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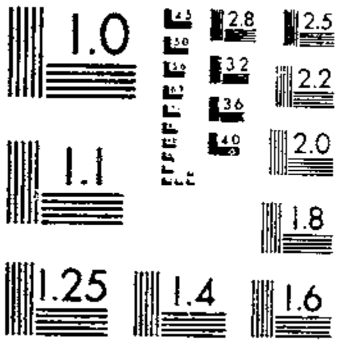

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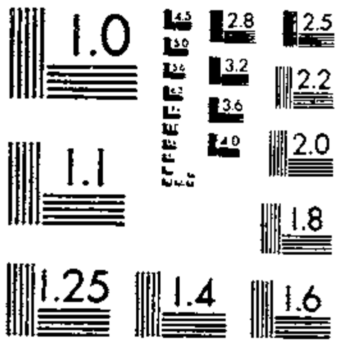

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Growth and Carbohydrate Content of Important Mountain Forage Plants in Central Utah as Affected by Clipping and Grazing[1,2]

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INTRODUCTION

Sustained forage production on western mountain range lands, together with the welfare of the livestock industry and the other enterprises these lands support, depends largely on the vigor and persistence of the herbaceous perennials that are the principal forage-producing plants of the region. Since these plants die back near the soil line upon approach of winter, it is imperative that they should make proper growth and store sufficient foods during the growing season to carry them through the winter period and to produce initial growth in the spring. Thus it follows that the harvesting by livestock of the forage crop when it is most needed and when the herbage is palatable and nutritious must be so controlled as to permit the plants to carry on their proper growth and nutritional functions. To determine the nature of such control, it is necessary to study the

[1] Received for publication July, 1941.

[2] The chemical analyses involved in this study were made under the supervision of the senior author in the Laboratory of the Botany Department of Riverside Junior College, Riverside, Calif. Ralph Stocking, formerly field assistant at the Intermountain Forest and Range Experiment Station, assisted in the chemical analyses, made some of the final calculations of chemical data, and reviewed the manuscript. The study was begun under the direction of C. L. Forsling, assistant chief of the Forest Service in charge of forest research, then director of the Intermountain station.

[3] Late head of the Botany Department of the Riverside Junior College, Riverside, Calif., and engaged during the summer months by the Intermountain station in the capacity of associate forest ecologist.

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growth and nutritional characteristics of the principal palatable forage plants as well as their reaction to harvesting and grazing.

Sampson (*10*),[5] in an earlier study bearing on the problem of correlating livestock grazing use with the growth requirements of mountain range vegetation, observed closely the above-ground growth and reactions of the plants under various systems of grazing and concluded that deferment and rotation of grazing are necessary for proper growth of the plants under rather heavy grazing use. Later, Sampson and Malmsten (*12*), as a means of determining plant response to harvesting, assigned index values, based upon calories of essential root constituents, to chemical data of roots. For plants harvested four times in a season for three consecutive years, the index was less than 100; for plants harvested twice yearly, more than 250; for plants harvested once yearly, more than 300.

Sampson and McCarty (*13*), working with California needlegrass (*Stipa pulchra*), and McCarty (*5*, *6*), working with wild oat (*Avena fatua*), wild-rye (*Elymus ambiguus*), and mountain muhly (*Muhlenbergia montana*), found that the annual growth cycles of grasses are influenced by environmental factors and by specific nutritional and reproductive processes. Initial growth of the herbage of the perennial grasses, according to their findings, is made by expenditure of carbohydrates [6] stored in the basal organs during the preceding season; accumulation of carbohydrates in both herbage and basal organs of the plant is inversely related to current rate of herbage growth; accumulation of carbohydrates is delayed until most of the herbage growth has been made; after one close clipping of the herbage, at any time during the yearly season of growth or at its close, carbohydrate content is less than normal in the renewed herbage and also in the stem bases and roots; and the quantity of carbohydrates stored in plants subjected to clipping is directly related to the total leaf area present during the storage period.

These findings, together with the results of the numerous investigations made concerning the growth requirements, life histories, forage yield, root development, and basal growth of range forage plants have great value as a basis for determining the proper season and degree of grazing use. The usefulness of the results of the nutritional studies is, however, limited by the fact that they were largely confined to the interval beginning with snow disappearance in the spring and ending with dissemination of the ripened fruit, and that they have not been tested under various harvesting and grazing treatments.

This bulletin presents both season and year-long growth and carbohydrate-nutritional data for two species of perennial forage grasses and two species of broadleaf herbaceous perennial forage plants native to the Wasatch Mountains in central Utah; as well as data on the trends of storage of carbohydrates in these plants under several controlled clipping treatments and as a result of livestock grazing during the 4-year period 1932–35.

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[5] Italic numbers in parentheses refer to Literature Cited, p. 50.

[6] Earlier (unpublished) studies by E. C. McCarty on *Agropyron smithii*, *Andropogon scoparius*, *A. hallii*, and *Bouteloua hirsuta*, indicated that of the several classes of foods utilized by plants, namely proteins, fats, and carbohydrates, the last is of greatest importance. Carbohydrates form the foundation material for the construction of fats and proteins.

Description of Study Areas

The study reported here was made at the Great Basin branch of the Intermountain Forest and Range Experiment Station, located in Ephraim Canyon, on the Wasatch Plateau, Utah. Field tests were on three separate areas in the vicinity of the branch headquarters, which is situated within the aspen-fir zone (*11*) of central Utah at an elevation of 8,850 feet. Location and description of each field unit are summarized briefly as follows:

HEADQUARTERS UNIT

Description.—Permanent enclosure of about 2 acres in an open, relatively flat parklike clearing, slope 5 percent, exposure southwest; 8,850 feet elevation, near center of aspen-fir zone.

Vegetation.—Almost pure stand of native mountain brome (*Bromus carinatus*)[7] planted in the spring of 1925. Area surrounded by dense stand of even-aged aspen (*Populus tremuloides*) with a mixture of Douglas-fir (*Pseudotsuga taxifolia*) and white fir (*Abies concolor*), in which the predominant herbaceous perennial making up the understory is sticky geranium (*Geranium viscosissimum*).

Soil.—Clay-loam of limestone origin. Total nitrogen, 0.389 percent; organic matter, 9.95 percent; moisture equivalent, 55.5 percent.

BLUEBELL UNIT

Description.—Temporary hurdle plots 16 by 16 feet in an open, flatlike area, slope 10 percent, exposure northeast; 9,000 feet elevation, near upper limits of aspen-fir zone.

Vegetation.—Grass-weed[8] type consisting chiefly of mountain brome, slender wheatgrass (*Agropyron trachycaulum*), oniongrass (*Melica bulbosa*), penstemon (*Penstemon rydbergii*), niggerhead (*Rudbeckia occidentalis*), and yarrow (*Achillea lanulosa*). Area surrounded by aspen intermixed with Douglas-fir and white fir.

Soil.—Clay-loam of limestone origin. Total nitrogen, 0.334 percent; organic matter, 7.2 percent; moisture equivalent, 32.4 percent.

DUNGEON UNIT

Description.—Permanent enclosure of 1 acre on an open, flatlike shelf, slope 13 percent, exposure west; 9,400 feet elevation, at upper limit of aspen-fir zone.

Vegetation.—Native stand of slender wheatgrass with slight mixture of Letterman needlegrass (*Stipa lettermani*), mountain brome, penstemon, yarrow, many-flowered sunflower (*Viguiera multiflora*), Fendler rose (*Rosa fendleri*), and common serviceberry (*Amelanchier alnifolia*).

Soil.—Clay-loam of limestone origin. Total nitrogen, 0.376 percent; organic matter, 16 percent; moisture equivalent, 34.6 percent.

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[7] This rather variable grass has been regarded by some botanists as three separate species, (1) California brome (*B. carinatus*), (2) big brome (*B. marginatus*), and (3) polyanthus brome (*B. polyanthus*). Frequently it has been known in the Forest Service by the name "the mountain brome."

[8] The term "weed," as here used, refers to the herbaceous, nongrasslike plants occurring on the range, often also referred to as "forb."

CLIMATE

Weather records are available for the headquarters field unit only. However, inasmuch as the two upper field units are within three-fourths of a mile (air-line distance) of the headquarters unit, it is believed that the following climatic data for the headquarters field unit are fairly representative for all.

Yearly maximum temperatures are reached in July and yearly minima in January (table 1). Average daily temperatures for June, July, August, and September, the growing season, are above 50° F. Temperatures have risen as high as 88 ° during July and dropped as low as 11° in September and 19° in June. The average length of the frost-free period is 87 days, although frosts have occurred during all months (*9*).

TABLE 1.—*Mean monthly air temperatures (1918–33) and precipitation (1914–33) at headquarters unit*

Month	Mean air temperature	Mean precipitation	Month	Mean air temperature	Mean precipitation
	° F.	*Inches*		° F.	*Inches*
January	21.4	3.15	August	58.1	1.80
February	23.3	2.85	September	50.1	1.56
March	23.2	4.11	October	38.9	1.92
April	34.8	3.54	November	29.0	2.19
May	42.8	2.44	December	20.3	3.26
June	53.7	.85			
July	60.1	1.81	Annual mean and total	38.0	29.48

More than three-fourths of the average annual precipitation of less than 30 inches occurs as snowfall during the winter period, October to April inclusive (*9*). Snowstorms have occurred in every month of the year. During the growing season, which averages approximately 145 days, precipitation occurs as thundershowers.

For the snow-free period of May 1 to September 30, before snow forms a continuous cover, average soil temperatures (averages of 8 a. m. and 5 p. m. readings, 1924–34) at the 6-, 12-, and 24-inch depths were 54.8°, 53.0°, and 50.8°F. (*9*). The soil is warmest in late July and coldest in May and September. When the ground is covered with snow, soil temperatures are almost the same at all three depths and remain practically constant.

Soil moisture is highest at the time of snow disappearance, averaging 30 percent of the dry weight of the soil. Thereafter, the moisture content of the soil decreases steadily, reaching the seasonal minimum in the latter part of June or in July.

Sampson, in earlier plant growth studies (*11*) at this same site, found that sunshine duration and intensity were practically the same in the three major vegetative types in Ephraim Canyon, namely, oak-brush, aspen-fir, and spruce-fir. This indicates that total length of day and sunshine duration and intensity, except for slight variations in direct sunlight from plot to plot in early morning and evening, were about the same at all three areas of the present study. Observations from a white cylinder-type atmometer during the months of July and August for a 3-year period indicate daily evaporation of 29.2 $cm.^3$ in July and 24.4 $cm.^3$ in August.

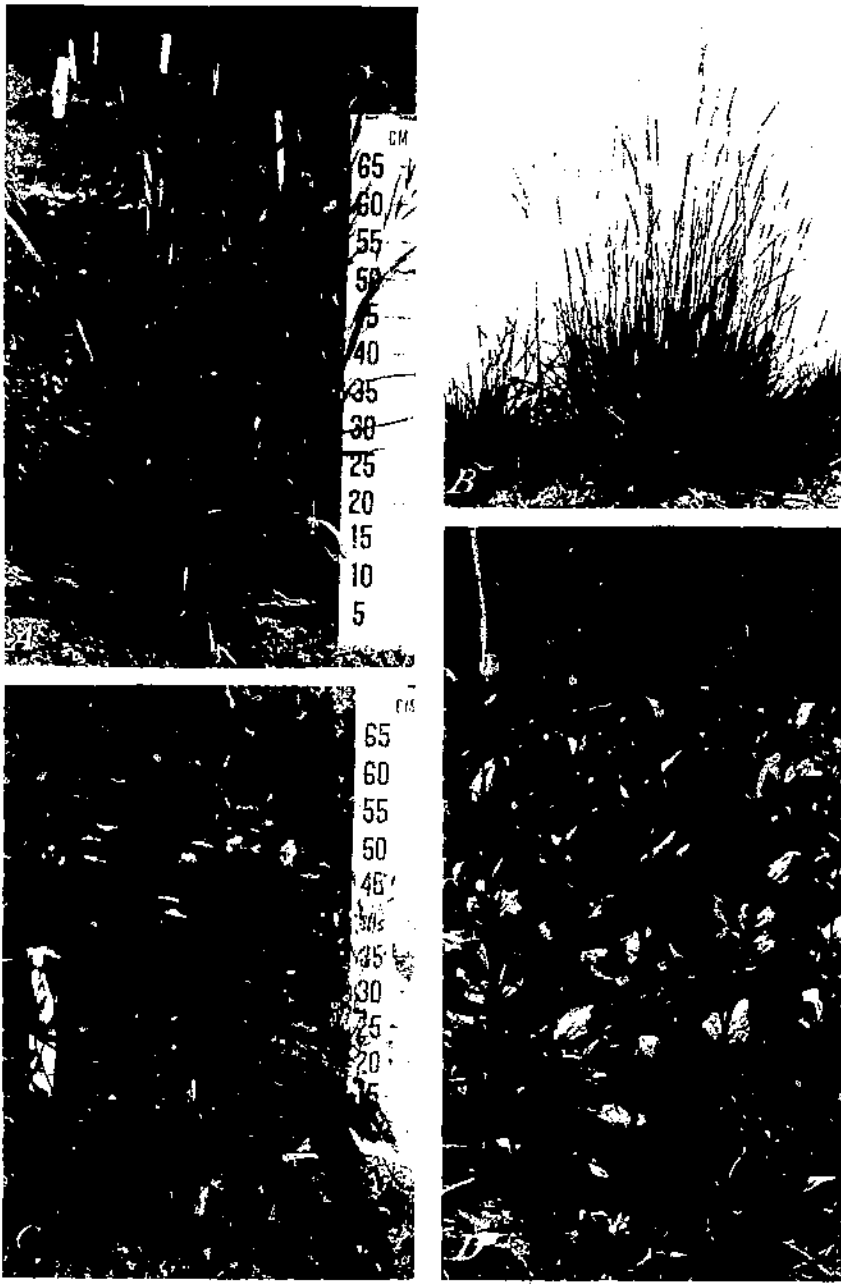

PLATE 1. Range forage plants used in the study: *A*, Mountain brome; *B*, slender wheatgrass; *C*, sticky geranium; and *D*, niggerhead.

SPECIES USED IN STUDY

Plant species used in the study were mountain brome, slender wheatgrass, sticky geranium, and niggerhead.

Mountain brome (pl. 1, *A*) is a moderately coarse-stemmed, short-lived perennial bunchgrass, widely distributed in the range States. The plant attains a height of 1 foot to 4 feet or more and has numerous basal leaves about 6 to 12 inches long and ¼ to ⅝ inch wide. It produces abundant seed, and is highly palatable to livestock, nutritious, and fairly resistant to drought (*15*). In the aspen-fir zone of central Utah, within which the experimental areas are located, mountain brome forms dense stands and is a key forage plant by means of which degree and intensity of grazing use are estimated.

Slender wheatgrass (pl. 1, *B*), a native perennial bunchgrass with erect, slender stems from 0.5 foot to 4 feet high, is also a key forage plant in central Utah. It is widely distributed, ranging from Newfoundland to Alaska and south to Missouri, Kansas, New Mexico, and California. It starts growth early, produces abundant seed, is very nutritious, highly palatable to livestock, drought resistant, and withstands grazing use (*15*).

Sticky geranium (pl. 1, *C*), also a key forage plant, is a native coarse, leafy, branched perennial herb 1 to 3 feet tall, widely distributed throughout the West. In palatability it is fair for sheep and fair to poor for cattle and horses (*15*). In the vicinity of the experimental areas it occurs abundantly, in association with mixed grasses and weeds.

Niggerhead (pl. 1, *D*) is a coarse perennial herb of the sunflower family with a stout ridged stem, occasionally 8 feet high, and a conspicuously cone-shaped head that is dark brown both before and after flowering. It is widely distributed, occurring in most of the Western States, and is considered the most important range species of the genus (*15*). In the vicinity of the experimental areas, niggerhead is not palatable to livestock until late fall.

GENERAL PLAN OF STUDY

The study had three phases: (1) Growth and nutrition phase, or determination of the character of annual growth and of the time, rate, extent, and type of carbohydrate storage in the plants under normal conditions and total protection from livestock grazing; and the (2) clipping and (3) grazing phases, or determination of the effect of several clipping treatments, and of seasonal livestock grazing, on carbohydrate storage in the roots and stem bases of the plants and on forage yield and plant vigor. Mountain brome and slender wheatgrass were included in all phases of the study. Sticky geranium was not included in the grazing phase, and niggerhead was included in the nutrition phase only.

Mountain brome was studied at Headquarters and Bluebell units; slender wheatgrass at Bluebell and Dungeon units; sticky geranium at Headquarters; niggerhead at Bluebell. The nutrition phase included studies at Headquarters on mountain brome and sticky geranium, at Bluebell on niggerhead, and at Dungeon on slender wheatgrass. The clipping tests were centered at Headquarters and Dungeon, and grazing tests at Bluebell only.

GROWTH AND CARBOHYDRATE FOOD RATIOS

On mountain brome and slender wheatgrass, the nutrition phase was carried on from May 1932 to May 1935, resulting in continuous year-long records. The investigation on sticky geranium began in May 1932 and was continued to mid-October yearly for 3 years, giving continuous records for three annual snow-free periods. That on niggerhead was started in June 1935 and carried continuously through April 1936.

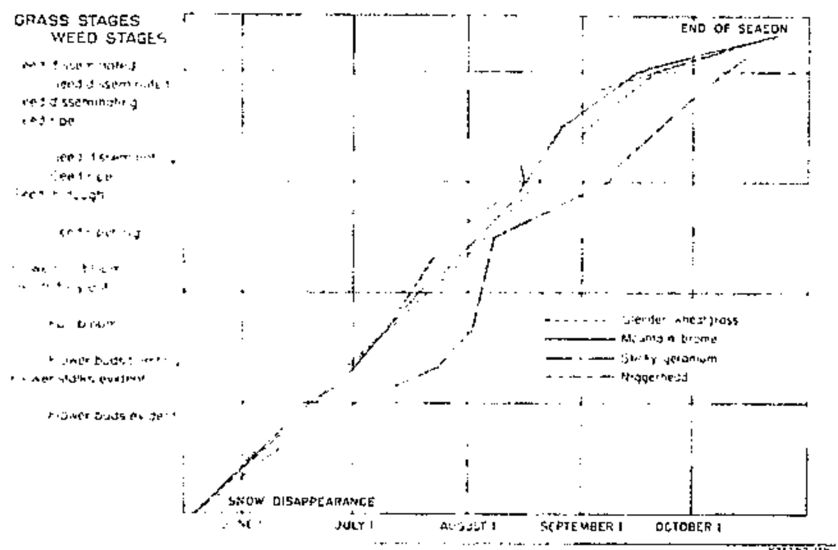

FIGURE 1. A comparison of the relative progress made by the four species of grasses and perennial herbs (weeds) used in this study, from snow disappearance to end of growing season. Based on averages for 1924–34.

METHODS OF MEASUREMENT AND ANALYSIS

GROWTH MEASUREMENTS AND PREPARATION OF SAMPLES

Maximum and average height growth were determined and phenological observations made at 5-day intervals throughout the snow-free period of each year on about 10 plants of each species in each field unit (fig. 1). Also, evidence of growth was noted on root samples collected during the winter season.

Collections of material for analyses were made between the hours of 9 a. m. and 12 noon. Each sample of the grasses included six to eight plants, and each sample of the other herbaceous plants included four to six plants. Samples were collected at 10-day intervals during the snow-free period and at monthly intervals during the rest of the season each year.

The grass samples were prepared by removing the soil from the roots with hand brushes and clipping the herbage from the stem bases. Herbage and roots of each sample were weighed and separately preserved in 95 percent alcohol. Herbage samples as prepared consisted only of culms and green leaves; all dead and discolored material and any inflorescence present were removed. Root samples (roots and stem bases) consisted of root crown and whatever fragments were not detached in harvesting or cleaning. The root samples, on the average, weighed more than 40 g. each; after start of active height growth, the weight of the herbage samples generally exceeded that of the root samples.

The preparation of sticky geranium and niggerhead samples was similar to that of the grass samples, except that the fibrous roots characteristic of these plants were split in half and all dead material scraped away with a dull knife. The root samples of sticky geranium averaged about 60 g. and those of niggerhead averaged more than 100 g. Herbage samples of sticky geranium averaged about 60 g.

CHEMICAL ANALYSES

The carbohydrates determined were acid-hydrolyzable hemicellulose, starch, sucrose, and reducing sugars.

The alcohol having been drained off, the samples were oven-dried at 75° C. for 24 hours, then ground and again dried for 12 hours at 80°. A 5-g. portion of each sample was used for the complete chemical analysis. It was extracted for 12 hours with hot alcohol to which was added a corresponding portion of the alcohol in which the sample had been preserved. The alcohol extracted the sugars; the hemicellulose and starches remained in the extraction thimble.

After the alcohol had been evaporated the residue 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 sulfate, according to the method described by Schaffer and Hartmann (*14*). The second portion was hydrolyzed according to the directions given in Official Methods (*1*). After neutralizing and making up to volume, the reduction power was determined. The resultant fraction is reported as total sugars, and the differences between the two determinations is reported as sucrose.

The residue remaining from the sugar extraction was dried in an electric oven, transferred to a ball mill, and rotated for 60 hours (for sticky geranium, 30 hours was sufficient). Distilled water, boiling hot, was added to the fine residual powder, and the container was placed in a water bath at 100° C. for one-half hour. After cooling, 6 cm.^{3} of saliva, a few drops of toluene, and approximately 0.1 g. 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 an aliquot portion of the former was hydrolyzed with 2.5 cm.^{3} of concentrated hydrochloric acid. After neutralizing and clearing, the reduction power of this solution was determined. This fraction, reported as starch, contains both true starch and water-soluble starch.

The residue remaining after the starch separation was washed and transferred to an Erlenmeyer flask, and 2.5 cm.^{3} of concentrated hydrochloric acid, diluted to 100 cm.^{3} with distilled water, was added. The hydrolysis was carried out on an electric hot plate, care being taken 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 by use of aliquot portions of this filtrate. This fraction is reported as hemicellulose.

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

Results of Observations

MOUNTAIN BROME

Annual growth of mountain brome is cyclic in nature (figs. 2 and 3), owing in part to the influence of climatic factors and in part to the plant's reproductive cycle (*2, 7*). Seasonal fluctuations in precipitation and temperature cause definite fluctuations in the growth rate. Depressions in growth rate also coincide with the advent of flowers and formation of fruit. The growth cycle includes seasonal growth of herbage, secondary herbage growth, and root growth. Annual herbage growth begins under the snow approximately 45 to 89 days before winter snow disappears. Secondary shoot growth follows the production of seasonal shoots and flower stalks. Root growth alternates with herbage growth in three main periods, (1) immediately preceding snow disappearance, (2) at the conclusion of seasonal shoot growth, and (3) at the close of the snow-free period in the autumn.

The combined sugars and starch content of the herbage tends to be very high immediately following snow disappearance, to reach its seasonal minimum during flower-stalk formation, and to rise to a secondary peak near the close of the snow-free period. After this secondary seasonal rise the values drop, probably as a result of translocation. A final upturn is caused by a rise in sucrose toward the end of the season, which may result from transformation of the insolubles.

Starch content shows almost the same fluctuations as the combined value. Sucrose content is also high at snow disappearance, but remains near the seasonal minimum throughout the remainder of the growing season, until the maximum near the close of the snow-free period. Reducing sugars, at their maximum at snow disappearance, steadily decline throughout the growing season to a minimum during seed dissemination, after which they increase slightly until the end of the season.

Conversely, hemicellulose is low in the herbage at snow disappearance, reaches its maximum during the formative growth stage, and declines fairly steadily when the fruit is developing and sugar and starch materials are being stored.

Sugar and starch storage in roots and stem bases is inversely related to rate of herbage growth. The trend of sugars and starch combined is from low values during the formative stage of shoot development to high values following the main seasonal and secondary herbage growth. Although individual fractions show similar trends, high values of sucrose and low values of starch coincide with declining autumnal temperatures, indicating transformation of insoluble to soluble carbohydrates, a change that undoubtedly influences the plant's hardening off. Maximum values of hemicellulose prevail during the formative growth stage; low values coincide with fruit development and with storage of sugars and starch. The latter fact suggests that hemicellulose is more important as a structural than as a storage material,

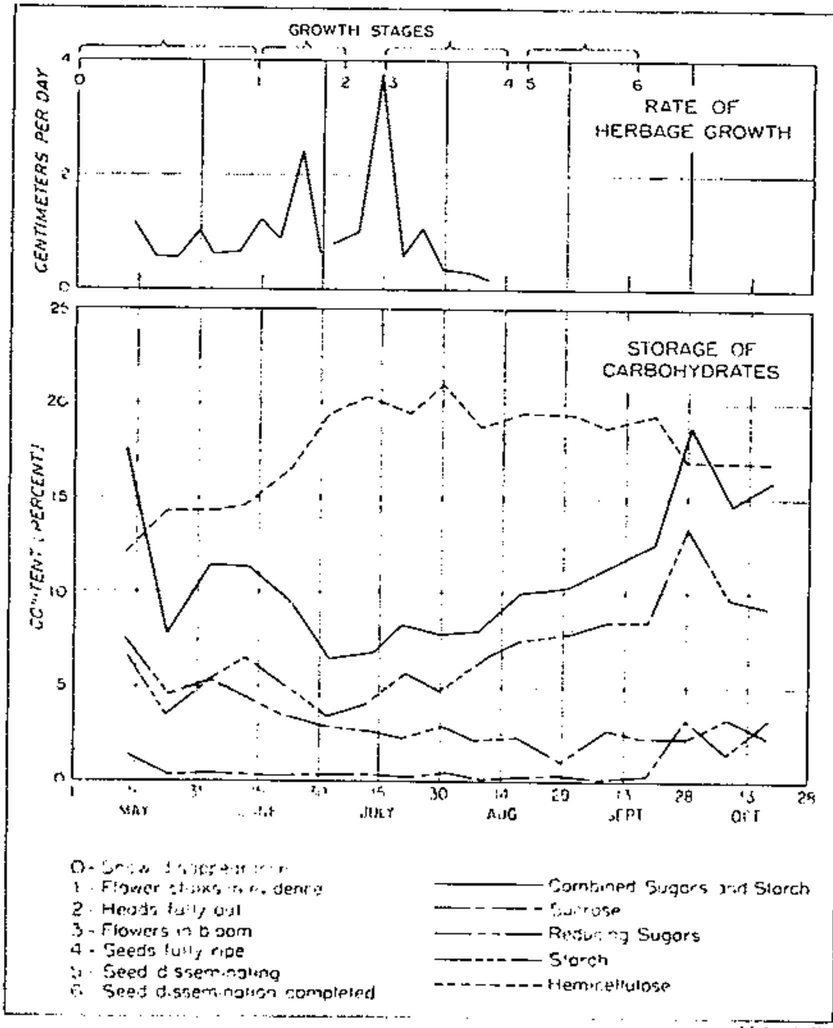

FIGURE 2.—Mountain brome: Annual herbage growth in relation to the trend of herbage storage of carbohydrates, 1932.

although it is possible that enzymatic transformations from hemicellulose are added to the sugars or the starch.

Of the sugars and starch stored in the basal organs of the plant during the autumn, approximately 75 percent is consumed by physiological activity during the winter period and by early spring growth in the form of production of herbage and adventitious roots. The

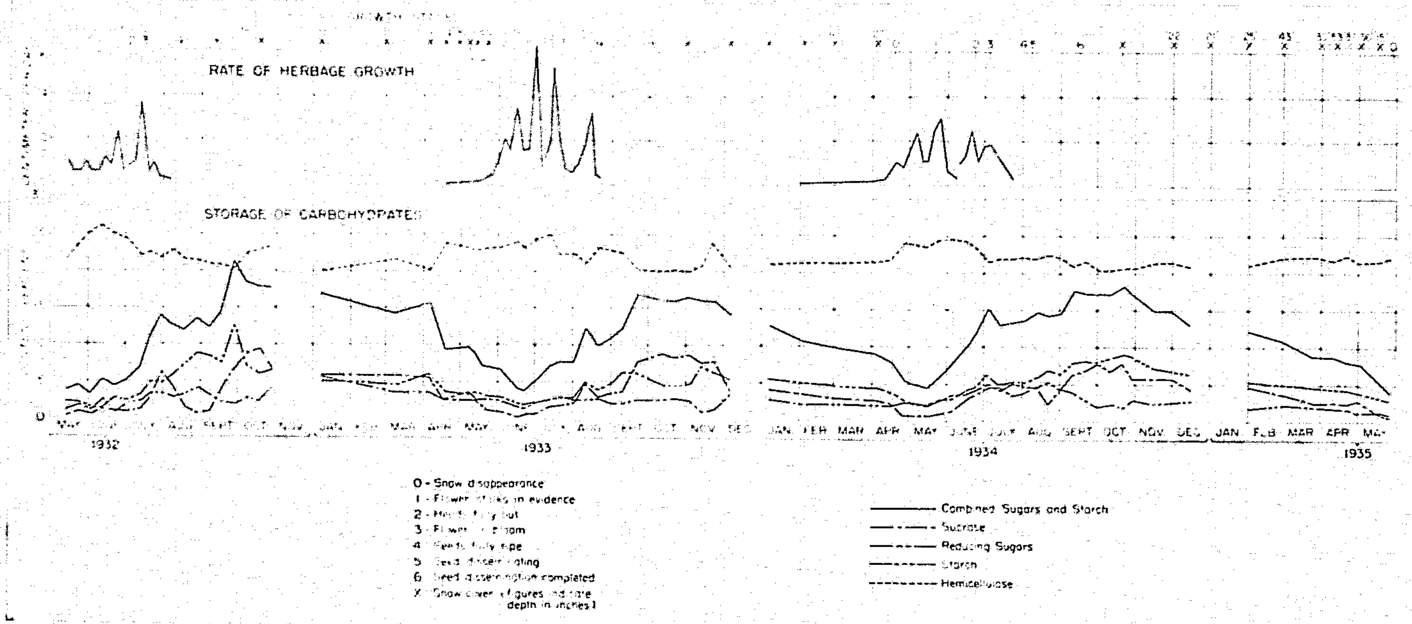

FIGURE 3.- Mountain brome: Annual herbage growth in relation to the trend of root and stem-base storage of carbohydrates, 1932–35.

remaining 25 percent ordinarily is not used, although it is diminished if the herbage of the plant is completely removed by clipping or grazing and renewed herbage growth follows immediately.

Inasmuch as the stored carbohydrates reach their normal minimum soon after snow disappearance, when not more than 10 percent of seasonal growth and development has taken place, it is clear that normal current growth and yield are almost solely the products of carbohydrates manufactured currently by photosynthesis.

Current seasonal growth and development, culminating in ripening of the fruit, keep the storage of carbohydrates at a minimum; in fact, evidence indicates that during periods of most active growth greater quantities of these materials are utilized than are currently manufactured (fig. 3). Carbohydrate storage reaches its maximum for the year during the autumn, starting after seeds have ripened. Physiological activity in the plant is not halted by the coming of winter snow. Enzymatic action is stimulated by autumnal temperatures, with the result that insoluble carbohydrates are transformed into soluble forms. Respiration and other physiological processes cause the sugars and starch content to decline progressively throughout the winter period.

SLENDER WHEATGRASS

Growth of slender wheatgrass definitely fluctuates according to season and stage of reproduction (figs. 4 and 5), much as does that of mountain brome. Comparison of the annual growth stages of the two grasses and their respective growth-rate curves reveals their similarity in these respects, with only minor differences resulting from differences in habitat.

In manufacture and storage of carbohydrates in herbage and in roots and stem bases, slender wheatgrass also follows the trend of mountain brome. Although the maximum of combined sugars and starch in the herbage is lower by 6 percent, the general trend of development and the storage of these materials, collectively and singly, is the same for the two species. The starch values are somewhat lower in slender wheatgrass and the hemicellulose value somewhat higher.

In the roots and stem bases as in the herbage, the combined total of sugars and starches is also lower for slender wheatgrass than for mountain brome, but the general trend and intervals of storage are the same. The individual carbohydrate fractions also are similar, except that sucrose is consistently lower in slender wheatgrass, making the sum total lower for this species. On the other hand, the starch and hemicellulose values tend to be slightly higher. Reducing sugars are about equal. The quantity of carbohydrates in each species varies from year to year, owing to differences in the length of the growing season and possibly to the differences of the two species in habitat.

As is true of mountain brome, normal growth and yield of slender wheatgrass are made almost entirely by expenditure of carbohydrates manufactured currently, and growth made prior to snow disappearance and the initial growth in the spring are made at the expense of carbohydrates stored during the previous autumn. Also the principal storage period is during the autumn. Storage after seed maturity, however, ranged from 1.15 percent in 1933 to 0.0 in 1934, whereas the range in mountain brome was from 5.94 percent in 1932 to 4.25 percent in 1934. The portion of the stored carbohydrates that normally remains in the roots and stem bases following early spring growth amounts to 30 percent in slender wheatgrass (table 2), as compared with 25 percent in mountain brome.

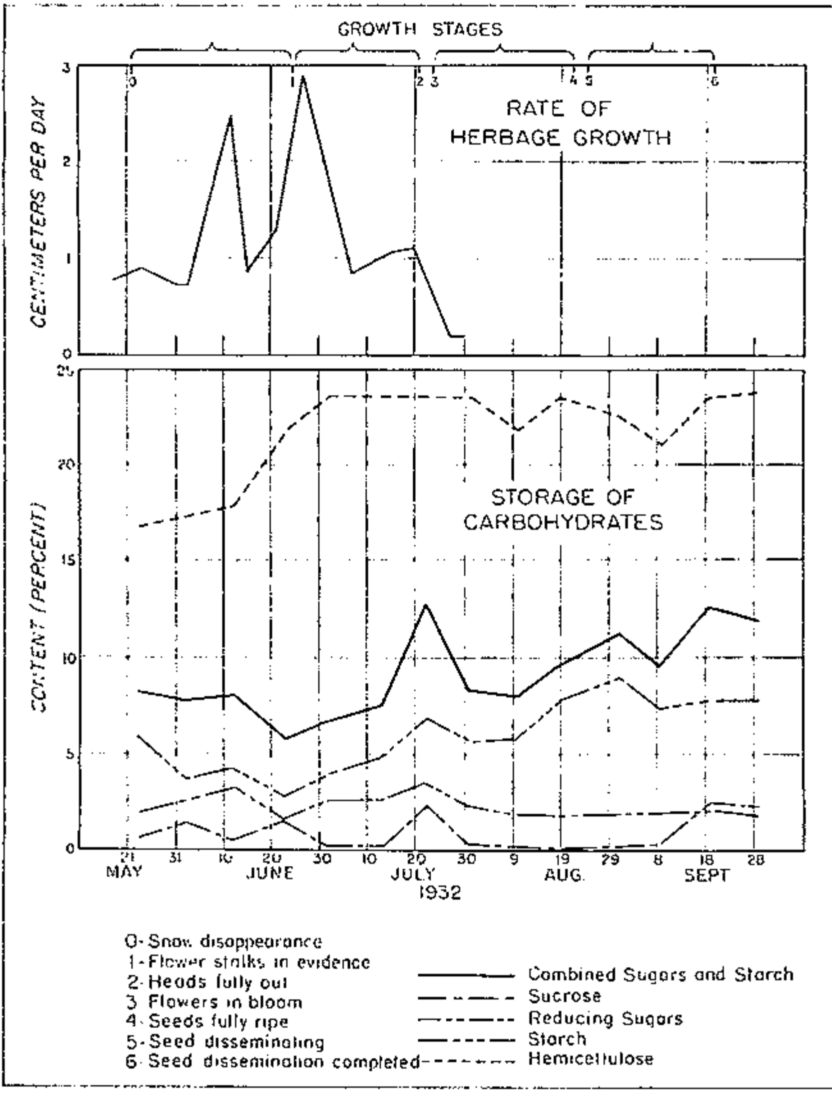

FIGURE 4. Slender wheatgrass: Annual herbage growth in relation to the trend of herbage storage of carbohydrates, 1932.

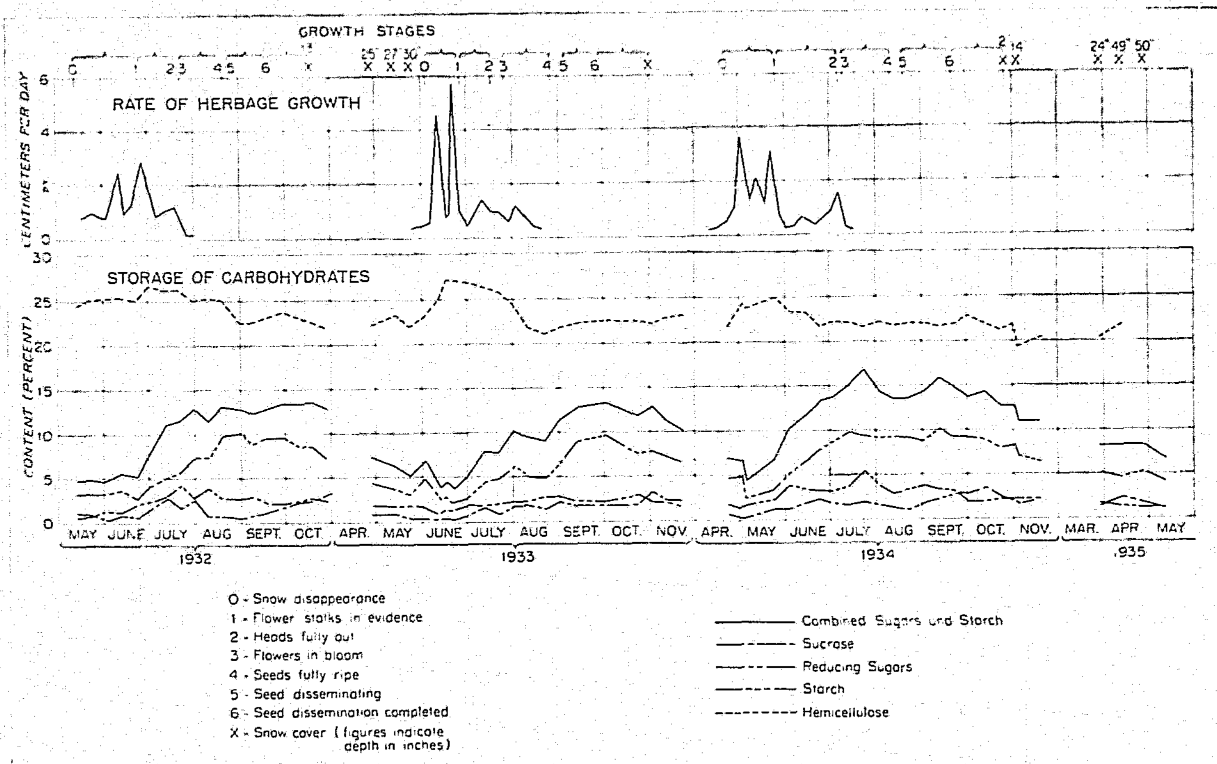

FIGURE 5.—Slender wheatgrass: Annual herbage growth in relation to the trend of root and stem-base storage of carbohydrates, 1932–35.

TABLE 2.—*Reductions in carbohydrate content of slender wheatgrass from end of storage period to 4-inch height growth, 1934–35*

Division of rest period	Carbohydrates in storage	Reduction in carbohydrates	Average daily reduction
	Percent	*Percent*	*Percent*
Shoot growth, Sept. 11–Oct. 22[1]	100 –80.22	19.78	0.482
Dormancy, Oct. 23–Dec. 30[2]	80.22–69.88	10.34	.150
Shoot growth, Dec. 31–Mar. 30[3]	69.88–51.95	17.93	.199
Root growth (new roots), Mar. 31–June 3[4]	51.95–41.99	9.96	.153
Early height growth, June 4–June 13[5]	41.99–30.89	11.10	1.11

[1] End of storage period. Excess of soluble over insoluble carbohydrates. Expansion of buds at basal nodes in response to favorable moisture conditions. These shoots may persist into winter in a dormant condition. (Storm Sept. 21, buds observed bursting Oct. 1.) Oct. 22 shoots 0.1 to 1.3 inches long and roots 0.2 inch long.

[2] Lower temperatures, surface soil frozen during most of this period. No growth activity observed.

[3] Soil thawed. New etiolated shoots 3 inches long observed March 25.

[4] On April 12 no further shoot growth was in evidence. Root growth observed on April 23. Snow disappeared June 3.

[5] Minimum level of carbohydrates June 13, 10 days after snow disappearance. Plants were 1 inch average height on June 5 and on June 17 the average height was 4.0 inches with a maximum of 9 inches.

As temperatures become lower in autumn the soluble forms of carbohydrates increase in slender wheatgrass at the expense of the insoluble forms, and during the winter, as a result of growth and physiological activity, carbohydrate content steadily declines (table 2).

BROADLEAF FORAGE PLANTS

Growth characteristics and manufacture and storage of carbohydrates follow the same general trends in sticky geranium and niggerhead, exemplifying broadleaf herbaceous forage plants, as in mountain brome and slender wheatgrass, although with some noteworthy differences. Annual growth fluctuates somewhat similarly with season and with stage of reproduction (figs. 6, 7, and 8). Sticky geranium, however, unlike the perennial forage grasses, makes no secondary herbage growth. Niggerhead produces secondary basal leaves during the autumn, just before the flower-stalk leaves begin to dry, and these remain green until the end of the snow-free period.

Newly formed roots were noted in geranium in mid-May, and again in late July during seed dissemination. Similar development in niggerhead was noted in mid-July, just before the plant bloomed. New root development of niggerhead may normally take place at other periods, but was noted only at the one period during the season of study.

Buds are usually formed in the crowns of both broadleaf species toward the end of the snow-free period. These buds elongate under the snow when conditions are favorable and produce the first shoots and leaves in early spring.

Sticky geranium starts active height growth early and matures earlier than the other plants. It is one of the first forage plants to display autumn color. Niggerhead develops later and continues growth later in the autumn.

Quantity of carbohydrates in the herbage was determined for sticky geranium (fig. 6), but not for niggerhead. General trends for sticky geranium are the same as for the grasses studied, but trends of reducing sugars and starch values differ somewhat in the two types of plants. Values of reducing sugars are higher and starch values are lower in geranium than in the grasses. This difference and the fact that the starch values in the roots and stem bases of geranium are exceptionally high suggest that sticky geranium may manufacture

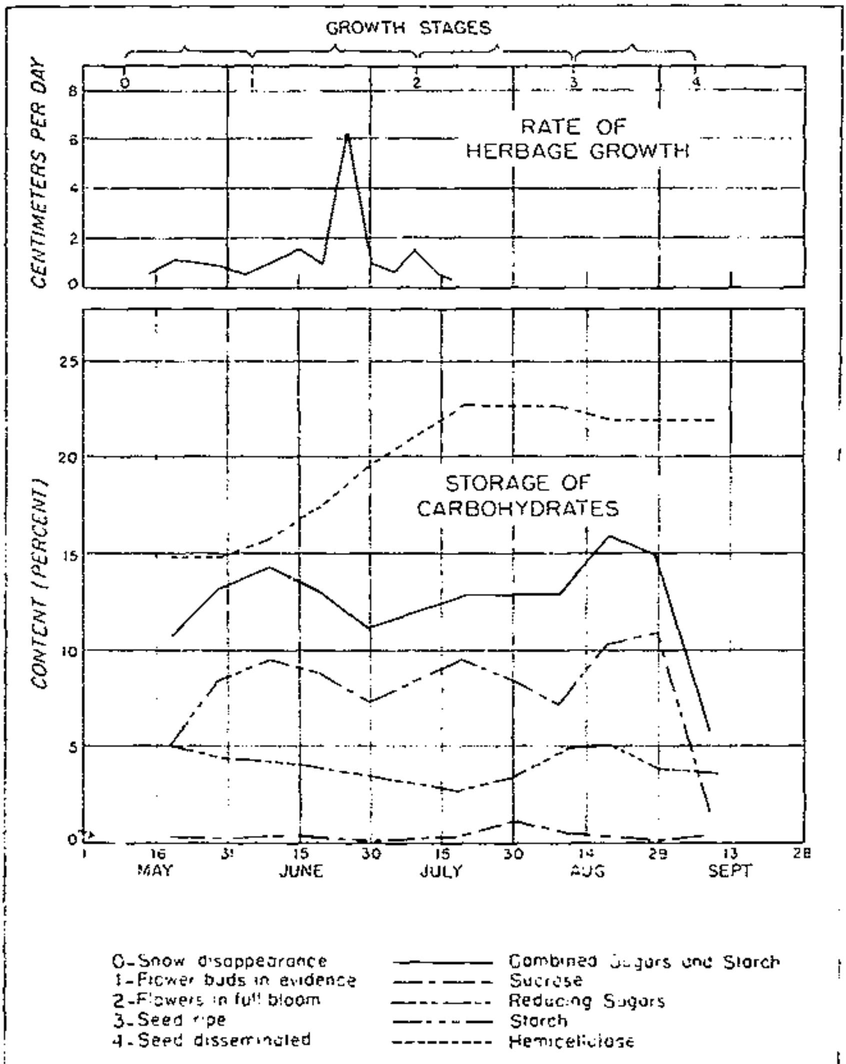

FIGURE 6. Sticky geranium: Annual herbage growth in relation to the trend of herbage storage of carbohydrates, 1932.

carbohydrates in the form of reducing sugars and store them in the form of starch. At the end of the snow-free period there is an abrupt decline in reducing sugars, and a slight drop in starch. Hemicellulose and sucrose values show trends similar to those in the grasses.

In carbohydrate storage in the roots and stem bases, niggerhead and sticky geranium differ outstandingly from the grasses. Differences include (1) abrupt beginning and rather brief duration of carbohydrate storage (table 3); (2) storage of greater quantities of

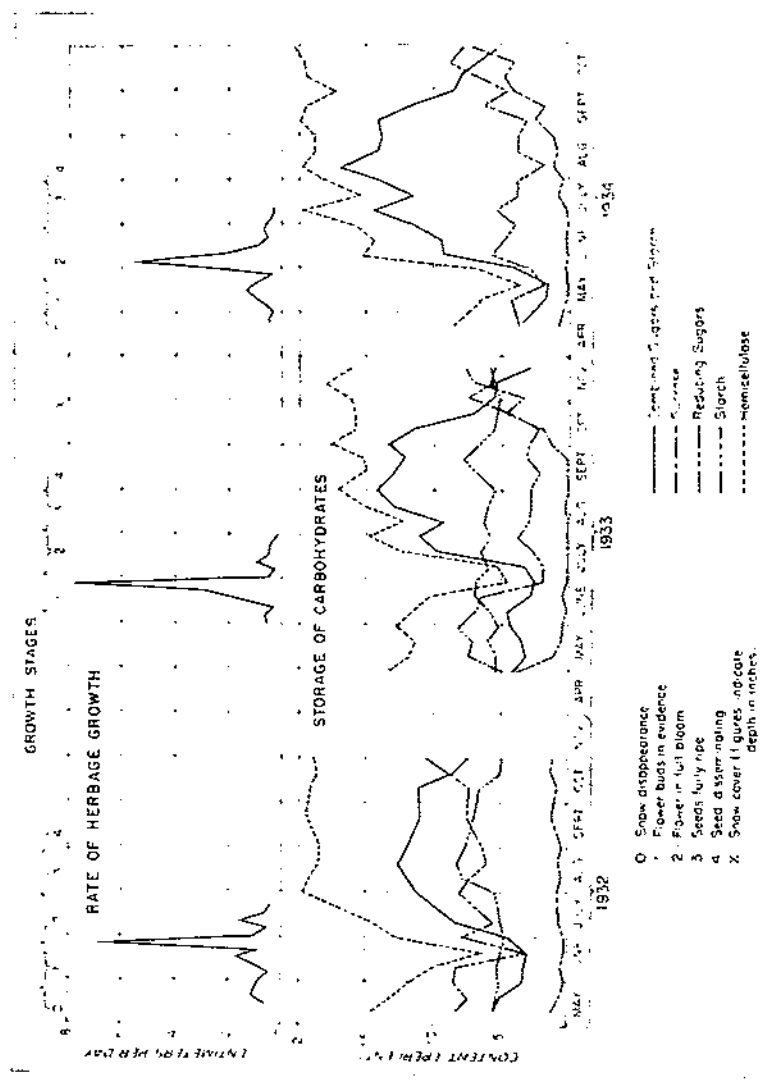

FIGURE 7.—Sticky geranium: Annual herbage growth in relation to the trend of root and stem-base storage of carbohydrates, 1932–34.

carbohydrates in the roots, especially of niggerhead; (3) higher starch values; and (4) low hemicellulose values.

These differences result chiefly from differences in growth habits. The fact that broadleaf plants produce large quantities of photosynthetic tissue within a comparatively short period would condition the time and manner of storage. The presence of large quantities of starch in the roots appears to be related to the production of large fibrous taproots.

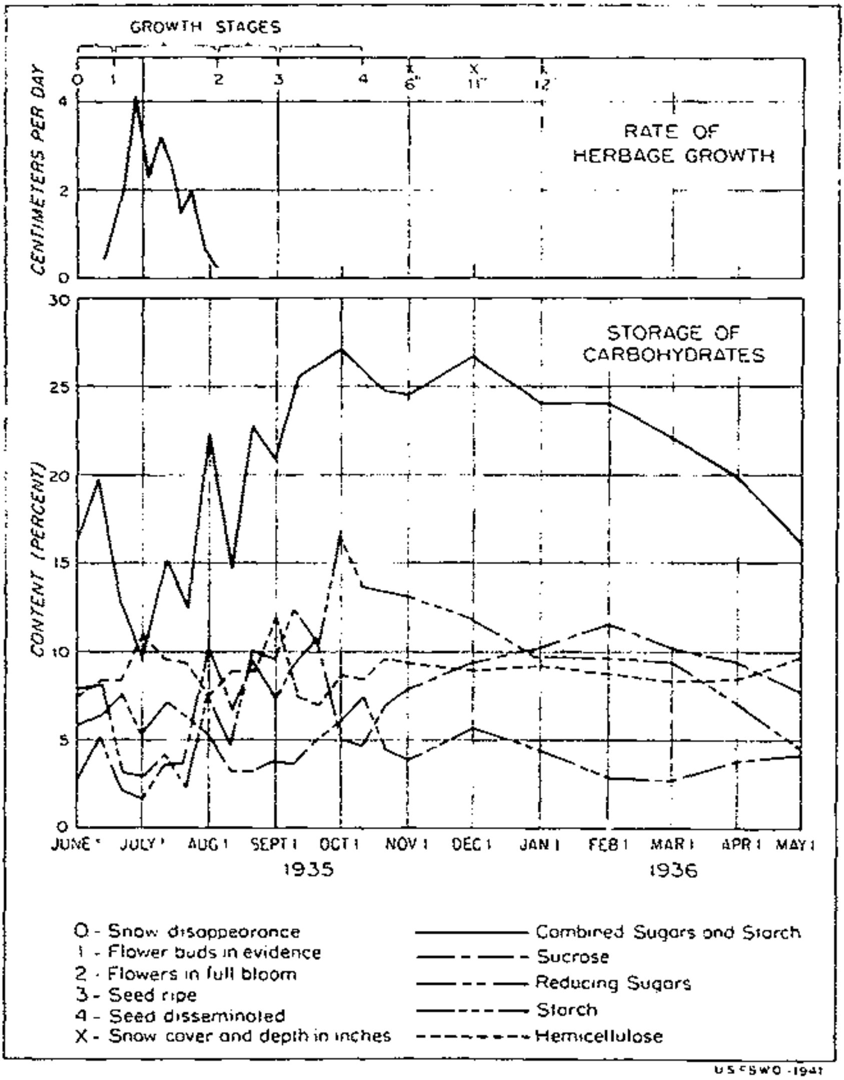

FIGURE 8. Niggerhead: Annual herbage growth in relation to the trend of root and stem-base storage of carbohydrates, 1935–36.

Growth and carbohydrate-storage relations of the broadleaf herbaceous plants are inversely related, as in the perennial grasses, the period of maximum storage following the cessation of active herbage growth.

TABLE 3.—*Minimum and maximum concentrations of combined sugars and starch in roots and stem base, and time required for change; three species, 1932–34; and niggerhead, 1935*

Species and year	Minimum content	Maximum content	Time required: Dates	Time required: Interval
Mountain brome:	*Percent*	*Percent*		*Days*
1932	3.20	21.11	June 2–Sept. 28	118
1933	3.02	16.45	June 21–Sept. 22	93
1934	4.50	18.09	May 11–Oct. 22	161
Average	3.57	18.55	June 3–Oct. 5	124
Slender wheatgrass:				
1932	4.77	13.37	June 2–Sept. 29	119
1933	3.71	13.33	June 21–Oct. 2	103
1934	4.32	15.67	May 1–Sept. 11	130
Average	4.27	14.12	May 30–Sept. 25	117
Sticky geranium:				
1932	6.38	19.58	June 19–July 29	40
1933	4.39	17.77	June 28–Sept. 29	93
1934	3.42	19.99	May 19–July 8	50
Average	4.73	19.11	June 12–Aug. 12	61
Niggerhead:				
1935	9.73	27.78	July 3–Oct. 2	91

On July 23, 20 days after minimum concentration, sugars and starches reached a total of 16.72 percent, but this was immediately reduced as a result of secondary growth.

EFFECTS OF CLIPPING

Concurrently with the growth and nutrition phase of the study, tests were made with a view to determining basic principles regarding the nature and extent of the manufacture and storage of the several carbohydrates under controlled clipping. Mountain brome, slender wheatgrass, and sticky geranium were clipped with hand shears at different stages of their normal growth cycle and in different frequencies.

PROCEDURE

The clipping plan followed for mountain brome and slender wheatgrass is outlined in table 4 and that for sticky geranium in table 5.

Twenty methods of clipping were applied to mountain brome and to slender wheatgrass (all of them close clippings, down to 1 inch from the soil line, except as otherwise specified), each treatment being applied on a series of four 1- by 0.5-m. plots designated by letter. In addition, a control plot (*Q*) was held unclipped. The mountain brome plots were mechanically arranged in series; the slender wheatgrass plots were placed throughout the enclosure. Five series of four plots each (*K, L, N, M, P*) were clipped once during the season, five were clipped twice (*D, E, H, I, J*), and five more three times (*A, B, C, F, G*); one series (*O*) was clipped eight times at 15-day intervals throughout the growing period; two series (*T, U*) were clipped three times at 5-day intervals during the early part of the season only; two (*R, S*) were clipped to a height of 4 inches from the soil line at regular intervals during the growing period.

The same general plan was followed with 16 treatments applied to sticky geranium, except that each was applied to a separate series of 8 individually staked plants located throughout the timbered area, and all were close clippings. Six series were clipped once (*H*, *K*, *L*, *M*, *N*, *P*); 5 twice (*D*, *E*, *F*, *I*, *J*); 4 three times (*A*, *B*, *C*, *G*); and 1 at 15-day intervals (*O*). Differences in time and number of clippings were due to differences in growth habit between this plant and the grasses. The early and 4-inch clippings were omitted.

All clippings were timed according to the stage of development of the control group, beginning at the date of snow disappearance each year, except for series *O*, *S*, *T*, and *U*. The clipped herbage was oven-dried and its weight in grams was recorded.

TABLE 4.—*Clipping plan followed for six different series of plots of slender wheatgrass and mountain brome, 1932–34* [1]

Average elapsed time (days)	Stage of development [2]	Clipped once (*K*, *L*, *M*, *N*, *P*)	Clipped twice (*D*, *E*, *H*, *I*, *J*)	Clipped 3 times (*A*, *B*, *C*, *F*, *G*)	Clipped each 15 days (*O*)	Early clipping (*T*, *U*)	Clipped to 4 inches (*R*, *S*)
0	Snow disappearance					*U*	
5						*T*, *U*	
10						*T*, *U*	
15	Plants 4 inches high	*K*	*D*, *E*, *I*	*A*, *C*	*O*	*T*	
20	Plants 6 inches high		*I*	*A*, *C*, *F*	*O*		
35	Flower stalks first evident						
40	Heads high in boot	*L*	*H*				
45					*O*		
50	Heads showing						
60	Heads fully out			*B*, *C*	*O*		*R*, *S*
65	Flowers in bloom			*B*			
75	Seeds in milk	*M*	*D*, *J*	*F*	*O*		*R*, *S*
80							
85	Seeds in dough			*B*, *G*			*S*
90					*O*		*R*
95	Seeds fully ripe	*N*		*G*			
100	Seed dissemination begun		*E*, *H*				*S*
105					*O*		
110							
125							*S*
135	Seed all disseminated		*J*	*F*, *G*	*O*		*S*
145				*A*			
165	End of season	*P*					

[1] Unless otherwise specified, all clippings were made at a height of 1 inch from the soil line. Series *O* was not clipped.
[2] Stages of development based on control plot, series *O*. See figures 2 and 5.

TABLE 5.—*Clipping plan followed for sticky geranium, 1932–34* [1]

Average elapsed time (days)	Stage of development [2]	Clipped once (*K*, *L*, *H*, *M*, *N*, *P*)	Clipped twice (*I*, *F*, *D*, *E*, *J*)	Clipped thrice (*A*, *C*, *B*, *G*)	Clipped each 15 days (*O*)
0	Snow disappearance				
15		*K*	*I*, *D*, *E*	*A*, *C*	*O*
20	Plants 2 to 4 inches high	*L*	*I*, *F*	*C*	
25	Flower buds in evidence				
30					*O*
35		*H*	*F*	*C*, *B*	
40	Buds bursting				
45					*O*
50	Full bloom			*A*, *B*	
55		*M*	*D*		
60					*O*
65			*J*		
75				*B*, *G*	*O*
85	Seed ripe	*N*	*E*		
90					*O*
95				*G*	
105					*O*
110	Seed disseminated				
115			*J*	*A*, *G*	
120					*O*
130	End of season	*P*			

[1] All clippings were made at a height of 1 inch from the soil line.
[2] Stage of development based on control series *O*, which was not clipped.

At the close of the snow-free period of each of the three years of treatment, roots of plants on one of three successive plots of each grass series and roots of two sticky geranium plants of each series were removed and analyzed for carbohydrate content. The fourth grass plot of each series and the remaining two sticky geranium plants of each treatment were used as checks. Methods of preparing the samples and of determining carbohydrate content were the same as in the nutrition phase.

Yields were recorded in the dry weight of the herbage present at the time of clipping. Herbage produced after the plots were clipped was not measured, inasmuch as this would have upset the clipping schedule. Consequently, yield data for the various clipped plots only represent the quantity of herbage produced from the date on which active growth began until time of clipping.

Results With Mountain Brome

PLOTS CLIPPED ONCE

As noted in table 6, the differences in total quantity of carbohydrates stored under the various systems of clipping are not great, but they are believed to be significant. The fact that they are small is due in part to inevitable loss in the digging and cleaning processes of roots weakened or dead as a result of clipping, as well as some of the smaller live roots. Season also influenced the values; as, for example, the abnormally long growing season following clipping in 1934. But the general trends indicated are the same for all years under the various clipping treatments.

The quantity of the combined carbohydrates stored was less as time of clipping approached the end of the growing season. Plots on which the plants were clipped when 4 inches high and prior to the upturn of the carbohydrate storage trend (series *K*) ranked highest in storage of sugars and starch, except during the last year, when they came second to the end-of-season clipping (series *P*). Plants clipped when seed was ripe (series *N*) contained less stored carbohydrates than any others and considerably less than those on the control plot, despite the fact that usually 67 percent of the normal maximum quantity of carbohydrates is stored at that stage. Plants clipped when seed were in the milk stage (series *M*) had intermediate values. Through a mistake in clipping no data were obtained for plots clipped when heads were high in the boot (series *L*). In the first 2 years, plots clipped at the end of the snow-free period, when all herbage growth was complete, showed nearly as high combined carbohydrate values as plots clipped when plants were 4 inches high and exceeded them in the last year.

Sufficient time elapsed between the end-of-season clipping and the lifting of the plants on the control plots to account for part of the difference between the quantities stored. The relations indicated were essentially the same in each year of the study, although yearly influence was noticeable. In exceptionally dry 1934, when the growing season extended into the fall, the plants on all plots had an unusually long period of growth remaining after they were clipped, were able to produce sufficient herbage to manufacture the necessary carbohydrate foods, and hence stored almost normal supplies.

TABLE 6.—*Mountain brome: Carbohydrates stored in roots and stem bases at end of each growing season, in percent of dry weight, under different systems of clipping, 1932–34* [1]

Series and time of clipping	Reducing sugars (A)			Sucrose (B)			Starch (C)			Total sugars and starch (A+B+C)			Hemicellulose		
	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934
UNCLIPPED CONTROL [2]															
Q unclipped	4.33	3.19	7.22	6.82	5.56	5.06	6.88	6.42	7.47	18.03	15.17	19.75	20.75	21.18	20.12
CLIPPED ONCE EACH SEASON [3]															
K 4-inch height	2.52	2.82	2.74	6.08	5.66	7.88	7.34	5.85	6.34	15.94	14.33	16.96	21.61	22.06	20.29
M seed in milk	2.12	2.38	6.72	4.92	4.58	3.81	5.01	4.69	5.19	12.05	11.65	15.72	21.15	22.27	21.06
N seed fully ripe	1.24	1.34	5.97	4.45	4.61	4.62	4.48	4.07	4.90	10.17	10.02	15.49	23.82	23.73	20.75
P end of season	2.86	2.67	7.22	3.17	5.27	3.68	9.09	5.89	7.02	15.12	13.83	17.92	22.00	23.28	18.39
CLIPPED TWICE THROUGHOUT SEASON [4]															
I 4- and 6-inch height	2.14	1.45	2.68	6.01	5.21	7.89	6.38	4.47	6.64	14.53	11.13	17.21	22.16	23.08	19.58
D 4-inch height and seed in milk	2.60	1.41	3.54	5.08	4.82	6.16	5.97	3.85	6.82	13.65	10.08	16.52	25.15	23.83	21.57
E 4-inch height and seed dissemination	2.52	2.24	4.05	5.25	5.24	6.54	6.27	4.17	6.99	14.04	11.65	17.58	23.12	23.39	21.69
H heads high in boot and seed dissemination	2.41	1.44	2.31	4.88	5.06	7.97	4.40	3.66	4.64	11.69	10.16	14.92	24.06	23.95	20.16
J seed in milk and seed dissemination	2.12	2.11	2.26	4.44	4.22	6.55	4.36	4.57	4.05	10.92	10.90	12.86	24.52	23.26	21.61
CLIPPED 3 TIMES THROUGHOUT SEASON [5]															
C 4- and 6-inch height and heads showing	3.11	4.27	4.24	6.30	5.42	5.74	6.21	6.12	8.01	15.62	15.81	17.99	23.02	21.31	20.42
A 4- and 6-inch height, 10 days after seed dissemination	2.08	2.94	3.47	6.94	5.18	6.29	5.52	3.43	5.90	14.54	11.55	15.66	24.51	23.27	21.93
F 4-inch height, seed in milk and dissemination	2.83	1.24	4.04	1.75	3.93	6.82	5.38	2.54	5.26	9.96	7.71	16.12	24.13	24.18	20.99
B heads showing, flowers in bloom, and seed in dough	3.26	2.06	3.21	4.73	5.63	7.11	5.22	3.81	6.59	13.21	11.50	16.91	24.06	22.11	19.70
R heads showing, flowers blooming, seed in dough (clipped to 4 inches)	4.30	3.97	6.35	3.65	5.70	3.53	6.75	7.38	5.96	14.70	17.05	15.84	22.60	19.38	19.96
G seed in dough, fully ripe, and dissemination	2.85	2.84	3.43	6.83	5.12	6.56	4.70	4.20	5.50	14.38	12.16	15.49	23.50	22.73	21.74

CLIPPED AT 15-DAY INTERVALS THROUGHOUT GROWING SEASON

Q beginning 15th day; clipped to 1 inch	1.04	0.79	(7)	3.18	5.80	(7)	2.11	2.87	(7)	6.66	7.46	(7)	23.34	23.80	(7)
S beginning 30th day; clipped to 1 inches	3.45	3.49	7.16	3.75	7.21	3.37	6.71	4.87	5.18	13.91	15.14	15.71	22.25	20.68	19.75

CLIPPED 3 TIMES IMMEDIATELY AFTER SNOW DISAPPEARANCE

Time of collection, series, and clipping dates	1933	1934	1935	1933	1934	1935	1933	1934	1935	1933	1934	1935	1933	1934	1935
Collected on 15th day:															
Q unclipped	1.77	2.28	1.47	0.38	0.47	0.18	2.01	2.38	4.81	1.16	5.13	6.46	23.09	25.50	22.16
U clipped 0, 5th, and 10th day	.71	1.51	2.72	.25	.16	.51	1.66	1.95	2.64	2.62	3.63	5.87	24.21	24.14	21.19
Collected on 20th day:															
Q unclipped	1.42	1.83	.97	.51	.17	1.95	1.09	2.34	4.73	3.92	1.34	7.65	23.15	25.94	20.56
T clipped 5th, 10th, and 15th day	.87	1.06	1.58	.08	.20	.45	1.80	1.58	1.36	2.75	2.84	6.39	23.72	26.70	21.71
Collected at end of season															
Q unclipped	3.10	7.22	3.51	5.56	5.06	5.66	6.12	7.47	8.60	15.17	19.75	17.77	21.18	20.12	18.01
U clipped 0, 5th, and 10th day	3.28	7.60	9.32	8.42	1.15	1.45	5.24	6.65	1.60	16.94	18.40	15.37	19.75	18.55	17.52
T clipped 5th, 10th, and 15th day	3.07	7.71	8.02	6.56	5.71	2.69	5.29	7.27	5.02	15.52	20.75	15.73	20.50	15.37	17.96

Calculations made on basis of ash-free dry weight and expressed as reducing sugar. Clipping to 1-inch height unless otherwise specified.
Samples collected Oct. 23, 1932; Oct. 23, 1933; Oct. 14, 1934.
Samples collected Oct. 21-22, 1932; Oct. 23, 1933; Oct. 11, 1934. No data obtained for series I.
Samples collected Oct. 18-21, 1932; Oct. 19-21, 1933; Oct. 11, 1934.
Samples of *C*, *A*, *F*, *B*, *G* collected Oct. 18-19, 1932; Oct. 18-19, 1933; Oct. 13-14, 1934. *P* collected Oct. 25, 1932; Oct. 24, 1933; Oct. 15, 1934.
Samples collected Oct. 22-23, 1932; Oct. 23-24, 1933; Oct. 15, 1934.
Plants mostly dead.
Samples collected June 16 and 21 and Oct. 24, 1933; May 8 and 13 and Oct. 15, 1934; June 11 and 17 and Oct. 10-11, 1935.

The length of the interval between clipping and the end of the snow-free period and the resultant quantity of photosynthetic tissue present during the normal autumn storage period (August and September at the study areas) appear to be the determining factors in the quantity of carbohydrates stored. Close clipping disrupts the natural growth processes, lengthening the vegetative period. At the same time new growth is stimulated and there is a tendency to repeat the normal growth stages of the plant—for example, production of flower stalks. This new growth draws upon the carbohydrates already stored, reducing the total stores present at the close of the snow-free period. When this period is of maximum length, as in the clipping of plants that have attained a height of only 4 inches, the growth cycle can be completed and almost normal quantities of carbohydrates stored. On the other hand, when plants are clipped at seed ripe, the average of 70 days remaining is insufficient for complete regrowth and adequate carbohydrate storage. Moreover, close clippings made when seeds are ripe seem to inflict permanent injury on the plants, related to the process of reproduction. Reproduction leads to physiological inertia or fatigue, and in annuals is followed by death of the plant (*8*). Removal of the flower stalks and seeds at this stage involves a very severe loss of material, restoration of which would require an excessively long growing period.

Clipping at the end of the growing season (series *P*), when storage is practically complete and only a few basal leaves of the plants remain green, renders any substantial regrowth impossible, hence the stores are not depleted to any great extent. However, yearly close clipping at that time may result in severe injury, inasmuch as complete removal of herbage to a height of 1 inch leaves the crowns of the plants exposed to winter temperatures.

The individual sugars and starch fractions of the clipped groups showed reactions similar to those of the combined group. The diminution in starch, which appears proportional to length of interval between clipping and the beginning of the winter season, exceeded that in total sugars (table 6). The hemicellulose fraction showed no significant change in the clipped groups, which further indicates that hemicellulose is used mainly for structural purposes and not as a stored food.

A significant relation is evident between the 1932 yield of each once-clipped group and its yield in subsequent years (fig. 9). Plots clipped only at the end of the season produced greater yields in 1934 than in 1932. Those clipped only when the plants first reached 4 inches high yielded little, since foliage development is normally not far advanced at that time; but the yields were maintained throughout the course of the study. Yield of the plots clipped at intermediate growth stages was reduced, that on plots clipped when seed was ripe showing the greatest reduction of all. Annual yield, therefore, is related not only to quantity of carbohydrates manufactured currently by the plant but also to quantity stored in the basal organs of the plant during the preceding autumn. Reduction of autumn stores results in a weakened condition of the plants at the start of active height growth the following season, and thus limits the quantity of forage produced in that season.

The effect of clipping on the vigor of mountain brome was clearly evident. Plants clipped when 4 inches high had sufficient growing time remaining to complete their growth cycle, producing flower stalks and viable seed (table 7). Plants clipped at intermediate stages did not have sufficient growing time for these functions; the flower stalks they produced were short, and their seed not mature. Also, a greater proportion of these later-clipped plants died than of those clipped early or at the end of the growing season (pl. 2).

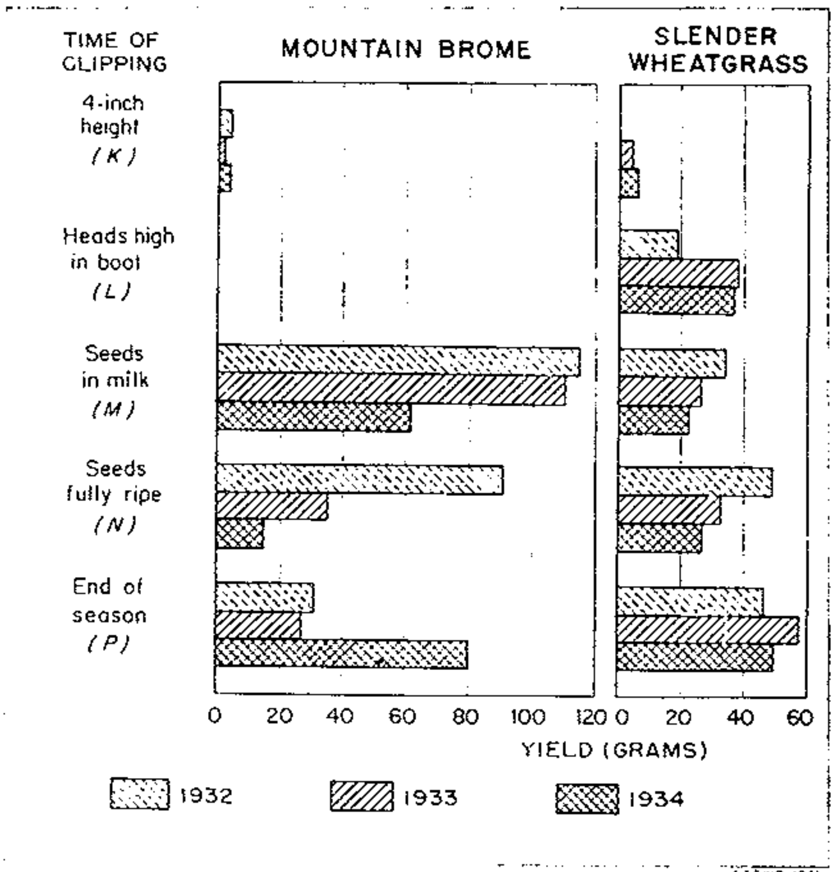

FIGURE 9. Yields from a single clipping at different stages of seasonal growth; mountain brome and slender wheatgrass; 1932-34. (Series *L* for mountain brome, misclipped, is omitted.)

PLOTS CLIPPED TWICE

Results of clipping to a height of 1 inch twice during the growing season clearly show that close clipping either during or at the close of the intense reproduction period results in less storage of carbohydrates (tables 6 and 7). During the 3 years of the study, plants clipped early (series *I*) stored 73 to 87 percent as much carbohydrate as the control plants, and plants clipped during reproduction plus an additional clipping later in the season (series *J*) stored only 61 to 65 percent.

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TABLE 7.—*Mountain brome yields and combined sugar and starch stores, 1932–34, and number of flower stalks and height in 1934, under different methods of clipping during growing seasons* [1]

Series [2] and time of clipping	Yield (1932=100)	Range of sugar-starch stores [3]	Flower stalks	Average end-of-season height
	Percent	*Percent*	*Number*	*Cm.*
UNCLIPPED CONTROL				
Q—unclipped		100	176	65
CLIPPED ONCE EACH SEASON [4]				
K—4-inch height	64.2	86–94	40	43
M—seed in milk	53.1	67–80	1	15
N—seed ripe	16.9	56–78	30	9
P—end of season	253.0	84–91	145	62
CLIPPED TWICE EACH SEASON				
I—4-and 6-inch heights	60.2	73–87	43	
D—4-inch height and seed in milk	58.2	66–84	3	
E—4-inch height and seed dissemination begun	66.5	77–89	131	
H—heads high and seed dissemination begun	13.0	65–76	21	
J—seed in milk and dissemination ended	19.7	61–65	2	
CLIPPED 3 TIMES EACH SEASON				
C—4- and 6-inch heights, heads showing	83.8	87–104	19	
A—4- and 6-inch heights, 10 days after seed dissemination begun	50.5	76–81	59	
F—6-inch height, seed in milk and dissemination	26.5	51–82	2	
B—heads showing, flowers in bloom, seed in dough	43.9	73–86	0	9
R—heads showing, flowers in bloom, seed in dough (clipped to 4 inches)	110.5	80–112	8	15
G—seed in dough, fully ripe, and dissemination ended	15.7	78–80		
CLIPPED FREQUENTLY DURING GROWING SEASON [5]				
O—every 15 days (8 clippings to 1 inch)	9.4	37–49	0	4
S—every 15 days (6 clippings to 4 inches)	72.2	77–100	2	10

[1] All clipping to 1 inch except as specified.
[2] No data obtained for series *L*.
[3] Based on series *Q*.
[4] Series *K* was 10 cm. when cut; *M*, 62; *N*, 55; *P*, 62.
[5] Series *O* yielded 22.5 cm. of regrowth after clippings in 1934; *S*, 11.5; *R*, 14.6; *B*, 11.

Loss in forage yield was also much greater for plants subjected to clipping during the more intense growing period (fig. 10 and table 7). The 1934 yield of plots clipped in midseason, in series *J*, was only about 20 percent of the 1932 yield, whereas the plots clipped early (series *I*) yielded 60 percent. Mortality was high in plants clipped twice during the later growing period; many of the tussocks were dead at the end of the experiment. On the early clipped plots, although some tussocks died, survival was good.

On the three series of plots first clipped when the plants were 4 inches high and clipped again during the early (series *I*), middle (series *D*), and late (series *E*) parts of the growing season, when reproduction was active, total quantity of carbohydrates stored did not differ greatly, but it is clear that series *D* suffered most (tables 6 and 7). This difference is also reflected slightly in forage production; series *D* yielded only 58 percent as much in 1934 as in 1932, whereas

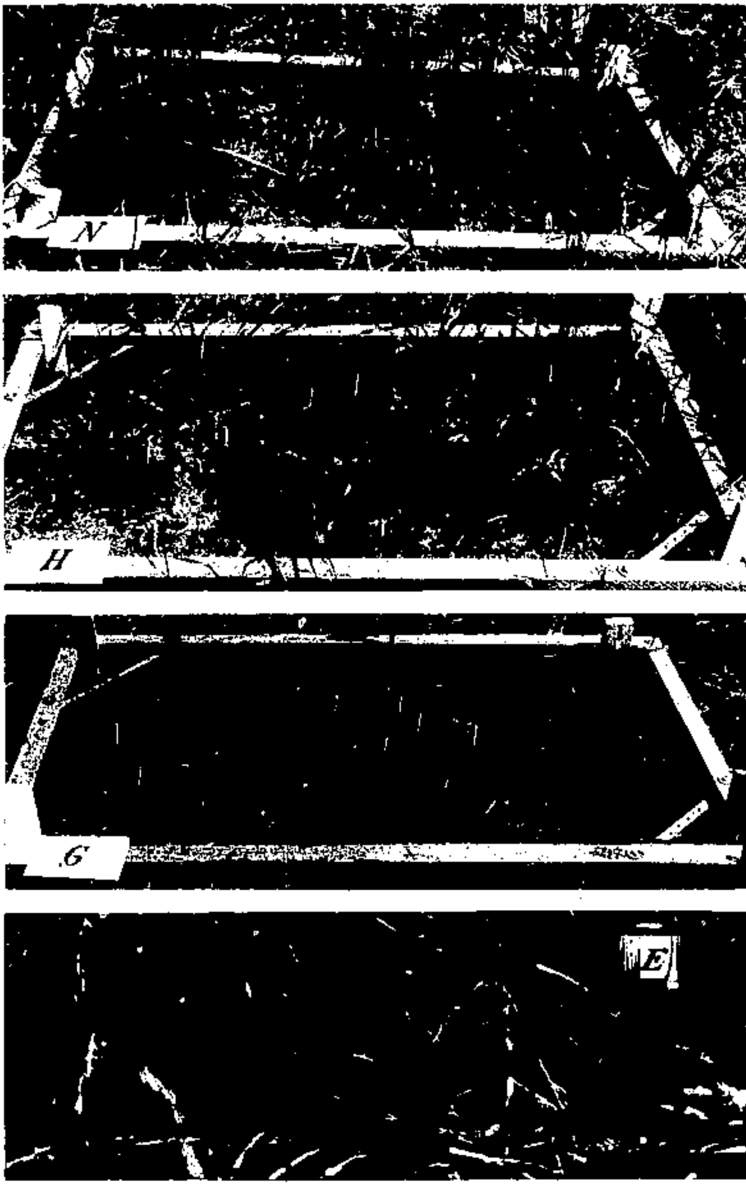

PLATE 2.—Plots of mountain brome at the end of season after 2 years' clipping to a height of 1 inch from the soil line during the reproduction period, compared with one clipped before and after the reproduction period: Series *N*, clipped once during the reproduction period (seeds ripe); series *H*, clipped once during the reproduction period and once later (heads high in boot and seed disseminated); series *G*, clipped twice during the reproduction period and at the end of the growing season (seed in dough, seed ripe, and seed disseminated); series *E*, clipped before and after the reproduction period and the normal maximum storage period (plants 4 inches high and seed dissemination begun). White pegs mark positions of former living plants.

the plants on the two other plots yielded 60 percent and 66 percent, respectively.

Results on three series of plots where the plants were first clipped in the early, middle, and late parts of the growing season and were

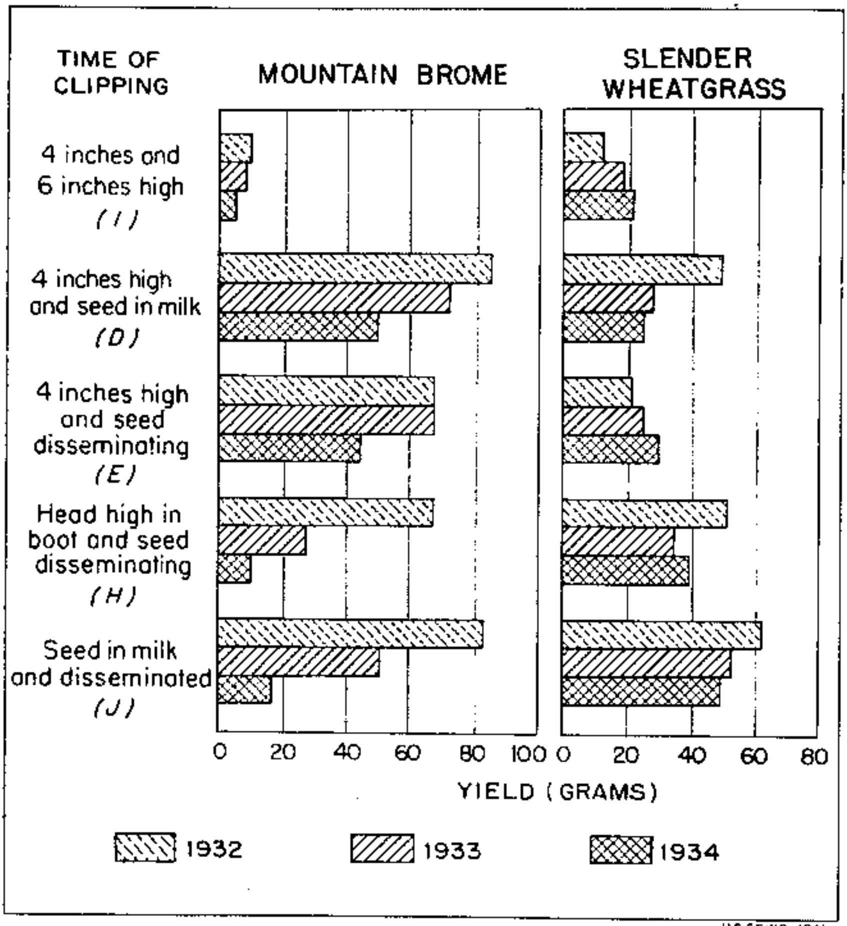

FIGURE 10. Yields from two clippings at different stages of seasonal growth; mountain brome and slender wheatgrass; 1932-34.

clipped a second time late in the season (series *E*, *H*, and *J*) give further evidence that close clipping is more detrimental if made later in the growing season when reproduction is active. Series *H* and *J* yielded only 14 percent and 20 percent of their 1932 yields, whereas series *E* yielded approximately 67 percent. The same relationship holds good with respect to carbohydrate storage, series *J* faring worse and series *H* and *E* successively better.

PLOTS CLIPPED THREE TIMES

Results on plots clipped three times to a height of 1 inch during the growing season corroborate the evidence already presented, that early clipping permits greater yield and greater storage of carbohydrates than later clipping (fig. 11 and tables 6 and 7). It was evident also that close clippings are detrimental if made during the most active period of growth and reproduction, which begins with flower-stalk formation, usually when the plants are 6 inches high, and ends when the seeds mature (pls. 3 and 4).

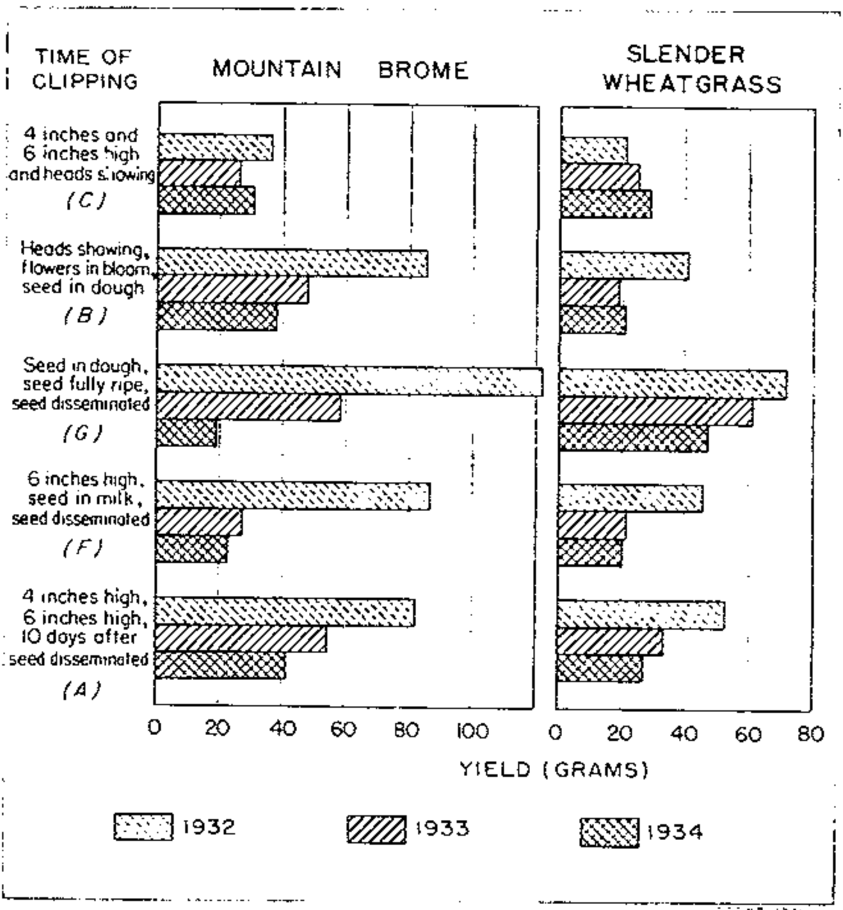

FIGURE 11. Forage yield of mountain brome and slender wheatgrass clipped three times at various stages of growth, 1932–34.

PLOTS CLIPPED THROUGHOUT SEASON WITHOUT RESPECT TO GROWTH STAGE

Plants clipped to a height of 1 inch at 15-day intervals throughout the growing season, beginning 15 days after snow disappearance (series *O*), produced less foliage and stored less carbohydrates in their roots than plants treated otherwise (fig. 12 and table 7). At the end of the first and second years of treatment the combined sugars and starch in the roots of these plants amounted only to 37 percent and 49 percent, respectively, of the quantities in the roots of the control series. At the end of the third year of treatment, insufficient plants remained to make up a 5-g. sample of roots for analyses. Forage

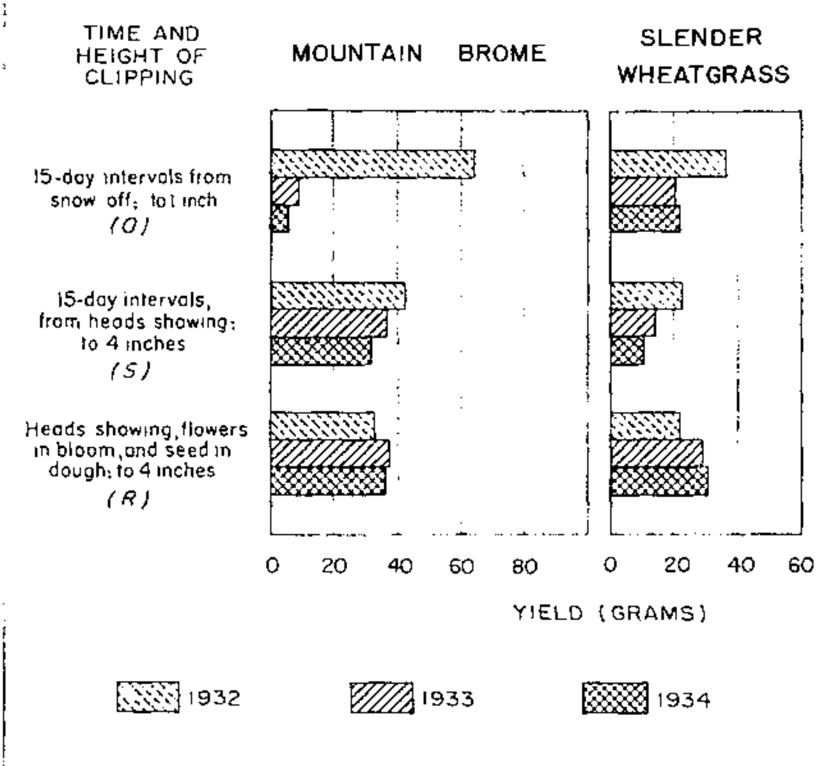

FIGURE 12. Forage yields of mountain brome and slender wheatgrass after clipping at 15-day intervals to 1 inch (series *O*) and 4 inches (series *S*) and clipping to 4 inches three times during active growth period (series *R*). Close-clipped series *O* indicated greatest reduction in yields of all plots, whereas the moderate clipping to 4 inches is among those with lowest reduction. Series *R*, clipped at the same intervals as series *B* (fig. 11), showed a slight gain.

yield showed similar trends; at the end of the third year of treatment it amounted only to about 9 percent of the 1932 yield. Continuous removal of the photosynthetic tissue prevents sufficient carbohydrate storage and leaves the plants in a weakened condition, with the result that the plants die of starvation or are winter-killed (*3*).[9]

Differences in carbohydrate storage between plants clipped at various frequencies were not marked. Carbohydrate reserves of

[9] This conclusion is supported also by unpublished data collected by the senior author on *Agropyron Smithii*, *Andropogon scoparius*, *A. hallii*, and *Bouteloua hirsuta*.

PLATE 3. Flower stalks of mountain brome from plants: *Q*, unclipped; *A*, clipped before and after the reproduction period; and *H*, clipped once early in the active period of reproduction and once during seed dissemination. Close clipping during the reproduction period not only injures the plants but also prolongs vegetative growth, which results in subnormality of growth and carbohydrate storage.

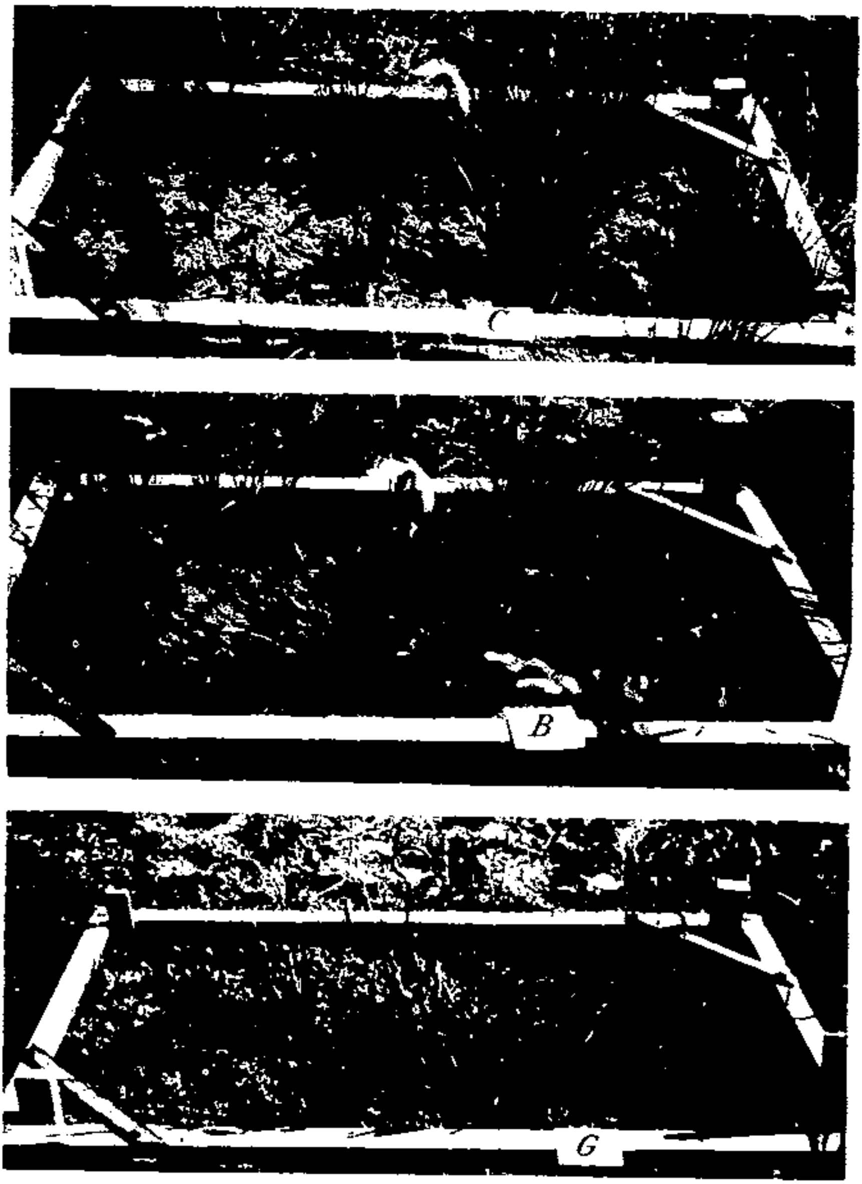

PLATE 4. Plots of mountain brome plants at end of third season of clipping three times a year to a height of 1 inch from the soil: Series *C*, twice before reproduction is active and once in early reproduction; series *B*, thrice during active reproduction period; series *G*, twice during period of seed ripening and once after active reproduction. On all these plots, plants were lost as a result of clipping made during the active growing season. Loss was greatest on the plots that received two clippings during this period, especially on the one clipped during the seed-ripening period.

plants clipped twice and three times during the growing season nearly equalled those of plants clipped once. Quantity of carbohydrate reserves in the plants at the end of the growing season appears to be influenced more by time and degree of clipping than by frequency. When, however, clippings are made both frequently and intensely, as in the continuously clipped plots, low values of yield and carbohydrate reserves result.

PLOTS CLIPPED FOUR INCHES FROM SOIL LINE

In addition to the 1-inch clippings, plants of two series (*R*, *S*) were clipped to a height of 4 inches from the soil line; series *S* at the same 15-day intervals as series *O*, but starting 35 days later, and series *R* at the same three stages in the middle of the growing season as series *B*.

The plants clipped to a height of 4 inches at 15-day intervals (series *S*, see pl. 5 and table 6) had consistently greater quantities of combined sugars and starch in their roots than those in series *O*, and in 1933 had practically as much as the control group. In 1934 the yield of plants in series *S* was about 72 percent of their 1932 yield, whereas that in series *O* was only about 9 percent (fig. 12, table 7).

Similar although smaller differences were found in the two series *R* and *B* clipped three times during the middle of the growing season to 4 inches and 1 inch, respectively (table 6). The plants clipped to 4 inches showed more sugars and starch storage in each year except 1934, a year when the growing season was prolonged. Their yield increased slightly during the experiment. Final yield (in 1934) of the series clipped to 1 inch was only about 44 percent of its 1932 yield, whereas in the series clipped to 4 inches it was slightly over 110 percent (table 7).

The results of the 4-inch clippings also demonstrate that subsequent forage yield and quantity of carbohydrates stored appear to be related to the quantity of photosynthetic tissue left after harvesting. The 4-inch clippings left herbage sufficient to manufacture and store nearly normal supplies of carbohydrates. It is believed, however, that prolonged clippings at 15-day intervals or clippings concentrated in the middle of the active growing season, even to a height of 4 inches, would eventually result in permanent injury to the plants.

The individual fractions of reducing sugars, sucrose, and starch followed the same trends under the various clipping treatments as the combined fractions.

PLOTS CLIPPED REPEATEDLY DURING EARLY GROWTH

At the close of the first year of the study, a question was raised concerning the effects of repeated clipping close to the soil line during the early growth period. Accordingly, two series of six plots each (*T* and *U*) were established at the time of snow disappearance in 1933 and clipped three times at 5-day intervals, the clipping starting on series *U* at the time of snow disappearance and, on series *T*, 5 days after snow disappearance.

Five days after the third and final clipping of each series, the roots of the plants on one plot of each series were removed and analyzed for carbohydrate content in comparison with roots of unclipped plants. At the end of the growing season, the roots of the plants on a second plot were similarly compared with roots of unclipped plants. This same procedure was followed each year for 3 years. The resulting data are presented in table 6.

These data show (1) no significant difference in the quantity of carbohydrates stored by the two clipped series, either at the end of the early clipping period or at the close of the growing season; (2) considerable difference in quantity of stored carbohydrates between the clipped plants (2.6 to 6.4 percent) and the unclipped plants (3.9 to 7.6 percent) at the end of the early clipping period; and (3) as great a carbohydrate content in the clipped plants as in the unclipped plants at the close of the growing season.

Nutritional deficiency appeared in the herbage after the first clipping. Growth seemed to be retarded and new foliage did not attain a healthy color until about 10 days after the final clipping. Branching from the crown was delayed and diameters of flower stalks reduced. The flowers did not open and dead stamens were found in the floral bracts along with caryopses. The roots of the clipped plants were short and matted and many of them were dead. Depletion of carbohydrates by the end of the third clipping amounted to about 78 percent of the total stored during the previous autumn, in contrast to 70 percent in the control group.

Sufficient time remained in the growing season after the final clippings, however, to allow the plants to recover, at least in part, and complete their growth cycle. At the close of the growing season, roots of plants in the clipped groups contained as much carbohydrate as those of plants in the control group, and in some cases more.

Results with Slender Wheatgrass

Results with slender wheatgrass under the several clipping treatments were in most cases similar to those with mountain brome. General relations were the same for both grasses under all clipping treatments. A descending trend in carbohydrate storage was evident as clipping was delayed (tables 8 and 9). The significant points of difference displayed by slender wheatgrass in comparison with mountain brome in the clipping tests were (1) consistently lower values of carbohydrates; (2) maintenance of greater percentage of forage yield; (3) increase of forage yield in the early clipped plots; (4) smaller differences between the results of the different clipping systems, especially between 4-inch clippings and 1-inch clippings; and (5) ability of slender wheatgrass plants to maintain yield and store fair quantities of carbohydrates under close and frequent clippings.

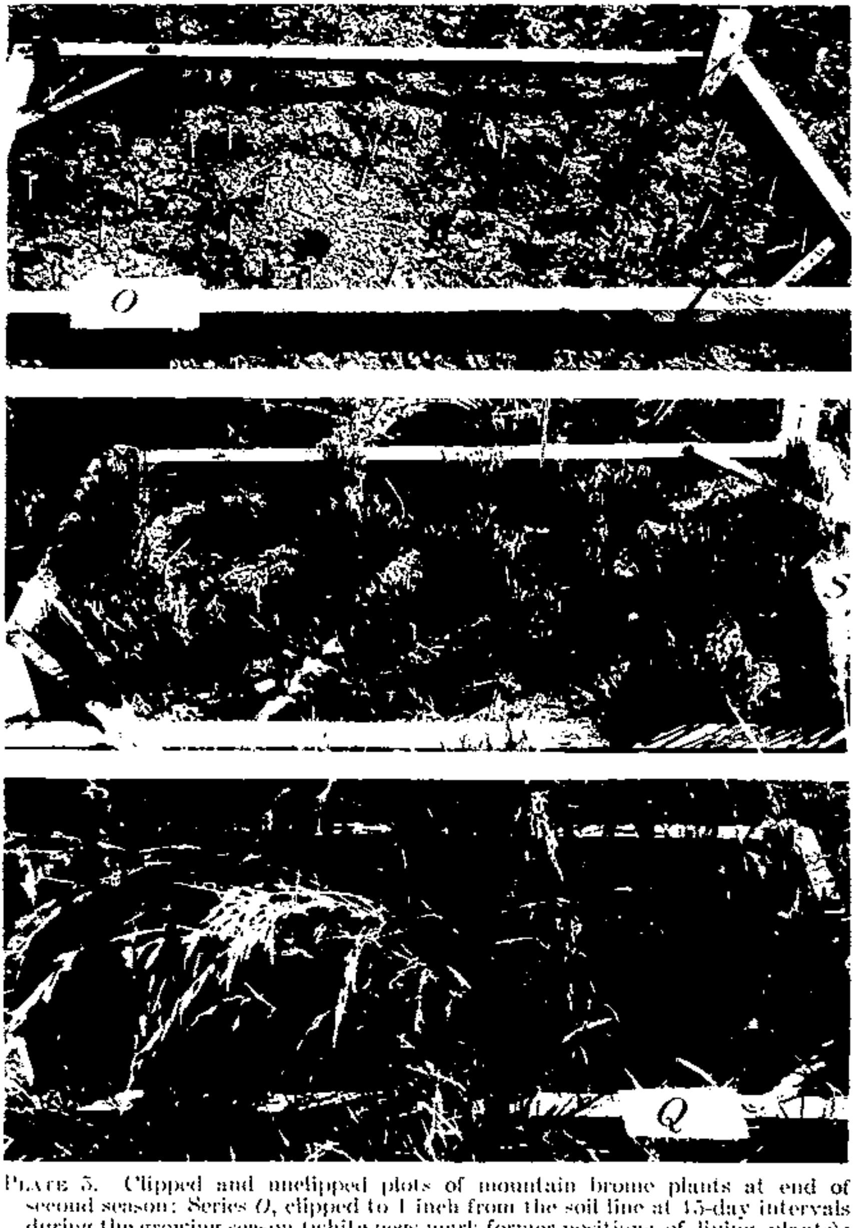

PLATE 5. Clipped and unclipped plots of mountain brome plants at end of second season: Series *O*, clipped to 1 inch from the soil line at 15-day intervals during the growing season (white pegs mark former positions of living plants); series *S*, clipped to 4 inches from the soil line at 15-day intervals during the reproduction period; series *Q*, unclipped. Clipping to 1 inch from the soil line at 15-day intervals resulted in low carbohydrate storage and high mortality of the plants; clipping to 4 inches from the soil line at the same intervals allowed moderate carbohydrate storage and did not appear to damage the plants.

TABLE 8.—*Slender wheatgrass yields and combined sugar and starch stores, 1932–34, and number of flower stalks and height in 1934, under different methods of clipping during growing seasons* [1]

Series and time of clipping	Yield (1932=100)	Carbohydrate stores [2]	Flower stalks	Average end-of-season height
	Percent	*Percent*	*Number*	*Cm*
UNCLIPPED CONTROL				
Q—unclipped		100	63	34
CLIPPED ONCE EACH SEASON [3]				
K—4-inch height	[4] 82.9	86-93	29	18
L—heads high in boot	101.8	81-88	3	10.5
M—seed in milk	68.7	67-84		4.5
N—seed ripe	52.4	60-79		26
P—end of season	104.7	89-92	45	25
CLIPPED TWICE EACH SEASON				
I—4- and 6-inch heights	181.4	80-86	41	
D—4-inch height and seed in milk	40.3	70-79	0	
E—4-inch height and seed dissemination begun	136.8	75-85	51	
H—heads high and seed dissemination begun	76.4	68-85	2	
J—seed in milk and dissemination ended	80.4	69-78	0	. .
CLIPPED THREE TIMES EACH SEASON				
C—4- and 6-inch heights, heads showing	140.9	80-90	8	. . .
A—4- and 6-inch height, 10 days after seed dissemination begun	54.8	85-87	([4])	
F—6-inch height, seed in milk and dissemination	46.1	66-90	0	
B—heads showing, flowers in bloom, seed in dough	51.7	82-87	0	7
R—heads showing, flowers in bloom, seed in dough (clipped to 4 inches)	142.8	86-93		10
G—seed in dough, fully ripe, and dissemination ended	67.2	76-87	0	
CLIPPED FREQUENTLY DURING GROWING SEASON [6]				
O—every 15 days (8 clippings to 1 inch)	62.5	59-80	0	2.5
S—every 15 days (6 clippings to 4 inches)	47.6	71-89	0	10.5

[1] All clipping to 1 inch except as specified.
[2] Based on series *Q*.
[3] Series *K* was 8 cm. when cut; *L*, 14; *M*, 25.5; *N*, 27; *P*, 25.
[4] Total yield very small.
[5] Clipped.
[6] Series *O* yielded 12.0 cm. of regrowth after clippings in 1934; *S*, 2.6; *B*, 2.6; *R* 6.5.

TABLE 9.—*Slender wheatgrass: Carbohydrates stored in roots and stem bases at end of each growing season, in percent of dry weight, under different systems of clipping, 1932–34* [1]

Series and time of clipping	Reducing sugars A			Sucrose B			Starch C			Total sugars and starch A + B + C			Hemicellulose		
	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934
UNCLIPPED CONTROL [2]															
Q unclipped	2.78	2.17	[illegible]	[illegible]	[illegible]	[illegible]	9.74	[illegible]	[illegible]	15.47	13.37	16.71	20.53	22.91	21.98
CLIPPED ONCE EACH SEASON [2]															
K 6-inch height	2.75	2.20	[illegible]	[illegible]	2.52	3.86	9.22	6.86	8.02	13.44	11.57	15.07	22.01	21.52	21.27
L heads half out	2.17	.84	2.71	2.18	2.77	2.8[illegible]	7.01	6.71	9.06	11.65	11.37	14.66	20.72	22.19	21.21
M seed in milk	2.30	[illegible]	3.08	[illegible]	[illegible]	[illegible]	[illegible]	3.88	7.16	10.30	8.91	11.04	22.50	23.28	21.51
N seed fully ripe	1.87	1.80	2.71	.82	[illegible]	[illegible]	[illegible]	3.16	7.08	9.60	8.03	13.21	21.75	22.17	22.11
P end of season	[illegible]	2.06	[illegible]	[illegible]	[illegible]	[illegible]	7.73	7.01	8.46	13.28	12.21	11.94	21.00	22.32	21.20
CLIPPED TWICE THROUGHOUT SEASON [3]															
I 3- and 6-inch heights	2.06	1.97	[illegible]	1.91	2.25	2.61	8.2[illegible]	[illegible]	8.68	12.20	10.72	14.31	21.75	21.99	22.17
D 6-inch height and seed in milk	1.78	1.11	2.18	1.92	2.08	2.67	7.1[illegible]	[illegible]	7.8[illegible]	[illegible]	9.50	12.90	22.72	19.66	22.23
E 6-inch height and seed dissemination	2.70	2.09	[illegible]	2.17	2.27	3.32	7.29	[illegible]	7.19	[illegible]	10.06	11.28	[illegible]	24.36	22.87
H heads half out and seed dissemination	2.37	[illegible]	2.81	[illegible]	.77	3.71	7.78	7.17	7.66	[illegible]	9.03	[illegible]	22.27	23.77	21.03
J seed in milk and seed dissemination	2.03	1.88	2.72	3.17	1.48	3.47	[illegible]	7.02	7.0[illegible]	10.7[illegible]	9.27	13.02	23.07	23.61	22.66
CLIPPED 3 TIMES THROUGHOUT SEASON [3]															
C 3- and 6-inch height and heads showing	2.58	1.83	3.07	2.47	2.62	[illegible]	8.07	6.26	8.70	13.12	10.71	17.07	21.25	21.10	21.42
A 3- and 6-inch height, 10 days after seed dissemination	2.30	1.86	3.87	1.83	2.21	4.23	8.08	7.17	8.18	12.27	11.77	14.76	23.36	23.33	21.39
F 6-inch height, seed in milk and dissemination	2.66	1.38	2.78	1.96	2.71	4.32	6.16	4.07	7.97	10.75	8.81	15.07	22.07	22.12	21.10
B heads showing, flowers in bloom, and seed in dough	2.21	1.97	2.73	2.21	2.65	3.35	7.88	7.02	7.66	12.36	11.64	13.64	23.10	22.88	22.26
R heads showing, flowers blooming, seed in dough (clipped to 1 inches)	2.11	2.21	2.07	2.16	4.09	4.22	8.07	7.58	9.32	12.67	11.51	15.51	21.50	21.30	21.06
G seed in dough, fully ripe, and dissemination	3.27	1.90	3.66	1.49	1.51	3.12	7.83	6.67	7.79	12.57	10.17	14.60	23.74	22.64	22.00

See footnotes at end of table.

TABLE 9.—*Slender wheatgrass: Carbohydrates stored in roots and stem bases at end of each growing season, in percent of dry weight, under different systems of clipping, 1932–34*—Continued

CLIPPED AT 15-DAY INTERVALS THROUGHOUT GROWING SEASON[4]

Series and time of clipping	Reducing sugars (A)			Sucrose (B)			Starch (C)			Total sugars and starch A+B+C			Hemicellulose		
	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934
O beginning 15th day, clipped to 2 inches	2.30	1.84	2.91	.75	2.58	2.70	5.48	4.97	7.67	8.53	9.39	13.31	21.75	22.58	21.90
S beginning 30th day, clipped to 1 inches	2.37	1.88	2.68	1.52	2.84	4.85	6.35	5.56	8.33	10.21	10.28	14.86	21.75	21.47	21.53

CLIPPED 3 TIMES IMMEDIATELY AFTER SNOW DISAPPEARANCE[7]

Time of collection, series, and clipping dates	1933	1934	1935	1933	1934	1935	1933	1934	1935	1933	1934	1935	1933	1934	1935
Collected on 15th day:															
Q unclipped	1.41	1.59	2.08	.41	.59	1.39	2.64	2.87	2.68	4.46	5.17	5.55	27.33	21.17	21.60
C clipped 0, 5th, and 10th day	.95	.95	1.13	.01	.26	.77	.90	1.98	2.59	1.89	3.19	4.40	24.98	21.67	21.52
Collected on 20th day:															
Q unclipped	1.36	2.13	2.65	.33	.48	.15	2.02	2.65	3.38	3.71	5.26	6.18	27.07	24.76	18.39
T clipped 5th, 10th, and 15th day	.39	.90	1.02	.81	.28	1.02	1.09	1.81	1.60	2.29	2.99	3.64	21.14	21.62	22.67
Collected at end of season:															
Q unclipped	2.17	3.28	3.70	4.57	1.39	2.16	7.13	9.04	7.63	13.87	16.71	13.49	22.91	20.98	18.15
C clipped 0, 5th, and 10th day	2.20	2.60	4.11	3.17	1.65	1.69	5.51	7.87	8.85	10.91	15.12	13.68	21.48	19.96	18.33
T clipped 5th, 10th, and 15th day	2.32	2.59	1.28	3.39	1.17	1.02	6.89	7.71	7.89	12.60	14.17	13.19	22.10	22.06	20.17

Calculations made on basis of ash-free dry weight and expressed as reducing sugar. Clipping to 1-inch height unless otherwise specified.
[2] Samples collected Oct. 26, 1932, Oct. 17, 1933, Oct. 12, 1934.
[3] Samples collected Oct. 25–26, 1932; Oct. 16–17, 1933, Oct. 12, 1934.
[4] Samples collected Oct. 21–27, 1932, Oct. 13–14, 1933, Oct. 11–12, 1934.
[5] Samples of C, A, L, R, G collected Oct. 17–20, 1932, Oct. 12–13, 1933, Oct. 11, 1934. P collected Oct. 27, 1932, Oct. 17, 1933, Oct. 3, 1934.
[6] Samples collected Oct. 26–27, 1932, Oct. 16–17, 1933, Oct. 11–13, 1934.
[7] Samples collected June 16 and 21 and Oct. 17, 1933; May 9 and 11 and Oct. 15, 1934, June 18 and 22 and Oct. 9, 1935.

The smaller values of carbohydrates in slender wheatgrass under clipping treatments are explained by the fact, shown in the nutrition phase of the study, that slender wheatgrass plants normally have less stores of carbohydrates in their roots and stem bases than mountain brome. Its growth habits explain in part other differences. Slender wheatgrass is a long-lived perennial plant and therefore may have been less influenced by age than the short-lived mountain brome. Also, slender wheatgrass produces more short basal leaves than mountain brome and is capable of enlarging its tuft area by tillering (pl. 1, *B* and *C*). Because of the shorter basal leaf growth, slender wheatgrass plants naturally have more photosynthetic tissue remaining after each clipping than mountain brome and therefore are able to store more carbohydrates; and the plant's ability to increase by tillering makes it more resistant to close clippings. Genetic differences of the two plants, also, may account in part for their different responses to the clipping treatments.

Results With Sticky Geranium

In general, the results with sticky geranium showed trends similar to those with mountain brome and slender wheatgrass. The plants subjected to clipping before and after the intensive growth and reproductive period showed more carbohydrate storage and less loss percent of forage yield than those clipped during the middle of the active growing season. The differences in this plant's responses to the several clipping treatments, and the variability of the results obtained in some cases, can be attributed chiefly to the growth habits of the species. Sticky geranium puts forth many long-stemmed leaves that grow from the crown of the plant (plate 1, *D*). As is shown by the results of the nutrition phase (figs. 6 and 7), this herbage matures relatively early, enabling carbohydrate storage to begin promptly and be completed in a relatively short time. This accounts for the favorable results from clippings late in the growing season. Figures 13 and 14 give comparative yields.

The fact that only two plants were used for each analysis in the clipping series may have resulted in minor discrepancies in some of the results. Moreover, close clipping of sticky geranium takes all photosynthetic tissue and herbage must again be produced from the crown before manufacture of carbohydrates can be resumed. Thus clipping causes severe shock to the plants.

The quantity of combined sugars and starch in the roots and stem bases of the plants clipped once during the season was lowest when the clipping was made during or at the immediate close of the intensive reproductive period (table 10), with the exception that in 1933 plants clipped after flower buds were in evidence stored more carbohydrates than plants clipped earlier. The growing season in 1933 was shorter than normal, decreasing the storage period of the plants clipped early and preventing regrowth in the plants clipped later in the season, and this caused less diminution of foods already stored in these plants. The several individual sugars and starch fractions showed trends similar to those of the combination (fig. 6). The main differences were in the values for starch and reducing sugar.

Results with plants clipped twice at various stages of growth (fig. 13 and table 10) vary somewhat, with no marked differences in

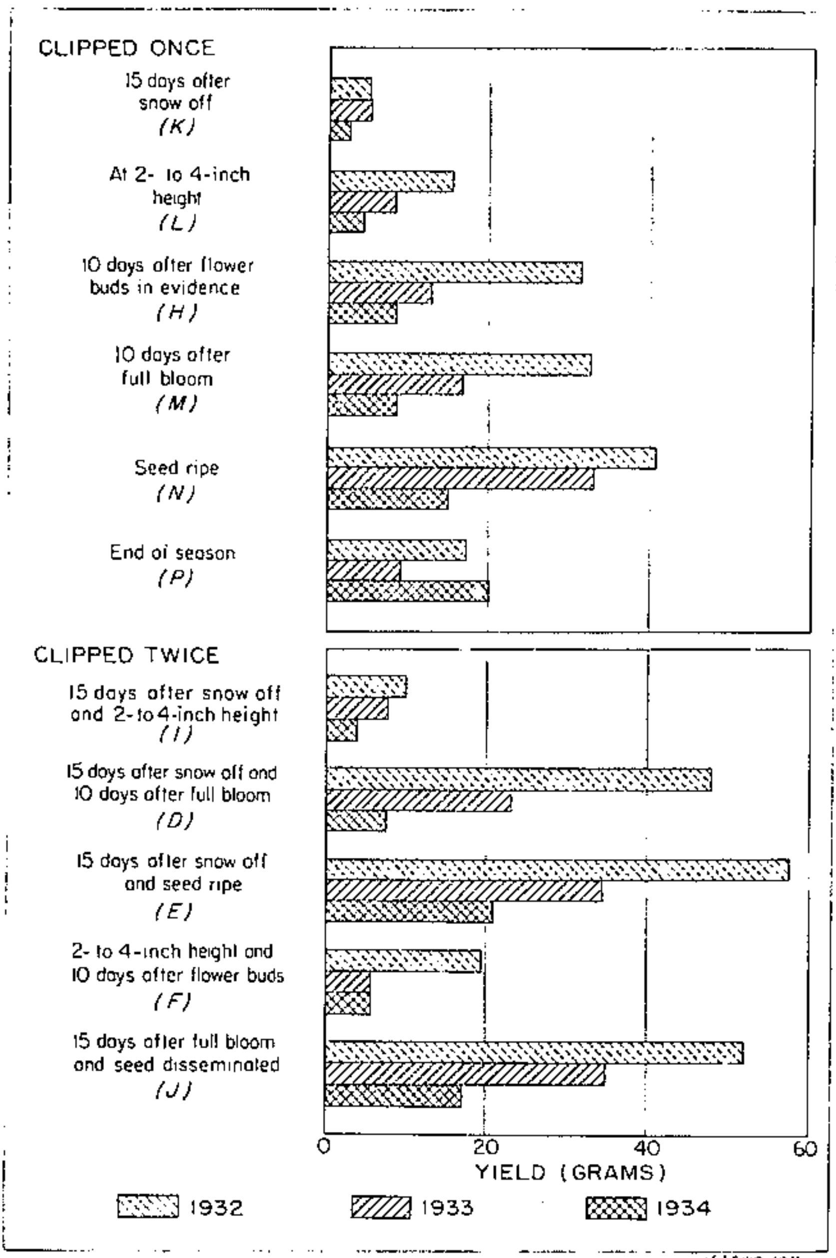

FIGURE 13.—Forage yields of sticky geranium from 1 and 2 clippings throughout the growing season, 1932–34.

quantities of carbohydrates stored except in series *D* during the last year. This series, clipped 15 days after snow off and again 10 days after full bloom, showed a steady loss in percent of forage yield.

Plants clipped three times during the early or late portion of the growing season (fig. 14 and table 10) had higher carbohydrate storage than plants clipped three times during midseason or plants clipped

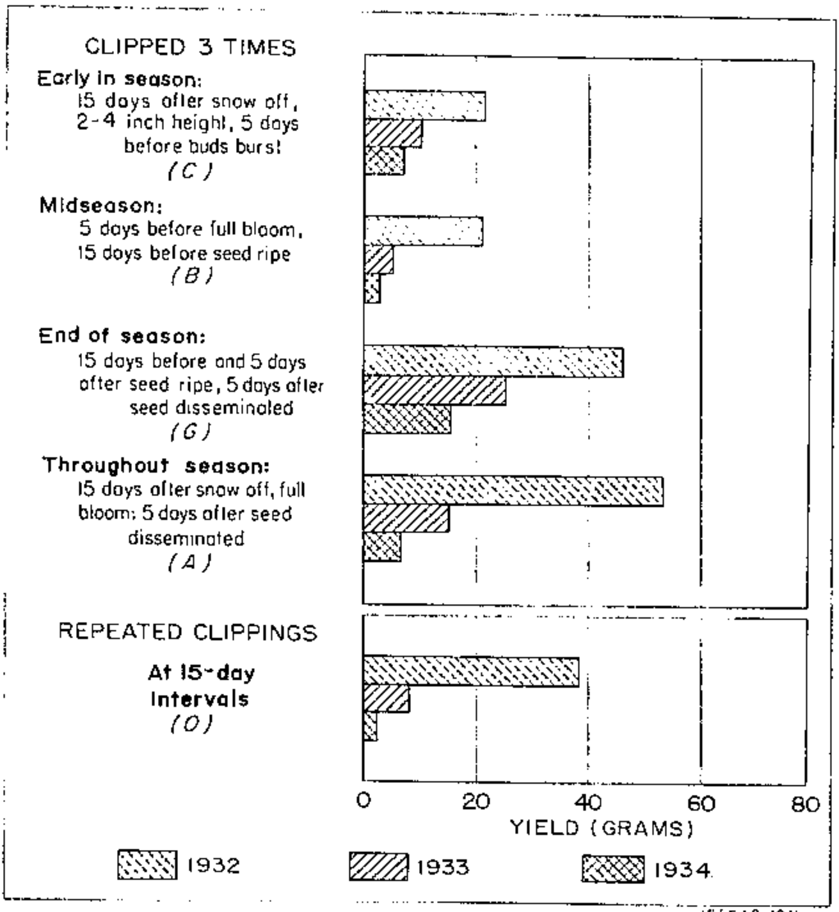

FIGURE 14.—Sticky geranium yields from 3 clippings during season, and from clippings at 15-day intervals, 1932–34.

three times throughout the season. The percentage of yield, also, was higher in the plants clipped early and late.

Plants clipped at 15-day intervals throughout the growing season had less carbohydrate storage and more reduction in yield than plants clipped under any other system (fig. 14 and table 10). Plants remaining after the third year of this treatment were nearly dead and furnished barely enough roots for the chemical analyses.

TABLE 10. *Sticky geranium: Carbohydrates stored in roots and stem bases at end of each growing season, in percent of dry weight, under different systems of clipping, 1932–34* [1]

Series and time of clipping	Reducing sugars (A)			Sucrose (B)			Starch (C)			Total sugars and starch (A+B+C)			Hemicellulose		
	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934
UNCLIPPED CONTROL [2]															
Q—unclipped	11.57		8.26	0.26	5.10	2.62	8.21	11.60	7.80	20.07	16.70	18.68	5.40	......	......
CLIPPED ONCE EACH SEASON [3]															
K—15 days after snow off	8.49	3.00	5.78	0.52	2.04	2.21	8.61	9.91	10.54	17.62	14.95	18.53	5.82	5.08	3.91
L—2- to 4-inch height (20 days)	8.65	4.20	7.07	.10	.75	4.45	7.03	8.47	6.28	15.78	13.12	18.40	5.50	5.00	4.69
H—10 days after flower buds in evidence	8.78	2.30	7.91	.54	3.95	3.52	7.61	11.01	3.66	16.96	17.29	15.09	6.29	5.67	5.67
M—10 days after full bloom	8.48		6.77	.40	7.60	2.01	7.01	8.40	3.73	15.89	16.00	12.51	5.66		3.74
N—seed ripe	8.57	1.96		.30	1.87		5.72	9.00		11.57	15.92		6.02	5.88	......
P—end of season	11.01	3.99	6.65	.32	1.57	6.28	8.24	13.52	7.17	19.60	19.08	19.98	7.26	7.32	......
CLIPPED TWICE THROUGHOUT SEASON [4]															
I—15 and 20 days after snow off	6.59	1.59	5.26	0.44	1.23	5.71	7.58	7.85	10.09	14.61	13.67	21.00	6.67	4.56	4.48
D—15 days after snow off and 10 days after full bloom	7.29	6.34	5.89	.75	1.76	1.02	7.80	6.92	2.87	15.84	15.02	12.78	5.23	5.03	5.47
E—15 days after snow off, seed ripe	6.91	1.01	6.67	.86	1.08	1.57	9.98	10.77	9.14	17.78	15.86	17.38	6.01	5.37	4.92
F—20 and 35 days after snow off	8.07	3.66	5.37	.48	3.22	7.69	6.37	10.06	8.18	14.92	16.94	21.24	6.30	6.25	5.30
J—15 days after full bloom, seeds disseminated	9.43	5.00	5.84	.32	2.12	4.29	7.23	8.33	8.24	16.98	15.75	18.37	6.36	5.75	3.27
CLIPPED 3 TIMES THROUGHOUT SEASON [5]															
C—beginning of season	9.60	3.20	5.08	0.20	3.07	4.26	7.65	11.74	6.98	17.45	18.01	16.32	6.43	6.32	4.30
B—middle of season [6]	7.98	1.13		.81	2.54		3.01	4.17		11.80	11.14		4.81	5.00	......
G—end of season	7.77	5.57	8.13	.22	3.85	3.53	8.22	8.88	0.78	16.21	18.30	18.44	6.70	5.80	......
A—beginning of season, full bloom, and end of season	9.81	5.20	8.93	1.98	2.34	1.39	3.95	3.27	2.75	15.77	10.90	13.07	–	5.42	4.85

CLIPPED AT 15-DAY INTERVALS [2]

9 from snow off	6.81	1.24	1.70	0.20	1.00	1.30	3.26	3.38	1.49	10.27	8.62	4.55	5.30	5.01	2.74

[1] Calculations made on basis of ash-free dry weight and expressed as reducing sugar. All clippings to a height of 1 inch above ground line.
[2] Samples collected Oct. 13, 1932; Oct. 11, 1933; Oct. 10, 1934.
[3] Total sugars.
[4] Samples collected Oct. 12-13, 1932; Oct. 10-11, 1933; Oct. 10, 1934.
[5] Samples collected Oct. 11-12, 1932; Oct. 9-10, 1933; Oct. 10, 1934.
[6] Samples collected Oct. 11, 1932; Oct. 9-10, 1933; Oct. 10, 1934.
[7] 1934 results lost in analysis.
[8] Samples collected Oct. 13, 1932; Oct. 11, 1933; Oct. 10, 1934.

EFFECTS OF GRAZING

Preliminary tests of the storage of carbohydrates in roots and stem bases of mountain brome under grazing by range cattle were made at the Bluebell field unit during the 4 years 1932-35. Similar tests of slender wheatgrass were made during 1935 only.

TREND OF CARBOHYDRATE CONTENT

Root samples of six to eight ungrazed mountain brome and slender wheatgrass plants located inside an enclosure were taken at approximately 10-day intervals during the period from June 2 to September 10, inclusive, 1935. On the same dates, root samples from six to eight plants of the same species that had been moderately grazed by cattle were taken in the vicinity of the enclosure. Grazing left the plants 2 to 6 inches high and was restricted to the period from mid-June to mid-September. Mountain brome was grazed first and to a greater degree, because of its higher palatability, doubtless due to the higher sugar content as indicated in the nutrition phase. The plants analyzed were grazed, on the average, three times during the season.

The carbohydrate content of the mountain brome that was grazed was significantly less shortly after grazing began than that of the ungrazed plants (fig. 15). On July 26 it averaged about 73 percent; by August 26 it had diminished to 55 percent; and by September 10 it increased only to about 66 percent, or less than the corresponding percentage for any of the clipped lots except the plants clipped at 15-day intervals.

The carbohydrate content of the roots and stem bases of grazed slender wheatgrass plants remained within 90 percent of that of the ungrazed plants until July 16 (fig. 15). Thereafter it diverged abruptly and on July 26 and on September 11 was only 70 percent.

Two points stand out in these results that agree with the results of the nutrition and clipping phases:

The carbohydrate content of the roots and stem bases of the two grasses reached the seasonal minimum during the formative growth stage and the seasonal maximum after current seasonal and secondary herbage and root growth was completed.

Grazing, especially during the reproductive period and during the normal storage period, reduced the quantity of carbohydrates stored in the roots of the plants at the end of the growing season.

CARBOHYDRATE STORAGE BY SEASON OF GRAZING

Figure 16 shows the quantity of carbohydrates stored in the roots and stem-bases of mountain brome and slender wheatgrass plants under (1) moderate grazing during the summer season (from mid-June to mid-September), (2) moderate grazing after seed maturity, and (3) total protection. The chemical determinations were made in each case with root samples of six to eight plants collected at the end of the snow-free period, in mid-October of each year.

As shown by figure 16, the plants grazed season-long (grazed on the average three to four times during each season to heights of 3 to 6 inches) had consistently less carbohydrates stored in their roots at the end of the season especially in 1932 and 1933, when grazing was somewhat heavier. In 1935, carbohydrate stores in grazed mountain brome ranged from 47 to 68 percent of those in ungrazed plants and

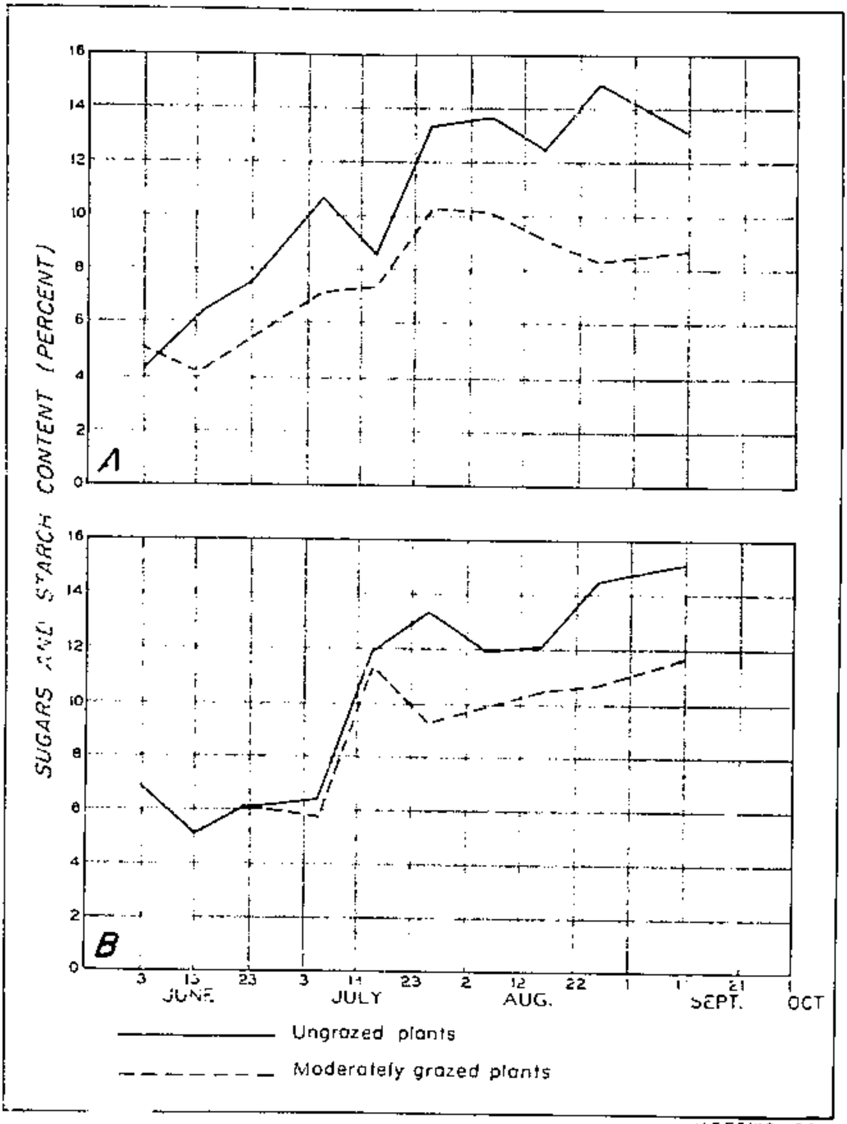

FIGURE 15.—Trend of the combined sugars and starch content of roots and stem-bases of grazed and ungrazed (A) mountain brome and (B) slender wheatgrass plants in 1935. In mountain brome new root growth (0.5 to 2 cm.) and new shoot growth (2 cm.) appeared about August 16.

in slender wheatgrass amounted to about 70 percent. Plants grazed only after seed maturity, near the end of the growing season, had 84 to 96 percent as much carbohydrate storage as the ungrazed plants, or considerably more than plants grazed during the intense growing period. The latter results resemble those with plants clipped at the end of the season (plot *P*), which had from 84 to 91 percent of normal carbohydrate stores.

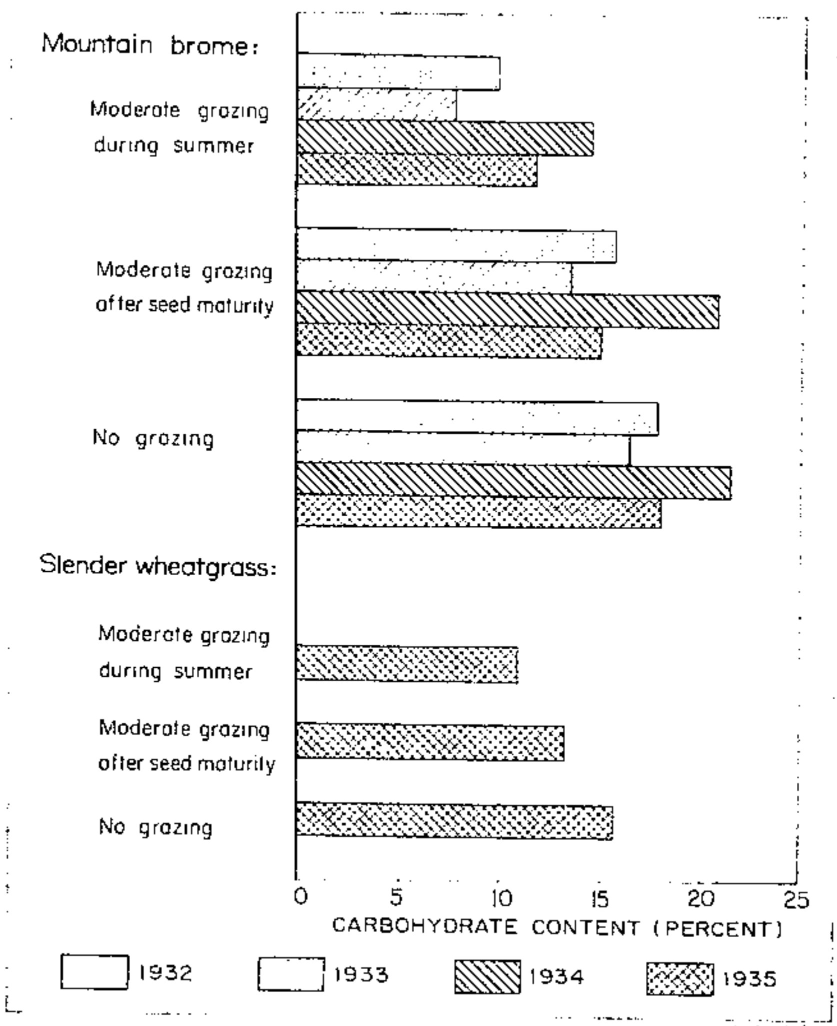

FIGURE 16. Sugar and starch content of roots and stem-bases of mountain brome (1932-35) and slender wheatgrass (1935) under grazing.

SUMMARY AND CONCLUSIONS

The findings of these studies of the growth and carbohydrate nutrition of two perennial range grasses and two broadleaf herbaceous range plants native to the Wasatch Mountains in central Utah, under natural conditions and total protection, clipping, and cattle grazing, are of importance as a basis for conservation measures and wise grazing use on western mountain range lands.

Annual growth of the plants is a cyclic process in which intervals of rapid growth alternate with intervals of depression in growth rate. Seasonal fluctuations in precipitation and temperature cause definite fluctuations in the growth rate. Depressions in growth rate also coincide with the advent of flowers and formation of fruit.

The annual cycle includes growth of herbage, growth of roots, flowering, and secondary growth of herbage. The annual herbage growth begins before the winter snow disappears. Root growth occurs in early spring immediately after winter snow disappears; at the conclusion of shoot growth; and near the close of the snow-free period, alternating with herbage growth. Secondary herbage growth takes place during the autumn when the foliage developed in the spring is drying. Shoot buds form in the crown of the plants during the following secondary herbage growth. These buds persist under the winter snow and produce the early spring shoots.

The storage of carbohydrates is also cyclic and is related to the cycle of annual growth in the following manner:

Storage of carbohydrates is at a minimum during the periods of greatest growth. Maximum storage occurs during the autumn (August and September) with the completion of secondary herbage growth.

Early growth in the spring is dependent upon reserve foods in the plants. Approximately 75 percent of the total carbohydrates stored in the autumn are consumed in the production of 10 percent of the herbage growth. Subsequent growth is dependent upon the currently assimilated foods.

During the winter metabolic activities are greatly reduced. Respiration at a low rate continues in the living tissues and the soluble carbohydrates increase at the expense of the insoluble carbohydrates. High concentrations of sugars in the basal organs appear to be associated with cold resistance and survival.

Sucrose and starch are the principal carbohydrates stored. Hemicellulose appears to be more important as a cell-wall constituent.

The quantity of carbohydrates stored is greater in the broadleaf plants than in the grasses. Proportions of the several carbohydrate fractions also vary somewhat for the two types of plants; sugar content is greater in the grasses and starch content is greater in the broadleaf plants. Carbohydrate-storage values were higher in mountain brome than in slender wheatgrass; sugar storage in particular was higher in mountain brome.

The various systems of clipping applied to mountain brome, slender wheatgrass, and sticky geranium yielded the following results:

With few exceptions, forage yield of all plants clipped (generally to a height of 1 inch) was lower at the close of the study than at the beginning. The exceptions were plants clipped at the close of the growing season, those clipped three times during the season to a height of 4 inches, and slender wheatgrass plants clipped when 4 to 6 inches high.

Carbohydrate storage of all clipped plants, except the sticky geranium plants clipped at the close of the growing season, was lower than those of unclipped plants.

Among clipped plants, highest percentages of yield and greatest carbohydrate storage occurred in plants clipped early—when 4 and 6 inches high—and at the close of the growing season—when foliage was dry. For mountain brome and slender wheatgrass plants clipped to 1 inch when they first reached 4 inches and those clipped at the close of the growing season, carbohydrate reserves averaged about 90 and 88 percent, respectively, of those in unclipped plants. Lowest carbohydrate storage, and greatest percentage of loss in forage yield, occurred in plants clipped to 1 inch at 15-day intervals season long and during the growing periods—flower-stalk formation to seed ripening. The plants clipped when seed were ripe average only 67 percent of the control-plot values. Others clipped when seed were in the milk stage averaged about 73 percent of the carbohydrate reserves of unclipped plants.

The quantity of reserve carbohydrates stored in the roots and stem bases of the plants is related to the amount of foliage present during the normal storage period—August and September at the study area—and is less as the interval decreases between clipping and the normal storage period. Close removal of herbage (clipping to 1 inch) at any time during the storage period reduces the carbohydrate reserves, but if done at the beginning it not only prevents normal storage of carbohydrates but also stimulates regrowth, at the expenditure of carbohydrate foods previously stored. If herbage is clipped early in the season when sufficient time yet remains for the plant to make new growth and complete the normal growth cycle before the onset of winter, near-normal carbohydrate reserves are attained.

Similar results with the two grass species were obtained by clipping twice and three times to a height of 1 inch during the growing season. Plants clipped early and at or near the close of the season maintained a greater percent of forage yield and had greater carbohydrate reserves than plants clipped during the middle of the season when reproduction was in progress. When early and close clippings (three clippings at 5-day intervals) were repeated, however, the immediate results were distinct etiolation and reduced carbohydrate stores; but with no further clippings the plants completed near-normal carbohydrate stores by the end of the season.

When clipped three times to a height of 4 inches from the soil line the mountain brome and slender wheatgrass plots attained above-average yields and carbohydrate reserves. In the mountain brome and slender wheatgrass plants clipped to this height every 15 days during the growing season, the carbohydrate reserves averaged about 86 percent and 77 percent, respectively, of the reserves in the unclipped plants.

Of plants clipped during the growing season, those clipped twice and three times nearly equalled those clipped once in carbohydrate reserves. This indicates that quantity of carbohydrate reserves in the plants at the end of the season is influenced less by frequency of clipping than by time and degree of clipping. When clippings were made both frequently and intensely, as to a height of 1 inch at 15-day intervals, low values were obtained in both yield and carbohydrate reserves.

The several clipping treatments of sticky geranium furnished evidence similar to that from tests on the two grasses, in that plants clipped at the close of the growing season maintained a greater percent of yield and higher carbohydrate reserves than plants clipped during the main part of the growing season.

Results obtained from cattle grazing closely resembled those from comparable clipping treatments. The seasonal trend of carbohydrate reserves under repeated grazing was markedly below that of the ungrazed plants, and at the end of the season (October 10) the total reserves for mountain brome and slender wheatgrass amounted to about 66 percent and 70 percent of the reserves in ungrazed plants. Under moderate season-long grazing (3 to 4 inches from mid-June to mid-September) during the 4-year period 1932-35, carbohydrate reserves of mountain brome averaged about 59 percent of those in ungrazed plants, whereas under moderate grazing after seed maturity they averaged about 88 percent. Similar treatments of slender wheatgrass yielded 70 percent and 85 percent, respectively, in carbohydrate reserves.

From these results the following conclusions are drawn with respect to proper season and intensity of grazing on high mountain summer ranges in the West, supporting stands of mountain brome, slender wheatgrass, and sticky geranium plants:

1. Although presence of snow and influence of other adverse climatic elements make it necessary to utilize high mountain ranges during the summer season when the plants are growing and producing herbage, such grazing should be so coordinated with the critical growth and developmental stages of the principal perennial forage plants that the plants may assimilate and store sufficient plant foods to maintain growth and produce herbage for forage in subsequent years.

2. Critical periods in the life cycle of the plants studied, as measured by the carbohydrate reserves at the end of the growing season and yield and vigor of the plants, are (1) from flower stalk formation to and including seed ripe—the active reproduction period; and (2) during the forepart of the normal carbohydrate-storage period, which in the mountains of Utah takes place during August and September. Carbohydrate storage is at a minimum during the reproduction period and subsequent storage is greatly reduced by close utilization during that period. Moreover, reproduction leads to physiological inertia or fatigue (8), and close harvesting during this period appears to inflict added injury on the plants. Again, harvesting during the normal storage period, particularly at the beginning, delays and prevents normal storage. Usually insufficient time remains in the growing season before the date when maximum storage takes place to allow for sufficient regrowth and normal storage. Grazing should be slackened during these periods.

3. Early grazing, when plants are 4 to 6 inches high, provided it is not too frequent, and grazing near the close of the growing season, when the herbage is dry or drying, appear to be the safer periods of use if grazing is to be restricted as to periods. Other factors, however, such as the uprooting of plants by pulling and trampling by livestock, as the result of early grazing on wet and spongy soil; or the lack of sufficient forage at this time to maintain livestock in thrifty condition, as outlined by previous investigations (*4, 11*), prevent too early grazing use. On the other hand, reduced palatability of the plant herbage and adverse weather conditions also militate against extended fall grazing. Restriction of actual grazing periods may not therefore be practicable.

4. The key to practical and sound continued use of the annual forage crop produced on high western mountain ranges supporting stands of mountain brome and slender wheatgrass appears to be moderate use grazing the grasses to an average height of 3 to 4 inches at about monthly intervals or less frequently; and allowing, at least periodically, for the slackening in the intensity of grazing during the intense reproductive period and the forepart of the fall storage period.

5. It is recommended that such grazing use be rotated so that no given portion of the range is grazed at the same time every year. This provision will allow for the production of seed and the reseeding of the range previously found to be necessary (*10*, *4*) and may also obviate the necessity of slackened grazing during the critical periods of plant growth.

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