Carbohydrate Reserves of Sand Reedgrass under Different Grazing Intensities[1]

TOMMY G. WELCH[2]

Graduate Research Assistant, Range Science Department, Colorado State University, Fort Collins.

Highlight

Stored carbohydrates of sand reedgrass increased from a low in late May and early June to a maximum in late September and early October. Starch was the major stored carbohydrate. The concentration of starch in the roots decreased slightly with increased grazing intensity. The results of this study combined with information on the morphological development, extent of root system, and other physiological aspects of sand reedgrass can be used in developing grazing management systems for sand reedgrass.

Sand reedgrass (*Calamovilfa longifolia*), a tall, sod-forming, warm-season grass with large, spreading rhizomes, is one of the prominent plants in the sandhills vegetation of northeastern Colorado. Sand reedgrass is a preferred or "sought-after" species by cattle only during May and early June, but, because it is abundant, it is a major component of cattle diets throughout the summer months. This plant decreases under heavy summer grazing (Dahl and Norris, 1965). Branson (1953) pointed out the importance of position of apical meristem and ratio of vegetative to reproductive stems in the response of a grass to grazing. The results of a study by Dahl[3] at the Eastern Colorado Range Station showed that apical meristem of reproductive shoots of sand reedgrass remained below the soil surface until June, shoot apices of vegetative stems remained below or near the soil surface throughout the growing season and were not subject to removal by grazing. There were approximately twice as many vegetative stems as reproductive stems. Therefore, the level of reserve carbohydrates may be a more important factor in the reaction of sand reedgrass to heavy grazing than position of apical meristem.

Reserve carbohydrates are those carbohydrates that are alternately accumulated and utilized by the plant during the growth cycle. Sucrose, fructosans, and starch are the most important reserve carbohydrates with glucose and fructose less significant. These carbohydrates are stored in the roots, rhizomes, stem bases, and corm-like organs of grasses. Carbohydrate reserves are used for initiation of growth in the spring, for regrowth following defoliation, and for respiration during the winter. Defoliation of a grass generally reduces the carbohydrate reserves. The degree of reduction depends on the frequency, intensity, and time of foliage removal (Weinmann, 1952; Troughton, 1957; Cook, 1966; Everson, 1966).

The objectives of this study were to determine seasonal trend, constituents (starch and soluble carbohydrates), and concentrations of the reserve carbohydrates in the roots and rhizomes of sand reedgrass as affected by grazing intensity. Basic knowledge of this plus morphological information are essential in developing grazing management systems that will utilize this species and its associates in the most efficient manner.

Methods and Materials

The study was conducted at the Eastern Colorado Range Station near Akron, in the sandhills of the northeastern part of the state. The climate is semi-arid and is characterized by hot summers; mild, dry autumns; cold winters; and moist, cool springs. The average annual precipitation is about 15 inches with most falling as rain during the growing season (Dahl et al., 1967). Reppert (1960) gives a detailed description of the station.

---

[1] Adapted from a thesis submitted in partial fulfillment of the requirements for the M.S. degree in Range Science at Colorado State University under the direction of Dr. J. J. Norris and Dr. Bill E. Dahl. Published with approval of the Director of the Colorado Agricultural Experiment Station as Scientific Series Paper No. 1220.

[2] Present address: Graduate Teaching Assistant, Range Science Department, Utah State University, Logan.

[3] Results of an unpublished study in 1961 and 1962 on the position of apical meristem of sand reedgrass by Bill E. Dahl, formerly Assistant Range Conservationist, Eastern Colorado Range Station, Akron, Colorado. Results on file at ECRS.

The study area was on deep sand range sites in two moderately grazed pastures, two heavily grazed pastures, and three exclosures. Vegetation on these areas is composed primarily of sand reedgrass, blue grama (*Boutelous gracilis*), needleandthread (*Stipa comata*), and sand sagebrush (*artemisia filifolia*). The soils are Blakeland loamy sand and Valentine sand. Stocking rates averaged about 1.0 and 0.7 acre/yearling steer-month for moderate and heavy grazing, respectively. The pastures were grazed at these intensities from about May 1 to October 1 during the years 1955 through 1966. Exclosures were not grazed by livestock.

Samples of roots and rhizomes were collected on 17 dates from July 1965 to November 1966. Sampling intervals varied from two weeks to several months. Samples were collected more frequently in the spring and early summer to determine when the reserves were at their lowest point and when storage began. After this period, samples were collected according to the following phenological stages: 1.) anthesis (early and late anthesis in 1965), 2.) seed in soft dough stage and, 3.) seeds mature. The last sample of the calendar year was taken in November after the plants became dormant. The first sample of the following year was taken in March before plants began growth.

To determine the effect of repeated foliage removal on the reserve carbohydrates, an area of sand reedgrass about 15 ft square was mowed repeatedly to a stubble height of 1 inch or less in 1966. The plants were not allowed to reach a height over 6 to 8 inches in the early part of the growing season and were kept below 3 to 4 inches during the remainder of the growing season. This plot was sampled on the same dates as the other study areas.

At each sampling date, several groups of plants in similar phenological development were selected in each pasture and exclosure. A representative sample of the roots and rhizomes of these plants was obtained by removing a sod approximately 12 inches square and 10 inches deep from each group. Soil was shaken from the roots and rhizomes and the plant tops were removed. Samples were collected from the same general areas on each sampling date.

Sods taken in a given pasture were composited. Also, sods taken from the exclosures in one heavy intensity pasture and the moderate intensity pasture were combined. The sample from the other exclosure was used as the replicate.

The composited samples were washed with water to remove any remaining soil. Roots and rhizomes were separated, ground with a hand-operated meat grinder, weighed, and placed in separate jars containing a measured amount of 80% ethanol (50 ml of 80% ethanol/g of oven-dry plant material). A portion of each sample was used to determine oven-dry weight. About 2 hr elapsed between removal of the sod and when the plant parts were placed in the ethanol. The material in ethanol was macerated with a Waring Blendor, filtered, and stored in a freezer until it could be chemically analyzed. The residue was oven-dried, ground through a 40-mesh screen, and sealed in jars.

The filtrate was analyzed for soluble carbohydrates by the anthrone reagent method (Johnson et al., 1964; Everson, 1966). Starch was extracted from the residue with perchloric acid (Pucher et al., 1948; Everson, 1966). Starch content was then determined by the anthrone reagent method. The concentration of carbohydrates was expressed as mg/g of oven-dry plant method.

Ascending paper chromatography was used to separate

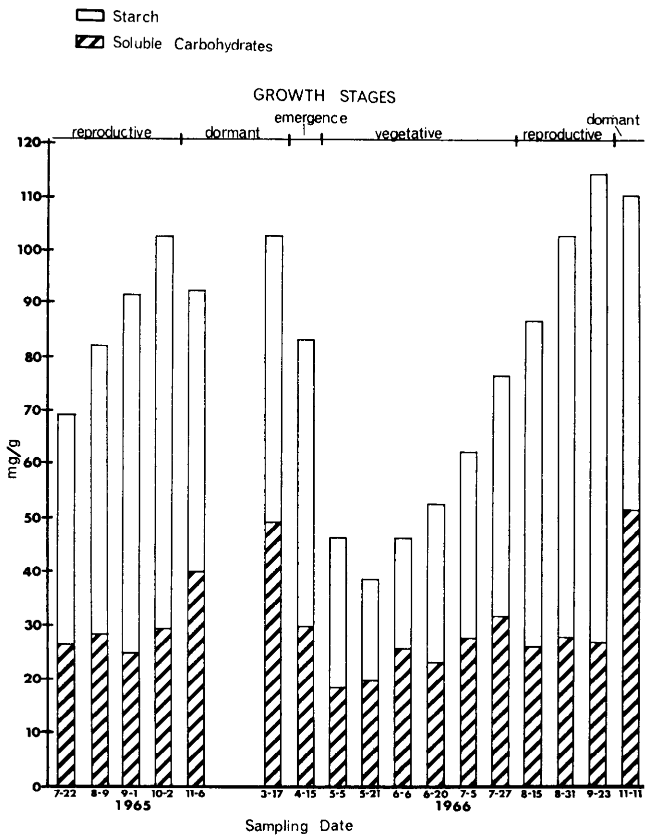

FIG. 1. Seasonal trend of reserve carbohydrate concentration (mg/g of oven dry roots and rhizomes) in sand reedgrass.

and identify the constituents of the soluble carbohydrate fraction (Olson[4]). Solvents used were n-butanol–acetic acid–water (40 : 10 : 19) and ethyl acetate–acetic acid–water (6 : 3 : 2). Aniline hydrogen phthalate and p-anisidine hydrochloride were used as color developers. Chromatograms were run in duplicate; one in each solvent. Glucose, fructose, and sucrose standards were run on each chromatogram to aid in identifying the spots of respective carbohydrates.

The data for each sampling date were analyzed statistically by split-plot analysis of variance. Least significant difference and smallest significant range were used to evaluate the reason for significant interactions. Data from all dates combined were analyzed similarly, thus, adding a split over time.

Results and Discussion

Seasonal Trend.—Fig. 1 shows that total carbohydrate concentration of the underground plant parts followed the typical U-shaped seasonal trend referred to by numerous workers (Cook, 1966). Carbohydrates were being accumulated when the first samples were collected in July 1965. The reserves increased to a peak in early October. They decreased after the beginning of dormancy, but were still at high levels just before new growth started in the spring of 1966. With initiation of

[4] Olson, G. G. 1963. Paper chromatography–anthrone determination of sugars. M.S. Thesis. Colorado State Univ., Fort Collins. 62 p.

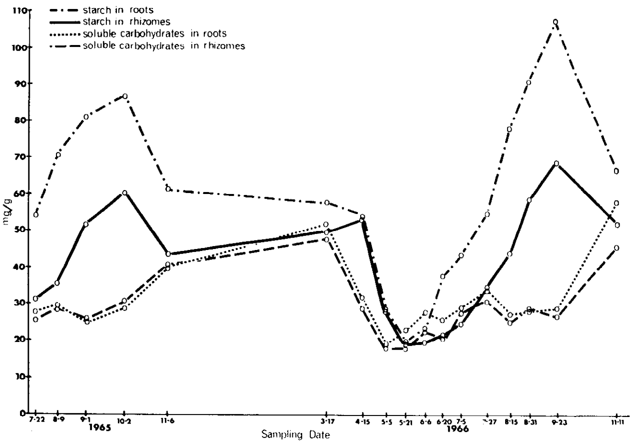

FIG. 2. Carbohydrate concentration (mg/g of oven dry plant material) in roots and rhizomes of sand reedgrass.

growth, reserves declined rapidly. The lowest concentration occurred on May 21. Thereafter, carbohydrate content increased steadily and the trend for the remainder of the growing season was similar to that of 1965.

The seasonal trend shows that accumulation of reserve carbohydrates in sand reedgrass begins early in the growing season. This agrees with the observation made by Hyder and Sneva (1959) that plants with a high proportion of vegetative stems, short internodes, and basal leafiness replenish reserves rapidly. In sand reedgrass, the carbohydrates began accumulating concurrently with the most rapid elongation of leaves and the greatest increase in dry weight. This indicated that sufficient leaf area was present by June 6 to provide photosynthate in excess of the plant demands for carbohydrates in respiration and growth.

The carbohydrate concentration was greater in the spring before growth began than the preceding fall after plants had become dormant. This may have been due to experimental error or to soluble carbohydrates being translocated from the stem bases to the roots and rhizomes after sampling was completed in the fall.

Throughout most of the growing season the starch content was significantly higher than the content of soluble carbohydrates. However, their concentrations were similar before the initiation of growth in the spring; when reserves were at their lowest point; when storage began; and after the plants were dormant in 1966. Soluble carbohydrate concentration was relatively constant throughout the growing season, but was higher during dormancy as a result of the conversion of starch to soluble carbohydrates at low temperature. The starch concentration fluctuated throughout the sampling period (Fig. 1). Thus, the seasonal variation of total reserve carbohydrates was the result of fluctuations in the starch content. The variability of the starch content and the relatively constant soluble carbohydrate concentration during the growing season resulted in a significant constituents–dates interaction.

Starch is the major stored carbohydrate of sand reedgrass. However, the soluble carbohydrates are the most readily available for use by the plants. The constancy of the concentration of these soluble carbohydrates throughout the growing season may indicate that they serve as the translocatable portion of the reserve carbohydrates. This relatively consistent concentration may also indicate that an equilibrium exists between the concentration of starch and soluble carbohydrates. The starch is apparently converted to soluble carbohydrates when the concentration of soluble carbohydrates is low, and the soluble carbohydrates are converted to starch when the concentration of soluble carbohydrates becomes high.

Underground Plant Parts.—Roots had a significantly higher concentration of total carbohydrates than the rhizomes from late June through November (Fig. 2). Total carbohydrate concentration in the roots was similar to the concentration in the rhizomes during initial spring growth. Because the carbohydrate concentration was greater in the roots for only part of the year, a significant plant parts–dates interaction resulted.

Soluble carbohydrate concentrations were similar in both roots and rhizomes throughout the year. However, the starch content was significantly higher in the roots during the periods when carbohydrates were being accumulated. A significant plant parts–constituents interaction resulted on these dates and for the whole experiment because of this higher starch concentration in the roots. Because the starch concentration was similar in roots and rhizomes for the early portion of the growing season and then became greater in the roots, a significant plant parts–constituents–dates interaction resulted (Fig. 2). This may indicate that starch is depleted at about the same rate from both roots and rhizomes, but that accumulation begins first in the roots.

Effect of grazing.—Only two dates, June 6, and August 15, 1966, showed a significant difference in carbohydrate concentration due to grazing treatment (Fig. 3). On June 6 the grazed plants had a higher concentration of carbohydrate reserves than the ungrazed plants. Plants in the exclosures began growth later than the grazed plants probably because the soils were cooler and wetter under the thick litter cover in the exclosures. On June 6 the carbohydrate reserves of the ungrazed plants were at the low point for the season, while the grazed plants had begun to replenish their reserves. Ungrazed and moderately grazed plants had a significantly higher carbohydrate concentration than heavily grazed plants on August 15. This differ-

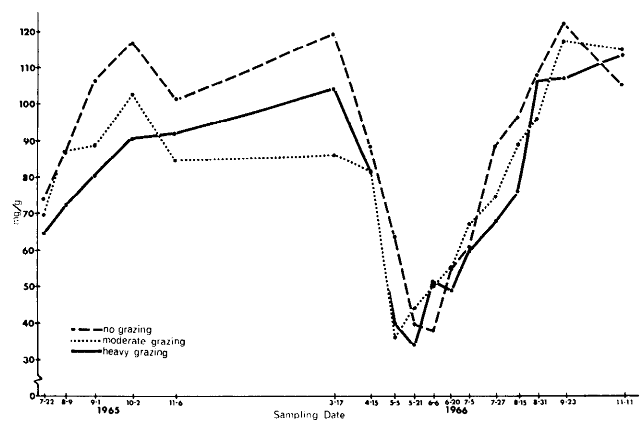

FIG. 3. Reserve carbohydrate concentration (mg/g of oven dry roots and rhizomes) of sand reedgrass under three intensities of grazing.

ence may be due to an apparent lag in the accumulation of reserve carbohydrates in the heavily grazed plants.

For all dates combined, a significantly higher concentration of carbohydrates occurred in the ungrazed plants. The ungrazed plants had a mean carbohydrate concentration of 86 mg/g while moderately grazed plants had 79 mg/g and heavily grazed plants had 75 mg/g. The concentration of reserve carbohydrates in the ungrazed plants was somewhat higher than in the grazed plants throughout most of the study period (Fig. 3). Although the concentration was not significantly higher for most of the individual dates, the cumulative effect when all dates were combined resulted in the significant difference.

The data from all dates combined have a significant grazing–constituents interaction because the starch concentration was lower in the underground parts of heavily grazed plants (45 mg/g) than in moderately grazed plants (50 mg/g). Also, starch concentration was lower in moderately grazed plants than in ungrazed plants (56 mg/g), whereas the soluble carbohydrates remained relatively constant in all grazing treatments and in both roots and rhizomes. The lower starch concentration occurred only in the roots of these plants, so a grazing—plant parts—constituents interaction also resulted. The lower starch content in the roots may indicate that an increase in grazing intensity reduces leaf area, which in turn reduces photosynthate production and starch accumulation. The biological significance of the small difference in concentration of starch in plants grazed at different intensities is uncertain.

Grazing intensity studies have shown generally that as intensity of grazing increased the root system was reduced. If the root systems of heavily grazed sand reedgrass plants have been reduced, then the total amount of reserve carbohydrates would be less than in the moderately grazed or ungrazed plants. This would account for the reduction in amount of sand reedgrass under heavy grazing. However, the size of the root system of sand reedgrass under different grazing intensities has not been studied. Research on the size of the root system is needed to complement the information on the concentration of reserve carbohydrates.

Effect of Repeated Foliage Removal.—Starch concentration of the underground parts of repeatedly mowed plants was as low as 7 mg/g on August 15, while plants from the other treatments averaged 61 mg/g. After the plants were dormant, the starch concentration was 14 mg/g on the mowed area and 58 mg/g on the other areas. The lowest concentration of soluble carbohydrates was 4 mg/g on August 31 for the mowed area, while the other areas averaged 28 mg/g. The mowed plants had a soluble carbohydrate concentration of 6 mg/g after dormancy, and the the other plants averaged 52 mg/g.

Cattle seek out early growth and regrowth of sand reedgrass. This would be the period when reserves are declining. If cattle graze the early growth and then graze the lush regrowth, as could be the case under heavy grazing, a situation similar to the repeatedly mowed area (but not as intensive) may result. Carbohydrate reserves are required for the initiation of growth when little or no photosynthetic tissue is present. The critical level of reserve carbohydrates needed for survival is not known.

Constituents.—Paper chromatograms of soluble carbohydrates in the roots and rhizomes for all sampling dates showed that glucose, fructose, and sucrose were the constituents of the soluble carbohydrate fraction. Carbohydrates in the residue were primarily starches. These constituents were the same as those found in the reserve carbohydrates of switch cane (*Arundinaria tecta*), a warm season grass morphologically similar to sand reedgrass (Lindahl et al., 1949). The carbohydrate reserves of big bluestem (*Andropogon gerardi*), another grass morphologically similar to sand reedgrass, were composed of similar carbohydrates, but had, in addition, a considerable amount of fructosan (Crockett[5]).

Chromatograms of samples collected in November showed two additional unidentified carbohydrates believed to be di- or tri-saccharides. These carbohydrates were probably intermediaries in the transformation of starch to sucrose and monosaccharides. The conversion of starch to soluble carbohydrates occurs when the temperature is near or below freezing.

---

[5] Crockett, J. J. 1960. Effects of intensity of clipping on three grasses from grazed and ungrazed areas in west-central Kansas. M.S. Thesis. Fort Hays State Coll., Fort Hays, Kansas. 68 p.

Paper chromatograms showed that the soluble carbohydrates in samples from the mowed area from August 15 to the end of the sampling period had one carbohydrate in addition to those found in samples from the other areas; the additional carbohydrate had a R_F value similar to the one reported for xylose (Lederer and Lederer, 1957). Xylose is a primary constituent of hemicellulose. Therefore, the presence of xylose in the soluble carbohydrates of plants with reserves maintained at a low level (near 20 mg/g) for about two months may indicate that hemicellulose was being broken down to provide energy for the plant.

Conclusions

Total carbohydrate concentration of sand reedgrass followed the typical U-shaped seasonal trend with reserves declining during early growth, then accumulating throughout the remainder of the growing season. The seasonal trend was due to fluctuations in the starch concentration, thus, starch was considered to be the major stored carbohydrate. The soluble carbohydrate concentration remained relatively constant throughout the growing season, and for this reason they were believed to be important as translocatable carbohydrates and as the most readily available carbohydrates for use by the plants.

The roots and rhizomes had similar concentrations of soluble carbohydrates throughout the year, but starch concentration was higher in the roots during the period when carbohydrates were accumulating. This may indicate that accumulation begins first in the roots.

The effect of grazing on the concentration of total carbohydrates was not significant for most of the sampling dates. For all dates combined there was a significant grazing effect. This effect was due to a higher concentration of starch in the roots of ungrazed plants than in the roots of moderately grazed plants and a higher starch concentration in the roots of moderately grazed plants than in the roots of heavily grazed plants. This may be due to a reduction of photosynthetic tissue with increased grazing intensity which apparently results in reduced starch accumulation in the roots.

The constituents of the soluble carbohydrate fraction from the roots and rhizomes for all dates were glucose, fructose, and sucrose. Roots and rhizomes taken from the repeatedly mowed area had an additional carbohydrate after the reserves were maintained at a low level for about two months. The additional carbohydrate was believed to be xylose. This may indicate that hemicellulose was being broken down to furnish simple carbohydrates for use by the plants.

Management implications cannot be concluded from this study. However, these findings combined with information on the morphological development, extent of root system, and other physiological aspects of sand reedgrass can be used in developing grazing management systems for sand reedgrass.

Future studies on carbohydrate reserves should be designed to determine the critical level of reserve carbohydrates needed for survival. Also, morphological studies should be conducted along with carbohydrate reserve studies to determine if a morphological factor may be limiting rather than the level of carbohydrate reserves when plants are heavily defoliated.

LITERATURE CITED

BRANSON, F. A. 1953. Two new factors affecting resistance of grasses to grazing. J. Range Manage. 6:165–171.

COOK, C. W. 1966. Carbohydrate reserves in plants. Utah Agr. Exp. Sta. Utah Resources Series 31. 47 p.

DAHL, B. E., AND J. J. NORRIS. 1965. The effect of grazing intensity on native sandhill ranges. Colorado Agr. Exp. Sta. PR 162. 2 p.

DAHL, B. E., A. C. EVERSON, J. J. NORRIS, AND A. H. DENHAM. 1967. Grass–alfalfa mixtures for grazing in eastern Colorado. Colorado Agr. Exp. Sta. Bull. *In Press.*

EVERSON, A. C. 1966. Effects of frequent clipping at different stubble heights on western wheatgrass (*Agropyron smithii*, Rydb.). Agron. J. 58:33–35.

HYDER, D. N., AND F. A. SNEVA. 1959. Growth and carbohydrate trends in crested wheatgrass. J. Range Manage. 12:271–276.

JOHNSON, G., C. LAMBERT, D. K. JOHNSON, AND S. G. SUNDERWIRTH. 1964. Colorimetric determination of glucose, fructose, and sucrose in plant materials using a combination of enzymatic and chemical methods. J. Agr. and Food Chem. 12:216–219.

LEDERER, E., AND M. LEDERER. 1957. Carbohydrates. 4. Paper chromatography of sugars, p. 245–259. *In* E. Lederer and M. Lederer, Chromatography; a review of principles and applications. Elsevier Publishing Co. New York.

LINDAHL, I., R. E. DAVIS, AND W. O. SHEPHERD. 1949. The application of the total available carbohydrate method to the study of carbohydrate reserves of switch cane (*Arundinaria tecta*). Plant Physiol. 24: 285–294.

PUCHER, G. W., C. S. LEAVENWORTH, AND H. B. VICKERY. 1948. Determination of starch in plant tissues. Anal. Chem. 20:850–853.

REPPERT, J. N. 1960. Forage preference and grazing habits of cattle at the Eastern Colorado Range Station. J. Range Manage. 13:58–65.

TROUGHTON, A. 1957. Chemical composition, p. 49–68. *In* A. Troughton, The underground organs of herbage grasses. Commonwealth Bur. Pastures and Field Crops Bull. 44.

WEINMANN, H. 1952. Carbohydrate reserves in grasses, p. 655–660. *In* Proc. VI Int. Grassland Congr., Penn. State College.