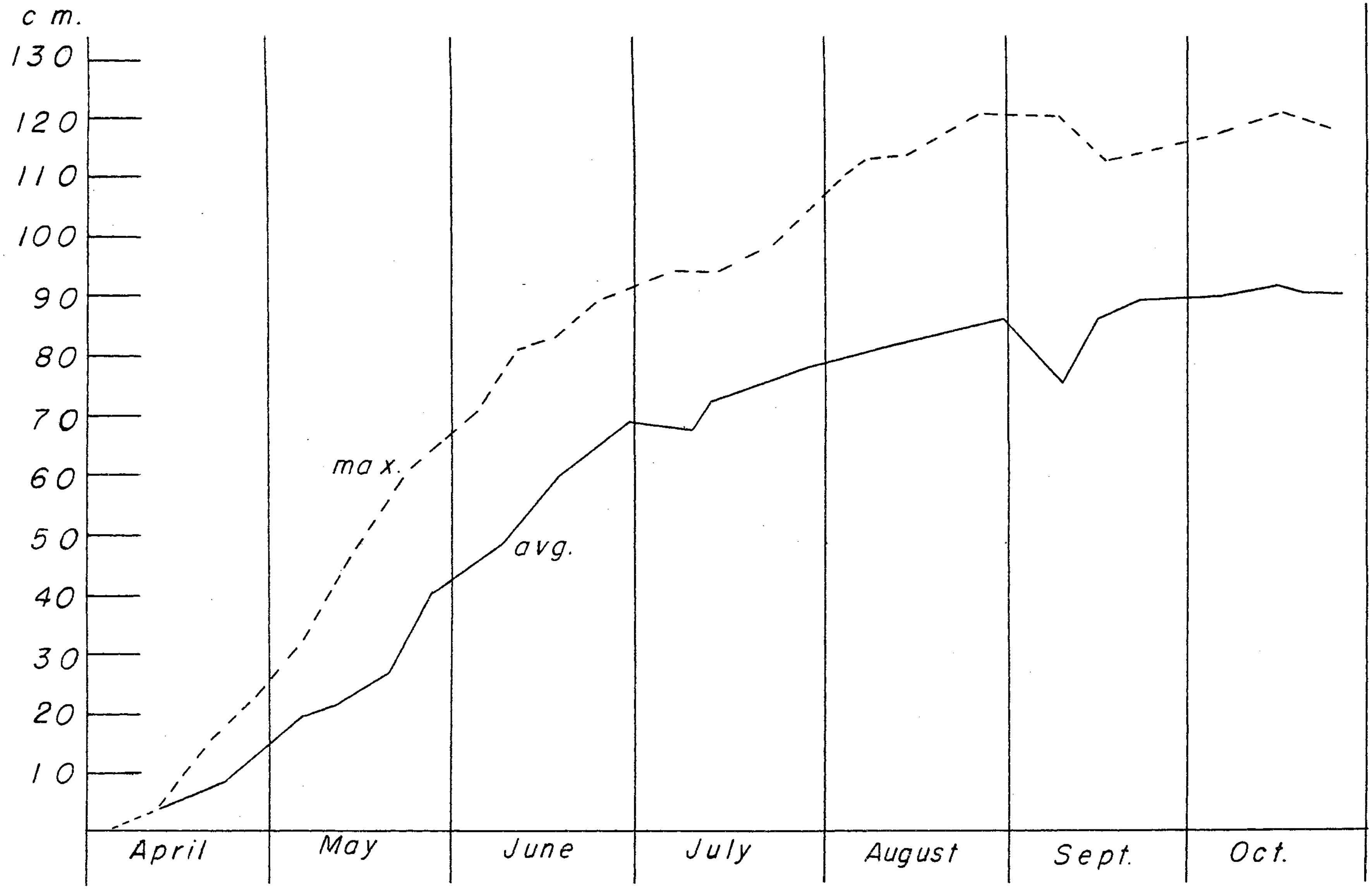

Figure 12. Average and average maximum height of switchgrass.

present study was 144 cm in height. The absence of a decline in height in switchgrass was unique among the four species studied.

Fifteen of the original twenty clones were measured on September 15, 1962. The average height on that date was 89.2 cm as compared with a height of 84.7 cm in 1961. The average maximum height was 119.7 cm in 1961 and 123.8 cm in 1962.

The average height in the greenhouse increased slowly until the first half of June, at which time growth became more rapid (Figure 3). The greatest average height was 83.0 cm and occurred on October 9. This was 7 cm less than the greatest average height in the field. The average maximum height was greatest on August 30, when it measured 112 cm. There was only a very slight decline following this. The tallest single culm measured was 122 cm in height.

The leaves of switchgrass had already reached their greatest length when measurements were begun on June 17 (Figure 7). At that time the average length was 37 cm, and the average maximum length was 47 cm. The length steadily declined from that date. By the middle of October, no living leaves were found. The longest single leaf recorded measured 60 cm.

The average leaf length in the greenhouse reached a peak of 27 cm on August 10, and then decreased slightly. The average maximum leaf length reached a peak of 38 cm on July 28. The longest single leaf measured was 42 cm. Very little decline in leaf length was evidenced in the greenhouse.

The greatest average leaf width recorded in the field was 8.5 mm (Figure 8). This width was maintained throughout the month of July then decreased steadily until mid-October when all leaves were dead. The greatest average maximum width recorded (10.6) was on the first day of measurement, June 17. The widest single leaf observed was 13 mm.

The leaf width measurements from the greenhouse varied a great deal from week to week. The greatest average width recorded was 6.8 mm on July 15 and again on August 10. The average maximum width reached a peak of 8.5 mm on August 10. There was only a comparatively small decrease in leaf width in the greenhouse specimens. The widest single leaf recorded was 10 mm.

The greatest average stem diameter for switchgrass was recorded on July 13, and was 2.7 mm (Figure 9). A decline followed that lasted until mid-October when it became impossible to distinguish the living culms. The greatest average maximum diameter was 3.9 mm recorded on July 13 and August 10. The largest culm measured was 5.0 mm in diameter.

In the greenhouse, the greatest average stem diameter (2.3 mm) occurred on July 14. The average maximum diameter was at its greatest on September 7, when it measured 3.3 mm. The largest single culm measured was 3.9 mm in diameter. Again there was relatively little decrease in size in the greenhouse.

Comparison of the four species

All four species grew at a relatively constant rate until mid-June, although indiangrass and switchgrass grew slightly faster and developed earlier than did big and little bluestem. Big bluestem showed the latest development of the four species. From late June until mid-September very little increase occurred in the vegetative portion of indiangrass, and almost none in the two bluestems. From mid-September until the end of the study in late October, these three species decreased in height due to the death of leaves. Switchgrass, however, continued to grow in height throughout the season, since the culms and not the leaves formed the basis of measurement.

Considering the vegetative portion of the plant only, the average height of big and little bluestem was practically identical, while indiangrass was approximately 10 cm taller than either.

The average height on September 15 was 4.7 cm more in 1962 than in 1961 in little bluestem, 1 cm more in big bluestem, and 4.5 cm more in switchgrass. Indiangrass was 12.2 cm shorter in 1962 than 1961.

Indiangrass had the greatest average maximum height in the field (127 cm), but was only 10 cm taller than switchgrass (117 cm). Little bluestem reached a height of 70 cm. Although big bluestem typically is conspicuous with tall seed stalks, it showed the lowest average maximum height (66 cm) of the four species. The cause for this low average was that, while many clones produced tall, "showy" seed stalks, others produced only small, inconspicuous stalks and many produced none at all. In the greenhouse big bluestem produced the tallest seed stalks (153 cm) of the four species. Switchgrass was the next tallest (112 cm) and little bluestem the third (95 cm). Indiangrass, which was the tallest species in the field, was the shortest in the greenhouse, with a maximum height of 87 cm.

All four species began growth in the greenhouse nearly three weeks before they began in the field. The plants in the greenhouse remained below 10 cm in height for almost two months after growth began. The plants in the field increased rapidly in height once growth began, and soon surpassed the greenhouse specimens. Only a slight decline in vegetative height and almost no decline in seed stalk height was shown by the specimens in the greenhouse. The field specimens, with the exception of switchgrass, showed a decrease in both vegetative and seed stalk heights.

All four species approached their maximum leaf length when measurements began in mid-June. By the middle of August, all four were definitely decreasing in length. Switchgrass showed a much sharper decline than the other species. Practically all leaves of switchgrass were dead by the middle of October. The other species had measurable leaves when the study ended in late October. It should be noted that no frost had occurred prior to the end of the study.

Indiangrass had the longest average leaf length (41 cm) of the four species. Switchgrass leaves reached 37 cm, big bluestem 34 cm, and little bluestem 31 cm. The length of leaves in switchgrass and indiangrass appeared to be the most uniform of the four species, with 7 cm and 10 cm, respectively, separating the greatest average and the maximum length. The difference was near 16 cm in big and little bluestem.

In the greenhouse, indiangrass and big bluestem leaves increased in length during late May and early April, and then in late April a decline of 2 to 5 cm was recorded. The decrease in length represented approximately one-third of the total length at that time. The decline was present in both average and average maximum leaf lengths, but was not evident in little bluestem or in switchgrass.

Although all four species attained greater lengths in the field, their relative position was unchanged in the greenhouse. Indiangrass still had the longest average leaf length, and little bluestem the shortest. Although a slight decline in length was recorded near the end of the study, it was not significant compared with the decline in the field.

Switchgrass leaves reached the greatest average width (8.5 mm) of the four species. Indiangrass reached 8.2 mm, big bluestem reached 5.8 mm, and little bluestem reached 2.9 mm.

Once the leaves had expanded in the greenhouse, their width was much more consistent that those in the field. There was only a gradual increase in width, reaching a peak in the latter half of July. Big bluestem showed the greatest average width (7.0 mm) of the species in the greenhouse. Switchgrass and indiangrass had greater widths in the field than in the greenhouse, but big and little bluestem had their greatest width in the greenhouse. Again, little decline was shown in the greenhouse specimens.

There was very little variation in the diameter of the culms, except in the case of switchgrass where the apparent death of the aerial parts occurred. Switchgrass culms showed the greatest average diameter (2.7 mm). Indiangrass reached 2.2 mm, big bluestem 1.8 mm, and the flattened stems of little bluestem reached a thickness of 1.2 mm.

All four species reached their greatest culm diameter in the greenhouse on July 15. All species, except big bluestem showed a greater stem diameter in the field than in the greenhouse.

CHAPTER V

SUMMARY

The phenology and rate of growth was studied for four species of grass, little bluestem, big bluestem, indiangrass, and switchgrass, in a relict prairie near Stillwater, Oklahoma.

Shoot formation began in all four species during the week preceeding April 3. All measured phenomena began on approximately the same date in little bluestem, big bluestem, and indiangrass, but occurred several weeks earlier in switchgrass.

All four species were found to begin growth in the greenhouse nearly 3 weeks before they began in the field. Big bluestem showed a slightly later development than the other species.

From late June until mid-September, very little increase occurred in the vegetative portion of little bluestem, big bluestem, and indiangrass. This period coincided with the formation of reproductive structures. Switchgrass was found to increase in height throughout the season.

Death of leaves caused a decline in many measurements. There was a drop of the weekly soil temperature at the one-half inch level on September 15 which coincided with a decline in height of all species except switchgrass.

Big bluestem, although typically conspicuous, was found to have the shortest average maximum height. The average heights of big

bluestem were practically identical with those of little bluestem.

Three species (little bluestem, big bluestem, and switchgrass) reached a greater height in 1962 than in 1961, while indiangrass was shorter in 1962.

The average leaf lengths and widths were much more consistent than the average heights, and very little variation was found in the diameter of the culms once maturity had been reached.

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APPENDIX

Weekly Height of Plants in 1961
(height in cm.)

Week ending on:	Little bluestem		Big bluestem		Indian-grass		Switch-grass	
	avg.	max.	ave.	max.	ave.	max.	ave.	max.
April 22	9	13	7	11	11	14	7	10
April 29	11	18	10	16	15	21	12	16
May 6	16	26	13	22	20	31	18	27
May 13	21	31	17	26	24	37	20	36
May 20	25	37	20	32	30	46	26	47
May 27	29	41	25	37	35	50	39	60
June 10	35	50	33	47	47	62	48	70
June 17	41	58	37	52	51	70	58	82
June 24	42	58	40	53	51	66	64	83
July 1	45	57	41	55	51	66	67	88
July 8	42	56	40	55	53	66	67	92
July 15	41	53	44	58	56	69	71	93
July 22	44	58	43	58	55	70	74	93
July 29	42	59	44	60	56	72	77	97
August 5	42	59	43	60	56	73	76	103
August 12	42	61	43	60	56	72	79	108
August 26	42	70	45	65	60	85	85	117
Sept. 9	43	70	43	66	59	99	74	117
Sept. 16	44	70	44	63	59	116	84	116
Sept. 23	40	69	39	61	52	127	87	109
Oct. 7	39	69	35	54	41	125	89	112
Oct. 14	33	69	29	50	36	123	92	114
Oct. 21	32	68	26	47	32	125	89	115
Oct. 28	26	66	19	40	22	110	90	114

Weekly Length of Leaves in 1961
(length in cm.)

Week ending on:	Little bluestem		Big bluestem		Indian-grass		Switch-grass	
	avg.	max.	avg.	max.	avg.	max.	avg.	max.
June 17	26	42	27	39	37	50	37	47
July 1	30	41	29	43	36	50	37	46
July 15	30	44	32	45	41	51	35	39
July 29	28	44	31	51	36	49	30	35
August 12	31	46	34	47	34	46	21	26
August 26	27	40	32	46	34	45	16	21
Sept. 23	24	36	29	40	26	40	10	13
Oct. 28	16	24	14	21	14	22	-	-

Weekly Width of Leaves in 1961
(width in mm.)

Week ending on:	Little bluestem		Big bluestem		Indian-grass		Switch-grass	
	avg.	max.	avg.	max.	avg.	max.	avg.	max.
June 17	2.5	3.9	5.4	6.3	6.0	7.5	7.0	10.6
July 1	2.6	3.5	5.0	7.1	7.0	8.9	8.5	9.8
July 15	2.5	3.3	5.0	6.5	8.0	9.9	8.5	9.9
July 29	2.6	3.3	5.8	7.2	8.2	10.5	8.1	10.0
August 12	2.8	3.6	5.5	7.0	8.2	10.3	7.2	9.4
August 26	2.9	3.9	5.6	7.2	7.0	9.1	6.1	7.7
Sept. 23	2.7	3.8	4.8	6.7	6.4	8.8	3.8	4.8
Oct. 28	2.2	3.9	3.1	4.2	4.2	5.7	-	-

Weekly Diameter of Stems in 1961
(diameter in mm.)

Week ending on:	Little bluestem		Big bluestem		Indian-grass		Switch-grass	
	avg.	max.	avg.	max.	avg.	max.	avg.	max.
June 17	1.2	1.8	1.8	2.6	2.0	3.0	2.3	3.4
July 1	1.0	1.5	1.5	2.5	2.1	3.6	2.6	3.8
July 15	1.0	1.5	1.6	2.6	2.2	3.8	2.7	3.9
July 29	1.0	1.7	1.4	2.4	2.0	4.0	2.6	3.9
August 12	0.9	1.9	1.6	2.4	1.9	4.2	2.6	3.9
August 26	0.9	2.0	1.3	2.6	1.9	4.1	2.2	3.6
Sept. 23	0.8	1.9	1.3	2.4	1.6	4.2	2.1	3.6
Oct. 28	0.9	1.9	1.0	1.8	1.5	3.9	2.5	3.6

VITA

H. L. Hutcheson

Candidate for the Degree of

Master of Science

Thesis: DEVELOPMENTAL GROWTH OF FOUR SPECIES OF RANGE GRASSES IN NORTH-CENTRAL OKLAHOMA

Major Field: Botany

Biographical:

Personal Data: Born in Tipton, Oklahoma, October 6, 1937, the son of H. Leon and Norma Emily Hutcheson.

Education: Attended grade school in Tipton, Oklahoma; graduated from Tipton High School in 1955; received the Bachelor of Science degree from the Oklahoma State University, with a major in Natural Science, in May, 1960; completed requirements for the Master of Science degree in May, 1963.

Professional Experience: Held a teaching assistantship at Oklahoma State University from September, 1960 to May, 1961.

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