Carbohydrate Reserves of Six Mountain Range Plants as Related to Growth[1]

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Highlight

The total available carbohydrate reserves of six native mountain range plants were studied through a growing cycle. The reserves showed somewhat similar trends as plants advanced in growth during their annual cycle. Minimum root reserves were reached during the early spring after producing approximately 15 percent of their annual growth. Maximum reserves were reached at or near flowering. The average level of root reserves at any one period varied widely among species, however.

The general trend of seasonal carbohydrate reserves is similar for most perennial plants. However, growth behavior or environmental conditions may influence the level of storage. Knowledge of reserve levels for plants allows correlation of grazing practices with the physiology of the plant.

With the onset of new growth there is universally a decline in stored carbohydrates (Jameson, 1963; Cook, 1966). The decline of reserves during early growth is well known. The magnitude and time of carbohydrate low may vary widely among species. Research indicates the storage of carbohydrates in roots and stem bases is inversely related to rate of herbage production (McCarty, 1938; McCarty and Price, 1942).

Mooney and Billings (1960) reported the carbohydrate cycle for several alpine plants. Early shoot growth utilized considerable carbohydrate reserve material but adequate amounts were present even at the lowest point of the cycle to maintain growth. McCarty (1938) and McCarty and Price (1942) found approximately the first 10 percent of the annual growth consumed about 75 percent of the root reserves before any replenishment occurred. Bluebunch wheatgrass (*Agropyron spicatum*) produced approximately 45 percent of the annual growth before ceasing to decrease carbohydrate reserves (McIlvanie, 1942).

When studying total water soluble carbohydrates in range grasses in Oregon, Hyder and Sneva (1963) found a definite low occurred early in growth, followed by a high accumulation during June and July. The reserve carbohydrates decreased slightly during the fall for six native range grasses studied. Brown (1943) reported late autumn to be the most favorable period for storage of carbohydrates in the underground parts of Kentucky bluegrass (*Poa pratensis*). The carbohydrates were synthesized more rapidly than they were used during the cool weather following early spring growth.

Experimental Area and Procedures

During 1965 and 1966 the carbohydrate levels were determined for six native range species at three replications on typical mountain range approximately 22 miles northeast

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FIG. 1. Distribution and location of plants on a typical southwest slope in a sagebrush-grass type.

of Logan, Utah. All study sites represented the open, sagebrush-grass vegetative type (Fig. 1).

The translocation of total available carbohydrates for two grass species, beardless wheatgrass (*Agropyron inerme*) and Letterman needlegrass (*Stipa lettermanii*); two browse species, snowberry (*Symphoricarpos vaccinioides*) and rabbitbrush (*Chrysothamnus viscidiflorus*); and two forb species senecio (*Senecio integerrimus*) and geranium (*Geranium fremontii*) were evaluated. Duplicate root samples from each of the six species were collected from each location at two-week intervals to study fluctuations of carbohydrate reserves throughout the growing season. Collections of root material commenced on May 11, and terminated August 27. In September and October, following summer dormancy, collections of root samples from the two grass species were made to determine the effect of fall regrowth on the carbohydrate root reserves.

Root samples were removed to a depth of 12 inches for carbohydrate reserve determinations. Cubes of soil, 12 $\times$ 12 $\times$ 12 inches, were placed in wooden boxes with a bottom constructed of one-eighth inch mesh screen and the soil washed from the roots by gentle agitation. The samples were blotted dry and cut into short segments starting immediately below the crown. Caution was taken to remove all visible dead root material. Only live roots less than 0.25 inch in diameter were collected from the browse and forbs. Root material of larger dimension was considered to have large amounts of xylem and cortex with little storage value.

After the samples were cut into short segments they were covered with 95 percent ethanol to prevent enzyme activity. The samples were then taken to the laboratory and placed in an air-draft dryer at 90 C for 2 hours and then dried for approximately 48 hours at 70 C. After drying, the samples were ground in a Wiley micromill equipped with a 40 mesh screen.

A 1-gram sample of the root material was placed in a Waring blender with hot 80% ethanol for 10 minutes (Noggle, 1953). The mixture was filtered through a Buchner funnel fitted with Whatman No. 40 filter paper and the alcoholic filtrate stoppered and retained for further analysis. The ethanol extraction removed alcohol soluble carbohydrate constituents, thus reducing the amount of carbohydrate material involved with later extractions.

The residue was removed from the filter paper, placed in a 250 ml beaker in an ice bath before addition of perchloric acid (Pucher, et al., 1948). Three ml of 72% perchloric acid and 4 ml of water were added rapidly to the residue with constant agitation. After 30 minutes, with occasional shaking, the mixture was centrifuged, the liquid decanted and saved. The residue was again treated with 7 ml of the perchloric acid-water mixture and allowed to stand for 30 minutes to assure complete removal of starch (Pucher, et al., 1948). The mixture was then filtered into the decanted liquid from the first perchloric acid extraction and washed twice with water.

The perchloric acid liquid was neutralized with approximately 10 ml of 25% sodium hydroxide and allowed to cool. After cooling, the mixture was added to the alcoholic extraction and diluted to a constant volume. An aliquot of the combined filtrate was evaporated on an electric hot plate until the odor of alcohol had disappeared. The solution was clarified with barium hydroxide and zinc sulfate (Moyer and Holgate, 1948), filtered through Watman No. 42 filter paper and made to a constant volume. An aliquot of the clarified solution was inverted and the total available carbohydrates determined by a modification of Forsee's photocolormetric method (Morell, 1941).

The percent transmittance of the sugar solutions was read at a wave length of 420 mμ. The readings were compared to a standard glucose curve and the values converted to milligrams of glucose per gram of plant sample by dividing the value by a conversion factor of 0.90.

Results and Discussion

Letterman Needlegrass and Beardless Wheatgrass.—Carbohydrate reserves of beardless wheatgrass and Letterman needlegrass followed the general depletion pattern described by McCarty (1938), McCarty and Price (1942), and Mooney and Billings (1960). Data collected for May 11, represents collections from only two locations. Thereafter the data were collected from three locations. Inclement weather prevented collection of root material from more than two locations on the first sampling date. While the number of samples constituting the average for the first date was from only two locations, the information was of considerable value.

Roots of Letterman needlegrass contained 86.7 mg of total available carbohydrates per gram of root material at the initiation of sampling. By May 18 when the grass had reached the three leaf stage, this value had reduced to 49.2 mg. It increased to 107.1 mg by the end of May (Fig. 2).

The carbohydrate reserves were replenished through the four-leaf stage after which they receded temporarily. The decrease continued until the early boot stage (July 1). Following the boot stage, on July 12 the carbohydrate reserves replenished to a seasonal high of 112.4 mg per gram of root sample which occurred during late anthesis to the milk-dough stage. At seed production there was a temporary decrease followed by a replenishment to

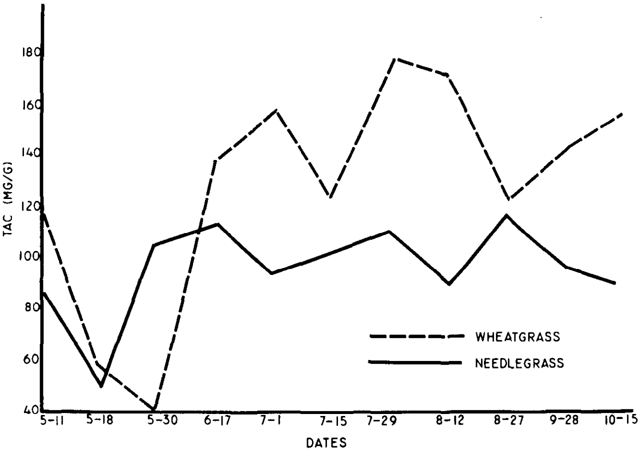

FIG. 2. Total available carbohydrate (TAC) reserves of beardless wheatgrass and Letterman needlegrass from initial growth to maturity. Values are averages expressed as milligrams of glucose equivalents per gram of root.

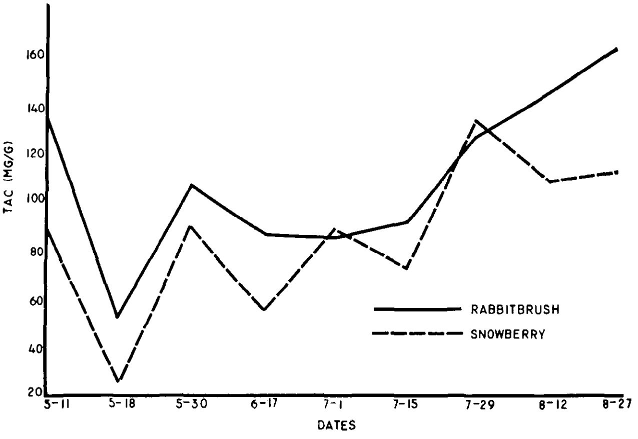

FIG. 3. Total available carbohydrate (TAC) reserves of little rabbitbrush and snowberry from initial growth to maturity. Values are averages expressed as milligrams of glucose equivalents per gram of root.

120.4 mg as the plant approached maturity by August 27.

While the general depletion and replenishment pattern followed a trend similar to previously reported studies, mid-season fluctuations were not understood. McCarty (1938) and McCarty and Price (1942) reported mountain brome (*Bromus carinatus*) began depleting the reserves with the development of flower stalks. This depletion continued until seeds were fully developed. After seed development, the carbohydrate reserves steadily increased through seed dissemination with no marked fluctuations. A marked increase occurred prior to fall dormancy. In the present study this same trend was evident in Letterman needlegrass. Initial fall dormancy and seed dissemination occurred concurrently.

Beardless wheatgrass was in the three-leaf stage at the initiation of the sampling and the root reserves were 116.6 mg per gram of sample (Fig. 2). With continued growth the reserves diminished to a seasonal low of 40.8 mg on May 30. The carbohydrate low for beardless wheatgrass coincided with the 4- to 5-leaf stage when development of the boot stage was initiated. This was two weeks later in the season than with Letterman needlegrass and at a much later phenological stage of development.

A rapid increase in the root reserve occurred after the seasonal low. Carbohydrate content increased to 137.4 mg and it coincided with the late boot stage (June 17). The increase continued through the next collection period at which time beardless wheatgrass was in the early heading stage (July 1). At anthesis, which occurred by July 15, the reserves were diminished to 124.0 mg. The depletion was found to be temporary as the highest seasonal reserve of 180.0 mg occurred 28 days later when the wheatgrass was in the hard dough stage. As beardless wheatgrass went into maturity the reserve declined from 175.3 mg to 125.3 mg August 27. The final fall concentration was still slightly higher than the initial concentration of 116.6 mg during the spring.

Regrowth occurred for both grasses during the fall. Hence, on September 28, and October 15, root samples showed that Letterman needlegrass reserves underwent a continual decline as a result of regrowth, going from 120.4 mg to 93.0 mg per gram of material (Fig. 2). Conversely beardless wheatgrass showed an increase from 125.3 mg to 152.6 mg per gram of root sample during the same period.

Although not investigated in this study, the leaf area index of the two plants may possibly explain the behavior of the root reserve. Brougham (1956) indicated rates of growth were correlated to the percentage of light intercepted by the leaves. Since beardless wheatgrass produced larger leaves and thus had more leaf area it would be possible with slow fall growth that the leaf area was sufficient to produce more carbohydrate material than was being used. In addition, it is possible that storage of reserve carbohydrates in the stubble and stem bases of beardless wheatgrass could have been greater than in Letterman needlegrass. This additional amount of stored carbohydrates would allow root reserves to increase slightly as a result of continued translocation to the roots, in addition to providing for some fall growth.

Little Rabbitbrush and Snowberry.—Roots of little rabbitbrush contained 137.4 mg of total available carbohydrates per gram of root material at the initiation of spring sampling (Fig. 3). The plants were in the late leaf-bud stage. One week later the seasonal low (55.6 mg) of total available carbohydrate reserve occurred when the rabbitbrush plants were in an early leaf stage and flower buds were present. Following the seasonal carbohydrate low, root reserves increased to 107.2 mg on May 30 when the basal leaves of the rabbitbush were mature and the apical leaves were in the process of unfolding. The increase appeared to coincide with a period of high photosynthetic activity which was in excess of the amount needed for growth.

Two weeks later on June 17, the reserves of little rabbitbrush decreased slightly to 91.9 mg with little change in phenology. At this time the apical leaves had developed to three-quarter size. No other change in phenology was evident. Leaf development, however, was occurring at a more rapid rate than during the earlier sampling period. The lower carbohydrate level remained relatively stable for a period of 4 weeks during which time leaf development was completed and flower buds had become evident. With the onset of flowering the root reserves of little rabbitbrush displayed a rapid increase through the maturing process, increasing from 93.1 mg (July 15) to 163.0 mg per gram of root sample (August 27).

The carbohydrate root reserves of snowberry were 86.7 mg per gram of root sample at the initiation of the study in early spring. They declined to a seasonal low of 25.6 mg one week later. The low level for snowberry occurred at almost the same stage of phenological development as rabbitbrush, when the leaves were one-half to three-fourths mature and leaf buds still remained at the apex of the stems. Following the minimum seasonal carbohydrate level, snowberry portrayed a most unique food reserve pattern, as it progressed to a peak of 92.5 mg per gram when vegetative development was about one-half complete on May 30, dropping when apical leaves were three-fourths mature (June 17) and then increased to 91.6 mg per gram (July 1) of root sample before any appreciable change occurred in leaf development. The initiation of flower buds resulted in an additional decline which was followed by the seasonal maximum of 141.4 mg at the time of full flower development on July 29. Contrary to other work, where it was found that maximum reserves were reached at maturity (Jameson, 1963; McCarty, 1938), the carbohydrate content of snowberry declined slightly during late flowering and maturation. After this decrease on August 12, a rather stable plateau occurred during the remainder of the season.

Senecio and Geranium.—Senecio is an early-growing forb, therefore the first collection was made when the plants were already in full leaf, just prior to flower bud formation. The root reserves were at the seasonal maximum at this time

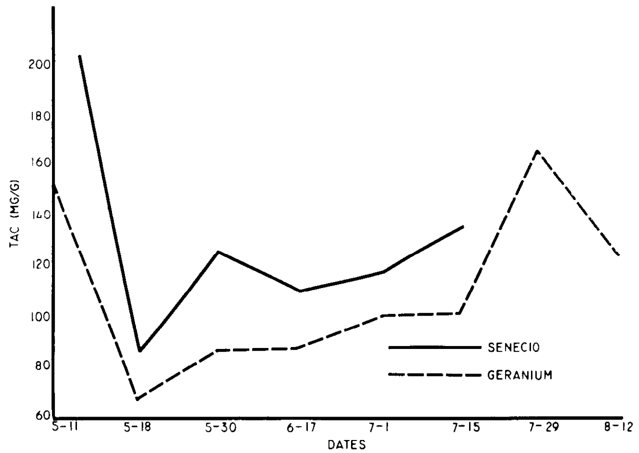

FIG. 4. Total available carbohydrate (TAC) reserves of Fremont geranium and senecio from initial growth to maturity. Values are averages expressed as milligrams of glucose equivalents per gram of root.

and contained 265.0 mg per gram of sample. One week later the carbohydrate content diminished to 81.0 mg as the plant initiated flower bud development. With the onset of flowering it rose to 127.9 mg on May 30, only to decline slightly in the late flower stage on June 17 (Fig. 4). Following the decline reserves increased until maturity, reaching 131.2 mg per gram of sample at the end of the growing season which occurred on July 15. Two weeks after maturity few plants remained and the species was no longer collected. In the present study senecio did not replenish the original carbohydrate reserve level of the roots that were present during early spring.

The carbohydrate reserve level of geranium roots was 150.1 mg per gram during early spring (Fig. 4). The plants had produced an average of two leaves per plant which were approximately one-third mature. Geranium plants displayed a sharp decline in root reserves one week later when an average of three leaves of one-half mature size were evident. The carbohydrate level then increased to 86.7 mg per gram on May 30. At this stage an average of six leaves, all of mature size were present. The increase in leaf area was most likely associated with an increase in root reserves. By June 17, the geranium plants exhibited occasional flowering but the carbohydrate level remained rather constant.

The onset of full flowering occurred about July 1, and corresponding with flowering was a marked rise in total available carbohydrates. Within a two-week period, all geranium plants were in full flower and the reserves declined to 105.1 mg per gram.

Following this slight decrease of carbohydrate reserves an increase to 161.2 mg per gram occurred on July 29. This level was the seasonal maximum and occurred when the plants were in late flower and seed set had begun. For an unknown reason, the reserves declined 2 weeks later when the plants were at full maturity. The trend in total available carbohydrate storage for Fremont geranium was similar to the trend described by McCarty and Price (1942) for sticky geranium *(Geranium viscossissimum)*. Sticky geranium likewise displayed a similar pronounced decline in root reserves with the onset of maturity.

Conclusions

Beardless wheatgrass was the last plant, chronologically and physiologically, to reach the minimum carbohydrate level in its roots during early growth. Carbohydrate reduction during early growth approached one of the lowest values recorded for any species analyzed. After descending to the minimal value the carbohydrate concentration increased quickly to the highest late season reserve recorded.

The reserve level of needlegrass was similar to that of beardless wheatgrass except it occurred earlier and was somewhat lower. A late season decline occurred at the time of seed development while with the beardless wheatgrass this decline occurred during flower development.

Snowberry and little rabbitbrush contained intermediate concentrations of available carbohydrates throughout the growing season compared with other species. However, the fluctuation of reserves throughout the season for snowberry was pronounced. No explanation was available for the fluctuation. Rabbitbrush root reserves increased steadily from a seasonal low through a mid-season plateau to a maximum value at maturity.

At the time of initial growth, senecio contained the highest carbohydrate level in the roots of the plants studied. Senecio plants grew faster and were in a more advanced stage of phenology than the other species. The reduced growth period resulted in rapid changes in total available carbohydrates in a short period of time.

The root reserves of geranium increased slowly through mid season. A late season maximum occurred at the time of full flower followed by a slight decline with maturity.

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Abstracting Journal Articles

Past procedure with all articles published in the Journal of Range Management has been for authors to prepare abstracts for Biological Abstracts. This practice was discontinued with the September 1969 issue (Volume 22, Number 5). Beginning with that issue, abstracts of articles appearing in the Journal of Range Management will be prepared by Biological Abstracts from the "Highlight" of each article, supplemented as necessary.

Authors preparing articles for the Journal should consider this use of the "Highlight" when it is being prepared.