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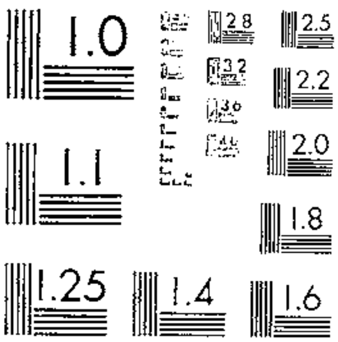

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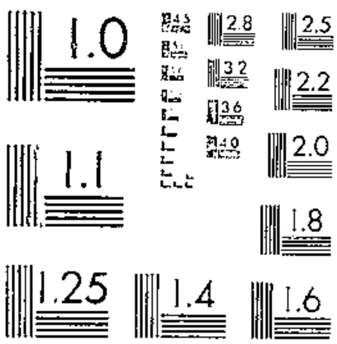

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WASHINGTON, D. C.

THE RELATION OF GROWTH TO THE VARYING CARBOHYDRATE CONTENT IN MOUNTAIN BROME[1,2]

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INTRODUCTION

Mountain range lands furnish abundant and varied forage for livestock. Although broad-leaved plants of these lands are valuable for grazing, perennial grasses, because of favorable growth habits, are better adapted to this use. Preservation of these range grasses depends upon the manufacture and storage of carbohydrates by the plant in excess of those consumed in growth. Any system of grazing that permits complete and frequent removal of the green shoots, thereby preventing manufacture and storage of carbohydrates, is injurious and may result in the destruction of the grass cover. Such

[1] Received for publication June 1, 1937.

[2] *Bromus carinatus.* This rather variable grass has been regarded by some botanists as composed of three separate species: (1) California brome (*B. carinatus*), (2) big brome (*B. marginatus*), and (3) polyanthus brome (*B. polyanthus*), although these were frequently lumped together in the Forest Service as "big mountain bromes."

[3] This posthumous bulletin appears in a form only slightly modified from that in which it was prepared by the author who, as head of the Botany Department of the Riverside Junior College, Riverside, Calif., was engaged during the summer months by the Intermountain Station in the capacity of associate forest ecologist. The chemical analyses involved in the study were made in the laboratory of the college under Dr. McCarty's immediate supervision.

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excessive use leads to retrogressive succession, which may in turn be followed by erosion and general impoverishment of the soil (*19*).[4]

Annual growth of a perennial grass is related to environmental factors and to specific nutritional and reproductive processes. Considerable regularity is manifested in the succession of these physiological processes. Initial growth of the herbage in the spring is made at the expense of the carbohydrate accumulations stored in the basal organs during the preceding season. Concentration of carbohydrates in both herbage and basal organs of the plant is inversely related to the rate of herbage growth. This relationship is maintained throughout the entire annual cycle of growth. The accumulation of carbohydrate stores is delayed, therefore, until most of the annual herbage growth is produced (*18, 20*).

One complete clipping of the herbage at any time during the active growing period or at the close of the current season of growth causes diminished carbohydrate concentration in the renewed herbage growth as well as in the stem bases and roots of the plant (*12, 18, 20*). Since carbohydrate accumulation occurs during the closing phase of the annual growth cycle, the amount stored in plants subjected to clipping is directly related to the total leaf area present at the beginning of the storage period (*18*).

Previous food-storage studies of grasses have been largely confined to the growth interval between snow disappearance and ripening and dissemination of the fruit. On mountain ranges annual growth of a grass has been considered to take place during the period from snow disappearance in the spring to its reappearance in the autumn. However, the carbohydrate concentration in the basal organs of mountain brome (*Bromus carinatus*) and other grasses is at the minimum level at the outset of the snow-free period, suggesting the occurrence of incipient growth stages prior to melting of the snow in the spring. Furthermore, maintenance of the native range grasses presupposes grazing use in agreement with their nutritional requirements. Therefore, additional information concerning the behavior of the carbohydrate fractions throughout the annual growth cycle of important range grasses is needed, as well as accurate determination of their nutritional and food-storage responses under definite systems of grazing use.

THE PROBLEM

The object of the present study was to determine for mountain brome (fig. 1), an important forage plant common to a large part of western mountain ranges, the following basic information necessary in the development of proper grazing practices for mountain range lands:

1. The character of growth.
2. The annual march and autumn and winter behavior of carbohydrates.
3. The relation between the march of carbohydrates and annual growth.

THE EXPERIMENTAL AREA

The experimental area is located at the Great Basin branch of the Intermountain Forest and Range Experiment Station in Ephraim Canyon, Utah. The soil of the area, a dark-colored clay loam, of limestone origin, contains considerable organic matter and has a

[4] Italic numbers in parentheses refer to Literature Cited, p. 25.

good water-holding capacity. The dominant vegetation is characteristic of the aspen-fir type at that altitude (8,850 feet), with an understory of snowberry (*Symphoricarpos oreophilus*) and a generous admixture of perennial grasses, predominantly mountain brome and broad-leaved herbaceous plants.

The experiment was conducted within an enclosure which was seeded to mountain brome in the spring of 1925. Samples of plant

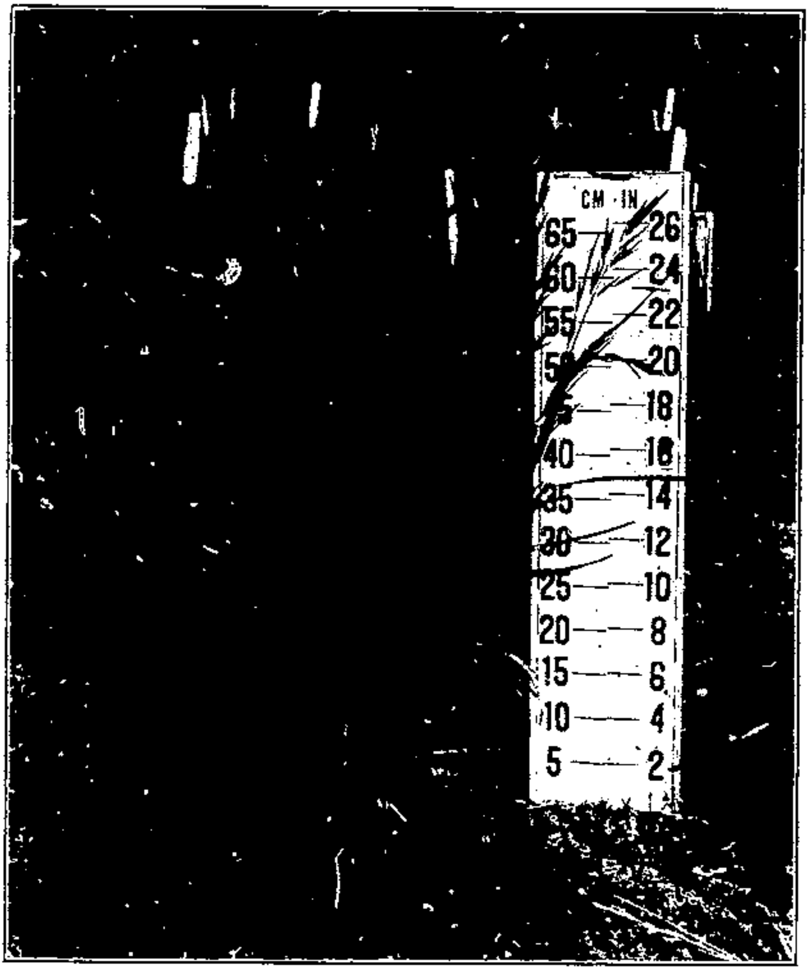

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FIGURE 1.—Mountain brome (*Bromus carinatus*), a highly palatable range forage grass.

material for food-march determinations were collected from an area within the enclosure approximately 75 by 100 feet.

METHODS EMPLOYED

COLLECTION AND PREPARATION OF SAMPLES

Random sampling was employed and all collections were made between the hours of 9 a. m. and 12 noon. The samples were taken approximately at 10-day intervals during the snow-free period and at monthly intervals during the winter. From 6 to 10 plants yielded a stem-base and root sample weighing approximately 40 g; the herbage from these plants generally exceeded that weight. Samples were prepared by clearing the soil from the roots with a small hand brush and cutting the tops from the bulblike stem bases. Herbage samples analyzed consisted of the culms and green leaves from which all dead or discolored material, and inflorescence when present, were removed. Root samples consisted of the bulblike stem bases and root fragments, ranging from 1 to 10 cm in length, that were not detached in harvesting and cleaning. After preparation, all samples were preserved in 95-percent alcohol.

CHEMICAL ANALYSES

After oven drying and grinding, a 5-gram portion of each of the preserved samples was used for the complete chemical analyses. Each portion was extracted with hot alcohol, and to the extract was added a corresponding portion of the alcohol in which the sample had been preserved. The residue remaining after the alcohol had been evaporated from this extract was dissolved in distilled water, transferred to a volumetric flask, and made up to volume. After it had been cleared, aliquot portions of the sample were pipetted into two smaller volumetric flasks. One flask was made up to volume, and the reducing sugars were determined by use of copper sulphate according to the method described by Schaffer and Hartman (*21*). The second portion was hydrolyzed according to the process described in Official Methods (*2*). After neutralizing and making up to volume, the reduction power was determined and the resultant fraction reported as total sugars. The difference between the two determinations was sucrose.

The residue remaining from the sugar extraction was dried in an electric oven, transferred to a ball mill, and rotated for 60 hours. Distilled water, boiling hot, was added to the fine residual powder and the container placed in a water bath at 100° C. for one-half hour. After cooling, 6 cc of saliva, a few drops of toluene, and approximately one-tenth of a gram of sodium chloride were added, and the suspension was agitated for 12 hours at 37°. The container was then transferred to an incubator and maintained at that temperature overnight. Subsequently, the container was placed in boiling water for 1 hour to arrest the enzymic action. The solution was then separated from the residue, and aliquot portions of the former were hydrolyzed with 2.5 cc of concentrated hydrochloric acid. After neutralizing and clearing, the reduction power of this solution was determined. Although this fraction is reported as starch, it actually contains both true starch and water-soluble starch.

After being washed, the remaining residue was transferred to an Erlenmeyer flask, and 2.5 cc of concentrated hydrochloric acid, diluted to 100 cc with distilled water, was added. The hydrolysis was carried out with an electric hot plate, care being used to keep the volume constant. The suspension was finally diluted with distilled water, neutralized, transferred to a volumetric flask, and made up to volume. Upon filtering and clearing, the reduction power was determined, using aliquot portions of this filtrate. This fraction is reported as hemicellulose.

The several solutions of the unknown substance were cleared with basic lead acetate solution, and deleaded with disodium phosphate. All determinations were made in duplicate, the results being reported as reducing sugar, based upon the ash-free dry weight of the sample.

GROWTH MEASUREMENTS

Maximum and average height-growth measurements of check plants were made at 5-day intervals, and a cumulative growth curve was constructed from the average measurements. The slope of the curve was determined by lines drawn tangent to the curve at convenient points. The tangents of the angles formed by the convergence of these lines upon the X-axis were computed, and rate curves were constructed from the resultant values (*8*).

GROWTH STAGES

The annual growth cycle of mountain brome includes four definite developmental stages and offers a convenient basis for presenting the experimental data. These stages are:

1. Snow disappearance to flower stalks first in evidence.[5]
2. Flower stalks first in evidence to heads fully out.
3. Heads fully out to flowers in bloom.
4. Flowers in bloom to seeds fully ripe.

In 1932, the four intervals were, respectively, 33, 20, 11, and 30 days in length. An additional 31 days was required for the dissemination of the fruit.

CLIMATE OF THE EXPERIMENTAL AREA

The climate of the experimental area is typical of that of mountainous regions. It is characterized by a short growing season with relatively uniform temperatures and by frequent frosts occurring during the early and late snow-free period.

AIR TEMPERATURES

Extreme temperatures are comparatively rare. In general, the daily maxima and minima increase progressively from snow disappearance to the seasonal maximum in July. Average daily temperatures are fairly uniform and are generally above 50° F. during the months of June, July, August, and September; this was also true for these months during the experimental period except September 1934 (table 1). Temperatures have risen as high as 88° during July and dropped as low as 11° in September and 19° in June.

The extreme maximum temperatures recorded during the growing season of the years 1931 to 1934, inclusive, were 88°, 83°, 84°, and 84° F., respectively; and the extreme minima, 15°, 19°, 30°, and 25°.

The 1931 extreme temperatures were record high and low, the former occurring on July 23 and 24, the latter on May 21, 27 days after snow disappearance.

[5] Flower stalks were considered to be in evidence when a slight swelling, caused by the inflorescence, could be detected by drawing the thumb and finger over the surface of the uppermost leaf sheath.

TABLE 1.—*Monthly mean maximum, mean minimum, and mean air temperatures during the growing seasons of 1932 to 1934, inclusive, Ephraim Canyon, Utah*

Month	1932			1933			1934		
	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean
	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.
May	55.5	31.3	43.4	47.8	24.7	36.3	62.2	37.1	49.6
June	65.2	38.6	51.9	71.7	42.4	57.0	62.7	37.5	50.1
July	73.1	46.2	59.6	75.7	49.4	62.6	76.8	48.4	62.6
August	71.2	44.8	58.0	72.3	42.3	57.3	72.2	46.2	59.2
September	66.5	37.1	51.8	68.3	40.1	54.2	62.6	34.4	48.5
October	50.5	25.2	37.8	58.9	32.4	45.6	55.8	30.2	43.0

Frosts have occurred during all months. Killing frosts may occur when the minimum temperature declines to 26° F., whereas light frosts may result between 27° and 32°, inclusive. Records for a decade, 1925–34 (*18*), show that an average of 3.4 killing frosts and 7.1 light frosts occur annually during the first growth stage, "snow disappearance" to "flower stalks first in evidence"; whereas during the 3 years of the study an average of 2.3 killing frosts and 8.7 light frosts occurred. The remainder of the growth stages during the experimental period were free from frost except for three light frosts during the second growth stage in 1934.

SOIL TEMPERATURES

As shown in table 2, temperatures of the soil at a depth of 6 inches show greater variation than those at depths of 12 or 24 inches, the near-surface temperatures being more closely related to air temperatures. The surface layer warms up following snow melt in the spring and if sufficient soil moisture is present, freezes as winter approaches. Frost may occur at a depth of 8 inches, as was noted on January 6, 1933.

When removing root samples during the winter snowfall period, it was observed that the surface layer of soil remains frozen under the snow until about 8 weeks to 3 months prior to snow disappearance, depending upon the current weather conditions, at which time melting usually occurs and the soil may become entirely free from frost while there is yet a snow cover. Complete thawing of the soil was noted in early April 1933 under a snow cover of 36 inches, and in early February 1934 under a snow cover of 27 inches.

Soil thawing prior to the melting of the snow may be partly a result of heat conduction from the deeper soil stratum; additional heat is released at the upper surface by the absorption of the snow-melt water. Spreading fluorescein on the snow surface during warm weather revealed well-defined channels and a general downward percolation of water throughout the entire snow mass (*5*). The greatly augmented soil-moisture supply apparent when root samples were taken during the several winters of the study evidenced the penetration of this water into the soil. In fact, where snow cover is deep, a thin sheet of ice may be formed at the soil surface.

TABLE 2.—*Mean*[1] *soil temperatures at various depths during the growing seasons of 1932 to 1934, inclusive, Ephraim Canyon, Utah*

Month	Temperatures at depth indicated in—								
	1932			1933			1934		
	6 inches	12 inches	24 inches	6 inches	12 inches	24 inches	6 inches	12 inches	24 inches
	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.
May	46.0	43.0	40.0	34.3	33.5	33.7	54.8	51.8	48.1
June	57.2	52.3	48.4	59.6	53.2	47.2	56.2	53.8	51.1
July	62.7	59.2	55.4	64.5	60.7	56.3	65.2	61.8	57.8
August	59.7	58.2	55.8	62.2	59.5	56.8	62.7	60.0	58.4
September	52.3	52.5	52.2	56.7	55.6	54.2	55.5	55.7	55.3
October	40.3	43.1	45.1	44.8	46.2	47.4	44.0	45.8	47.4
Seasonal range	22.4	16.2	15.8	30.2	27.2	23.1	21.2	16.0	11.0

[1] Temperature at 8 a. m. plus that at 5 p. m. divided by 2.

PRECIPITATION

Mean annual precipitation for the area for the period 1914–33 totals 29.48 inches, and as shown in the following tabulation most of the precipitation falls during the winter months (Oct. 1 to May 1):

	Inches		Inches
January	3.15	August	1.80
February	2.85	September	1.56
March	4.11	October	1.92
April	3.54	November	2.19
May	2.44	December	3.26
June	.85		
July	1.81	Total annual	29.48

Total precipitation from May to October during 1932, 1933, and 1934, as shown in table 3, averaged less than one-third of the annual total. Precipitation from snow disappearance to seeds ripe for these same years was 4.48, 3.04, and 4.13 inches, respectively. Snowstorms have occurred in every month of the year; they are frequent in late May and usual in September. Short summer thunderstorms and occasionally hailstorms prevail during the snow-free period, although rains may continue for a week during the summer rainy season in July.

TABLE 3.—*Monthly precipitation, April to October 1932–34, Ephraim Canyon, Utah*

Year	April	May	June	July	August	September	October	Total (May to October)
1932	1.92	1.50	0.91	2.45	2.70	0.21	1.11	8.88
1933	3.36	5.75	.02	2.09	1.10	.83	1.03	10.82
1934		2.08	.32	1.73	1.42	.27	1.62	7.44
Average								9.05

TEMPERATURE RELATIONS OF THE GROWTH STAGES

Maximum and minimum air temperatures that occurred during the several growth stages of the plant in the course of the study are compared with the 10-year mean records in figure 2. As shown in this

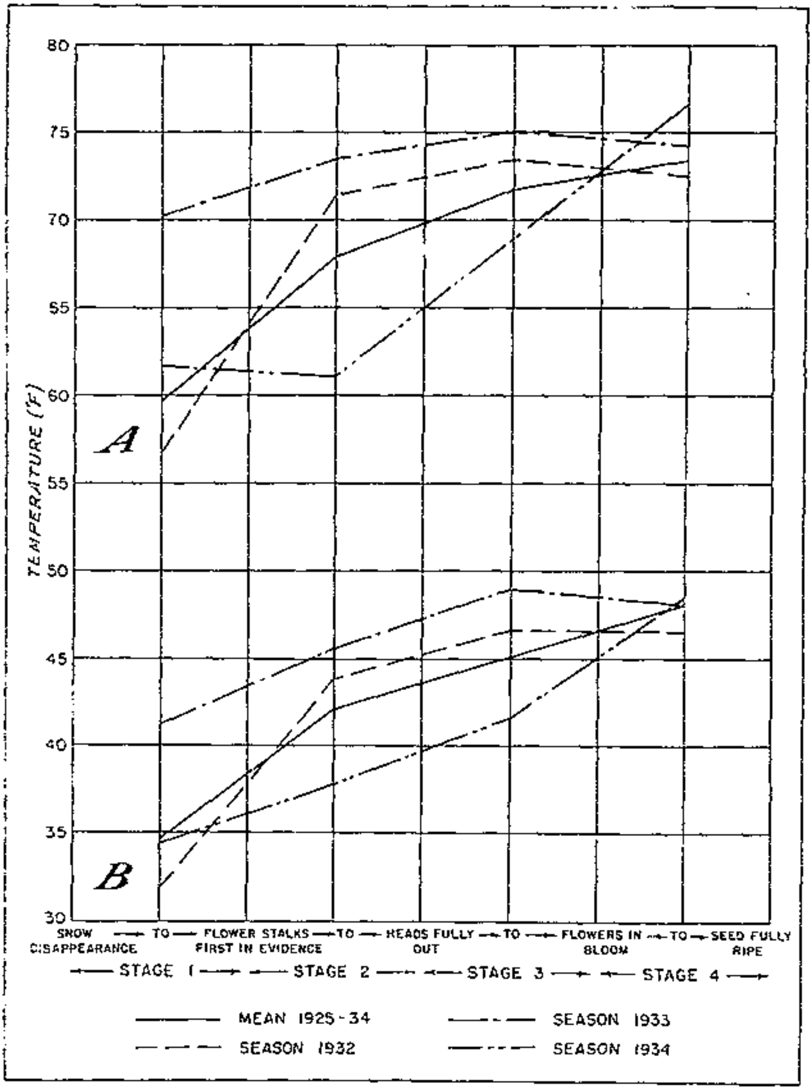

FIGURE 2.—Mean maximum (*A*) and mean minimum (*B*) air temperatures for 1932, 1933, and 1934, and average maximum and minimum air temperatures for the period 1925–34, in relation to the average developmental stages of mountain brome.

figure, maximum and minimum temperatures during the several growth stages in 1932 approached the 10-year mean while the temperatures during the growth stages of 1933 were above average for all stages and those for 1934 were below except for the first and last stages. Thus, years of near-average, above-average, and below-

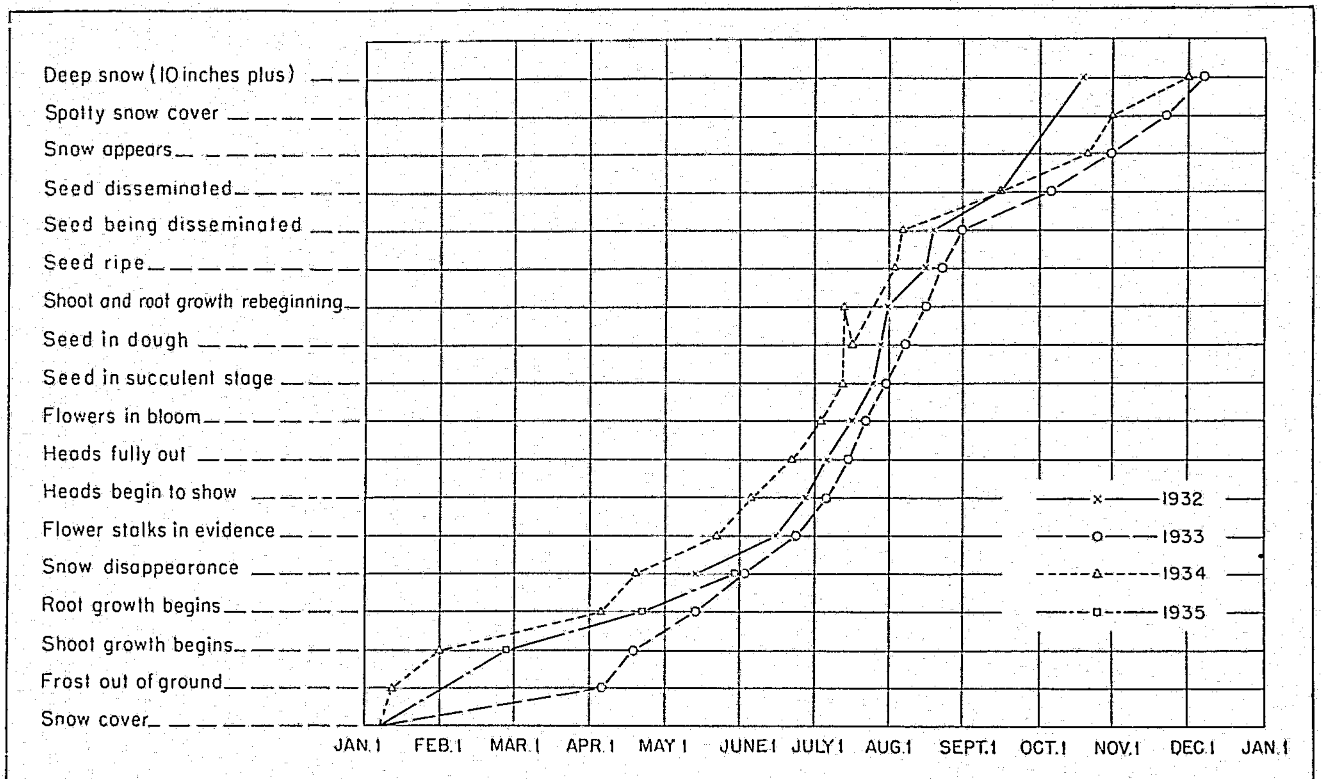

FIGURE 3.—Annual growth stages of mountain brome, Ephraim Canyon, Utah, 1932-35.

average temperatures during the growth stages of the plant occurred in the course of the study.

The variations in temperature during the growth stages were reflected in the length of the active growth period of the plant. In 1932, when temperatures approached the mean, the length of the growth interval between snow disappearance and seeds ripe was 94 days. The length of the growth period in 1933 was 81 days with temperatures above the mean, and in 1934, 106 days with temperatures below the mean.

The prevailing temperatures during the growth stages of the plant are also reflected in the length of the growth stages. The growth stage "snow disappearance" to "flower stalks first in evidence" in 1933 was 11 days shorter than the same period in 1932, as the result of higher-than-average temperatures. On the other hand, the growth stage "flower stalks first in evidence" to "heads fully out" in 1934 was 13 days longer than the same period in 1932, as the result of lower-than-average temperatures (fig. 3).

GROWTH STAGES AND THE MARCH OF THE CARBOHYDRATES

THE ANNUAL GROWTH CYCLE

Annual growth of mountain brome is cyclic in nature, owing in part to atmospheric temperatures and in part to the plant's reproductive processes (fig. 4). The growth cycle includes current seasonal growth of herbage, secondary herbage growth, and root growth. Current seasonal growth includes growth made prior to snow disappearance and the vegetative shoots which produce the flower stalks. Secondary herbage growth consists of shoots which arise from buds situated at the base of the stems of current seasonal growth. Root growth includes the adventitious roots which grow from the plant crown and spring from the basal nodes of the stem.

GROWTH PRIOR TO SNOW DISAPPEARANCE

Initial growth of mountain brome occurs some 45 to 89 days prior to spring snow melt and is usually confined to the production of leaves although root growth also may occur. In 1933 active shoot growth was noted on April 18 under a snow cover of 34 inches (fig. 3). Although the snow depth increased to 54 inches in May, the shoots meanwhile attained a height of 6 cm. Growth of adventitious roots was discernible on May 13; when the snow disappeared on June 2 they were 4 cm long. During 1934 and 1935, new shoot growth began approximately February 1 and February 27, respectively; root growth was observed on April 5 and April 21, respectively; while the dates of snow disappearance were April 19 and May 28. Askenasy (*1*) made comparable observations showing that sweet cherry buds increased in size during the rest period. Simon (*22*), on the other hand, reported that many trees produce roots during the most intense rest period of their buds.

The concentration of the carbohydrates in the herbage during this period was at a maximum (fig. 5), while the corresponding values in the roots and stems approached the minimum (fig. 4). The concentration of the sugar and starch fractions in the etiolated shoots collected at snow disappearance in 1932 and in 1934 was 17.84 and 18.04 percent, respectively (table 4), while the combined sugar and starch

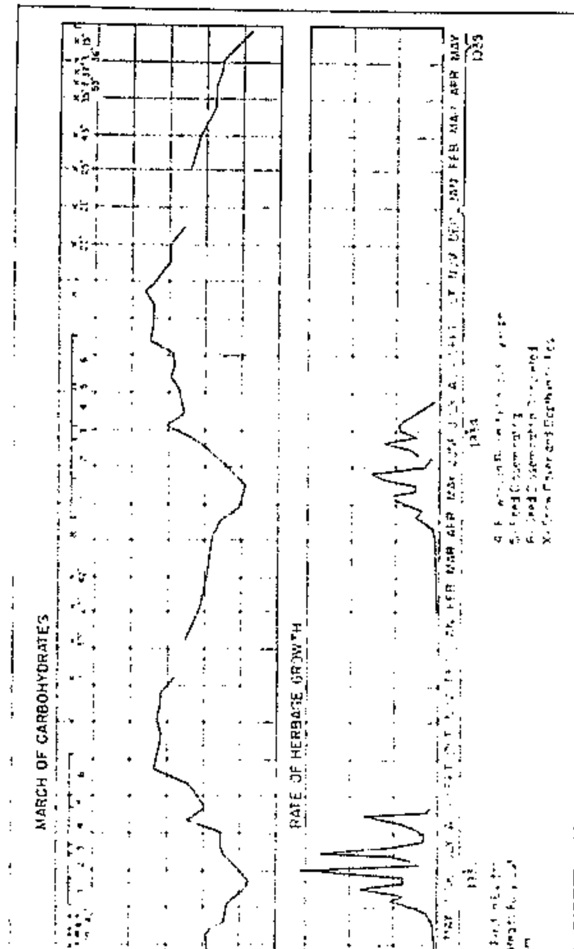

FIGURE 1.—The changes of the combined fractions, reducing sugars, sucrose, and starch in roots and stem bases in relation to growth of mountain brome.

values in newly developed shoots collected on March 30, 1935, 59 days prior to snow disappearance, were 18.13 percent. Comparison of these values with the concentrations of the combined sugar and starch values in the herbage throughout the snow-free period in 1932 (fig. 5) identifies them as the maximum values. The combined sugar and starch fractions in the stem bases and roots at snow disappearance in the years 1932 to 1935, inclusive, were 3.70, 6.77, 8.01, and 4.11 percent, respectively (table 5), whereas the maximum stores of these carbohydrates during the autumn in the same years were 21.11, 16.45, and 18.09 percent, respectively. The concentration of the hemicellulose increased in the basal organs prior to snow disappearance.

TABLE 4.—*Carbohydrate fractions in mountain brome herbage samples collected at or prior to snow disappearance, 1932, 1934, and 1935*

Date of snow disappearance	Date of collection	Reducing sugars	Sucrose	Total sugars	Starch	Reducing sugars, sucrose, and starch	Hemicellulose
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
May 13, 1932	May 13, 1932	8.76	1.28	10.04	7.80	17.84	11.50
Apr. 19, 1934	Apr. 16, 1934	3.91	1.02	4.93	13.11	18.04	9.32
May 28, 1935	Mar. 30, 1935	2.39	3.66	6.05	12.08	18.13	8.05

TABLE 5.—*Carbohydrate fractions in stem bases and roots of mountain brome at snow disappearance, 1932–35*

Date of snow disappearance	Date of collection	Reducing sugars	Sucrose	Total sugars	Starch	Reducing sugars, sucrose, and starch	Hemicellulose
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
May 13, 1932	May 13, 1932	1.14	0.22	1.36	2.34	3.70	21.03
June 2, 1933	June 2, 1933	2.67	1.22	3.89	2.88	6.77	23.14
Apr. 19, 1934	Apr. 18, 1934	1.87	2.24	4.11	3.90	8.01	21.76
	Apr. 26, 1934	2.27	.66	2.93	2.54	5.47	23.62
	May 4, 1934	2.07	.68	2.75	2.16	4.91	23.66
May 28, 1935	May 28, 1935	.88	.42	1.30	2.81	4.11	22.25

SNOW DISAPPEARANCE TO FLOWER STALKS FIRST IN EVIDENCE

The rate of herbage growth after snow disappearance and until flower stalks are first in evidence begins to show marked fluctuation, after which the growth rate is retarded and the growth curve declines. This decline is followed by a secondary rise of higher magnitude followed in turn by another retardation. During this growth stage in 1932, relatively low atmospheric temperatures prevailed and frequent frosts occurred; whereas during the same period in 1933 temperatures were higher and there were no killing frosts. In 1934, frosts of all kinds were few but the temperature level resembled that of 1932. Such temperature characteristics were reflected in the growth of the herbage (fig. 4).

Coincident with the periods of acceleration and retardation of the rate of herbage growth during this period, pronounced fluctuations in the concentration of the several carbohydrate fractions in the herbage occurred (fig. 5). Although the sucrose values were high at snow disappearance, this fraction was reduced to the seasonal minimum during the first 10 days of the snow-free period. Also, as the result of acceleration in herbage growth, the seasonal maximum diminutions of these several fractions occurred in the stem bases and roots during this same period, although the hemicellulose fraction continued to increase (fig. 6).

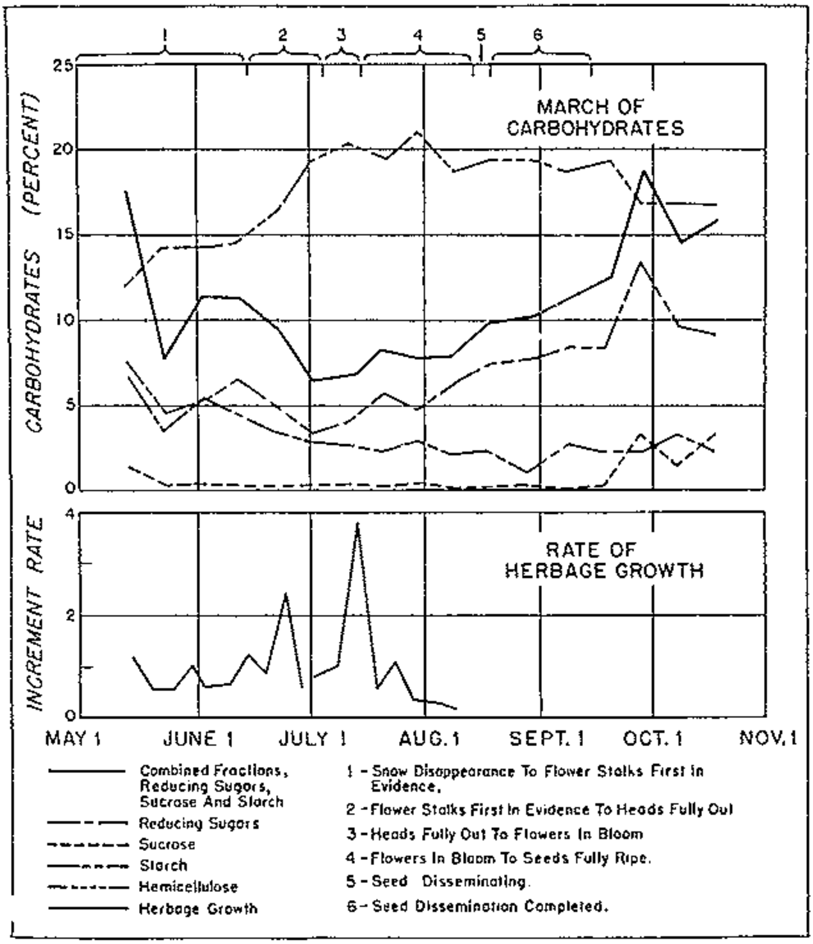

FIGURE 5.—The change of carbohydrates in the herbage in relation to annual growth of mountain brome, Ephraim Canyon, Utah, 1932.

FLOWER STALKS FIRST IN EVIDENCE TO HEADS FULLY OUT

The growth stage between the time when flower stalks are first in evidence and that when heads are fully out is characterized by the maximum growth rate of the herbage; 70 to 80 percent of the annual top growth is completed by the time the heads emerge from the sheaths. Rapid growth of the inflorescence and acceleration in the lengthening of the flower stalks also characterize this interval.

A marked decline in the starch fraction and a lesser decline in the reducing sugars were immediately reflected in the herbage as the result of the accelerated growth of the vegetative shoots. The simultaneous increase of hemicellulose in the herbage, however, was approximately equal to the loss of the combined sugar and starch values, and the sucrose fraction continued at the minimum level.

Low concentrations of the sugar and starch fractions prevailed in the basal organs in 1932; small increases were noted in 1933. Low growth rate coincided with the low mean temperatures of this stage of development in 1934, however, and the initial stores of sugar and starch were deposited. This accumulation confirmed the results of previous grass studies to the effect that low or declining carbohydrate values in the basal organs appeared during intervals of accelerated growth rate, and high or ascending values accompanied low or declining growth rate of the herbage (*12*, *13*, *20*).

HEADS FULLY OUT TO FLOWERS IN BLOOM

The growth stage occurring between the time when heads are fully out and that when flowers are in bloom is usually completed in approximately 10 days, and during it both acceleration and decline in the rate of herbage growth take place.

All sugar and starch values in both herbage and stem bases and roots increased while the hemicellulose fraction in the stem bases and roots decreased sharply and varied somewhat in the herbage.

FLOWERS IN BLOOM TO SEED FULLY RIPE

During the growth stage between the time when flowers were in bloom and that when seed were fully ripe additional height growth of the flower stalks usually follows the expansion of the flowers and the current seasonal herbage growth is completed before ripening of the fruit. New adventitious roots and secondary shoots were also produced during this growth stage.

Concentration of the sugar and starch values of both herbage and stem bases and roots rose during the early part of this stage but decreased during the latter part, occasioned by the accelerated utilization of carbohydrates by the secondary herbage growth. The decline in the sugar and starch values in the basal organs occurred subsequent to July 30, August 11, and July 3, respectively, of the years 1932, 1933, and 1934. Hemicellulose in both herbage and roots continued to show opposite reaction to that of the starches and sugars.

SEED FULLY RIPE TO THE END OF THE SNOW-FREE PERIOD

Drought may delay root growth and secondary shoot growth until the growth stage occurring between the time when seed are fully ripe and the end of the snow-free period. But this period is usually characterized by ripening of the fruit accompanied by waning vitality in the current seasonal shoots, manifested chiefly by the drying and browning of the fruit stalks. Following these events a condition of more or less complete dormancy is reached.

Additional starch and sucrose were noted upon the cessation of secondary growth; in 1932, maximum values coincided in both herbage and basal organs. Annually throughout the experiment maximum sugar and starch values in both herbage and stem bases and roots were deposited before the permanent autumnal snowfall. Secondary

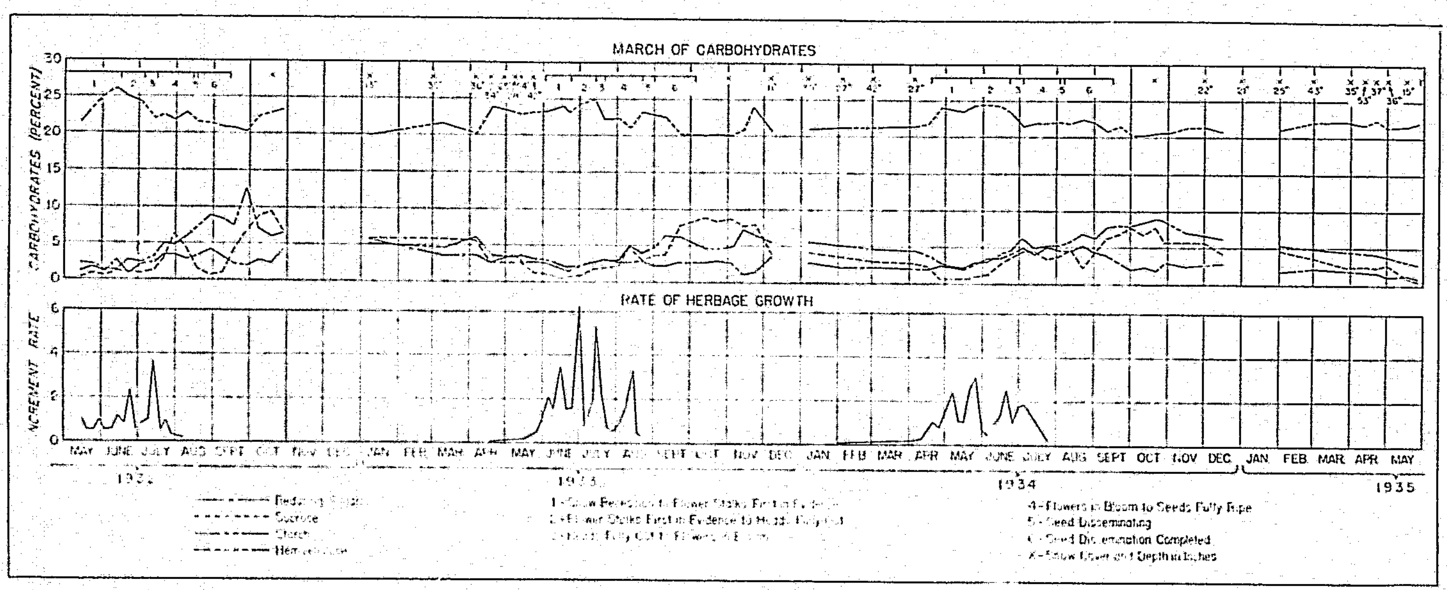

FIGURE 6.—Changes of the several carbohydrate fractions in roots and stem bases in relation to annual growth of mountain brome, Ephraim Canyon, Utah, 1932–35.

shoots may remain green until the appearance of permanent snow cover, resulting in some additions to the carbohydrate stores (Oct. 22, fig. 6). The hemicellulose values usually remained low, although this fraction increased at the end of the snow-free period in 1932.

GROWTH AND CARBOHYDRATE STORAGE

THE GROWTH MADE FROM STORED FOOD

Growth made previous to snow disappearance is largely confined to cell division and, owing to low temperatures and perhaps to the limited light intensity underneath the snow, the photosynthetic power of the young etiolated leaves may be considered as negligible. However, the building of protein and protoplasm, incident to meristem activity, and the differentiation and enlargement which follows cell division, consume relatively large amounts of the soluble carbohydrate stores.

When little growth other than the swelling of the buds was yet perceptible in 1933, the loss in the combined sugar and starch fractions, based upon the maximum storage values of these materials found on September 28 of the previous autumn, amounted to 56 percent. At snow disappearance, June 2, the diminution amounted to 67.9 percent, whereas the maximum height growth attained on this date was but 6.6 percent of the total annual increment. By June 21, when approximately 25 percent of the current annual herbage growth had been made, the stored sugar and starch fractions were diminished by 81 percent of the maximum. Losses in stored sugars and starches which occurred during a comparable period in 1934, based upon the values found September 22, 1933, amounted to 35 percent at initial growth of the herbage, 55.9 percent at snow disappearance, and 72.6 percent when the minimum concentration of these carbohydrates was reached, May 14. Diminutions in the total stores observed when shoot growth began in the spring of 1935 were 40 percent, and 77 percent at snow disappearance.

Thus, growth made previous to snow disappearance and during early spring, which consists of the production of herbage and adventitious roots, consumes approximately 75 percent of the combined sugar and starch accumulations stored in the basal organs of the plant during the previous fall period. These findings agree essentially with those of Korstian, who, in a study of certain conifers, determined that the stored foods were exhausted during the incipient stages of current growth (*10*). However, the amount of these carbohydrate stores consumed before snow disappearance appears to be disproportionate to the amount of growth made, and exemplifies the capacity of meristematic activity to monopolize the available carbohydrate supply of the plant.

The residual sugar and starch fractions not used in early growth, approximately 25 percent of the maximum stores of these foods, are not ordinarily used. However, if the herbage growth is removed by clipping, and if renewed herbage growth follows immediately, diminution of this residual in the stem bases and roots of the plant results. This was demonstrated by clipping two series of plots three times, 1 inch from the soil line. The first clipping was made at snow disappearance, the second 5 days later, and the third at the end of the second 5-day period. On the fifth day following the third clipping, the basal organs of each plot were removed and analyzed. Although on these dates the seasonal level in the unclipped plants showed a diminution of 80 percent and 81 percent, respectively, the residual sugar and starch values in the stem bases and roots of the clipped plots were reduced to 86.8 percent and 87.5 percent. In a study of *Stipa pulchra*, diminutions in the basal organs resulting from one clipping ranged from 2 percent to 56 percent (*20*), and in *Avena fatua* the diminution was proportional to the rate of growth at the time of clipping (*12*). These results indicate that following complete removal of the herbage the residual sugars and starch may be used to produce new shoots. Hence, the residual carbohydrates represent an excess of the storage function which may be compared to the characteristic excess of biological functions in general.

INDEPENDENT GROWTH AND YIELD

Since stored carbohydrates reach a minimum level practically at snow disappearance, as shown in the previous section, and since the maximum height growth of the herbage at that stage does not exceed 10 percent of the total annual height growth of the plant, it is clearly evident that normal current growth and yield are independent of stored sugars and starches and are products of the carbohydrate foods manufactured currently in the herbage of the plant. In this respect, therefore, annual growth of a perennial grass plant is comparable to that of wheat or other annual grasses. Previous food-march studies of grasses (*13, 20*)[6] confirm this finding.

THE STORAGE OF CARBOHYDRATES

As shown by figure 6 the changes of the acid-hydrolyzable hemicellulose and of the combined sugar and starch fractions are more or less in inverse proportion. This behavior suggests that enzymatic transformations from the hemicellulose may be added to the sugar or to the starch fractions. Significant declines in the concentrations of the hemicellulose aggregating 2.35, 2.88, and 1.42 percent were observed between August 9 and September 28, August 21 and September 22, and August 2 and October 22, during 1932, 1933, and 1934, respectively. The sugar and starch fractions increased during this same period.

That the hemicellulose may be a possible source of the less complex carbohydrates is further suggested by the behavior of these several materials in the basal organs under the winter snow cover. The diminutions in the combined sugar and starch fractions, January 6 to June 2, 1933, December 6, 1933, to April 16, 1934, and December 1, 1934, to May 28, 1935, were 10.01, 6.0, and 10.53 percent, respectively. The increases in the hemicellulose during these intervals were 3.11, 1.25, and 1.04 percent, respectively. Since carbohydrate synthesis under the winter snow cover was entirely suspended, the additional hemicellulose in each instance probably was constructed from materials derived from the sugar and starch fractions.

On the other hand, the hydrolytic products resulting from the diminution in the hemicellulose during the respective intervals, August 9 to September 28, 1932, August 21 to September 22, 1933, and August 2 to October 22, 1934, or between the seed-fully-ripe

[6] Also unpublished data on *Agropyron smithii*, *Andropogon scoparius*, *A. hallii*, and *Bouteloua hirsuta*.

stage and the completion of the storage process, were in all probability utilized in the metabolic functions of the plant. Although the quantities of the transformed carbohydrate materials were small in each case, the hemicellulose may be considered stored food. However, the speed of these transformations is apparently very slow, possibly so slow as to fail to supply sufficient soluble sugars to satisfy the demand when such foods are being used at a rapid rate.

When considered in relation to the nutritional requirements of the plant, the relative values of the hemicellulose and of the sugar and starch fractions are by no means equal. The sugar and starch fractions fluctuate with changes in growth acceleration, whereas this relationship does not obtain in the hemicellulose values. Moreover, when clipping is practiced in sufficient intensity to decrease sugar and starch values pronouncedly, the hemicellulose tends to equal, or to exceed, the amount contained in the controls (*12*, *13*). Graber et al. (*6*), in the study of alfalfa, determined that the diminution in the sugar and starch materials in the roots of the plant at fall dormancy was proportional to the frequency of cutting of the top growth, but that no marked variations in the hemicellulose resulted from the clippings. Furthermore, in certain grass studies, plants with greatly diminished stores of sugar and starch showed a high mortality during the winter, despite the absence of comparable diminution in the hemicellulose fraction.[7] These facts lead to the conclusion that the sugars and starches (chiefly sucrose and starch) are the more potent of the stored carbohydrate foods, and that the presence of such foods in relatively high concentration is essential to winter survival as well as to vigorous growth during the succeeding season. Conversely, the behavior of the acid-hydrolyzable hemicellulose suggests that this carbohydrate is employed largely as structural material.

Storage of the sugar and starch fractions presumes the synthesis of these materials in excess of their use in the metabolic functions of the plant. Evidence from this study, however, indicates utilization of these materials in excess of their manufacture during intervals of active growth.

Accumulation of a considerable portion of the carbohydrate stores occurred during the flowering stage and the development of the fruit in 1932 and 1933. During 1934, the initial accumulation appeared after the vegetative shoots were fully developed. As has been previously shown, this initial accumulation attended low growth rate, which coincided with the low temperatures prevailing between "flower stalks first in evidence" and the blooming stage of 1934. During each year of the study carbohydrate storage ceased simultaneously with new root growth and secondary shoot growth; a loss of slightly more than 2 percent, principally in the sucrose and starch of the combined sugar and starch fractions, resulted. As revealed by the variations in the concentrations of the sugar and starch fractions, the storage of these materials is inhibited by vegetative growth, the process of which is completed after the seed matures.

For the purpose of discussion, the start of seed dissemination may be considered as the date of seed maturity when many fruits are brown, with white, firm endosperms. The inflorescence and fruit stalks also are then mature. In 1932, 1933, and 1934, seed matured August 18, September 1, and August 6. Permanent snowfall came on October 18,

[7] Unpublished data on *Agropyron smithii*.

October 31, and October 20. Carbohydrate determinations corresponding to these dates may be selected from the food-march series (fig. 6). In 1932, determinations were made on August 18 and October 18, whereas the determinations made on August 31 and November 2 correspond approximately to the dates of seed maturity and the permanent snow of 1933. By interpolation, the combined sugar and starch stores on August 6, 1934, were 13.84 percent, and the total deposits of these materials on October 22 were 18.09 percent. The amounts of the stored sugar and starch fractions on the latter dates, or at the time of the permanent snowfall of each of the years 1932 to 1934, inclusive, were 5.94, 5.78, and 4.25 percent, respectively, in excess of the values found at seed maturity. It is obvious, therefore, that carbohydrate accumulation is incomplete at seed maturity, the autumn being the period of storage of these materials. These several steps of carbohydrate storage in the growth cycle of mountain brome conform to the same general pattern found in former grass studies (*18*).[8]

THE REST PERIOD

The interval of comparative inactivity when active herbage growth ceases began in 1932 on September 28, when the seed had been disseminated and the herbage was mature. Comparable intervals were noted September 22 and September 11, respectively, in 1933 and 1934. At this time no further additions were made to the carbohydrate stores, and the insoluble foods exceeded the sugar fractions in concentration. This condition corresponded to the middle rest period which Johannsen (*9*) described as the interval of complete inactivity. However, the physiological activity in mountain brome does not cease with the end of active growth or the so-called rest period, which, according to Simon (*22*), represents merely a reduction in some processes and modification in others.

Invariably, the characteristically low autumnal temperatures stimulated enzymatic action, resulting in increased concentrations of sucrose at the expense of the starch fraction. These reactions began after secondary growth, the maximum concentrations of sucrose being reached before the first permanent snowfall of the winter. The maximum concentrations of sucrose during the autumns of 1932 and 1933 exceeded those of the starch fractions, indicating relationship to the depth of the frost in the soil. In the autumn of 1934, however, with little or no frost in the soil, the starch fraction persisted in excess of the sucrose concentration throughout the winter. Transformations from the insoluble to the soluble in the carbohydrate constituents of plants are related to low temperatures, according to Miyaké (*14*), Lewis and Tuttle (*11*), Korstian (*10*), and others. Müller-Thurgau (*15*) concluded that diastatic action was stimulated at the freezing point. Hopkins (*7*) showed that the rate of respiration increased with decline in temperature from 37.4° to 32° F.

These transformations of insoluble carbohydrates into soluble forms result, in part, in an increased water-holding capacity. The plant is exposed to the desiccating influence of low relative humidity and deficient soil moisture before the first permanent snow. The moisture content of the stem bases and roots of the plant during the autumn was maintained at 32 to 45 percent, whereas the soil moisture

[8] Unpublished data on species listed in footnote 6.

ranged from 8 to 17 percent. It is even conceivable that a relatively high autumnal sap concentration affords some protection against excessive water loss due to the low relative humidity of both air and soil.

The hardening off of the plant also is affected by the increase of sugars during the autumn. Although the snow blanket affords protection against extremely low temperatures, the formation of an ice sheet at the soil surface may expose the young growth to freezing. The newly formed shoots are relatively high in sugar concentration, which appears to be a factor in their resistance to low temperatures. Chemical analyses showed an increase in sucrose in the stem bases and roots from 0.85 percent on September 8 to 9.3 percent on October 18, 1932; increases in this fraction also occurred during corresponding periods in 1933 and 1934. Supplementary to the increase in sucrose before the first permanent snowfall, marked diminutions in the reducing sugars developed. In this connection, Newton (*16*) reports that the precipitation of proteins due to freezing is prevented by the presence of sucrose in solution in the cell sap. Chandler (*4*) found that apple and peach blossoms placed in solutions of sugar and glycerin became more resistant to cold, while Newton and Brown (*17*) showed that higher sugar concentrations prevailed in the hardier varieties of wheat. Although hardiness in plants appears to depend upon a number of cell constituents, the presence of the sugars in relatively high concentration is obviously a contributing factor. This evidence warrants the conclusion that relatively high concentrations of the sugars in the basal organs and in the newly developed shoots of mountain brome are associated with resistance to low temperatures and are essential to winter survival of the plants.

APPLICATION OF RESULTS TO RANGE MANAGEMENT

RANGE GRASSES ARE LIVING ORGANISMS

The study of the march of carbohydrates in relation to growth of mountain brome reemphasizes the fact that range grasses, the key forage plants of mountain ranges, are living organisms and must be managed as such. Early spring growth, which is produced before snow disappears, is made at the expense of carbohydrates stored in the roots and stem bases during the previous autumn. Subsequent herbage growth, new root development, flower-stalk formation, seed production, secondary herbage growth, and other growth stages, follow in a regular order. The reappearance of a permanent winter snow cover causes a temporary halt in current herbage growth, but the physiological activity continues. Autumnal temperatures stimulate enzymatic action, resulting in the transformation of the insoluble carbohydrates into soluble forms for winter use.

The various growth stages are essential to the living grass plant and provision must be made in range management plans for their development in proper sequence if the plants are to remain on the range and contribute their maximum forage value.

MODERATE GRAZING ESSENTIAL

Since the carbohydrates stored during the previous autumn in the roots and stem bases of mountain brome reach their minimum level when not more than 10 percent of the total seasonal height growth of the plant has been attained, it is clear that subsequent normal growth and yield are independent of stored carbohydrates and that they are products of carbohydrates manufactured currently by photosynthesis. This indicates that enough herbage must be left after each grazing period to permit sufficient manufacture and storage of carbohydrates to maintain the life and proper vigor of the plants; in other words, moderate grazing is essential.

DEFERRED AND ROTATION GRAZING IMPORTANT

As shown by this study, storage of carbohydrates in mountain brome is at a minimum during the active growth stages, and evidence strongly indicates the utilization of these materials during these stages in excess of their manufacture. Also, maximum stores of carbohydrates are not deposited until seeds are matured and active growth has ceased. Most of the food manufactured by the plant is utilized to support its several growth processes; hence, maximum storage cannot take place until these growth stages are completed.

Continuous heavy grazing during the formation of the flower stalks, when carbohydrates stores are at a minimum, undoubtedly would inflict considerable injury on and disrupt the biological function of the plant, necessitating the use of part of the 25-percent residue of the carbohydrates stores to support regrowth. Continuous heavy grazing at or after seed maturity, during the autumn storage period, would not only prevent normal storage of carbohydrates but also would stimulate further herbage growth. This stimulated growth would be produced at the expense of the carbohydrates already stored, resulting in further depletion of carbohydrates, and the plant would enter the winter period with diminished stores. Consequently since it has been shown that sufficient carbohydrates must be stored in the roots and stem bases at the outset of the winter period to prevent winter-killing and to promote early spring growth, any system of grazing that will result in depleted carbohydrate stores will be detrimental to the plant.

Therefore, it is strongly indicated that some form of the deferred and rotation system of grazing (*8, pp. 60–65*) is important as a practical method of utilizing range grasses for forage for livestock. In this system of grazing, the plants are not grazed continuously during any one season nor at the same time in consecutive years. The plants are aided by this controlled use in depositing normal or near-normal stores of carbohydrates.

SUMMARY

A detailed field and laboratory study was made at the Great Basin branch of the Intermountain Forest and Range Experiment Station during the period 1932–34, to determine the character of growth and the time and amount of carbohydrate food storage in mountain brome (*Bromus carinatus*), a highly palatable range forage grass native to a large part of western mountain range lands. The experimental area is located at an elevation of 8,850 feet in Ephraim Canyon, Utah.

Annual growth of mountain brome is cyclic in nature, owing in part to atmospheric temperatures and in part to the plant's reproductive processes. The growth cycle includes current seasonal growth of herbage, secondary herbage growth, and root growth. Annual herbage growth begins some 45 to 89 days (depending upon the season) before winter snow disappears. Secondary shoot growth follows the produc-

tion of the current seasonal shoots and flower stalks. Three intervals of adventitious root growth were noted; they occurred immediately preceding snow disappearance, at the conclusion of current seasonal shoot growth, and at the close of the snow-free period in the autumn.

While the coming of the winter snow temporarily halts seasonal herbage growth, yet the physiological activity in mountain brome does not cease. Autumnal temperatures stimulated enzymatic action, resulting in the transformation of insoluble carbohydrates into soluble forms.

Except for the hemicellulose fraction, carbohydrate storage is inversely related to the rate of growth of the herbage, i. e., high growth rate, low carbohydrate storage. Minimum values prevail in the roots and stem bases during the active growth stages of the plant, and evidence indicates the utilization of carbohydrates in excess of their manufacture during the most active growth periods. Maximum storage occurs during the autumn period after current seasonal and secondary herbage growth is completed.

The general trend of the combined sugar and starch fractions is from low values during the formative stage of shoot development to high concentrations following current seasonal and secondary herbage growth. The starch values in both herbage and basal organs exceed the sugar values; their respective seasonal trends correspond to those of the combined sugar and starch fractions. Minimum sucrose concentrations in the herbage prevails from snow disappearance into September, and in the stem bases and roots during the formative period of herbage growth. The highest concentration of sucrose appeared in both herbage and basal organs coincident with declining autumnal temperatures. Maximum values of the reducing sugars in the herbage and low values in the stem bases and roots obtain during the formative stage of herbage growth. Although this fraction increases in the stem bases and roots as the current seasonal growth declines, low values were found in both herbage and basal organs simultaneously with the autumnal increase in sucrose concentrations. Maximum concentrations of hemicellulose prevail in the herbage and in the basal organs during the formative growth stage; low values coincide with the development of the fruit and the storage of the sugar and starch materials.

The study leads to the conclusion that sugars and starches (chiefly sucrose and starch) are the more potent of the stored carbohydrate foods. Conversely, the behavior of the acid-hydrolyzable hemicellulose suggests that this carbohydrate is employed largely as structural material.

Minimum values of carbohydrates in the roots and stem bases occurred shortly after snow disappeared, which clearly shows that annual herbage growth and yield of mountain brome are products of carbohydrates manufactured currently in the herbage. Hence, herbage growth of perennial mountain brome is comparable to the growth of wheat or other annual grasses.

Evidence from the study warrants the conclusion that relatively high concentration of the sugars in the basal organs and in the newly developed shoots of mountain brome are associated with resistance to low temperature and are essential to winter survival of the plants.

The results of the study have a direct bearing on practical range management in that they (1) reemphasize the fact that range grass plants are living organisms and that their individual growth requirements must be considered in grazing practices if they are to be maintained on the range, (2) stress that moderate grazing use is essential to allow for proper carbohydrate food storage, and (3) indicate the importance of some form of the deferred and rotation system of grazing as a practical method of utilizing range grasses as forage for livestock.

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