Carbohydrate Reserve Content of Mountain Range Plants Following Defoliation and Regrowth[1]

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Highlight

Following the establishment of a curve for carbohydrate reserve levels in the roots of six native range plants in relation to phenological development, the effect of heavy clipping at the time of carbohydrate low and carbohydrate high was studied. The carbohydrate reserves in all species except senecio were significantly affected by defoliation treatment. Results indicated that defoliation of grasses and forbs early in the season was more detrimental than defoliation late in the season, but defoliation of browse late in the season appeared to lower reserves more than early defoliation.

Physiological reactions of plants to grazing should be the basis for development of sound grazing practices. To date knowledge concerning the role of carbohydrate reserves has been inadequate to establish specific requirements for plant sustenance with respect to period and extent of defoliation. Renewed growth following clipping or grazing is generally made at the expense of accumulated carbohydrate reserves. Thus, any grazing system which permits complete and frequent removal of the foliage could be injurious and lead to death of the plant.

Nieland and Curtis (1956) found reserve accumulation any time during vegetative growth was an important factor in the plant's ability to withstand grazing. Results from crested wheatgrass (*Agropyron desertorum*) studies (Hyder and Sneva, 1959) and hardinggrass (*Phalaris tuberosa* var. *stenoptera*) (McKell, et al., 1966) support this view.

Experimental Area and Procedures

The objective of this study was to evaluate the carbohydrate reserve level in six range plants after attaining two rates of regrowth following 90% foliage removal at the time of the minimum and maximum reserve level on non-grazed plants.

Three experimental areas were located in typical sagebrush-grass types of the montane zone in the mountains of northern Utah. In the spring of 1965 sixteen plants of each of six species, beardless wheatgrass (*Agropyron inerme*), Letterman needlegrass (*Stipa lettermanii*), snowberry (*Symphoricarpos vaccinioides*), rabbitbrush (*Chrysothamnus viscidiflorus*), senecio (*Senecio integerrimus*) and geranium (*Geranium fremontii*), at each area were located by stakes. Four plants of each species at each location were clipped 90% when carbohydrate reserves were believed to be a minimum and when carbohydrate reserves were believed to be at a maximum as estimated by previous work (Donart, 1969). In each case two plants that were clipped and two that remained unclipped were excavated when regrowth of the clipped plants attained 10% of the total expected annual growth of the control plants. The two remaining clipped plants and two unclipped plants were excavated when regrowth of the clipped plants attained approximately 20% of the expected total annual growth of unclipped plants.

Excavation and preparation of root samples and analysis of the root material for total available carbohydrates (TAC) were conducted in the same manner as described by Donart (1969).

Data were analyzed by an analysis of variance to evaluate the effects of each treatment on the individual species. The mean carbohydrate values for treatment for each species were analyzed by the multiple range test (Duncan, 1955).

Results and Discussion

Letterman Needlegrass

Clipping at the carbohydrate low.—Ninety percent of the herbage of the needlegrass plants was removed on June 5, when the plants were in the three leaf stage. This was believed to be the period of low carbohydrate reserve according to previous work. On July 13, 38 days later, the clipped plants had attained approximately 10% regrowth (Table 1) and the roots were excavated. The TAC content for the clipped plants was 67.0 mg per gram of root sample as compared to 73.1 mg in unclipped plants (Fig. 1).

Twenty percent of the anticipated annual growth was reached by July 21. At this time the previously clipped plants contained 61.4 mg TAC, a slight decrease from the 10% regrowth value. Control plants had an average of 73.4 mg of root reserves at this time.

The root reserve level of the control plants increased slightly while the clipped plants decreased slightly. The decrease in root reserves with defoliation suggested heavy utilization of needlegrass by grazing would require more than 20% regrowth before it replenishes the carbohydrate reserves.

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Table 1. Length of time in days required for plants to regrow 10 and 20% after harvesting 90 percent at the time of the total available carbohydrate low and total available carbohydrate high.

Species	Days of regrowth TAC low		Days of regrowth TAC high	
	10%	20%	10%	20%
Needlegrass	38	46	36	58
Wheatgrass	16	23	33	56
Rabbitbrush	30	48	46	63
Snowberry	57	79	37	75
Geranium	40	45	35	56
Senecio	29	42	28	37

Clipping at the carbohydrate high.—The initiation of the second 90% clipping treatment occurred on July 16, when the plants were in late anthesis which coincided with the maximum carbohydrate reserve content. The average root reserves of the needlegrass plants after attaining the estimated 10% new growth (August 21) were 83.6 mg per gram of root sample as compared to 128.3 mg TAC from the control plants.

On September 12, the estimated regrowth had developed and the TAC level for the clipped plants was 101.4 mg. Control plants contained 132.6 mg TAC per gram of sample. Late season clipping significantly reduced carbohydrate root reserves and neither 10 nor 20% regrowth allowed for sufficient leaf area to replace the reserves expended by regrowth following defoliation.

Beardless Wheatgrass

Clipping at the carbohydrate low.—Wheatgrass plants were harvested 90% on June 10, when they were in the fifth leaf stage. Ten percent regrowth was present on June 26, and the roots were excavated for total carbohydrate analysis. The amount of time required to obtain 10% regrowth was 22 days less than with Letterman needlegrass.

The TAC for wheatgrass upon attaining an estimated 10% regrowth was 144.5 mg per gram of root sample (Fig. 1). Unclipped plants excavated on the same date had an average value of 249.2 mg.

The rapid rate of growth continued until 20% of regrowth had developed by July 3, when the second series of plants were excavated. The roots of the clipped plants contained an average of 60.4 mg TAC per gram of root sample compared to 71.8 mg for the control plants. The reduction in root reserves for the clipped plants reflected the effect of regrowth demands. The reason for the rather marked decrease in TAC content in the control plants since the first samples were taken was unknown.

Clipping at the carbohydrate high.—Clipping wheatgrass plants at the time carbohydrate reserves were considered to be maximum, occurred on July 16, when the plants were in the early boot stage. By August 18, 32 days later, 10% regrowth had developed. Root reserves for the harvested plants were 79.5 mg per gram. The TAC value for unclipped plants was 182.4 mg.

The continued regrowth, to an amount approximating 20% of the annual growth, produced a TAC content of 148.1 mg. This was almost double the content attained with only 10% regrowth. Unclipped plants had a TAC value of 172.5 mg.

In all cases regrowth following the clipping of wheatgrass plants resulted in an immediate and marked decrease in root reserves. Hanson and Stoddart (1940) observed a similar decrease in root carbohydrates following grazing trials of beardless wheatgrass. Results of the current study showed regrowth following early season harvesting continued to draw upon reserves up to 20%, but during late season harvesting, reserves were replenished between the time 10 and 20% regrowth occurred. Therefore, this would indicate beardless wheatgrass could tolerate grazing better in late stages of development if given time for regrowth.

Little Rabbitbrush

Clipping at the carbohydrate low.—The rabbitbrush plants were harvested 90% on June 2, when the leaves were one-half to three-quarter mature size and the TAC content was lowest.

By July 2, 10% regrowth had developed. The TAC of the roots of the clipped plants was 112.2 mg per gram (Fig. 1). Control plants had an average of 123.8 mg of TAC per gram of root sample.

By September 8, 20% regrowth was produced. A few flower stalks, ranging from three to eight per clipped plant, were evident at the time of excavation and could have been responsible for the delay in additional growth. The clipped plants contained an average of 128.1 mg of root reserves compared to 120.1 mg for the control plants. The clipped plants grew at a slower rate and produced fewer stems. Therefore, the slight increase in root reserves could not be considered beneficial. Carbohydrates from stem storage might have been utilized which would have allowed root reserves to increase at the expense of plant vigor.

Clipping at the carbohydrate high.—The carbohydrate reserves of rabbitbrush were highest when the plants reached anthesis on July 24. By September 8, the clipped plants produced 10% of the annual growth of the control plants. The clipped plants contained an average of 89.9 mg of TAC per gram, while the control plants contained 102.2 mg of carbohydrate reserves.

Twenty percent regrowth occurred by September 25. Both the control and clipped plants had

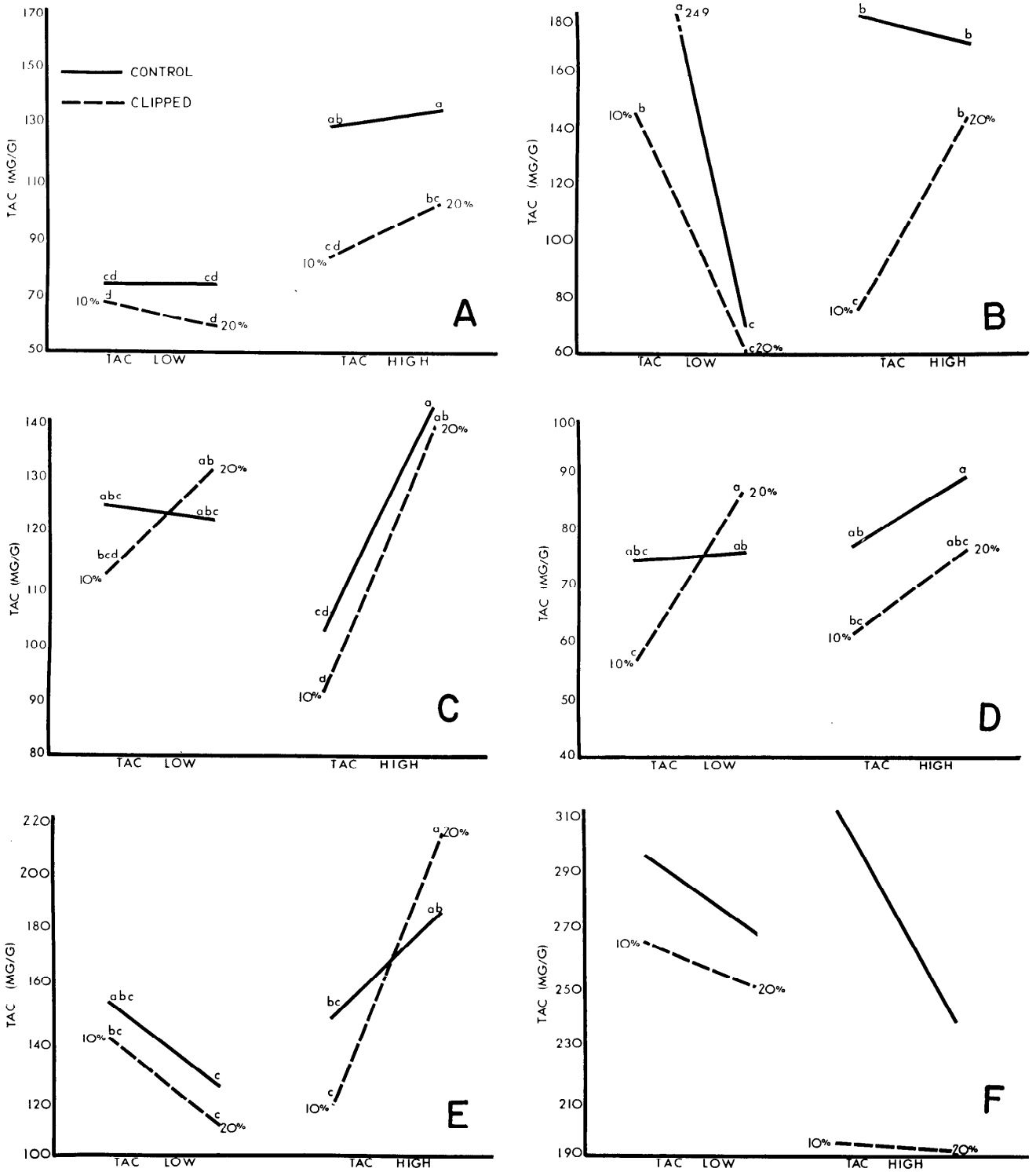

FIG. 1. Total available carbohydrates for control and clipped plants when harvested at the carbohydrate low and high and allowed to regrow 10 and 20%. (A) Letterman needlegrass; (B) beardless wheatgrass; (C) rabbitbrush; (D) snowberry; (E) geranium; and (F) senecio. (Different lower case letters within a species indicate significance at the 5% level.)

completed flowering. The control plants contained an average of 137.4 mg TAC and the clipped plants contained 130.8 mg of reserve carbohydrates.

Snowberry

Clipping at the carbohydrate low.—Snowberry plants were harvested 90% on June 2, when the plant leaves were one-half to three-quarters mature size. By July 29, 10% regrowth had occurred and the TAC content of the clipped plants was 57.4 mg per gram of root sample (Fig. 1). The control plants contained an average of 74.3 mg.

The twenty percent regrowth was present by August 20. Roots of the clipped plants contained an average of 86.2 mg of reserve carbohydrates as compared to 76.1 mg for the control plants. This indicated the plant could withstand early season grazing if it was given sufficient time to recover.

Snowberry plants showed no regular pattern for root reserves with respect to stage of growth. Part of the carbohydrate reserves utilized in foliage and flower production of snowberry plants may have come from storage in the stems, in the vicinity of the lateral buds (Priestly, 1962).

Clipping at the carbohydrate high.—By July 16, snowberry plants were in full flower, and the reserve storage was considered to be maximum. Ten percent regrowth was attained by August 22, and the average root reserves of the clipped plants were 61.7 mg. This was 15.4 mg higher than control plants excavated on the same date.

By September 29, the clipped snowberry plants attained 20% regrowth. The clipped snowberry plants were the latest of all plants studied to obtain 20% regrowth following the late harvesting period. The TAC for the clipped plants after attaining the 20% regrowth stage was 75.2 mg while control plants contained 89.2 mg.

Fremont Geranium

Clipping at the carbohydrate low.—The plants were harvested on June 2, when they were believed to have a minimum carbohydrate reserve value. At this time an average of three leaves of one-half mature size were present. The ten percent regrowth occurred on July 12. The TAC fraction at this time was 143.6 mg per gram of root material. Control plants excavated on the same date contained 156.9 mg of root reserves.

The additional 10% regrowth developed rapidly. Twenty percent of expected total regrowth was present by July 17, requiring only 5 days more than the initial 10%. After 20% regrowth the clipped plants contained 110.9 mg while control plants averaged 125.6 mg TAC. The 20% regrowth stage occurred when unclipped geranium plants were in full flower. Clipped plants which attained 20% of expected regrowth also possessed some flower stalks on this date.

Clipping at the carbohydrate high.—Maximum reserve storage occurred when the plants were in late flower on July 16. Ten percent regrowth following defoliation occurred by August 20, and the TAC level was 120.3 mg per gram. This value was 28.3 mg less than the reserve level of the control plants. Ten percent regrowth following defoliation when food reserves were high resulted in the greatest depletion of the root reserve level of geranium. Likewise, the newly produced foliage during this period was not as large or as vigorous as foliage on control plants.

Plants which were allowed to regrow to 20% of expected total growth after clipping attained this development by September 10. At this time the clipped plants contained TAC content of 210.2 mg. This reserve level was the highest of any recorded for the geranium plants during the season. The root reserve value for the control plants was 186.8 mg per gram of sample. A rapid increase and subsequent high value for the clipped plants indicated geranium was capable of replenishing its reserves rapidly if allowed sufficient leaf area to do so.

Senecio

The differences between the clipped and unclipped senecio plants were the greatest of any species studied. Experimental variation was also greater than with the other species. A short annual growth span and several extreme variations in root reserve content resulted in much variability among samples. The unusual growth pattern presented by senecio might also be part of the answer to the large experimental error. Plants which were observed to flower one year were found to remain vegetative the next. Conversely, senecio plants flowered during the second year in areas where it was not observed to do so the first year.

Clipping at the carbohydrate low.—Senecio plants were harvested to 90% on May 26, at which time the root reserves were believed to be minimal from previous analysis. Flower buds were just beginning to develop. Ten percent regrowth was present on June 24 and the TAC content was 265.8 mg per gram of root sample. Control plants collected on the same date contained an average of 295.6 mg of root reserves. The control plants collected at the time of 10% regrowth were in late flower development.

The 20% regrowth stage occurred on July 7. The TAC values for the clipped and control plants at this time were 250.0 mg and 267.9 mg respectively. Control plants collected at the time of the 20% regrowth stage had set seed. Senecio plants subjected to the clipping treatment did not produce seed stalks.

Clipping at the carbohydrate high.—By June 3, the senecio plants were in full flower which cor-

responded with the carbohydrate reserve high, and the plants were harvested 90%. Ten percent regrowth was produced by July 1, when the control plants were in late flower. At this time the clipped plants had a TAC content of 143.8 mg per gram. Roots of the control plants contained 312.3 mg of reserve substances. The great difference was correlated with the poor growth response of senecio plants to heavy foliage removal at the time of full flower development.

Twenty percent regrowth occurred by July 10, after the seed of control plants had matured. The clipped plants contained 191.5 mg TAC while the control plants had an average of 230.1 mg per gram of root sample. Twenty percent regrowth on the previously clipped senecio plants occurred at the end of the growing season. This would indicate heavy clipping at the time of the high carbohydrate level would result in a marked reduction in reserve materials available for growth at the start of the next growing season.

Conclusions

Defoliation and subsequent regrowth of plants during early spring caused a marked depletion of root reserves. When these plants produced regrowth amounting to 10% of total anticipated current growth, the depletion of reserves was pronounced. When harvested plants were allowed to produce 20% regrowth, the TAC reserve was often restored. Both grasses and forbs continued to draw on root reserves even when 20% regrowth was produced. The shruby species, however, restored their root reserves to a level comparable to unclipped plants if allowed to produce 20% of their total anticipated regrowth following defoliation during early spring when root reserves were lowest.

Defoliation of plants during the late growing season when they were believed to have a maximum level of root reserves also caused plants to use their reserves to produce regrowth. All species depleted their reserves to produce 10% regrowth following late season defoliation but their reserves were replenished somewhat when allowed to grow an additional 10%. Even though there was some replenishment of food reserves when allowed to produce 20% regrowth, the food reserves in the roots were still lower than in unclipped plants in most cases.

The results suggest that defoliation of both grasses and forbs early in the season when carbohydrate reserves are low is considerably more detrimental than defoliation late in the season when carbohydrate reserves are high if there is ample opportunity for regrowth before fall dormancy occurs. Defoliation of browse species appeared to lower the carbohydrate reserves to about the same extent when harvested in either the early season or in the late season.

Literature Cited

DONART, G. B. 1969. Carbohydrate reserves of six mountain range plants as related to growth. J. Range Manage. 22: 411–415.

DUNCAN, D. B. 1955. Multiple range and multiple F test. Biometrics 11: 1–42.

HANSON, W. R., AND L. A. STODDART. 1940. Effects of grazing upon bunch wheatgrass. Agron. J. 32: 278–289.

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

MCKELL, C. M., R. D. WHALLEY, AND V. BROWN. 1966. Yield, survival, and carbohydrate reserve of hardinggrass in relation to herbage removal. J. Range Manage. 19: 86–89.

NIELAND, B. M., AND J. CURTIS. 1956. Differential response to clipping of six prairie grasses in Wisconsin. Ecology 37: 355–365.

PRIESTLY, C. A. 1962. Carbohydrate resources within the perennial plant. Commonwealth Bur. Hort. and Plant. Crops Tech. Comm. 27. 116 p.

Election Results

Selected by the membership to serve the Society in 1970 and following years are—

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Charles L. Leinweber

Bredemeier will automatically succeed to the presidency in 1971, while the two new directors will serve for the three-year term 1970–72.

Ballots were mailed to all members on October 1, 1969, and 1,695 were returned bearing an eligible postmark dated November 30 or before. This represents a return of approximately 45%.

Ballots were counted by the Election Committee consisting of Robert W. Appleman, Carlton S. Fonte, Herbert I. Jones, Floyd E. Kinsinger, James A. Lees, Myrvin E. Noble, and Francis T. Colbert.