

Seasonal Carbohydrate Reserve Cycles in Eight Desert Range Species¹

PATRICK I. COYNE AND C. WAYNE COOK²

NDEA Fellow and Professor, Department of Range
Science, Utah State University, Logan.

Highlight

Delineation of seasonal carbohydrate reserve cycles in important range plants is fundamental to development of a physiological index to proper season and intensity of range use. Carbohydrate reserves were studied with relation to growth stage of eight desert range plants in northern Utah. Most species showed definite seasonal trends. Results indicated that maximum plant vigor in relation to carbohydrate reserves depends upon reserve storage sometime at the end of the growth period.

An index to proper season and intensity of range use based upon the normal process of photosynthesis and physiological functions of carbohydrate storage would be a boon to range management.

Depletion of carbohydrate reserves normally accompanies defoliation (Brown, 1943; Cook et al., 1958; Jameson and Huss, 1959; Sullivan and Sprague, 1953; Weinmann, 1943, 1949). The extent and duration of this depletion is associated with the season, frequency, and intensity of herbage removal.

Reduction of carbohydrate reserve levels lowers plant vigor, herbage yield, and rate of growth (Cook et al., 1958; Weinmann, 1946). Spring growth also may be delayed (Cook et al., 1958; McCarty, 1938) and plants may be more susceptible to winter injury (Kust, 1960) and disease (Weinmann, 1946).

Most perennial plants studied with respect to

carbohydrate reserve cycles show at least some behavior similarity. Plants store reserves during periods of slow herbage growth, particularly in the fall when elaboration of carbohydrates exceeds the demands of growth and assimilation. Reserves are used during periods of rapid herbage growth, such as initial growth, subsequent regrowth, and for respiration and slight growth during winter (Cook, 1966; Priestly, 1962; Troughton, 1957; Weinmann, 1961).

Several comprehensive reviews have presented information on carbohydrate reserve cycles as related to stage of growth and environmental factors (Cook, 1966; Jameson, 1963; Priestly, 1962; Troughton, 1957; Weinmann, 1948). Stage of growth is the most important factor influencing carbohydrate reserve concentrations in plants. Therefore, fundamental to studying the effects of defoliation on carbohydrate reserve is the delineation of annual carbohydrate cycles in non-defoliated plants.

This study involved the determination of seasonal fluctuations of carbohydrate reserves in roots and crowns of eight desert range species protected from grazing. These included three browse, two suffrutescent, and three grass species as follows: big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia arbuscula* var. *nova*), shadscale (*Atriplex confertifolia*), Nuttall saltbush (*Atriplex falcata*), winterfat (*Eurotia lanata*), Indian ricegrass (*Oryzopsis hymenoides*), needleandthread (*Stipa comata*), and squirreltail (*Sitanion hystrix*). In addition to roots and crowns, carbohydrates in the twigs were studied in big sagebrush, shadscale, and winterfat.

Study Areas and Methods

Plants were collected from two locations in northern Utah during 1967 and 1968. The climate is semi-arid with warm dry summers and cold winters. Annual precipitation was 29 cm for both years compared to an average of 24 cm during the preceding 10 years. Precipitation distribution varied widely between 1967 and 1968. Thirty-four percent of the total fell in June, 1967 compared to only 15% in June, 1968. Less than 2% of the total came in August, 1967 while 25% was recorded in August, 1968.

Soils at the study areas are representative of those of Great Basin Valleys. Parent material is either of sedimentary origin or alluvial outwash from adjacent mountain ranges (Gates, 1956). The biotic communities included in this study constitute a part of the Northern Desert Shrub Biome (Fautin, 1946).

¹ Adapted from a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree in Range Science at Utah State University by the senior author. Financial support provided by the Bureau of Land Management, Contract No. 14-11-0008-2849, is gratefully acknowledged. Journal Paper No. 992, Utah Agricultural Experiment Station, Logan. Received December 12, 1969; accepted for publication June 16, 1970.

² Present address is Head, Department of Range Science, Colorado State University, Fort Collins, Colorado.

Plant roots were excavated to a depth of 30 cm. Root samples from woody species included those roots with diameters of approximately 8 mm or less. Woody crowns were defined as the tissue between the first stem branch and the first concentration of roots. All the fibrous grass roots in the top 30 cm of soil were collected. The lower 3 cm of grass culms were designated as crowns. Samplings were carried out weekly from March through June, biweekly in July and August, and monthly from September to November.

The number of plants collected on each location at each date was dependent upon the amount of roots and crown on a particular plant. This varied from two to four on all species except Nuttall saltbush and squirreltail grass which required from 5 to 10 plants. All plants of each species at each location for a single date were composited by root and crown material respectively.

The 1967 data indicated that the underground parts of sagebrush, and possibly other woody species, might be of secondary importance relative to carbohydrate storage. Throughout 1968 previous year's twigs were sampled in big sagebrush, shadscale, and winterfat. Current year's twigs were sampled in these species after July 12, 1968. All leaves and seedstalks were removed from both twig fractions.

Plant parts were washed in cold water at the site of collection. The washed tissue was sectioned and placed into pint fruit jars, covered with 95 percent ethanol, and sealed tightly. Samples were dried at 70 C, ground to pass a 40-mesh screen, and stored in tightly capped jars until analyzed. Concentration of total available carbohydrates (TAC) was determined for each sample by using 0.2 N sulfuric acid hydrolysis according to Smith et al. (1964). Results were reported in milligrams of glucose equivalent per gram of dry sample. Total available carbohydrates consist of starch, dextrins, fructosans, sucrose, and reducing sugars, but not structural carbohydrates such as pentosans, hemicellulose, and cellulose (Smith et al., 1964; Weinmann, 1947).

The average length of current year's growth and the average growth stage were recorded for all species at each collection date. The percent of soil moisture by weight at 30 cm depth was determined gravimetrically at each sampling date during 1968.

Data for 1968 are presented graphically in figures 1-8. Similarities and differences of 1967 data are discussed. Each point on the graph represents the average of two locations.

Results and Discussion

Big Sagebrush

Clearly defined seasonal trends in total available carbohydrate (TAC) were generally lacking in the crowns and were not pronounced in the roots (Fig. 1). Maximum crown storage of TAC at plant maturity for both years of the study was only about 34 mg/g of sample with a minimum of about 18 mg. Lack of definite trends of carbohydrates in underground storage organs has been reported in the literature for other species (Weinmann, 1961).

Growth began earlier and initially phenology advanced more rapidly in 1967 than 1968. However, by mid-June, the growth stages were the same for corresponding dates. Differences between years were not significant although fall regrowth caused a reduction of reserves in 1968.

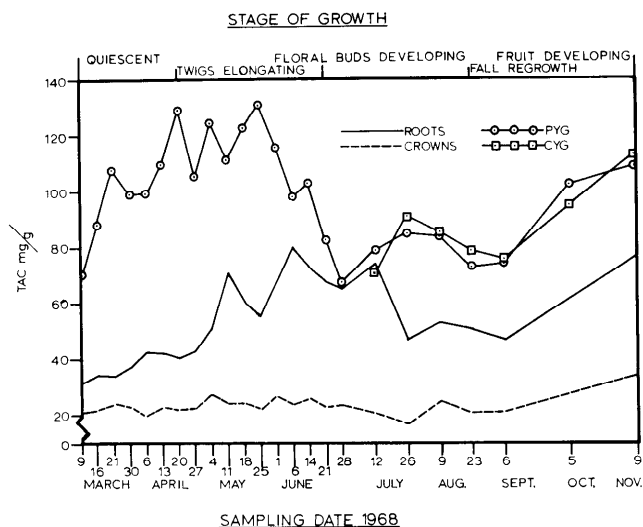


FIG. 1. Total available carbohydrates (TAC) (mg of glucose equivalent/g) in roots, crowns, previous year's twig growth (PYG), and current year's twig growth (CYG) of big sagebrush as related to stage of growth.

Twigs of big sagebrush, which were studied only in 1968, showed significantly greater storage than the roots and displayed a more pronounced seasonal trend (Fig. 1). It was noted that TAC concentrations in roots and previous years' twigs increased slightly during spring growth. This would not be expected since most species reported in the literature decrease in TAC as growth begins (Cook, 1966; Troughton, 1957). However, big sagebrush retains a large proportion of its leaves throughout the winter. According to literature reviews (Jameson, 1963), early spring decline in carbohydrates within perennial plants is apparently caused by their utilization in the production of new leaves. Evidently, existing leaves of big sagebrush can more than support the demands of the plant for carbohydrates during initial spring growth.

A time lag was observed between TAC accumulation in the twigs and in the roots. This may indicate that excess photosynthate is stored largely in the twigs and the remainder used to support new growth. Eventually, excess TAC exceeds twig storage capacity and is translocated downward.

In big sagebrush, twigs are apparently an important site of reserve storage. Cook et al. (1959) observed that this species stored considerable carbohydrates in the twigs just behind the point where new growth would occur. This would appear to be an efficient adaptation provided the twigs are not removed by grazing. If grazed, much of the stored carbohydrates could be directly removed by the animals.

Overwinter loss of TAC was 50% and 27% in roots and crowns, respectively. Fruit development and winter respiration contributed to this loss.

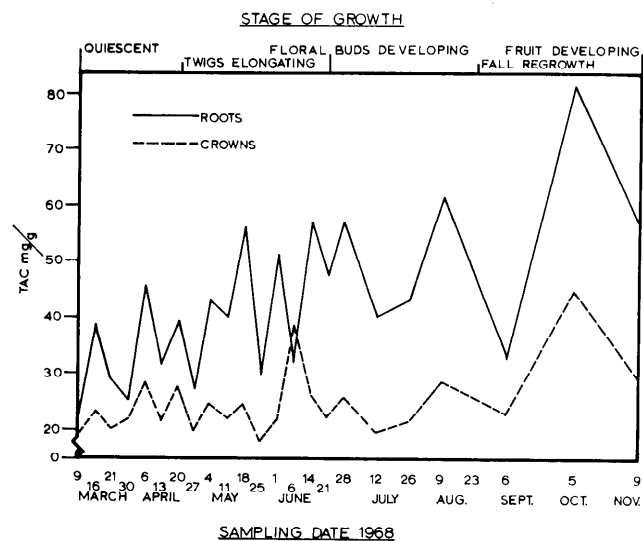


FIG. 2. Total available carbohydrates (TAC) (mg of glucose equivalent/g) in roots and crowns of black sagebrush as related to stage of growth.

Generally, root TAC in big sagebrush increased from early growth until early seed stage, after which TAC leveled off or decreased. Twig TAC peaked during twig elongation and then declined sharply as flower stalks were elongating.

Black Sagebrush

This species was similar to big sagebrush in respect to a lack of pronounced trend in TAC concentrations in roots and crown (Fig. 2). However, the crowns did show somewhat of a pattern which closely resembled that of the roots although the magnitude of fluctuation was less in crowns than in roots.

Root TAC fluctuated erratically through both years, but generally showed a gradual increase from early growth in March to floral bud development in August. This buildup was followed by a rather sharp decline which lasted until early September of both years. The earlier fall decline in 1968 can be attributed to fall rains which caused renewed growth activity.

In 1967, root TAC leveled off following the fall decline and remained constant throughout flower opening and initial fruit development. Conversely, in 1968, TAC in both roots and crowns increased rapidly from September 6 until flowers began opening about October 5. Then TAC decreased almost as rapidly until at least the last sampling date, November 9. Differences in late season behavior between years may have been a result of fall regrowth in 1968.

Corresponding yearly mean TAC concentrations for roots and crowns were almost identical for both years. Nearly half of the root reserves and one-fourth of the crown reserves were lost over the

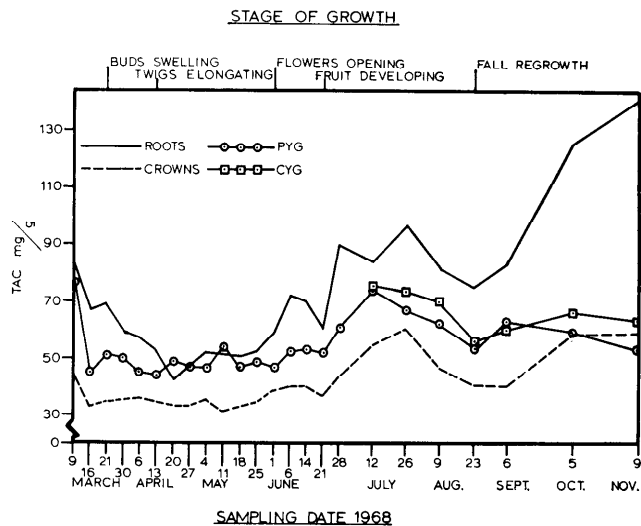


FIG. 3. Total available carbohydrates (TAC) (mg of glucose equivalent/g) in roots, crowns, previous year's twig growth (PYG), and current year's twig growth (CYG) of shadscale as related to stage of growth.

winter months. On the basis of big sagebrush studies, one could expect that twigs of black sagebrush would be sites of significant TAC storage.

The erratic nature of TAC trends in roots and crowns of black sagebrush cannot be adequately explained. Interplant variation seems unlikely since TAC concentrations were essentially similar for corresponding dates at both locations. Mean differences between locations were not significant. The relatively large amount of plant tissue comprising the sample of this species should dampen the fluctuation rather than amplify it. Neither can poorly-defined trends be attributed entirely to experimental error. The same sampling techniques were employed for both black sagebrush and the similar species, big sagebrush.

Shadscale

Rather definite seasonal trends in TAC were obtained for shadscale (Fig. 3). Both roots and crowns showed similar patterns in relation to stage of growth, but the latter was less pronounced. Reserve carbohydrates in roots and crowns were similar from March through June of each year. During the remainder of the season, roots accumulated carbohydrates much more rapidly than crowns. This resulted in a highly significant ($P < .01$) interaction between growth stage and plant parts. Carbohydrates in shadscale did show the expected draw-down during early growth and the buildup during plant maturity.

Spring drawdown of TAC in both roots and crowns occurred gradually over a 2 to 2½ month period. This was followed by a gradual replenishment period lasting from 3 to 3½ months. Spring drawdown in TAC was more extensive in 1967

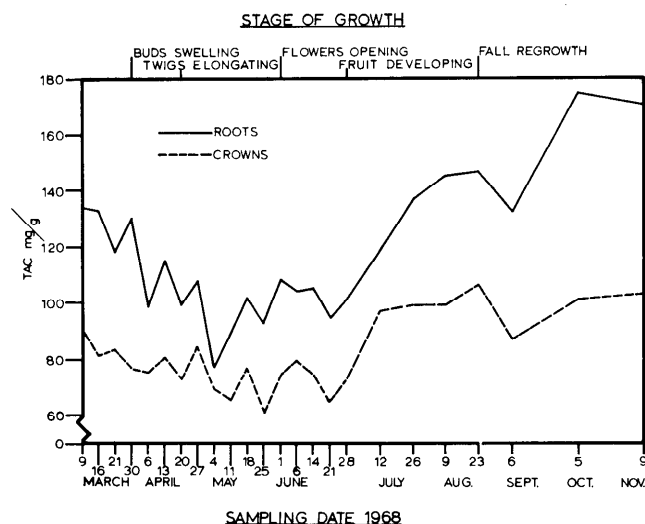


FIG. 4. Total available carbohydrate (TAC) (mg of glucose equivalent/g) in roots and crowns of Nuttall saltbush as related to stage of growth.

than in 1968 and recovery was delayed until June 23, 1967 (fruit development) compared to May 25, 1968 (flower opening). This can be explained by precipitation distribution and growing conditions. The greater spring precipitation in 1967 resulted in a faster growth rate, which in turn produced a greater demand for stored carbohydrates. The fraction of total seasonal elongation growth which had been attained by the end of spring depletion was approximately 58 and 27 percent in 1967 and 1968, respectively. The other notable difference between years was the secondary depletion of TAC due to fall regrowth in 1968 (Fig. 3).

Stored reserves were used during both years when the fruits were approaching maturity. The depletion was observed in roots only in 1967, but occurred in all plant parts in 1968. According to literature reviews (Jameson, 1963), the most important cause of mid-season depression in carbohydrates accumulation may be fruit development. This secondary drawdown was amplified in 1968 because of fall regrowth.

The trends of TAC in twigs were intermediate between those of roots and crowns. As with twigs of big sagebrush, mean TAC concentrations in previous and current-year twigs were not significantly different. Differences among roots, crowns, and twigs were highly significant ($P < .01$).

Winter drawdown of TAC in shadscale roots was only about 25% of the November concentration compared with 50% in sagebrush roots. Crown depletion was 19%. This reflects the deciduous nature of shadscale and probably a lower rate of metabolism while quiescent. Also, shadscale becomes quiescent much earlier than does sagebrush whose seed is usually not yet mature when the soil freezes.

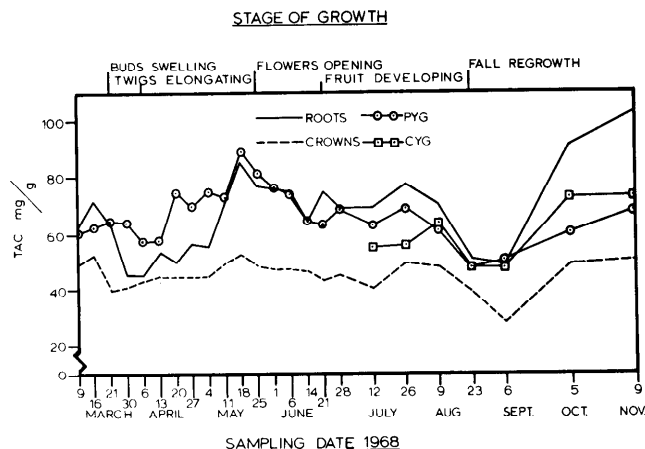


FIG. 5. Total available carbohydrates (TAC) (mg of glucose equivalent/g) in roots, crowns, previous year's twig growth (PYG), and current year's twig growth of winterfat as related to stage of growth.

Nuttall Saltbush

Concentrations of TAC in roots and crowns of Nuttall saltbush showed similar but definite trends during both years (Fig. 4). In all cases, the roots contained significantly higher concentrations of TAC than the crowns. Concentrations of TAC in roots and crowns were at least twice as high as those of the other four woody species studied.

Drawdown during rapid spring growth was extensive, but gradual. Replenishment was also gradual and, it was not completed until late August or September (mature fruit).

Trends in 1967 were quite similar to those for 1968, but differences between years were significant ($P < .05$). As with shadscale, drawdown was more extensive and recovery was delayed in 1967 compared to 1968. Likewise, fall regrowth resulted in a secondary TAC depletion cycle in 1968. In spite of these year differences, initial and final seasonal concentrations in roots and in crowns were essentially the same for both years.

Sixty percent of the total annual growth increment in 1967, and 30% in 1968, were completed by the end of spring drawdown. Overwinter reserve losses amounted to 20% in the roots and 17% in the crowns. The range of carbohydrate concentrations in the roots of Nuttall saltbush was considerably greater than the other woody species, reaching 116.7 mg/g in 1968. The carbohydrates accumulation phase generally was not completed until seed maturity or quiescence.

Winterfat

Few similarities were observed between the 2 years for winterfat (Fig. 5). In 1967, roots entered the growing season with relatively low TAC (49.3 mg/g) and remained at approximately the same level with only slight fluctuation until June 30, during fruit development. Beyond this point, a

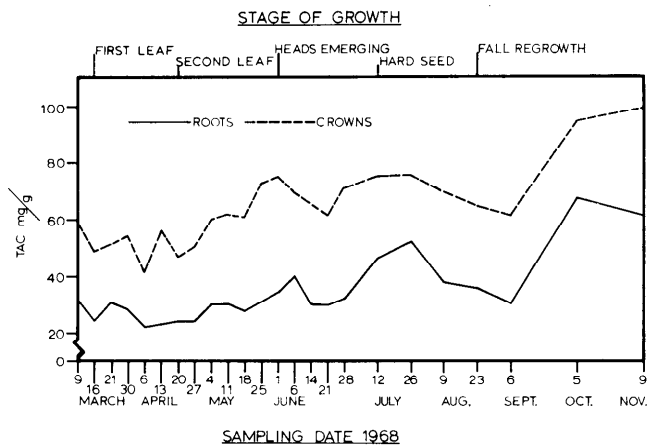


FIG. 6. Total available carbohydrates (TAC) (mg of glucose equivalent/g) in roots and crowns of Indian ricegrass as related to stage of growth.

gradual increase was detected which lasted until the latter stages of fruit development in late August, reaching a maximum for the year of 84.1 mg/g. During the next 2 weeks, TAC declined as the fruit matured and finally increased and leveled off becoming quiescent with TAC at 75.1 mg/g.

Patterns for TAC in crowns were similar to TAC in roots from July through November although TAC concentrations were somewhat lower than in the roots.

During 1968 (Fig. 5) the initial spring drawdown was rapid. Depletion generally ceased when only 7% of the annual growth increment was completed. Replenishment began almost immediately, but at a slower rate than depletion. In 1967, twig elongation was 60% complete when replenishment began. Root TAC had reached 70.6 mg/g by May 11, 1968 when floral buds were beginning to develop, thus requiring 5 weeks to replace what was used in 2 weeks.

Crown and twig trends in TAC were similar to the roots during 1968. Both TAC concentrations and TAC fluctuations were greater in the roots than in the crowns. Reserves in previous year's twigs showed a less-pronounced spring drawdown than the roots. The increase in twig reserves during the first 4 weeks of sampling may have represented translocation from underground parts to the twigs. Mean TAC concentrations in roots and in previous year's twigs were not significantly different. Differences between mean TAC storage in the two twig fractions were not significant ($P < .05$).

The secondary depletion cycle during fall regrowth and fruit development was as extensive as the initial spring cycle. However, recovery was rapid and peak root concentrations for the season (103.5 mg/g) was reached in November, as the plants approached quiescence. Minimum root concentrations for spring and fall were about equal.

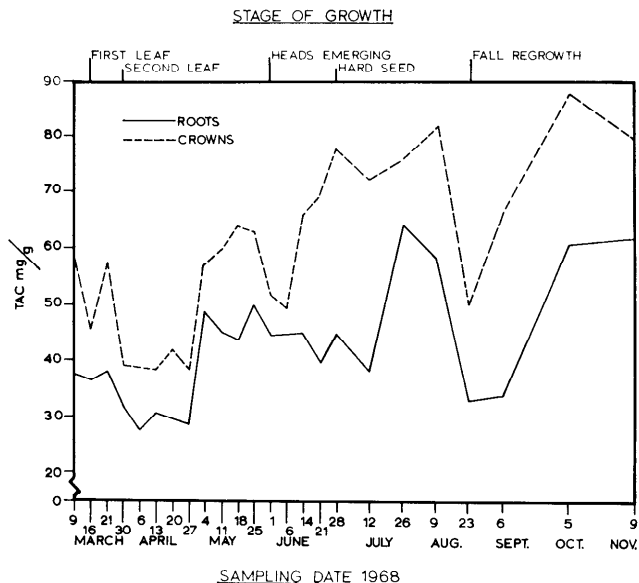


FIG. 7. Total available carbohydrates (TAC) (mg of glucose equivalent/g) in roots and crowns of needleandthread as related to stage of growth.

Winterfat lost the least amount of carbohydrates of any species during the winter months. Losses were 17 and 18% in roots and crowns, respectively.

Indian Ricegrass and Needleandthread

The relationship between TAC in the underground parts of these two grasses was opposite that of the browse species. In these grasses, the crowns accumulated higher concentrations of TAC than the roots throughout the season (Figs. 6 and 7). Similar results have been reported for other perennial grasses (Alberda, 1955; Baker, 1957; Norman, 1939; Sprague and Sullivan, 1950; Weinmann, 1949). TAC trends were essentially identical in both roots and crowns and either part alone could be used to safely determine the carbohydrate budget of the plant. Sampson and McCarty (1930) found that the same seasonal changes in carbohydrates occurred in the roots and crowns of California needlegrass (*Stipa pulchra*).

For both grasses, the extent and duration of TAC depletion during spring growth was greater in 1967 than in 1968 when precipitation was relatively higher. Growth rate was greater in the spring of 1967 than the spring of 1968, which thereby increased the demand for stored reserves. Fall depletion of TAC is evidently common in both species. The extent of depletion is proportional to the growth activity in the fall.

Mean differences between years for Indian ricegrass and needleandthread were greater than mean differences between these two species. Seasonal TAC cycles and magnitude of storage were comparable. However, fluctuation was more pro-

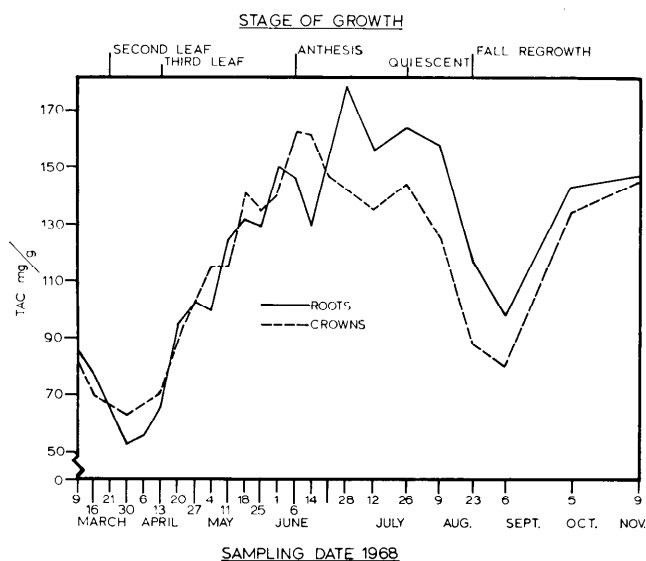


FIG. 8. Total available carbohydrates (TAC) (mg of glucose equivalent/g) in roots and crowns of squirreltail as related to stage of growth.

nounced in needleandthread. The spring depletion of TAC was more rapid in needleandthread than in Indian ricegrass, but storage after depletion was delayed longer in the growth cycle. Once storage of TAC began, the rate was more rapid in needleandthread than in Indian ricegrass.

Although the yearly mean TAC storage in roots of needleandthread was higher than in Indian ricegrass, the latter had a larger mean value for crowns so that over-all storage for both plant parts was not significantly different. Both grasses lost 34% of the TAC stored by November during the winter, but crowns of Indian ricegrass lost 41% compared to 20% for crowns of needleandthread. For Indian ricegrass, growth elongation was approximately 50 and 40% completed at the end of spring drawdown in 1967 and 1968, respectively. The corresponding values for needleandthread were 35 and 28%.

Squirreltail

Seasonal trends of TAC in roots and crowns of squirreltail were well-defined and definite (Fig. 8). Spring drawdown in TAC was rapid, but relatively light. Recovery of TAC took place almost immediately following initial drawdown. A wet spring, such as 1967, increased the extent and duration of a carbohydrate depletion similar to the other species.

Squirreltail accumulated significantly more carbohydrate reserves in 1968 than in 1967 ($P < .01$). Roots and crowns displayed similar seasonal trends, but in contrast to the other seven species studied, there was no significant difference between mean root and crown concentrations of TAC. McIlvanie (1942) reported that storage of reserves in roots and crowns of bluebunch wheatgrass (*Agropyron spicatum*) was nearly equal.

Growth elongation was generally 40 to 45% completed by the end of the spring depletion phase (second leaf). McIlvanie (1942) found that the equivalent value for bluebunch wheatgrass was 45%. Recovery of TAC was completed by anthesis during both years. Peak storage in the crowns at anthesis was 126.2 and 162.9 mg/g in 1967 and 1968, respectively. Carbohydrates declined slightly subsequent to anthesis while the caryopses were developing. Losses of TAC during the winter ranged from 37% in roots to 29% in crowns.

Squirreltail is extremely responsive to fall rains and as a result went through almost two complete life cycles during 1968. The second cycle in the fall caused a tremendous drain upon reserves previously stored at the end of the first cycle (Fig. 8) since the length of fall growth reached a value comparable with spring and early summer growth. Nevertheless, it made remarkable recovery and entered the winter with higher TAC concentrations than the previous year when fall regrowth was not pronounced.

McCarty (1938) found that in mountain brome (*Bromus marginatus*), spring growth utilized 75% of the stored reserves and fall growth only 15%. The corresponding values for squirreltail were 30 and 40%.

In 1967, crowns accumulated about 10 mg/g more TAC on the average than the roots. In 1968, roots stored 4.4 mg/g more than the crowns. Thus, although plant parts were not significantly different, this did cause a highly significant ($P < .01$) interaction between years and plant parts.

Summary and Conclusions

Carbohydrate concentrations were consistently higher in the roots of the five woody species than in the crowns. The reverse relationship was found for Indian ricegrass and needleandthread. Mean root and crown concentrations of TAC were not significantly different in squirreltail. With the exception of big sagebrush, carbohydrate trends were similar in all plant parts studied although magnitude of storage and degree of fluctuation varied between plant parts. All species, except sagebrush, showed the expected spring depletion of TAC in each plant part when growth began. In a similar manner these species showed replenishment of the reserves during advanced stages of phenological development and maximum TAC in the storage organs was reached at maturity.

Crowns of the sagebrush species appeared unimportant as storage organs. A slight increase in TAC was observed in roots and twigs of sagebrush when spring growth began. This might be a reflection of the evergreen nature of these species. Twigs of big sagebrush were considered more important as storage organs than roots or crowns with respect

to TAC concentrations. Twig concentrations of TAC were intermediate between roots and crowns of shadscale and were not significantly different from roots in winterfat.

Growth rate was generally directly related to soil moisture and inversely related to carbohydrate storage. This was particularly evident during the wet spring of 1967 and the wet fall of 1968.

This study suggests that maximum carbohydrate reserves are not attained until a plant completes its annual life cycle. Therefore, maximum plant vigor as a reflection of carbohydrate reserves depends upon the magnitude of TAC storage sometime at the end of the growth period.

Literature Cited

- ALBERDA, T. 1955. Variations in the carbohydrates of perennial ryegrass in 1954. Verslag Landbouwk. Onderzoek. p. 70-78. (English summary).
- BAKER, H. K. 1957. Studies on the root development of herbage plants. III. The influence of cutting treatment on the root, stubble and herbage production of a perennial ryegrass sward. J. Brit. Grassl. Soc. 12:197-208.
- BROWN, E. M. 1943. Seasonal variations in the growth and chemical composition of Kentucky bluegrass. Mo. Agr. Exp. Sta. Res. Bull. 360. 56 p.
- COOK, C. W. 1966. Carbohydrate reserves in plants. Utah Agr. Exp. Sta. Utah Resources Series 31. 47 p.
- COOK, C. W., L. A. STODDART, AND L. E. HARRIS. 1959. The chemical content in various portions of the current growth of salt-desert shrubs and grasses during winter. Ecology 40:644-651.
- COOK, C. W., L. A. STODDART, AND F. E. KINSINGER. 1958. Response of crested wheatgrass to various clipping treatments. Ecol. Monogr. 28:237-273.
- FAUTIN, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecol. Monogr. 16: 251-310.
- GATES, D. H. 1956. Ecology of plant distribution on the salt deserts of Utah. Unpublished Ph.D. dissertation. Utah State Univ. Library, Logan, Utah.
- JAMESON, D. A. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532-594.
- JAMESON, D. A., AND D. L. HUSS. 1959. The effect of clipping leaves and stems on number of tillers, herbage weights, root weights and food reserves of little bluestem. J. Range Manage. 12:122-126.
- KUST, C. A. 1960. The influence of harvest management on yields and food reserve trends in alfalfa grown in pure stands in grass mixtures. Diss. Abst. 20:3916.
- MCCARTY, E. C. 1938. The relation of growth to the varying carbohydrate content in mountain brome. U.S. Dep. Agr. Tech. Bull. 598. 24 p.
- MCLVANE, S. K. 1942. Carbohydrate and nitrogen trends in bluebunch wheatgrass, *Agropyron spicatum*, with special reference to grazing influences. Plant Physiol. 17: 540-557.
- NORMAN, A. G. 1939. Biochemical approach to grass problems. J. Amer. Soc. Agron. 31:751-760.
- PRIESTLY, C. A. 1962. Carbohydrate resources within the perennial plant. Commonwealth Agr. Bureaux, London. 116 p.
- SAMPSON, A. W., AND E. C. MCCARTY. 1930. The carbohydrate metabolism of *Stipa pulchra*. Hilgardia 5:61-100.
- SMITH, D., G. M. PAULSEN, AND C. A. RAGUSE. 1964. Extraction of total available carbohydrates from grass and legume tissue. Plant Physiol. 39:960-962.
- SPRAGUE, V. G., AND J. T. SULLIVAN. 1950. Reserve carbohydrates in orchardgrass clipped periodically. Plant Physiol. 25:92-102.
- SULLIVAN, J. T., AND V. G. SPRAGUE. 1953. Reserve carbohydrates in orchardgrass cut for hay. Plant Physiol. 28: 304-313.
- TROUGHTON, A. 1957. The underground organs of herbage grasses. Commonwealth Bur. Pastures and Field Crops Bull. 44. 163 p.
- WEINMANN, H. 1943. Effects of defoliation intensity and fertilizer treatment on transvaal highveld. Emp. J. Exp. Agr. 11:113-124.
- WEINMANN, H. 1946. Some fundamental aspects of modern pasture management. Rhod. Agr. J. 43:418-425.
- WEINMANN, H. 1947. Determination of total available carbohydrates in plants. Plant Physiol. 22:279-290.
- WEINMANN, H. 1948. Underground development and reserves of grasses. A review. J. Brit. Grassl. Soc. 3:115-140.
- WEINMANN, H. 1949. Productivity of Marandellas Sandveld pasture in relation to frequency of cutting. Rhod. Agr. J. 46:175-189.
- WEINMANN, H. 1961. Total available carbohydrates in grasses and legumes. Herbage Abst. 31:255-261.

Specialists in Quality NATIVE GRASSES

Wheatgrasses • Bluestems • Gramas • Switchgrasses • Lovegrasses • Buffalo • and Many Others
We grow, harvest, process these seeds

Your Inquiries
Appreciated

SHARP BROS. SEED CO.

Native Grasses Harvested in ten States

Phone 398-2231
HEALY, KANSAS