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CONTENTS

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THE CARBOHYDRATE METABOLISM OF STIPA PULCHRA

ARTHUR W. SAMPSON[1] AND EDWARD C. McCARTY[2]

THE PROBLEM

Observation and experimental evidence strongly indicate that the present extensive stands of annual grasses and other annual herbs characteristic of the valleys and foothills of California, were, prior to the advent of domestic herbivora, frequently dominated or conspicuously occupied by perennial bunch grasses.[14] Relicts of perennial grasses, notably of species of such genera as *Aristida, Poa, Festuca,* and *Stipa* (and *Agropyron* in the north), are found commonly on ranges where annual grasses now constitute most of the season's herbage. In a very few localities of this "winter annual" type are still to be found the highly palatable perennial grasses in such density as to furnish a large part of the forage. Economically the perennial grasses are to be preferred as the herbage yield is less subject to fluctuations than is that of the annual cover in seasons of departures from climatic norms, notably decreased rainfall. Also, because of their characteristically later maturity and correspondingly longer period of succulence, perennial grasses are superior for pasturage. Moreover, perennial grasses as a whole are more nutritious during the dry summer months than are the mature, less succulent, often less aromatic, and frequently more fibrous annual grasses. Stockmen appear to be justified in their desire to restock the foothill

[1] Associate Professor of Forestry, University of California, and Plant Ecologist in the Experiment Station.

[2] Associate Professor of Botany, Riverside Junior College, Riverside, California.

ranges with the choicest native perennial grasses. The restoration of such grasses will depend upon the adoption of management plans based upon the growth and nutritional requirements of the particular species concerned.

There are reasons for believing that knowledge of the carbohydrate metabolism of the plant is fundamental to the organization of rational revegetation plans. The object of this study, therefore, was to ascertain (1) the annual march of the carbohydrate foods in the herbage, stem bases, and roots of a common perennial bunch-grass; (2) the influence of a single harvest made at various stages of the annual growth of the plant; (3) whether a specific interval of food accumulation occurs in the developmental cycle of the plant, and if so, to note its relation to seasonal growth; and (4) the relative importance of stem bases and of roots as organs of food accumulation.

Although the conclusions here presented appear to be well founded, the experimental error being well within the bounds of the substantiating data, they must be considered preliminary to the formulation of a broad management plan of perennial grass types as a whole. The promise of highly valuable economic results in this field has prompted enlargement of the program to include studies of food accumulations of *Stipa pulchra* and certain other important range grasses from even-aged stock.

THE EXPERIMENTAL PLOT

The experimental plots were located on the slope of an extensive herbaceous type approximately one-half mile east of the campus of the University of California, Berkeley. This region lies in the Upper Sonoran Zone and the successional climax is grass. On the north and east facings a rather dense cover of shrubby growth occurs, presumably reflecting plant successions following repeated fires. A consociation of oak typifies the grassland association generally. Plantings of conifers and eucalyptus have been established somewhat systematically over the watershed. Scattered trees of eucalyptus are found on the plot selected, but their presence merely causes slight flecking over the plot at rather short daily intervals. Needle grass (*Stipa pulchra*) is a fairly tolerant species.

The soil classed as Olympic clay is residual in origin, from metamorphosed igneous rocks. At the surface it is of rusty grayish brown color, and the subsoil is reddish brown. It is dense and uniform in structure, compact, and the upper three or four inches are

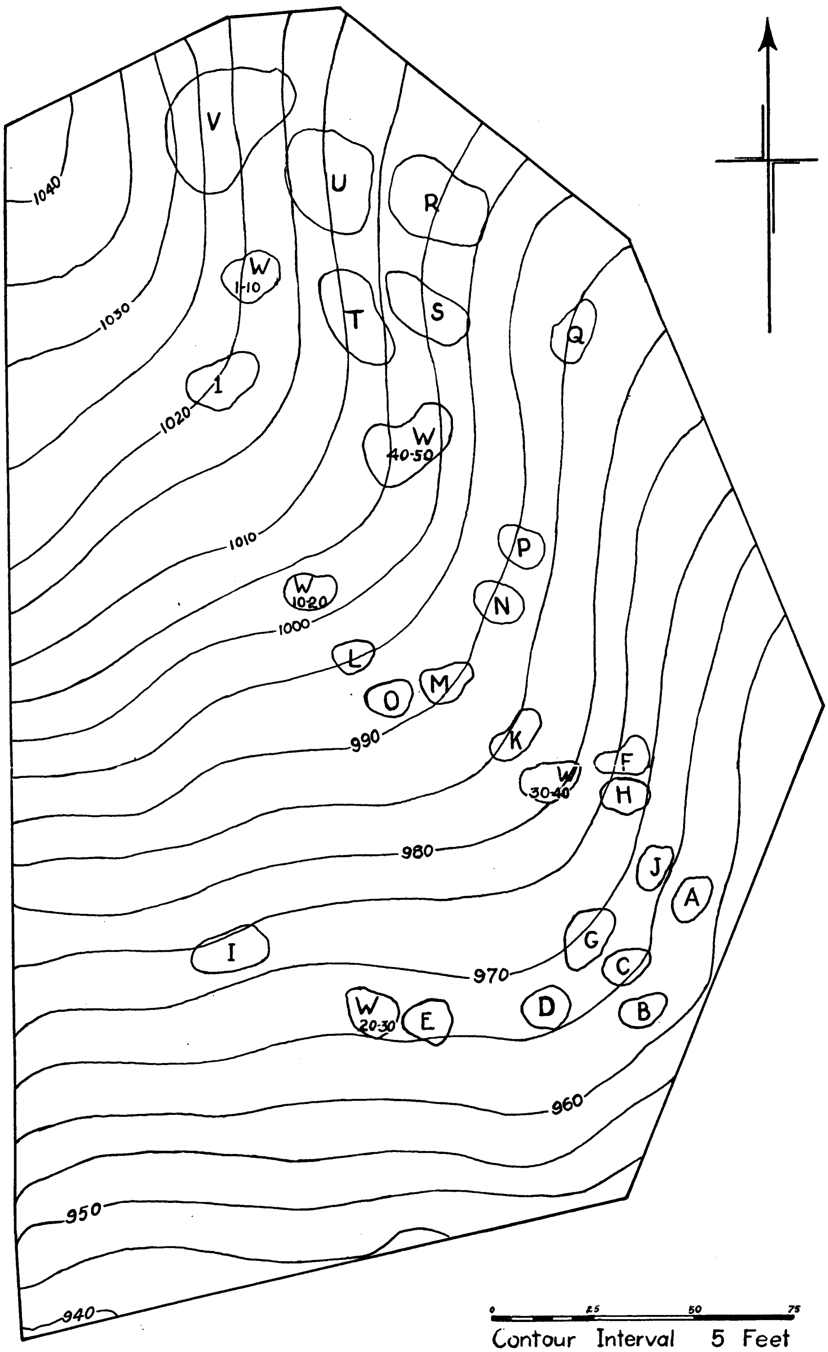

Fig. 1. Sketch showing location of the various groups of *Stipa pulchra*. The control plots "W" were located in five places over the area.

fairly high in organic matter. The deeper layers are occasionally marked with iron stains. Bedrock usually occurs a few feet from the surface and there is some outcrop. The area is well drained and slopes gently to the southeast (fig. 1). This soil type is extensively representative of grasslands. A relatively small proportion of this soil type is utilized for cultivated crops.

CLIMATIC FACTORS

Such factors as air and soil temperatures, precipitation, the evaporating power of the air, wind movement, and sunshine duration and intensity may all directly or indirectly affect the inception and the cessation of growth, as well as the growth rate of the plants. The periods of growth and rest in the habitat concerned, however, are determined chiefly by air temperature and precipitation.

Air Temperature.—The air temperature records were obtained by using a thermograph, checked daily against maximum and minimum standardized thermometers of the Weather Bureau type and exposed in a shelter approximately 4½ feet above the ground.

The relation of the growth rate to the air temperature may best be shown by its expression in terms of[(1)] physiological temperature coefficient,[(6)] and,[(2)] the exponential temperature summation based on the Van't Hoff-Arrhenius principle of doubled chemical efficiency (applied presumably also to plant growth within the optimum temperature range) for each 18° F increase in temperature. The formula used in deriving these indices is: $U = \frac{t\text{-}40}{18°F}$, where U is the index to be determined; t, the temperature value of the Fahrenheit scale of the thermometer; and where the index is the exponential (or log.) function of the temperature itself with reference to the thermometer scale (figs. 2 and 3).

Either summation plan shows clearly that temperature is a limiting factor in determining growth rate during the period from December to February. The similarity of the slopes and the differentials in their maximum and minimum extremes is essentially one of degree rather than of kind. Accordingly, either plan may be used in the study of the growth rate. The fact that the growth rate declined sharply in November, prior to a corresponding decline in the summed mean temperatures, may be accounted for by the periods, short though they were, of minimum temperatures recorded during that month. On only two occasions during the winter did freezing temperatures occur for any appreciable time. On several occasions, however, the temperature dropped for short periods below that at which growth of most higher plants ordinarily takes place. No injury to the leaf blades or to other aerial parts as a result of low temperatures was observed.

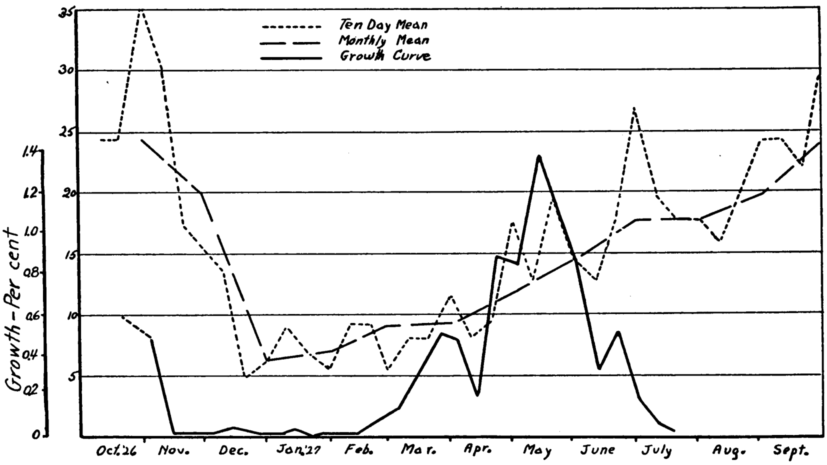

Fig. 2. Physiological temperature coefficient summation (Lehenbaur plan) expressed in 10-day periods and in monthly intervals, respectively, October, 1926, to October, 1927. The growth curve of *Stipa pulchra* is also shown.

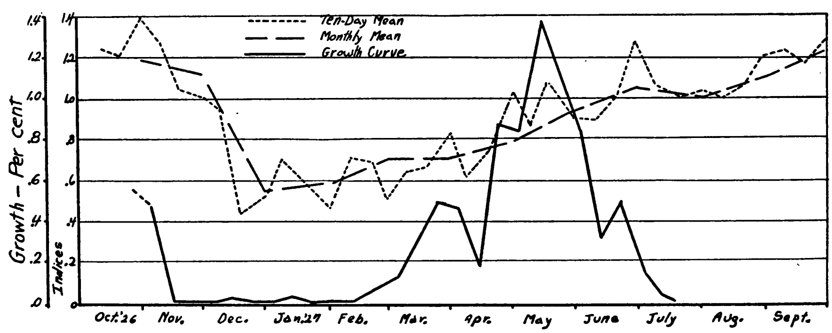

Fig. 3. Van 't Hoff-Arrhenius temperature summation plan, expressed in 10-day periods and in monthly intervals, respectively, October, 1926, to October, 1927. The growth curve of *Stipa pulchra* is also shown.

The most rapid period of growth was accompanied by gradually rising spring temperatures (fig. 4). This thermal rise continued, however, long after the inflexion in the growth rate occurred. The maximum temperatures recorded, even after growth had ceased, were not excessive.

Precipitation.—The precipitation was measured in standard rain gauges of the Weather Bureau type. Inception of growth in October was accounted for by rainfall, as is invariably the case. Figure 5 shows the distribution of the precipitation by 10-day intervals. It

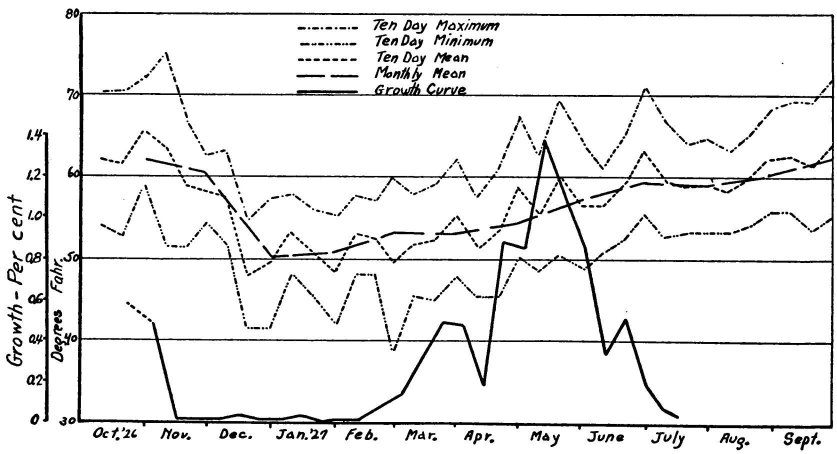

Fig. 4. Air temperature in degrees Fahrenheit expressed in 10-day periods and in monthly intervals, respectively, October, 1926, to October, 1927. The growth curve of *Stipa pulchra* is also shown.

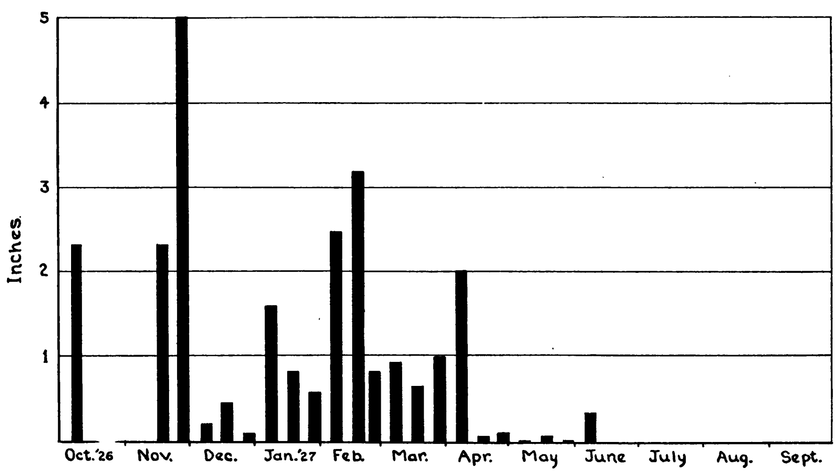

Fig. 5. Precipitation shown for 10-day intervals, October, 1926, to October, 1927.

will be noted that after the recording of the second rain the intervals between rainstorms were not very great, the season's precipitation being over by the middle of June. Beginning approximately April 15, however, the amount of rainfall for a time interval declined sharply.

That the humidity of the soil was well above the wilting coefficient from the time of the first rainfall, in October, to the end of the growth cycle, becomes evident if one will adopt the plan of comparing indices showing precipitation relations from a series of overlapping groups of five days each. This was done by numbering the days of the year consecutively, days 1 to 5 constituting the first five-day group; days 2 to 6 making up the second group; days 3 to 7, the third group, etc., through each month of the year. The respective groups were marked for the five-day period concerned as (1) dry—no rain, designated as D; (2) slightly moist—where .01 to .09 of an inch of rainfall was received, designated as M; (3) moist—where .10 to .50 of an inch of rainfall was received, designated as W; and (4) very moist or rainy—where .51 of an inch or more of rainfall was received, designated as R. Thus, October 9 showed a precipitation of .20 inch, which is the rainfall for the five-day period beginning October 5, and for that date gave a value of W, designated as moist.

On October 1, 1925, a rainfall of 1.04 inches, the first effective rain of growth potentiality of the season was received. Within four days slight greening of *Stipa* hummocks was observed, and prior to the coming of the second rainfall, on October 9, plumules arising from the seed crop that had been cast during the summer could occasionally be seen. Although no rain was received from October 10 to November 11, the humidity of the surface soil was ample for growth.

For October, 1926, the moisture indices showed 24 dry-day intervals, 1 moist-day interval, and one very moist-day interval. The winter and spring months following October, 1926, showed a sharp decrease in dry-day intervals (January, 1927, having none) and a corresponding increase in medium moist, moist, and very moist-day periods. These months are generally accompanied with correspondingly high total precipitation. A sharp decline in rainfall occurred in May, when only .13 of an inch of precipitation was recorded. No rainfall was received in July and August, and only .01 of an inch was recorded in September. In the latter part of June the upper two inches of soil were near the wilting point of vegetation. The greater part of the feeding roots of the older plants of *Stipa pulchra*, however, occur at depths of from 6 to 14 inches. A total of 25.30 inches of rainfall was received for the year, which is slightly less than the annual normal.

Humidity.—The relative air humidity, expressed in intervals of 10 days and in monthly means through the growth cycle, is high throughout the entire period (fig. 6). At no time do the summed points drop below 74 per cent and not uncommonly they are above

90 per cent. Daily dips of comparatively low humidity occurred occasionally. The relatively low evaporating power of the air is doubtless a factor of importance in the maintenance of a fairly moist surface soil during the normal growing period of the graminaceous vegetation.

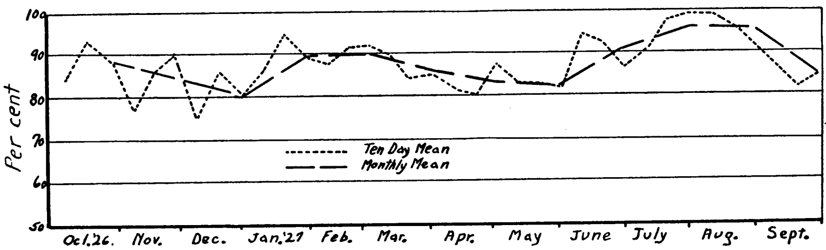

Fig. 6. Relative air humidity expressed in intervals of 10 days and in monthly periods, October, 1926, to October, 1927.

THE EXPERIMENTAL GROUPS

Twelve groups consisting of 90 plants each were selected. These groups were designated by letters and the plants of each staked and numbered consecutively from one to ninety. In order to make all the groups uniform and to remove the straw of the previous year's growth, the plants on all plots, including the controls, were clipped at a point five centimeters from the soil surface. All subsequent clippings were made in like manner. The initial harvest, made on October 14, 1926, was recorded as the first treatment for each group. Some green herbage was removed at this harvesting since growth had begun about October 5, preceding.

The Harvesting Plan—The harvesting plan is given in table 1. The second harvest in each group included all of the plants composing the group. Plants numbered 61 to 90 received no further treatment until the final harvest at the end of the annual growth cycle. At the time of the second clipping of each group the stem bases and roots of plants 1 to 30 were removed and prepared for analysis. The stem bases and roots of plants 31 to 60 were removed in 7 to 15 days following the second harvest. Although some herbage growth occurred in the interval no analyses were made of such growth. All groups were treated in a like manner, the second harvest of each group following that of the preceding group by an interval of from 15 to 30 days, depending upon the rate of growth during the interval (figs. 7 and 8).

The Control Groups.—Comparisons of the carbohydrate changes were made with group A. This group received no further treatment following the initial harvest of October 14. The growth rate study was made of fifty selected plants and contained in five plots which

TABLE 1

HARVESTING PLAN OF THE EXPERIMENTAL GROUPS, OCTOBER, 1926, TO AUGUST, 1927

Plant measurement	Dates harvested									
	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	Aug.
A	14									22
B	14	2								20
C	14		4							20
D	14			5						20
E	14			29						16
F	14				10					16
G	14					20				17
H	14						14			20
I	14						29			20
J	14							16		20
K	14							31		20
L	14								22	
M	14	1	14				14			
W	14									

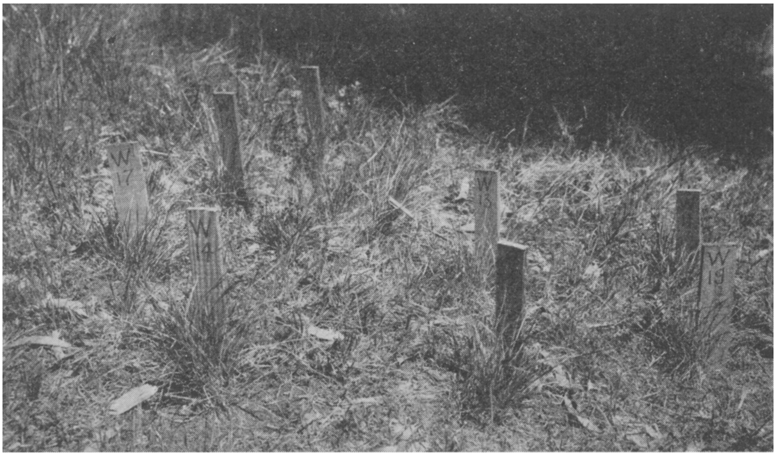

Fig. 7. Part of plot of series "W" of *Stipa pulchra* typifying the development of a group of undisturbed plants. Photographed March 20.

were located in as many places on the experimental area (fig. 7). Measurements of height growth were made at intervals of seven to twenty days throughout the period of the experiment. These measurements were made by means of a scale consisting of a stake 12 × 75

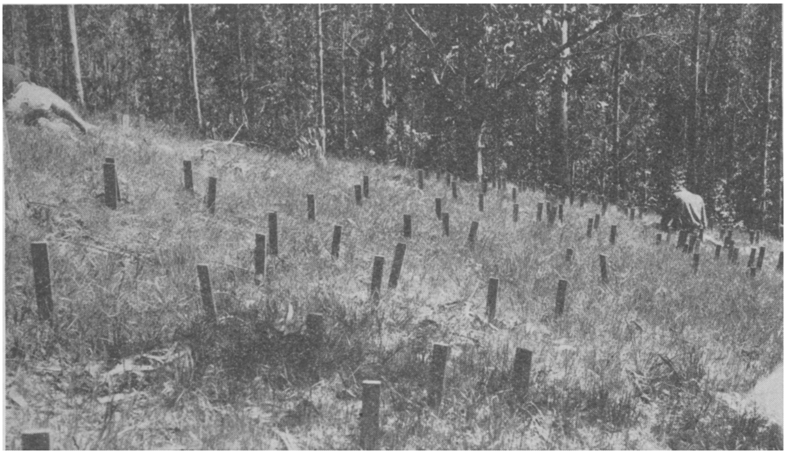

Fig. 8. View of a portion of the site selected for the study of *Stipa pulchra*. Note the rather wide spacing of the specimens. The cover over the plot as a whole consisted largely of annual species, of which *Bromus hordeaceus* predominated. Competition with the selected specimens of *Stipa* was prevented by removing the vegetation immediately around each specimen. Photographed March 20.

TABLE 2

AVERAGE AND MAXIMUM HEIGHT GROWTH OF THE PLANTS COMPOSING GROUP *W*, EXPRESSED IN CENTIMETERS AND AS A PER CENT OF THE TOTAL ANNUAL HEIGHT GROWTH, FOR 1926–27

Date of measurement	Average	Averaged height of plants	Maximum height	Maximum height
	centimeters	*per cent*	*centimeters*	*per cent*
Oct. 25	5.1	15.2	....	....
Nov. 1	6.7	20.0	....	....
Nov. 12	6.7	20.0	....	....
Dec. 4	6.8	20.3	12.9	20.2
Dec. 14	6.9	20.6	13.2	20.7
Jan. 4	7.0	20.9	13.1	20.5
Jan. 20	6.9	20.6	13.2	20.7
Jan. 29	7.0	20.9	13.8	21.6
Feb. 10	7.2	21.5	14.1	22.1
Feb. 26	7.5	22.4	14.6	22.9
Mar. 20	9.9	29.6	17.4	27.3
April 4	12.2	36.5	21.0	33.0
April 14	12.7	38.0	23.0	36.1
April 21	15.0	44.9	25.7	40.4
April 30	17.5	52.3	31.4	49.3
May 9	20.8	62.6	37.5	58.9
May 16	25.2	75.4	46.6	73.2
May 23	26.8	80.2	52.1	81.9
May 31	29.2	87.4	57.2	89.9
June 10	30.5	91.3	59.3	93.2
June 20	32.2	96.4	62.2	97.8
July 5	33.2	99.4	63.2	99.3
July 18	33.4	100.0	63.6	100.0

centimeters, having two short legs at the zero end of the stake. In making measurements of height growth, these legs were pressed into the soil at the base of the plant so that the zero point of the scale rested at five centimeters from the soil line. Two measurements were made at each interval, the one an average of all the shoots, the other being the height of the tallest shoot (table 2).

THE GROWTH CYCLE

Inception of Growth.—Growth of the herbaceous perennial vegetation in the upper Sonoran Zone begins a few days after the coming of the first autumn rains, in the habitat selected, usually early in November and occasionally in October. About half an inch of rainfall in a single storm is sufficient to initiate the production of basal leaf blades in the bunch grasses and to cause re-greening of the herbage of certain grass species which are dry and brown in summer. Germination of seeds of both annual and perennial vegetation characteristically lags behind the earliest appearance of leafage of most perennial grasses, including *Stipa pulchra.* When well established, however, the leafage and stalks of annual grasses are generally produced more abundantly than in vigorous stands of the needle grasses. On the plot studied the foliage of the annual grasses had matured and lost its verdure when their seed crop reached maturity, whereas the herbage of the needle grasses remained green and succulent from six to eight weeks after maturity and the casting of the seed. The striking difference in succulence of the herbage prolongs the period of high palatability of needle grasses in general, and doubtless accounts in a large measure for their limited population on pastures heavily stocked during spring and summer. On a range type where annual grasses predominate the herbage of the needle grasses, during the summer period is kept grazed close to the ground regardless of the abundant herbage of the annual grasses, or of the kind of livestock maintained on the area. With late seasonal grazing the period of growth of needle grasses is prolonged, but such activity is sometimes reflected in delayed inception of growth in the following season. That growth and other physiological responses, due to herbage removal, vary at different stages in the growth cycle of the plant, is quite as evident as in the pruning of a tree.

Annual Growth Cycle.—The annual growth cycle as here considered embraces the period beginning with growth inception and ending with the cessation of herbage growth. In the period studied, the growth cycle extended from October 5, 1926, to July 15, 1927, or about nine months. Approximately 90 per cent of the entire growth of the herbage, however, was made in five months, while 34 per cent, or about one-third of the entire increment was produced in the month of May. Flowering occurred during April 5 to 10 and the fruit was mature and mostly dispersed by May 20.

The Growth Curves.—The data from which the growth curves were constructed were derived from a series of measurements of group W and extended throughout the annual cycle, as shown in the previous section. In order that comparisons might be made from year to year, the respective measurements were converted into per cent,

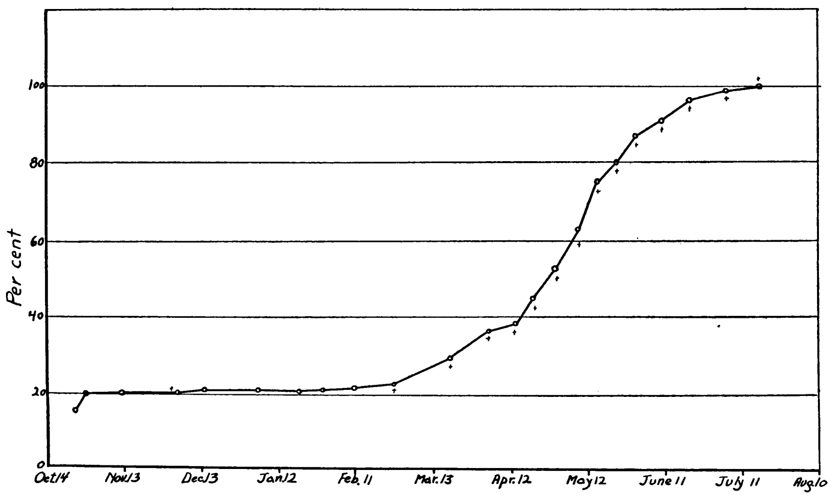

Fig. 9. The annual cumulative growth curve.

considering the average total height growth of the plants at the final measurement to be 100 per cent. These data were plotted, as shown in figure 9. The measurements of maximum growth included in table 2 show very close agreement. The annual curve is delineated into several S-type segments, suggesting as many 'grand periods of growth.'[9]

The curve of daily growth, derived by interpolation from the annual curve, offers a convenient means of designating these characteristics (table 3, fig. 10).

The particular features of the annual cycle are shown to be as follows:

1. Two intervals of very rapid growth occurred in alternation with an interval of exceedingly low growth rate. The annual maximum rate

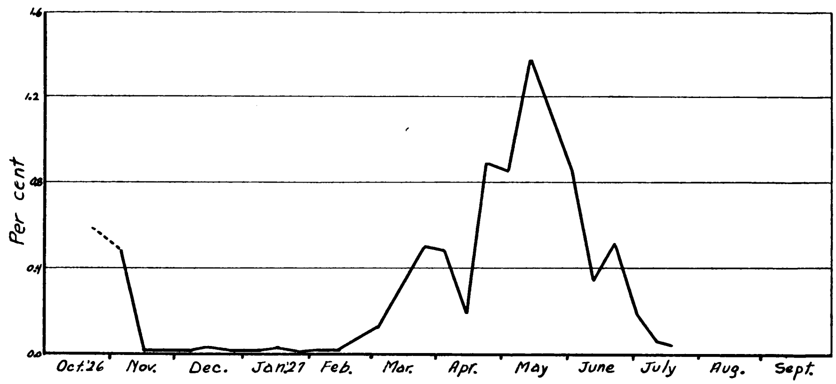

Fig. 10. Daily growth of the plants through the period of the experiment.

TABLE 3

INTERPOLATED READINGS FROM THE ANNUAL GROWTH CURVE OF 1926–27

	Readings annual curve, per cent	Growth 10-day interval, per cent	Daily growth, per cent
Oct. 25	15.2	......	......
Nov. 4	20.0	4.8	0.48
Nov. 14	20.1	0.1	0.01
Nov. 24	20.2	0.1	0.01
Dec. 4	20.3	0.1	0.01
Dec. 14	20.6	0.3	0.03
Dec. 24	20.7	0.1	0.01
Jan. 3	20.8	0.1	0.01
Jan. 13	21.0	0.2	0.02
Jan. 23	21.0	0.0	0.00
Feb. 2	21.2	0.2	0.02
Feb. 12	21.4	0.2	0.02
Feb. 22	22.2	0.8	0.08
Mar. 4	23.5	1.3	0.13
Mar. 14	26.5	3.0	0.30
Mar. 24	31.5	5.0	0.50
April 3	36.3	4.8	0.48
April 13	38.0	1.7	0.17
April 23	46.8	8.8	0.88
May 3	55.3	8.5	0.85
May 13	69.2	13.9	1.39
May 23	80.2	11.0	1.10
June 2	88.8	8.6	0.86
June 12	92.1	3.3	0.33
June 22	97.2	5.1	0.51
July 2	99.1	1.9	0.19
July 12	99.7	0.6	0.06
July 18	100.0	0.3	0.03

occurred in the month of May, in which the daily increment rose to 1.39 per cent of the total annual production of herbage. The lesser maximum rate occurred in October, and both intervals correspond to favorable conditions of temperature and moisture, as may be seen in figures 2, 3, 4, and 5. The period of very low growth rate occurred during the winter, and this activity showed relation to the temperature factor.

2. Approximately 79 per cent of the annual growth of herbage occurred after February 11. The remaining 21 per cent of the growth was in great part made following growth inception in October. Growth in height during November, December, and January, was barely measurable. Before the resumption of very active growth, photosynthesis became active, giving a sharp rise in carbohydrates early in February.

3. The growth rate was decidedly periodic in nature, in that intervals of rapid growth alternated with intervals of depression throughout the annual cycle. The prolonged period of depression which occurred from November to January was marked by root growth, while an apparent correlation with flowering was noted in April. Seed maturity occurred between May 10 and May 21, and this coincided with the rise to the maximum annual growth rate about May 13. Food accumulation in the stem bases also occurred following the decline in growth rate after that date. Again, the periodicity in the growth rate was associated with the annual march of the carbohydrates in the plant, the relation showing inverse proportionality throughout the annual cycle. Although several points of inflexion in the growth rate are shown in the growth curves (figs. 9 and 10), that which occurred following the rise to the annual maximum, about May 13 is the most significant. This point divided the season into two intervals, in the foremost of which vegetative activities were dominant, whereas in the latter those processes are characterized which are important in the reseeding of the range as well as in the growth of the plants during the subsequent season.

Periodic growth in the common sunflower has been reported by Reed and Holland;[11] in certain trees by Illick;[5] in the dairy cow by Brody and Ragsdale;[2] in the domestic fowl by Brody;[1] in the roots of *Tradescantia* and other plants by Priestley and Evershed;[10] in the tomato by Murneek;[8] and by others. The rise and fall in the growth rate preceding and following May 13 was equally rapid, as is shown by the precipitous inclination of the respective limbs of the curve. The growth studies of *Agropyron smithii*[7] revealed a similar rise and fall in the growth rate. Inflexion in the growth rate in this species did not show any correlation with the state of accumulation or diminution of plant foods, or with precipitation, soil moisture, or other external factors. On the other hand, flowering and food accumulation, as well as inflexion in the growth rate, tended to show relation to the time of growth inception in the spring. The occurrence of the annual maximum growth interval in *Stipa pulchra* may also be expected to occur at approximately the same time from year to year, at least in the absence of very wide departures from the usual in environmental factors.

4. A pronounced root growth was observed during the autumn. Each plant removed showed several growing adventitious roots, varying in length from two to twenty centimeters. While this growth was initiated after the rains in November, progress was noticeable at the harvests of December 14 and January 5. Owing to the decline in temperature, conditions appeared to be unfavorable to herbage growth. Little or none occurred during this interval in the W group. The moisture content of the soil, however, was very close to saturation and apparently quite favorable for root growth. Although lateral root branching may have occurred at other intervals during the growth cycle, no further development of adventitious roots was observed.

REGENERATION GROWTH

The term "regeneration" growth is here used to indicate that herbage growth which is produced immediately after a clipping. Regeneration growth occurred within a day or two after the general harvest of all the groups on October 14. The growth response of each plot harvested in turn after October 14, and including May 31, was equally prompt. Regeneration growth did not occur after the final harvests in August. In order to determine the degree of recovery from the second harvest of each of the several groups, measurements were made of the height growth of the herbage produced before and after such harvest. Plants numbers 61 to 90 of each group were used.

HEIGHT GROWTH

In all of the groups harvested between October 14 and March 20, inclusive, the sum of the height growths before and after the second harvest was equal to or greater than the average height growth as indicated by the control group W (tables 2 and 4).

TABLE 4

AVERAGE HEIGHT GROWTH OF EXPERIMENTAL GROUPS BEFORE AND AFTER THE SECOND HARVEST

Group	Number of plants measured	Date of harvest	Average height, centimeters	Average height, per cent
A	20	Oct. 25	4.3	10.0
		Aug. 22	38.6	90.0
		Total	42.9	
B	20	Nov. 2	5.9	14.4
		Aug. 20	35.1	85.6
		Total	41.0	
C	20	Dec. 4	9.2	22.4
		Aug. 20	31.9	77.6
		Total	41.1	
D	20	Jan. 5	8.2	20.7
		Aug. 20	31.4	79.3
		Total	39.6	
F	20	Feb. 10	5.8	15.1
		Aug. 16	32.6	84.9
		Total	38.4	
G	20	Mar. 20	6.4	18.8
		Aug. 17	27.6	81.2
		Total	34.0	
I	20	April 29	18.1	62.6
		Aug. 20	10.8	37.4
		Total	28.9	
J	20	May 16	20.9	72.3
		Aug. 20	8.0	27.7
		Total	28.9	
K	20	May 31	23.8	75.8
		Aug. 20	7.6	24.2
		Total	31.4	

These experimental groups included A, B, C, D, F, and G. Groups I, J, and K, on the other hand, showed a combined height growth materially less than the average of the W group. In these latter groups the second harvest in each case was made in the midst of the interval of rapid growth during April and May. While the growth rates were approximately equal at the time of the second harvests of the groups I and K, the latter more closely approximated the average height of the control W. The much greater growth of group K was probably due to the higher carbohydrate level at the time of the second harvest (table 6).

SEED PRODUCTION

Seed production in the several experimental groups again falls into two general divisions. Seed was produced in Groups A to G, inclusive, whereas the groups H, I, J, and K, produced no seed. In their several capacities for seed production, groups A to G formed a progressive series. Abundant seed was produced in groups A, B, C, and D, whereas the amount produced in groups E, F, and G, ranged from many, to only a few scattered seed stalks in a whole group of 30 plants.

THE METHODS OF ANALYSIS

Preparation of Samples.—The treatment of the harvested materials in the laboratory involved the separation of the herbage, the stem bases, and the roots. The herbage included all growth above five centimeters from the plant crown, or basal portion of the stems. The basal portions of the stems of *Stipa pulchra* form a compact crown which gives rise to adventitious roots. These portions were prepared for analysis by removing all roots and stubble, and are referred to in this paper as stem *bases*. The roots alone constituted the third sample of each harvest.

In the preparation of samples for analysis, all dead straw was removed from the herbage. Dead roots and discolored portions of the stem bases were also rejected. The roots were freed from earth by drawing them between the thumb and fingers, a process which also facilitated the detection of dead roots. The stem bases were cleaned by means of a circular polishing brush attached to the shaft of a fan motor. Preparation of the material for drying was completed usually within two hours after its removal from the field. The material was dried in a ventilated electric oven at 65° C. Following the grinding of the sample, drying was continued at 80° C. Separate analyses were made of the herbage, the stem bases, and the roots.

The Chemical Analyses.—The reducing sugars and sucrose were determined by the colorimetric method as outlined by Willaman and

Davison.[18] The dried samples were extracted first with benzol and then with alcohol. The dried alcoholic extract was dissolved in 100 to 200 cc of distilled water and the color developed in the usual manner, using 2 cc of the unknown, 4 cc of saturated picric acid, and 2 cc of 20 per cent sodium carbonate solutions. Comparisons were made in a Klett Colorimeter.

The polysaccharide determinations were made according to the process described by Thomas and Dutcher.[16] The residue from the alcoholic extract was ground to a suitable degree of fineness in a ball mill, 150 cc of distilled water added, and the whole immersed one hour in a bath of boiling water. After cooling, 2 cc of saliva and 0.1 gram of sodium chloride were added and the incubation carried out at 40° C, with constant shaking during the process. The suspension was then transferred to a 200 cc volumetric flask and made up to volume. After shaking for one-half hour and filtering, 40 cc of the filtrate was placed in a 50 cc volumetric flask to which 4 cc concentrated hydrochloric acid was added. The flask was then heated for three hours, using a funnel as a condenser. Neutralization was effected by using a concentrated solution of sodium hydroxide, care being exercised to avoid an excess of alkali. The contents of the flask were then made up to volume and the determination continued in the manner prescribed for the reducing sugars. All data are reported as grams of reducing sugar per 5-gram dry sample (tables 5 to 13 inclusive). It should be understood that the term 'polysaccharide' is used to designate that fraction obtained by enzymatic digestion. The term 'total carbohydrate' has been used for convenience in expressing the sum total of the reducing sugars, sucrose, and the fraction referred to above.

ANNUAL MARCH OF THE REDUCING SUGARS, SUCROSE, AND POLYSACCHARIDES IN THE PLANTS

Reducing Sugars.—In the herbage the general level of the reducing sugars was relatively high during the interval of vigorous spring growth and low during intervals of slow growth, as during the winter, and again in late summer (figs. 11, 12, table 5). Two maxima occurred, the lesser on February 10 at the onset of the active growth; and the other on May 31, the post-inflection period of declining growth velocity. The upward movement of the mean atmospheric temperature during January and February was accompanied by a similar concentration trend, suggesting conditions progressively more favorable to photosyn-

TABLE 5

REDUCING SUGARS, SUCROSE, AND POLYSACCHARIDES IN HERBAGE, EXPRESSED AS GRAMS OF REDUCING SUGARS IN A FIVE-GRAM OVEN-DRIED SAMPLE

Group	I Plant numbers	II Date of harvest	III Reducing sugars				IV Sucrose				V Total sugars		VI Polysacchardies				VII—Total carbohydrates	
			Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent
A	1-30	Oct. 14, 1926	0.079	1.58			0.041	0.82			0.120	2.40	0.141	2.82			0.261	5.22
	61-90		0.122	2.44	+0.86		0.077	1.54	+0.72		0.199	3.98	0.111	2.22	−0.60	21.3	0.310	6.20
B	1-30	Nov. 2, 1926	0.107	2.14			0.100	2.00			0.207	4.14	0.169	3.38			0.376	7.52
	61-90		0.102	2.04	−0.10	4.7	0.105	2.10	+0.10		0.207	4.14	0.109	2.18	−1.20	30.9	0.316	6.32
C	1-30	Dec. 4, 1926	0.104	2.08			0.059	1.18			0.163	3.26	0.147	2.94			0.310	6.20
	61-90		0.062	1.24	−0.84	40.4	0.087	1.74	+0.56		0.149	2.98	0.156	3.12	+0.18		0.305	6.10
D	1-30	Jan. 5, 1927	0.094	1.88			0.151	3.02			0.245	4.90	0.075	1.50			0.320	6.40
	61-90		0.048	0.96	−0.92	48.9	0.084	1.68	−1.34	44.4	0.132	2.64	0.051	1.02	−0.48	32.0	0.183	3.66
E	1-30	Jan. 29, 1927	0.146	2.92			0.046	0.92			0.192	3.84	0.084	1.68			0.276	5.52
	61-90		0.080	1.60	−1.32	45.3	0.119	2.38	+1.46		0.199	3.98						
F	1-30	Feb. 10, 1927	0.182	3.64			0.051	1.02			0.233	4.66	0.182	3.64			0.415	8.30
	65-90		0.063	1.26	−2.38	65.4	0.072	1.44	+0.42		0.135	2.70	0.112	2.24	−1.40	38.5	0.247	4.94
G	1-30	Mar. 20, 1927	0.167	3.34			0.060	1.20			0.227	4.54	0.103	2.06			0.330	6.60
	65-90		0.077	1.54	−1.80	53.9	0.093	1.86	+0.66		0.170	3.40	0.115	2.30	+0.24		0.285	5.70
H	1-30	April 14, 1927	0.150	3.00			0.058	1.16			0.208	4.16	0.169	3.38			0.377	7.54
	65-90		0.133	2.66	−0.34	11.3	0.095	1.90	+0.74		0.228	4.56						
I	1-30	April 29, 1927	0.127	2.54			0.087	1.74			0.214	4.28	0.147	2.94			0.361	7.22
	65-90		0.050	1.00	−1.54	60.7	0.090	1.80	+0.06		0.140	2.80	0.050	1.00	−1.94	66.0	0.190	3.80
J	1-30	May 16, 1927	0.143	2.86			0.052	1.04			0.195	3.90	0.129	2.58			0.324	6.48
	65-90		0.086	1.72	−1.14	39.9	0.060	1.20	+0.16		0.146	2.92	0.132	2.64	+0.06		0.278	5.56
K	1-30	May 31, 1927	0.199	3.98			0.136	2.72			0.335	6.70	0.122	2.44			0.457	9.14
	65-90		0.115	2.30	−1.68	42.2	0.100	2.00	−0.72	26.4	0.215	4.30	0.116	2.32	−0.12	4.9	0.331	6.62
L	1-30	June 22, 1927	0.070	1.40			0.140	2.80			0.210	4.20	0.110	2.20			0.320	6.40

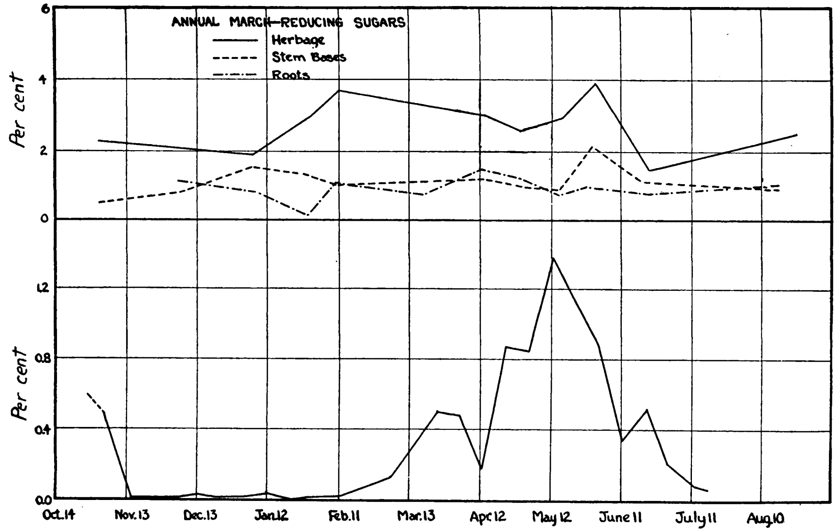

Fig. 11. Upper: Annual march of reducing sugars in herbage, stem bases, and roots. Lower: The daily growth of the plants.

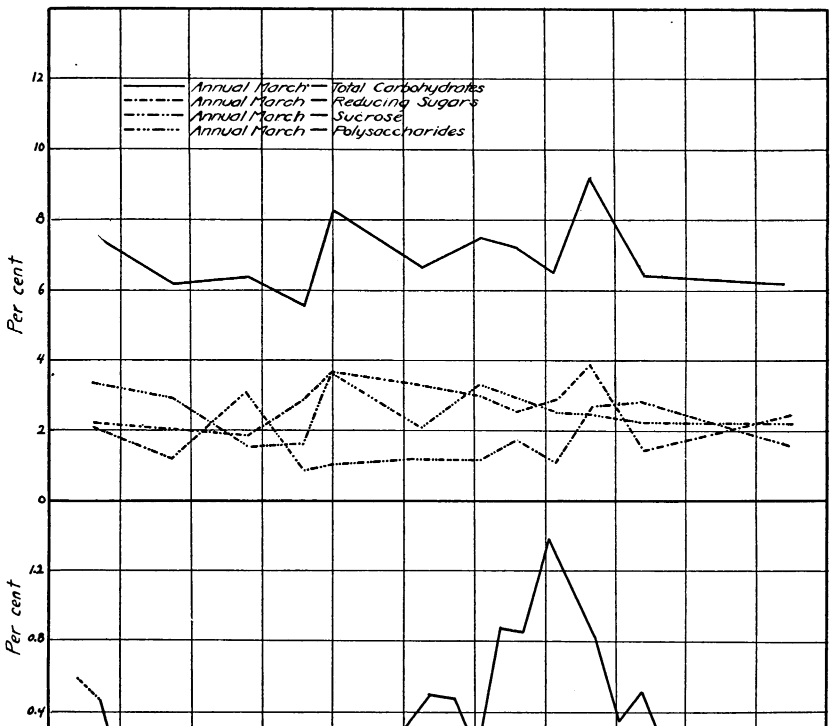

Fig. 12. Upper: The carbohydrates of the herbage. Lower: The daily growth of the plants.

thetic activity (fig. 4). The high level of carbohydrates of February 10 was maintained during the period of growth activity following that date, but decreased slightly as the growth rate rose to the annual maximum. With the inflection in the growth rate, which was about May 13, the concentration of reducing sugars rose and then in the

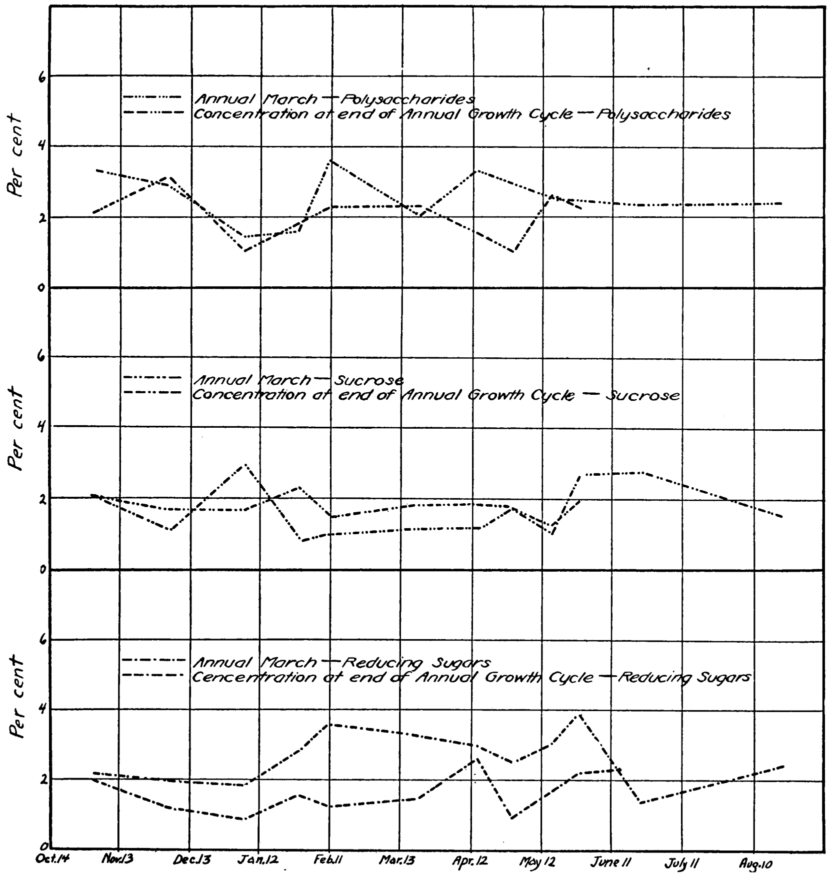

Fig. 13. The annual march of the total carbohydrates of the herbage, and the final level at the close of the growth cycle.

latter part of June promptly declined as the herbage approached maturity, a time approaching the rest period. The two inter-season high points of concentration correspond almost exactly to the high points of concentration in the total carbohydrates. Although some inconsistency obtained in the level of the reducing sugars, as shown by the final harvest (fig. 13), nevertheless those groups in which the second harvest was made early in the growth cycle tend to show low concentration of the reducing sugars, whereas those in which the second harvest was made later in the annual growth cycle tend to show high concentration. A pronounced difference in the state of maturity of the several groups was noticeable at this final harvest of all groups.

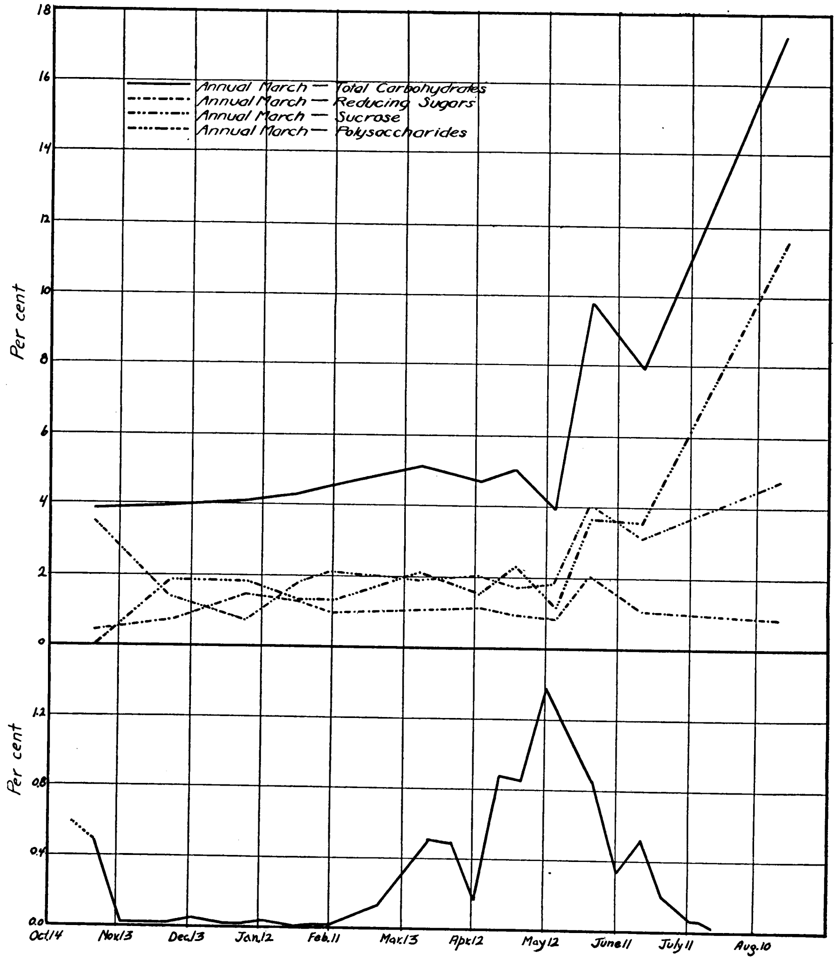

Fig. 14. Upper: The carbohydrates of the stem bases. Lower: The daily growth of the plants.

In the stem bases the concentration of the reducing sugars was lower than that in the herbage; and except for the post-inflection rise, it was practically constant for the remainder of the annual cycle (fig. 14, table 6).

TABLE 6

REDUCING SUGARS, SUCROSE, AND POLYSACCHARIDES IN STEM BASES, EXPRESSED AS GRAMS OF REDUCING SUGARS IN A FIVE-GRAM OVEN-DRIED SAMPLE

Group	I Plant numbers	II Date of harvest	III Reducing sugars				IV Sucrose				V Total sugars		VI Polysaccharides				VII Total carbohydrates		
			Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Total decline in per cent
A	1-30	Oct. 14, 1926	0.039	0.78			0.092	1.84			0.131	2.62	0.191	3.82			0.322	6.44	
	31-60		0.048	0.96	+0.18		0.080	1.60	−0.24	11.9	0.128	2.56	0.084	1.68	−2.14	55.9	0.212	4.24	35
	61-90		0.042	0.84	+0.06		0.245	4.90	+3.06		0.287	5.74	0.580	11.60	+7.78		0.867	17.34	
B	1-30	Nov. 2, 1926	0.022	0.44			0.171	3.42			0.193	3.86	0.000	0.00			0.193	3.86	
	61-90		0.088	1.76	+1.32		0.272	5.44	+2.02		0.360	7.20							
C	1-30	Dec. 4, 1926	0.036	0.72			0.070	1.40			0.106	2.12	0.091	1.82			0.197	3.94	
	31-60		0.036	0.72	0.00		0.066	1.32	−0.08	5.7	0.102	2.04	0.091	1.82			0.193	3.86	2
	61-90		0.035	0.70	−0.02	2.8	0.200	4.00	+2.60		0.235	4.70							
D	1-30	Jan. 5, 1927	0.075	1.50			0.038	0.76			0.113	2.26	0.091	1.82			0.204	4.08	
	31-60		0.036	0.72	−0.78	52.0	0.059	1.18	+0.42		0.095	1.90	0.053	1.06	−0.76	41.8	0.148	2.96	27
	61-90		0.070	1.40	−0.10		0.290	5.80	+5.04		0.360	7.20							
E	1-30	Jan. 29, 1927	0.061	1.22			0.092	1.84			0.153	3.06	0.065	1.30			0.218	4.36	
	61-90		0.040	0.80	−0.42	34.4	0.256	5.12	+3.28		0.296	5.92	0.532	10.64	+9.34		0.828	16.56	
F	1-30	Feb. 10, 1927	0.049	0.98			0.109	2.18			0.158	3.16	0.066	1.32			0.224	4.48	
	31-60		0.028	0.56	−0.42	43.5	0.037	0.74	−1.44	66.0	0.065	1.30	0.062	1.24	−0.08	60.0	0.127	2.54	43
	61-90		0.042	0.84	−0.14		0.208	4.16	+1.98		0.250	5.00							
G	1-30	Mar. 20, 1927	0.054	1.08			0.095	1.90			0.149	2.98	0.109	2.18			0.258	5.16	
	31-60		0.035	0.70	−0.38	35.2	0.029	0.58	−1.32	69.4	0.064	1.28	0.048	0.96	−1.22	55.8	0.112	2.24	56
	61-90		0.039	0.78	−0.30		0.206	4.12	+2.22		0.245	4.90	0.535	10.70	+7.25		0.780	15.60	
H	1-30	April 14, 1927	0.055	1.10			0.101	2.02			0.156	3.12	0.078	1.56			0.234	4.68	
	31-60		0.034	0.68	−0.42	38.2	0.049	0.98	−1.04	51.5	0.083	1.66	0.125	2.50	+0.94		0.208	4.16	11
	61-90		0.031	0.62	−0.48		0.229	4.58	+2.54		0.260	5.20	0.470	9.40	+7.84		0.730	14.60	
I	1-30	April 29, 1927	0.049	0.98			0.089	1.78			0.138	2.76	0.116	2.32			0.254	5.08	
	31-60		0.020	0.40	−0.58	59.2	0.048	0.96	−0.82	46.1	0.068	1.36	0.047	0.94	−1.38	59.5	0.115	3.30	35
	61-90		0.049	0.98			0.210	4.20	+2.42		0.259	5.18							
J	1-30	May 16, 1927	0.043	0.86			0.094	1.88			0.137	2.74	0.059	1.18			0.196	3.92	
	31-60		0.021	0.42	−0.44	51.1	0.054	1.08	−0.80	42.5	0.075	1.50	0.062	1.24	+0.06		0.137	2.74	30
	61-90		0.040	0.80	−0.06		0.335	6.70	+4.82		0.375	7.50	0.125	2.50	+1.32		0.500	10.00	
K	1-30	May 31, 1927	0.103	2.06			0.203	4.06			0.306	6.12	0.187	3.74			0.493	9.86	
	31-60		0.052	1.04	−1.02	49.5	0.094	1.88	−2.18	53.5	0.146	2.92	0.150	3.00	−0.74	19.7	0.296	5.92	40
	61-90		0.121	2.42	+0.36		0.220	4.40	+0.34		0.341	6.82	0.337	6.74	+3.00		0.678	13.56	
L	1-30	June 22, 1927	0.055	1.10			0.160	3.20			0.215	4.30	0.179	3.58			0.394	7.88	

In the roots the general behavior of the reducing sugars was similar to that in the stem bases, in that the concentration was relatively constant throughout the annual growth cycle (fig. 15, table 7).

Summarizing: In the herbage the concentration of reducing sugars was relatively high during intervals of active growth. However, where the second harvesting was made early in the growth cycle the

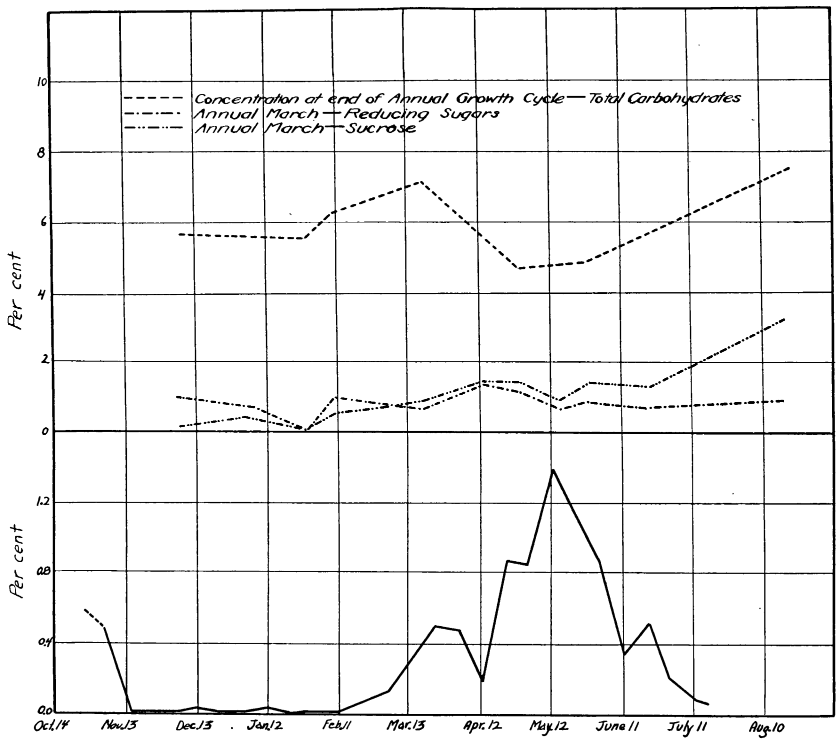

Fig. 15. Upper: The carbohydrates of the roots. Lower: The daily growth of the plants.

concentration was low, being in opposition to that in similar second harvests which were made later in the growth cycle. In the stem bases and roots the reducing sugars were similar in concentration and in constancy.

Sucrose.—*In the herbage* the concentration of sucrose was relatively low during active growth, suggesting a minor importance of this sugar in the metabolism of the actively growing portion of the plant. Two maxima occur, the greater in January, being in contrast with the levels of both of reducing sugars and polysaccharides. The

TABLE 7

REDUCING SUGARS, SUCROSE, AND POLYSACCHARIDES IN ROOTS, EXPRESSED AS GRAMS OF REDUCING SUGARS IN A FIVE-GRAM OVEN-DRIED SAMPLE

Group	I Plant numbers	II Date of first harvest	III Reducing sugars				IV Sucrose				V Total sugars		VI Polysaccharides*			VII—Total carbohydrates	
			Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Grams	Per cent	Per cent difference	Grams	Per cent
A	1–30	Oct. 14, 1926	0.033	0.66			0.072	1.44			0.105	2.10	0.077	1.54		0.182	3.64
	61–90		0.045	0.90	+0.24		0.165	3.30	+1.86		0.210	4.20	0.166	3.32	+1.78	0.376	7.52
B	1–30	Nov. 2, 1926															
	31–60		0.050	1.00			0.011	0.22			0.061	1.22					
C	1–30	Dec. 4, 1926	0.050	1.00			0.005	0.10			0.055	1.10					
	31–60		0.052	1.04	+0.04		0.006	0.12	+0.02		0.058	1.16					
	61–90		0.000	0.00			0.179	3.58	+3.48		0.179	3.58	0.103	2.06		0.282	5.64
D	1–30	Jan. 5, 1927	0.039	0.78			0.021	0.42			0.060	1.20	0.046	0.92		0.106	2.12
	31–60		0.026	0.52	−0.26	33.3	0.007	0.14	−0.28	66.7	0.033	0.66					
E	1–30	Jan. 29, 1927	0.000	0.00			0.000	0.00			0.000	0.00					
	61–90		0.000	0.00			0.162	3.24	+3.24		0.162	3.24	0.117	2.34		0.279	5.58
F	1–30	Feb. 10, 1927	0.050	1.00			0.027	0.54			0.077	1.54					
	31–60		0.027	0.54	−0.46	46.0	0.018	0.36	−0.18	33.3	0.045	0.90					
	61–90		0.037	0.74	−0.26	26.0	0.166	3.32	+2.78		0.203	4.06	0.112	2.24		0.315	6.30
G	1–30	Mar. 20, 1927	0.035	0.70			0.045	0.90			0.080	1.60					
	31–60		0.023	0.46	−0.24	34.3	0.017	0.34	−0.56	62.2	0.040	0.80					
	61–90		0.000	0.00			0.235	4.70	+3.80		0.235	4.70	0.122	2.44		0.357	7.14
H	1–30	April 14, 1927	0.067	1.34			0.076	1.52			0.143	2.86					
	31–60		0.027	0.54	−0.80	59.7	0.023	0.46	−1.06	69.8	0.050	1.00					
I	1–30	April 29, 1927	0.057	1.14			0.074	1.48			0.131	2.62					
	31–60		0.027	0.54	−0.60	52.6	0.026	0.52	−0.96	64.9	0.053	1.06					
	61–90		0.054	1.08	−0.06	5.3	0.112	2.24	+0.76		0.166	3.32	0.068	1.36		0.234	4.68
J	1–30	May 16, 1927	0.035	0.70			0.049	0.98			0.084	1.68					
	31–60		0.040	0.80	+0.10		0.035	0.70	−0.28	28.6	0.075	1.50					
K	1–30	May 31, 1927	0.042	0.84			0.070	1.40			0.112	2.24					
	31–60		0.040	0.80	−0.04	4.8	0.072	1.44	+0.04		0.112	2.24					
	61–90		0.060	1.20	+0.36		0.113	2.26	+0.86		0.173	3.46	0.068	1.36		0.241	4.82
L	1–30	June 22, 1927	0.032	0.64			0.065	1.30			0.097	1.94					

* Due to insufficient material the determination for polysaccharides was omitted in some instances.

somewhat lesser rise was in the post-inflection period of declining growth rate (fig. 12, table 5).

In the stem bases the concentration of sucrose was greater than that of the reducing sugars, but there was a close parallelism between the respective levels of these substances (fig. 14). The maximum concentration occurred in the post-inflection interval of the annual growth cycle, whereas the interval of very rapid growth showed a much lower level.

In the roots the concentration of sucrose was relatively constant throughout the annual growth cycle of the tops, and although the level gradually rose as root growth subsided, it was not so precipitous as in the post-inflection interval of the herbage growth (fig. 15, table 7). The large excess of sucrose, as shown by the final harvest in August, emphasized the importance of this sugar as an accumulation product in the roots and stem bases. There was a definite parallelism in the annual march of the sucrose with that of the reducing sugars.

Polysaccharides.—In the herbage the concentration of polysaccharides was not parallel to that of sucrose. The same general movements, however, obtained in that the high levels prevailed during intervals of low growth activity. Moreover, the low levels occurred during intervals of active growth (fig. 12). There is a definite parallelism in the seasonal march of the polysaccharides and that of the reducing sugars.

In the stem bases the general level of the polysaccharides was low during rapid growth activity of both roots and herbage. The maximum level was reached in the post-inflection interval (fig. 14).

THE CARBOHYDRATE BEHAVIOR IN REGENERATION GROWTH

The behavior of the carbohydrates of the stem bases following regeneration growth tends to show the same correlation with the growth rate as does the annual march of these materials in untreated plants (fig. 16, table 8). While a generally low carbohydrate level prevailed throughout the period preceding May 16, harvesting of the herbage was followed by a further decline in the carbohydrate concentration in the stem bases. The renewal of growth *following harvesting* was immediate. The decline in the carbohydrate level, including reducing sugars, sucrose, and polysaccharides (tables 6 and 8) was likewise immediate, having been found seven days after harvest in group H, and with no indication of recovery 15 days after harvest in groups F and G. Some degree of uniformity was shown. For example, the amount of the decline in the stem bases of group I, harvested for the first time April 29, was, respectively, 59.2 per cent of the reducing sugars,[3] 46.1 per cent of the sucrose, and 59.5 per cent

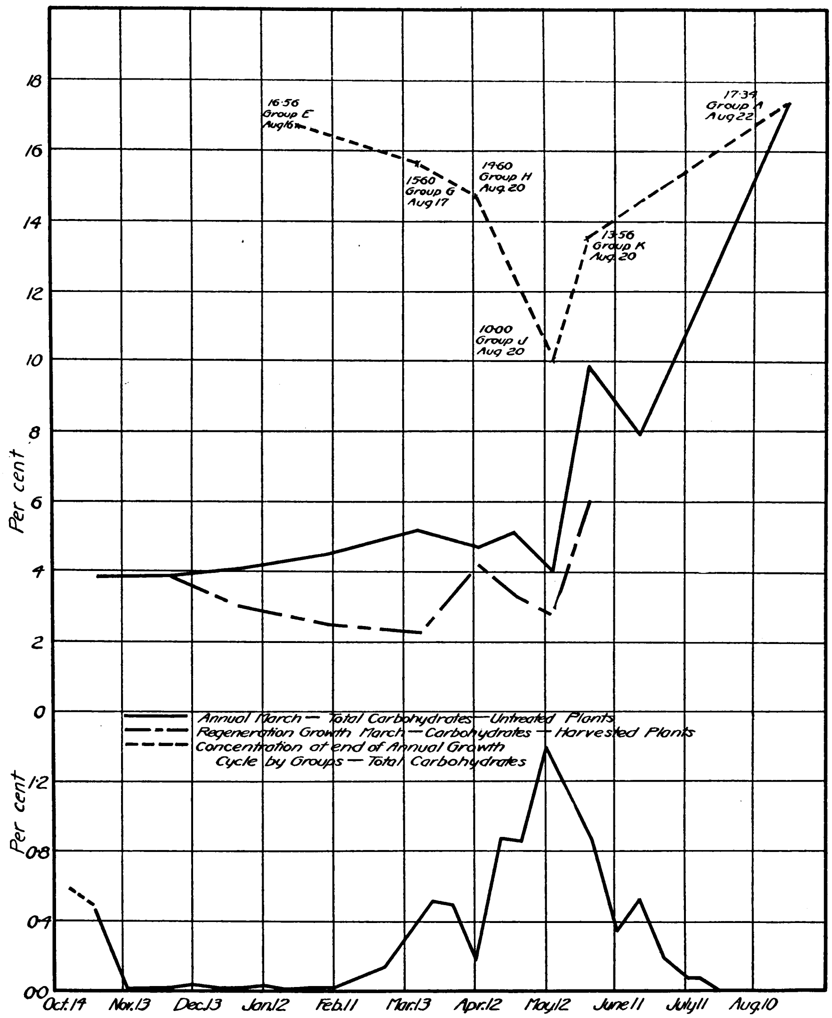

Fig. 16. Upper: The carbohydrates of the stem bases; comparison of annual march, regeneration growth and the concentration at the end of season. Lower: The daily growth of the plants.

[3] Table 6, column 3, group I; reducing sugars in sample on April 29 were .049 gm. The reducing sugars on May 9 were .020 gm., a difference from the first harvest of .029. Thus $\frac{.029 \times 100}{.049}$ or 59 per cent, represents the decline.

TABLE 8

REDUCING SUGARS, SUCROSE, AND POLYSACCHARIDES IN STEM BASES OF PLANTS NUMBERS 31–60, EXPRESSED AS REDUCING SUGARS IN A FIVE-GRAM OVEN-DRIED SAMPLE

Group	I Date of collection	II Reducing sugars				III Sucrose				IV Polysaccharides				V Total carbohydrates		
		Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Total decline in per cent
A	Oct. 25, 1926	0.048	0.96	+0.18	....	0.080	1.60	−0.24	11.9	0.084	1.68	−2.14	55.9	0.212	4.24	35.0
C	Dec. 14, 1926	0.036	0.72	0.00	....	0.066	1.32	−0.08	5.7	0.091	1.82	....	....	0.193	3.86	2.0
D	Jan. 20, 1927	0.036	0.72	−0.78	52.0	0.059	1.18	+0.42	....	0.053	1.06	−0.76	41.8	0.148	2.96	27.0
F	Feb. 26, 1927	0.028	0.56	−0.42	43.5	0.037	0.74	−1.44	66.0	0.062	1.24	−0.08	60.0	0.127	2.54	43.0
G	April 4, 1927	0.035	0.70	−0.38	35.2	0.029	0.58	−1.32	69.4	0.048	0.96	−1.22	55.8	0.112	2.24	56.0
H	April 21, 1927	0.034	0.68	−0.42	38.2	0.049	0.98	−1.04	51.5	0.125	2.50	+0.94	....	0.208	4.16	11.0
I	May 9, 1927	0.020	0.40	−0.58	59.2	0.048	0.96	−0.82	46.1	0.047	0.94	−1.38	59.5	0.115	3.30	35.0
J	May 23, 1927	0.021	0.42	−0.44	51.1	0.054	1.08	−0.80	42.5	0.062	1.24	+0.06	....	0.137	2.74	30.0
K	June 10, 1927	0.052	1.04	−1.02	49.5	0.094	1.88	−2.18	53.5	0.150	3.00	−0.74	19.7	0.296	5.92	40.0

of the polysaccharides, whereas group C, harvested December 4, was only slightly affected. Based upon the total carbohydrate concentration, the two groups (C and H), harvested early in the growth cycle, during low growth rate, showed only a slight decline (2 per cent and 11 per cent, column 7), whereas sharp decline toward low concentration occurred in those groups which were harvested later or during high growth rate. The loss to the plant due to decreased carbohydrate concentration following harvesting was seen in the decreased height growth of the herbage (groups I, J, and K, table 4, page 79). The concentration of the sugars in the roots following harvesting showed the same general behavior (table 9).

TABLE 9

SUGARS IN ROOTS OF PLANT NUMBERS 31–60, EXPRESSED AS REDUCING SUGAR IN A FIVE-GRAM OVEN-DRIED SAMPLE

Group	I Date of collection	II Reducing sugars				III Sucrose			
		Grams	Per cent	Per cent difference	Decline in per cent	Grams	Per cent	Per cent difference	Decline in per cent
B	Nov. 12, 1926	0.050	1.00	......	......	0.011	0.22	......	......
C	Dec. 14, 1926	0.052	1.04	+0.04	......	0.006	0.12	+0.02	......
D	Jan. 20, 1927	0.026	0.52	−0.26	33.3	0.007	0.14	−0.28	66.7
F	Feb. 26, 1927	0.027	0.54	−0.46	46.0	0.018	0.36	−0.18	33.3
G	April 4, 1927	0.023	0.46	−0.24	34.3	0.017	0.34	−0.56	62.2
H	April 21, 1927	0.027	0.54	−0.80	59.7	0.023	0.46	−1.06	69.8
I	May 9, 1927	0.027	0.54	−0.60	52.6	0.026	0.52	−0.96	64.9
J	May 23, 1927	0.040	0.80	+0.10	......	0.035	0.70	−0.28	28.6
K	June 10, 1927	0.040	0.80	−0.04	4.8	0.072	1.44	+0.04	......

That the loss resulting from harvesting may be temporary is shown by a comparison of the carbohydrate concentration in groups M and H, on April 14 (table 10).

TABLE 10

GROUP M.—REDUCING SUGARS, SUCROSE, AND POLYSACCHARIDES OF STEM BASES EXPRESSED IN GRAMS OF REDUCING SUGARS IN A FIVE-GRAM OVEN-DRIED SAMPLE

Plant numbers	Date of harvest	Reducing sugar		Sucrose		Total sugars		Polysaccharides		Total carbohydrates	
		Grams	Per cent	Grams	Per cent	Grams	Per cent	Grams	Per cent	Grams	Per cent
†1–90	Apr. 14	0.124	2.48	0.061	1.22	0.185	3.70	0.069	1.38	0.254	5.08
*Group M	Apr. 14	0.055	1.10	0.101	2.02	0.156	3.12	0.078	1.56	0.234	4.68

† Previous harvesting dates October 14 and December 14.

* Group H, from table 6, represents undisturbed growth.

Although group M was harvested three times prior to that of April 14, as compared to one harvesting of group H prior to April 14, the total carbohydrates in the stem bases were approximately the same in both groups. While a decline in the seasonal level of the carbohydrates following harvest and regeneration growth was shown in all groups, the amount was small, and restoration, as in group M, apparently occurred in those groups harvested early in the growth cycle. Again, on the basis of the food level at the close of the annual cycle, group E shows practically complete recovery from the second harvest made on January 29 (table 6, column 7). The groups which did not show maximum carbohydrate accumulations at the end of the cycle were—G, H, J, and K, harvested, respectively, March 20, April 14, May 16, and May 31, during high growth rate (fig. 16). The deficiencies in these groups were, respectively, 10 per cent, 15.8 per cent, 42.2 per cent, and 21.8 per cent (calculated from table 6).

These diminished food levels involve factors other than merely the second harvesting of the herbage. The second harvest of groups H, J, and K, were made preceding seed maturity, in the midst of seed maturity, and following that event, respectively. The diminution in the food level, however, showed relation to the increasing growth rate and to the time of harvesting, rather than to the advent of seed maturity. Although group K was harvested during a relatively high growth rate, food accumulation began approximately 15 days prior to the second harvest of this group. Thus according to quantitative food deposits in the stem bases at the end of the growth cycle the favorable intervals of harvesting were in the early period of low growth rate (autumn and winter), whereas the unfavorable intervals were during high growth rate (late spring and early summer). This conclusion is consistent with the results of the height growth measurements and seed production as previously indicated in this paper.

FOOD ACCUMULATION

According to the annual march of the carbohydrate concentration of the plant, a low level prevailed in the stem bases throughout the growth cycle prior to May 16. Although the concentration in the herbage was greater than that of the stem bases during this interval, low levels likewise occurred in the herbage. The inverse ratio which obtained between the food march and the growth rate both in the herbage and the stem bases shows the growth rate to be a factor in food accumulation. Accumulation implies an excess of foods above that utilized in growth processes. Such an interval occurred in the herbage between January 29 and February 10 (fig. 12). The carbohydrate concentration in the stem bases also increased following this interval but declined again as the growth rate rose to its annual maximum (fig. 14). A second interval of excess carbohydrates in the herbage occurred between May 16 and May 31, and a prompt rise in these foods in the stem bases and roots followed. Accumulation during this interval was favored by the declining growth rate and by a large leaf area, since approximately 73 per cent of the annual growth was completed by May 16.

TABLE 11

REDUCING SUGARS, SUCROSE, AND POLYSACCHARIDES IN HERBAGE OF PLANTS NUMBERS 61–90, AUGUST COLLECTION. EXPRESSED AS REDUCING SUGARS IN A FIVE-GRAM OVEN-DRIED SAMPLE

Group	Date of collection	Reducing sugars		Sucrose		Total sugars		Poly-saccharides		Total carbo-hydrates	
		Grams	Per cent	Grams	Per cent	Grams	Per cent	Grams	Per cent	Grams	Per cent
A	Aug. 22, 1927	0.122	2.44	0.077	1.54	0.199	3.98	0.111	2.22	0.310	6.20
B	Aug. 20, 1927	0.102	2.04	0.105	2.10	0.207	4.14	0.109	2.18	0.316	6.32
C	Aug. 20, 1927	0.062	1.24	0.087	1.74	0.149	2.98	0.156	3.12	0.305	6.10
D	Aug. 10, 1927	0.048	0.96	0.084	1.68	0.132	2.64	0.051	1.02	0.183	3.66
E	Aug. 16, 1927	0.080	1.60	0.119	2.38	0.199	3.98	....	....	....	....
F	Aug. 16, 1927	0.063	1.26	0.072	1.44	0.135	2.70	0.112	2.24	0.247	4.94
G	Aug. 17, 1927	0.077	1.54	0.093	1.86	0.170	3.40	0.115	2.30	0.285	5.70
H	Aug. 20, 1927	0.133	2.66	0.095	1.90	0.228	4.56	....	....	....	....
I	Aug. 20, 1927	0.050	1.00	0.090	1.80	0.140	2.80	0.050	1.00	0.190	3.80
J	Aug. 20, 1927	0.086	1.72	0.060	1.20	0.146	2.92	0.132	2.64	0.278	5.56
K	Aug. 20, 1927	0.115	2.30	0.100	2.00	0.215	4.30	0.116	2.32	0.331	6.62

Some variation in the total carbohydrate concentration of the herbage at the final collection in August occurred in the several experimental groups (table 11). Little or no relation is shown between the final level and the respective intervals of the second harvest of each group. Very probably the level found to obtain during the latter half of May and in the early part of June was of greater significance to the plant, since a pronounced rise in the food level of the stem bases occurred at the same time.

The final collection of the stem bases of groups E, G, H, and J showed a progressive decline in the food level (table 12). While the final concentration in group E was approximately equal to that of the control group A, the accumulation in group J was found to be the lowest of all the experimental groups. As the time of the second harvest approached the interval of seed maturity, the deficit in the accumulated foods became greater, group J having been harvested in the midst of that interval. Group K was harvested some ten or fifteen days after the seed had been cast; and although the food level was greater than that in group J, it was lower than that in the control group A. The concentrations of the several carbohydrates in the

TABLE 12

REDUCING SUGARS, SUCROSE, AND POLYSACCHARIDES IN STEM BASES OF PLANTS NUMBERS 61–90, AUGUST COLLECTION, EXPRESSED AS REDUCING SUGARS IN A FIVE-GRAM OVEN-DRIED SAMPLE

Group	Reducing sugars			Sucrose			Polysaccharides			Total carbohydrates	
	Grams	Per cent	Per cent difference	Grams	Per cent	Per cent difference	Grams	Per cent	Per cent difference	Grams	Per cent
A	0.042	0.84	0.06	0.245	4.90	+3.06	0.580	11.60	7.78	0.867	17.34
B	0.088	1.76	+1.32	0.272	5.44	+2.02					
C	0.035	0.70	−0.02	0.200	4.00	+2.60					
D	0.070	1.40	−0.10	0.290	5.80	+5.04					
E	0.040	0.80	−0.42	0.256	5.12	+3.28	0.532	10.64	+9.34	0.828	16.56
F	0.042	0.84	−0.14	0.208	4.16	+1.98					
G	0.039	0.78	−0.30	0.206	4.12	+2.22	0.535	10.70	+7.25	0.780	15.60
H	0.031	0.62	−0.48	0.229	4.58	+2.54	0.470	9.40	+7.84	0.730	14.60
I	0.049	0.98		0.210	4.20	+2.42					
J	0.040	0.80	−0.06	0.335	6.70	+4.82	0.125	2.50	+1.32	0.500	10.00
K	0.121	2.42	+0.36	0.220	4.40	+0.34	0.337	6.74	+3.00	0.678	13.56

stem bases of group A, at the close of the growth cycle, were 0.84 per cent reducing sugars, 4.90 per cent sucrose, and 11.60 per cent polysaccharides. Of this amount more than 87 per cent was shown to be available for use in the physiological processes incident to the life and growth of the plant.

TABLE 13

REDUCING SUGARS, SUCROSE AND POLYSACCHARIDES IN ROOTS OF PLANTS 61–90, AUGUST HARVEST, EXPRESSED AS REDUCING SUGARS IN A FIVE-GRAM OVEN-DRIED SAMPLE

Group	Reducing sugars			Sucrose			Polysaccharides			Total carbohydrates	
	Grams	Per cent	Per cent difference	Grams	Per cent	Per cent difference	Grams	Per cent	Per cent difference	Grams	Per cent
A	0.045	0.90	+0.24	0.165	3.30	+1.86	0.166	3.32	+1.78	0.376	7.52
C	0.000	0.00		0.179	3.58	+3.48	0.103	2.06		0.282	5.64
E	0.000	0.00		0.162	3.24	+3.24	0.117	2.34		0.279	5.58
F	0.037	0.74	−0.26	0.166	3.32	+2.78	0.112	2.24		0.315	6.30
G	0.000	0.00		0.235	4.70	+3.80	0.112	2.44		0.357	7.14
I	0.054	1.08	0.06	0.112	2.24	+0.76	0.068	1.36		0.234	4.68
K	0.060	1.20	+0.36	0.113	2.26	+0.83	0.068	1.36		0.241	4.82

The final concentration of the carbohydrates of the roots at the August collection showed a very general agreement with that of the stem bases, in that low levels prevailed in those groups harvested at seed maturity (table 13, fig. 15).

The importance of the polysaccharides and sucrose as accumulation products is suggested by the large excess of these foods over the reducing sugars. Large amounts of polysaccharides as food deposits have also been reported for other members of the tribe *Agrostideae* to which *Stipa pulchra* belongs.(3) Since the amount of the food deposits in the stem bases was proportionately much greater than in the roots, the former constitute the chief organ of accumulation in the species studied.

DISCUSSION

The Growth Cycle of Stipa Pulchra.—The growth cycle of *Stipa pulchra* is divided into definite intervals, which are characterized by different growth rates. Flowering, the development of seed, the deposit of carbohydrate foods in the perennial organs, and the maturity of the herbage follow growth inception in an orderly sequence.

Although the growth rate varies somewhat in accordance with the environmental complex, certain correlations with internal factors are also evident. The depression in growth rate which occurred between March 25 and April 14, coincided with the period of flowering and the formation of fruit. Similar correlations have been reported by Murneek.(8) While the rapid rise in the growth rate to the annual maximum in May was no doubt associated with the favorable external factors, the equally rapid decline in growth following immediately, appears to be related to the growth habits of the particular species. Again, this precipitous rise and fall in the growth velocity preceding and following May 13, marked a division point in which the low food level prevalent in the perennial organs throughout nearly four-fifths of the annual growth cycle, was superseded by the high level found to be characteristic of the rest period. The value of these several growth phenomena, when applied to grazing periods, lies in the regularity and the uniformity with which they occur from year to year.

Food Accumulation and Growth.—An inverse ratio between the food march and the growth rate obtained in the herbage as well as in the stem bases and roots. From this it may be inferred that prior to May 13 the utilization of food in the growth processes exceeded its availability, resulting in the low level of carbohydrates in the stem bases and roots which obtained during this period. Again, since the accumulation of foods implies an excess of such materials above that utilized for growth and other physiological processes, deposit in the stem bases and roots could not proceed until the change in the acceleration of the growth rate had taken place, in this instance being May 13. This conclusion is supported by the chemical analyses of the several groups. Again, the increment growth from April 29 to May 13 was approximately equal to that which occurred between May 13 and May 31 (table 3, fig. 10). The food deposited in the stem bases during the latter interval amounted to 44 per cent of the total increase which obtained in the late phase of the growth cycle. The concentration for the interval April 29 to May 16, on the other hand, showed an appreciable decline (groups I, J, and K, table 6). The growth acceleration of the former, however, was positive, whereas that of the latter was negative. Again, on April 29 only 52 per cent of the total annual leafage was available for the manufacture of carbohydrates, whereas 70 per cent was available on May 13. Food deposit, therefore, is related to low or to declining growth velocity and is also dependent upon the amount of leaf area available for its manufacture.

Injury Through Harvesting.—Injury following frequent harvesting has been established for a number of grasses and in diversified climatic associations.

In a study made by Sampson,[12] *Festuca viridula* plots were harvested three times annually for three years and no treatment at all was applied during the fourth and fifth years of the study. Vegetative growth, including the size of the tufts, decreased annually during the treatment, showing a decline in vigor. No flower stalks were produced during the fourth year while only a few appeared during the fifth year. Similar plots harvested once annually produced flower stalks as uniformly and abundantly as in the untreated or control plots.

Sampson and Malmsten[13] found that *Stipa lettermani* and *Agropyron violaceum,* clipped five times annually for three successive years, yielded in the third year of treatment only 12 per cent and 9 per cent, respectively, of the amount of herbage that was produced in the first year of treatment. *Bromus polyanthus,* a short-lived perennial, treated in a like manner, showed a mortality of 100 per cent.

Sarvis[15] found that *Stipa comata* disappeared entirely under frequent harvesting. *Stipa minor* as well as other grasses showed high mortality and lowered vigor as a result of clipping experiments.

McCarty[7] judged yields on a basis of their calculated values for the second year of treatment, thus attempting to eliminate seasonal variation from year to year. Quadrats of *Agropyron smithii,* harvested four times during one year, yielded 84 per cent of their calculated values during the second year of treatment. Quadrats harvested seven and eight times in one year yielded, respectively, 50 per cent and 40 per cent of their estimated values during the succeeding year. Quadrats of *Bulbilis*[4] *dactyloides,* clipped four times, were reduced to 71 per cent of their calculated values for the second year of treatment.

In each of the plots of *Agropyron* and *Bulbilis* the vigorous growth of the first year of treatment gave way to feeble vegetative activity, while the mortality due to winter killing was very high during the rest period. Chemical analyses of *Agropyron smithii*(7) showed low yields to be consistently associated with diminished food accumulations in the subterranean organs.

Waters(17) observed that the bulbs of *Phleum pratense* were depleted by the rapid growth of the plants, and if cut at such an interval, low vigor, low yields, and winter killing resulted.

Graber, Nelson, Luckel and Albert(4) reported that low yields and winter killing were associated with diminished food supply in the roots of alfalfa, and that the diminished food materials resulted from cutting in immature stages of growth.

In the present studies the reaction upon growth and food relationships resulting from one harvest distributed in the several groups throughout the growth cycle, may be summarized as follows:

1. Regeneration growth occurred in all plots harvested between October 14 and May 31, inclusive. The amount of growth in each case showed proportionality to the growth rate, as measured in group W, the untreated plants.

2. The carbohydrate concentration in the stem bases declined below the seasonal level coincident with the renewal of the growth processes after harvesting, and a loss varying from 2 per cent to 56 per cent was sustained. This loss was relatively small in groups C and H, clipped in each case when the growth velocity was low, but a greater loss was recorded in the remaining groups.

3. The groups harvested prior to the resumption of active growth (February 11) produced abundant seed and herbage, and came to maturity at the same time as did the untreated plants. Moreover, the stem bases and roots contained maximum carbohydrate food deposits at the close of the growth cycle (groups A and E, tables 6 and 7).

4. The groups harvested after the resumption of active growth, including those clipped on March 20 and later, produced few or no

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[4] From unpublished data.

seeds. Decrease in the carbohydrate accumulations at the end of the annual growth cycle resulted, the diminution varying from 10 per cent in group G, to 42 per cent in group J, based in each case upon the control group A (fig. 16, tables 6 and 12). The groups harvested on April 14 and later showed delay in the maturity of the herbage and produced an appreciably lesser growth in height than the average of group W.

The seasonal decline in carbohydrate foods of the stem bases resulting from the harvest of October 14, was closely approximated by that following the harvests of February 10 and April 29. Moreover, the losses sustained through harvesting January 5, and May 16, were approximately equal, but somewhat less in amount than in either of the clippings mentioned above. In other words, practically the same injury was imparted through harvesting in the midst of seed maturity and dispersal as during the period of inactive growth in January. Although harvesting within the first two or three weeks after growth inception is believed to be injurious, these results indicate for *Stipa pulchra* that such harvesting, or grazing, exerts practically the same influence upon the plant as similar treatment applied at seed maturity. While the actual seasonal loss was not great in any group, the decline following the harvests of December 4 and April 14 was 0.1 per cent and 0.5 per cent, respectively. The very low growth velocity coincident with these harvests tends to show that the decline in the carbohydrate level following such treatment is associated with the growth velocity, rather than with the interval of harvest (fig. 16). The general trend of the carbohydrate level in regeneration growth shows this same tendency. These materials doubtless contribute to the expanding herbage in the earlier stages of regeneration growth, resulting in a decline in concentration affecting both stem bases and roots.

Unlike the seasonal loss, the diminution in the accumulated carbohydrate foods at the end of the annual growth cycle showed direct relation to the amount of leaf area available for photosynthetic activity at the onset of the interval of food deposit. The interval of food deposit began in the stem bases about May 16 (fig. 14). Again, this interval may be presumed to have occurred simultaneously in all the groups.[7] At the onset of this interval of food deposit, the total leaf area of the groups E, G, and H, was 51 per cent, 43 per cent, and 33 per cent, respectively, of the annual yield, whereas the herbage had been entirely removed in group J. The capacities of these groups to manufacture carbohydrate foods may be presumed to have differed in like proportion. The analyses of the stem bases of these several groups at the end of the annual growth cycle, showed maximum accumulations in group E, and a diminution of 10 per cent, 16 per cent, and 42 per cent, respectively, in groups G, H, and J (fig. 16, tables 6 and 12). The amount of the accumulated carbohydrate foods in the plant depends, therefore, upon the total leaf area available for its manufacture when this period of the annual growth cycle is reached. Maximum food deposits in *Stipa pulchra* require the production of approximately 50 per cent of the annual herbage growth prior to the onset of the period of accumulation, and its continuance undisturbed by grazing until the close of the annual growth cycle. Therefore, the interval of harvest, as in *Agropyron smithii*,[7] appears to be of paramount importance.

Injury to range grasses through too early grazing has been definitely established. However, the rather generally accepted belief that grazing once or twice early in the growth cycle is unfavorable to subsequent large forage yields, to seed production, and to longevity of the stand of perennial grasses, apparently involves physical damage caused by tramping over wet soil and the uprooting of young plants, rather than unfavorable physiological responses due to such a practice. Serious damage from early seasonal grazing occurs particularly on hillsides when the soil is saturated with moisture. The present study shows that moderately intensive grazing in autumn and winter would not occasion irreparable injury to the *Stipa* cover. It is evident, however, that moderate utilization immediately following seed maturity would occasion some injury. On the other hand, grazing after the completion of the annual growth cycle would not cause serious injury through food depletion, since removal of the mature herbage would not be followed ordinarily by regeneration growth. The interval at which the greatest injury would appear to result from grazing *Stipa pulchra* is when increment growth is proceeding at maximum rate (fig. 16). While any management plan for the bunch grass type of the foothill range would have to take cognizance of the growth and reproductive requirements of the annual grasses, rotations presuming to favor *Stipa pulchra* should be organized to obtain light stocking in alternation with complete rest during the intervals of rapid growth velocity. Maximum stocking or intensive utilization should coincide with the period of maturity and completion of the annual growth of the plant. These studies strongly indicate that growth rate and food relationships of range plants are fundamental elements in the development of sound management plans.

CONCLUSIONS

1. The growth cycle of *Stipa pulchra* is an orderly process characterized by periodicity, in that intervals of rapid growth alternate with intervals of depression in the growth rate. The time of growth inception of the herbage on the range studied followed closely the early autumn rains. The rate of growth during the winter is controlled by atmospheric temperatures, whereas that of the spring and early summer is in part related to internal factors, among which the food level and the growth habits of the plant appear paramount. Cessation of growth in the summer is determined by the maturity of the herbage, and may be appreciably hastened by low soil humidity.

2. Active root growth occurred in the autumn and winter when herbage growth had practically ceased.

3. The advent of flowers and seed coincided with depression in the growth rate.

4. An inverse correlation existed between the annual march of the carbohydrate foods and the growth rate. Accumulation of foods, therefore, is related to low or to declining growth velocity, and is most active near the close of the annual growth cycle.

5. Removal of the herbage at any time prior to the maturity of the plant was followed by more or less vigorous regeneration growth.

6. Practically complete accumulation of carbohydrate foods occurred where from 43 to 50 per cent of the total annual herbage yield was produced prior to the peak in the growth rate. A deficiency in the accumulated food supply at the close of the annual cycle would apparently result in decreased growth during the subsequent year.

7. Grazing or clipping once or twice early in the growth cycle influenced little, if at all, the total herbage yield of *Stipa pulchra*. This treatment did not prevent the accumulation of maximum amounts of carbohydrate foods in the late part of the annual growth period.

8. Grazing or removal of the herbage between the time of flower stalk production and seed maturity prevents the accumulation of maximum amounts of carbohydrate foods and tends to prolong the vegetative growth of the plant.

9. Growth should proceed with a minimum of disturbance by grazing or other forms of harvesting during the intervals of rapid growth. Maximum utilization should follow cessation of growth and the maturity of the herbage.

10. The herbage of *Stipa pulchra* on the range studied retains its succulence for a period of nine or ten months.

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The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. C. Haas. April, 1923.
5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.
6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.
7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.
8. Effect of Salts on the Intake of Inorganic Elements and on the Buffer System of the Plant, by D. R. Hoagland and J. C. Martin. July, 1923.
9. Experiments on the Reclamation of Alkali Soils by Leaching with Water and Gypsum, by P. L. Hibbard. August, 1923.
10. The Seasonal Variation of the Soil Moisture in a Walnut Grove in Relation to Hygroscopic Coefficient, by L. D. Batchelor and H. S. Reed. September, 1923.
11. Studies on the Effects of Sodium, Potassium, and Calcium on Young Orange Trees, by H. S. Reed and A. R. C. Haas. October, 1923.
12. The Effect of the Plant on the Reaction of the Culture Solution, by D. R. Hoagland. November, 1923.
13. Some Mutual Effects on Soil and Plant Induced by Added Solutes, by John S. Burd and J. C. Martin. December, 1923.
14. The Respiration of Potato Tubers in Relation to the Occurrence of Blackheart, by J. P. Bennett and E. T. Bartholomew. January, 1924.
15. Replaceable Bases in Soils, by Walter P. Kelley and S. Melvin Brown. February, 1924.
16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Veihmeyer, O. W. Israelsen and J. P. Conrad. September, 1924.
17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. C. Haas. October, 1924.
18. Factors Influencing the Rate of Germination of Seed of Asparagus Officinalis, by H. A. Borthwick. March, 1925.
19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.
20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.