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Growth and Carbohydrate Trends in Crested Wheatgrass[1]

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The importance of carbohydrate reserves in perennial plants is well recognized and documented. The seasonal trend in depletion of reserves for initial growth and subsequent replenishment has become an important consideration in range management due to the fine contributions of Sampson and McCarty (1930), McCarty and Price (1942), McIlvanie (1942), Weinmann (1952), and many others.

This paper presents growing-season trends in herbage production and root carbohydrates by crested wheatgrass *(Agropyron desertorum)*.

Procedure

The work reported was conducted on Squaw Butte Range in southeastern Oregon. The bottom sites chosen for study represent the deeper, relatively rock-free soils in this area. Bluebunch wheatgrass *(Agropyron spicatum)*, sandberg bluegrass *(Poa secunda)*, and Junegrass *(Koeleria cristata)* are dominant native grasses found with big sagebrush *(Artemisia tridentata)* on these soils. Average precipitation is slightly over 11 inches.

In 1956 crested wheatgrass plants were removed from the field with a column of undisturbed soil 12 inches in diameter and 18 inches deep for potting. These were mature plants that had been seeded in 1952 and subsequently protected from grazing. Thirty-two plants were potted and arranged in a plastic-lined trench that was refilled with soil to maintain field conditions with respect to soil temperatures. Potting was completed March 20-27, 1956—about 10 days after snow melt. The plants were arranged by clump sizes into 4 groups identified as A (large), B, C, and D (small). Each pot was fertilized with ammonium nitrate at a rate equivalent to 20 lb. N/A. Applications were made in 1 quart of water. Additional irrigation of 1 quart was provided on June 12.

One pot of each size class was removed on each of 8 dates at 2-week intervals beginning April 24 and concluding July 24. The herbage was clipped from the 4 pots at ground level, dried in a forced-air electric oven at 90°C., and weighed to the nearest gram. Stem bases and roots were washed from the soil column, dried at 90°C., weighed, ground in a Wiley mill to pass through a 20-mesh screen, composited, and preserved in sealed containers for chemical determinations of total carbohydrates.

In 1957 studies were conducted under field conditions on 2 similar sites identified as site I and site II. On site I, 4 randomized blocks of seven 48-square-foot plots each were prepared and cleaned of old herbage in the fall 1956. On this site there was a mature stand of crested wheatgrass that had been drilled in 12-inch rows in the fall 1952 and subsequently protected from grazing. Herbage was harvested by hand clipping near ground level on 1 of 7 dates at 2-week intervals beginning May 7, 1957 and concluding July 30. The herbage was dried at 90°C. and weighed to the nearest gram. Also, root samples were taken from clipped plots on each date. Root samples, including 5 or 6 clumps on each plot, were obtained by excavating to a depth of about 8 inches at a distance of 6 inches from the crowns. The roots with stem bases were washed from the sods, dried, ground in a Wiley mill, composited, and sealed in glass containers for chemical determinations.

A 2 x 12 factorial experiment in 4 randomized blocks was prepared on site II. On this site there was an old stand of crested wheatgrass that had grown with-

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Table 1. Precipitation and atmospheric temperatures that provided favorable growing conditions in 1956 and 1957.

	Monthly precipitation (inches)			Mean monthly temp. (°F.)		
Month	'55-56	'56-57	20-yr. mean	'55-56	'56-57	20-yr. mean
October	0.49	2.57	1.01	49	48	48
November	1.80	0.18	1.11	34	38	36
December	2.05	0.75	1.46	31	31	29
January	3.20	1.40	1.24	29	18	25
February	1.00	1.19	1.03	26	34	29
March	0.65	3.21	0.82	36	38	34
April	0.20	0.75	0.67	47	44	43
May	3.04	2.70	1.40	52	51	50
June	0.80	0.24	1.34	55	59	56
Totals	13.23	12.99	10.08	359	361	350

out treatment for about 15 years. Individual plots were 8 x 12 feet in size. The 2-level factor included untreated and deheaded plants. Deheading was accomplished by cutting the culms at the base of the heads shortly after they emerged from the boot. The 12-level factor included 12 dates of harvest at weekly intervals beginning June 5, 1957 and concluding August 21. Herbage and root samples were taken on each date and processed in the manner described.

Carbohydrate concentrations were determined by the Shaffer and Hartmann modification of the Munson and Walker method (Browne and Zerban, 1941).[2] This determination obtains most of the carbohydrates in forms other than cellulose and lignin. The results are presented as total-carbohydrate concentrations in terms of glucose equivalent.

The growing seasons in 1956 and 1957 were unusually favorable. Precipitation and temperature records are presented in Table 1.

Results

Crested Wheatgrass Grown In Pots

Growing-season trends in the total-carbohydrate content of roots with stem bases and in herbage dry-matter yields by crested wheatgrass grown in pots during 1956 are presented in Figure 1.

Carbohydrate determinations were performed on composite samples. Mean values of triplicate determinations are presented.

Analyses of herbage yields gave highly significant differences among clump-size classes and among dates of removal. Mean herbage weights were 14, 13, 11, and 10 grams of dry matter, respectively, by size classes A (large), B, C, and D (small). Consequently, stratification by size classes was an important experimental control. Among dates of removal the final significant increase in yield was obtained in the period June 21-July 2, as measured by the 5 percent L.S.D. of 3.7 grams per pot. Mean herbage weights of plants were 19, 18, 16, and 16 grams, respectively, by size classes A, B, C, and D when clipped on and after July 2.

Analysis of root yields (with stem bases) gave highly significant differences among size classes, but dates of removal did not give significant variation. In fact, root weights did not manifest even a slight tendency for seasonal increases. Clump size stratification was of importance in root weight. Mean root weights were 66, 60, 53, and 37 grams of dry matter, respectively, by size classes A, B, C, and D. The root: top ratio was 3.1 to 1, as computed from the mean root weight of all plants and the mean herbage weight of plants removed on and after July 2.

The data of Figure 1 suggest that: (a) The depletion of carbohydrate reserves for initial growth probably was not excessive, (b) the accumulation of carbohydrates proceeded rapidly during the growing season and by head emergence in early June was high at about 27 percent, (c) herbage growth was completed by flowering time, and (d) the termination in herbage growth and initiation of reproductive activity were associated with a moderate decrease in carbohydrates that was not restored until after the seeds were filled.

Crested Wheatgrass Grown in The Field

Growing-season trends in the total-carbohydrate content of roots (with stem bases) and herbage dry-matter yields by crested wheatgrass grown in the field during 1957 are presented in Figure 2.

Carbohydrate determinations were performed on composite samples. Mean values of triplicate determinations are presented.

Statistical analysis of herbage yields gave highly significant differences among dates of harvest. The final significant increase in yield was obtained in the period June 4-18, as measured by the 5 percent L.S.D. of 330 lb/A. However, yield samples taken on and after July 1 averaged 1,490 lb/A, or 150 lb/A higher than on June 18.

Figure 2 data suggest that: (a) The accumulation of carbohydrates proceeded rapidly during the growing season and was slightly over 27 percent at the time of head emergence, (b) herbage growth was essentially complete by flowering time, (c)

[2]*Chemical determinations were performed by the Dept. of Agricultural Chemistry, Oregon State College, Corvallis, Oregon.*

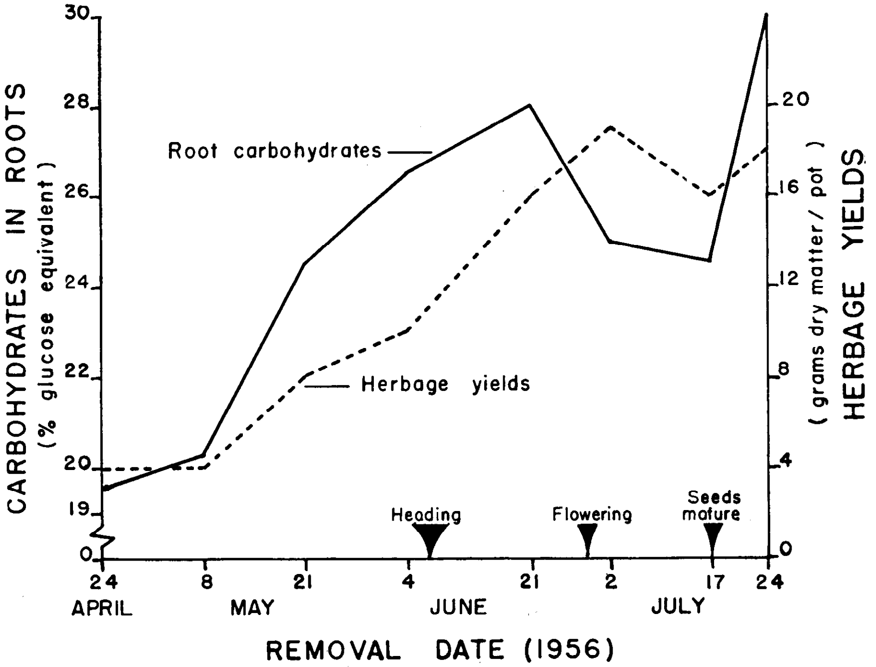

FIGURE 1. Seasonal trends of total carbohydrates in roots (with stem bases) and of herbage yields by crested wheatgrass grown in pots.

a slight decrease in total carbohydrates was associated with or slightly preceded the termination in herbage growth and initiation of flowering, and (d) a moderate increase in total carbohydrates occurred during the period of seed formation.

Figure 2 data began too late in the season to provide information pertaining to the level of carbohydrate depletion with initial growth. On May 7, when herbage production was just 24 percent complete, total-carbohydrate concentrations were over 23 percent.

Effects of Deheading upon Carbohydrate trends

Pre- and post-flowering trends in the total-carbohydrate content of roots and stem bases by untreated and deheaded crested wheatgrass plants grown in the field during 1957 are presented in Figure 3. Corresponding herbage dry-matter yields are presented in Table 2.

A paired comparison analysis of root carbohydrate values indicates no differences due to deheading. The mean difference was 0.4 percent glucose equivalent, and the standard deviation of individual differences was 1.23 percent. Since the greatest difference was just 2.2 percent on June 26, it seems likely that deheading did not influence root carbohydrate levels at any time. The primary objective in deheading was to find whether the carbohydrate decrease in June was directly associated with flowering activity. Root carbohydrates decreased in both treatments, although the decrease was slightly less in deheaded plants.

Statistical analysis of herbage yields gave highly significant differences among the 4 replications and among the 12 dates of removal. The differences in yields by untreated and deheaded plants were significant at the 5 percent level. However, deheading removed an average of 53 lb/A. of dry matter. Since the 5 percent L.S.D. for testing treatment means was 80 lb/A, it is clear that the removal of heads was responsible for the significant difference. No further effects of deheading were apparent. Among dates of harvest the final increase in yield occurred in the week June 26-July 3.

Considering mean carbohydrate values and herbage yields,

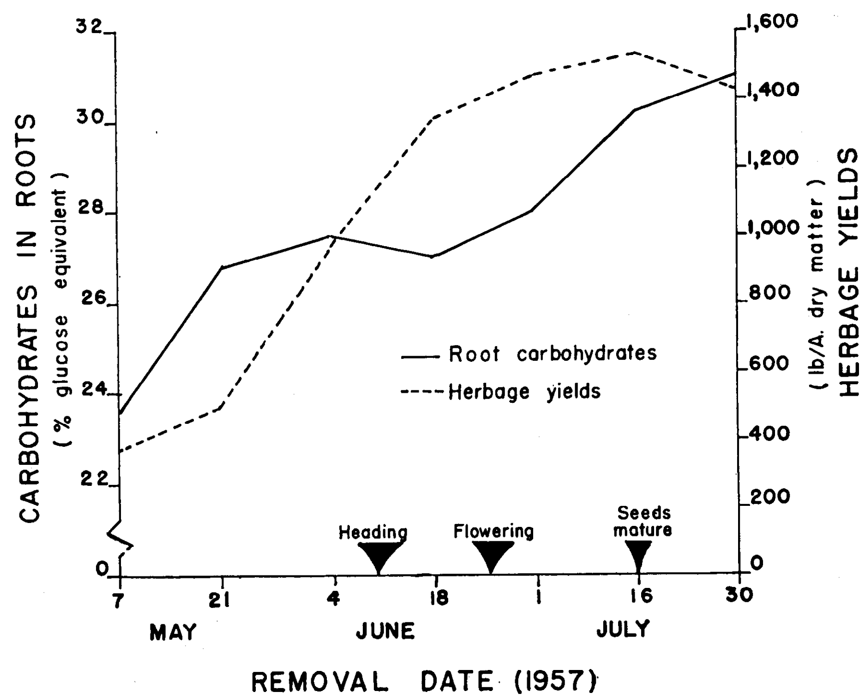

FIGURE 2. Seasonal trends of total carbohydrates in roots (with stem bases) and of herbage yields by crested wheatgrass grown in the field.

the data presented in Figure 3 and Table 2 suggest that: (a) Total carbohydrate levels were about 27 percent at heading time in early June, (b) herbage growth terminated by, or during, flowering activity, (c) a moderate decrease in total carbohydrate occurred by June 26 when flowering activity was just beginning, but recovery was prompt in the subsequent week during greatest flowering activity, and (d) total-carbohydrate levels fluctuated between 25.5 and 30 percent throughout July and August.

By August 21 the grasses were brown, and the herbage contained only 34 percent moisture. It seems unlikely that root storage levels increased at later dates.

Discussion and Conclusions

Growing-season trends in the total-carbohydrate content of crested wheatgrass roots (with stem bases) appear to be characterized by: (a) An early rapid increase during the growing season to a level near 27 percent at about the time of head emergence, (b) a moderate decrease at, or just prior to, flowering, and (c) a final recovery during or just following seed formation to a level approximately the same as that attained by head emergence.

An important period for the accumulation of carbohydrates coincided with the growing season. Reserves were restored most rapidly in May prior to head emergence in early June. The time and manner of depletion of reserves for initial growth was not investigated. However, it is recognized that the extent of depletion for initial growth might strongly affect the rapidity and time of recovery.

Some concern regarding the conclusion of early accumulation of carbohydrates in crested wheatgrass must be expressed, because delayed accumulation is sometimes represented as the classic pattern regarding food reserves.

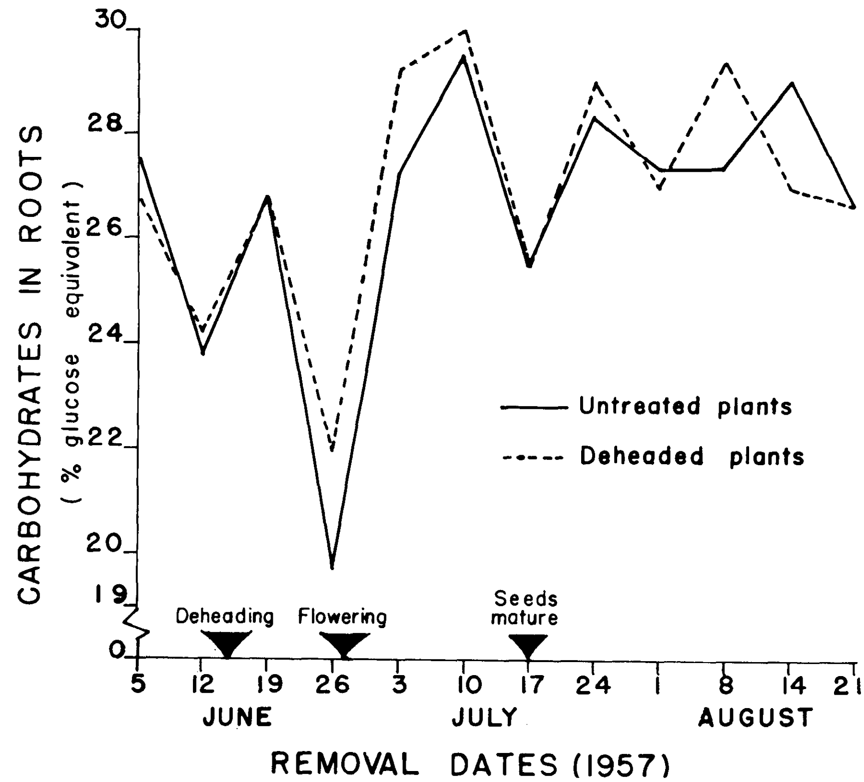

FIGURE 3. Pre-and post-flowering trends of total carbohydrates in roots (with stem bases) by untreated and deheaded crested wheatgrass plants grown in the field.

Delayed accumulation of reserves may be illustrated with data on California needlegrass (*Stipa pulchra*). Total carbohydrates in the stem bases of California needlegrass were low (about 4 percent) during the season of active growth (Sampson and McCarty, 1930). Flowering occurred when herbage growth was about 40 percent complete. Thereafter the composite demands of growth and reproductive activities consumed current production of carbohydrates. Terminal storage levels obtained after termination in growth and reproductive activities were about 17 percent.

In contrast with California needlegrass, flowering and seed formation are delayed in many species until herbage growth is essentially complete. Neiland and Curtis (1956) listed the duration of pre-flowering vegetative growth as an important factor in the ability of a grass to withstand grazing. It seems likely that the accumulation of food reserves is related to the sequence in growth and reproductive activities.

Moderately early accumulation of carbohydrate reserves may be illustrated with data regarding slender wheatgrass (*Agropyron trachycaulum*), which appeared to complete growth activity by flowering time. In the roots and stem bases of slender wheatgrass the combined sugars and starch were low (about 5 percent) at the early stage of growth (McCarty and Price, 1942). Storage levels remained low until head emergence, then increased rapidly to a level at flowering time (10 to 15 percent) that was as high as autumn storage levels in 2 of the 3 years reported. The authors of the present paper suggest that the increase in reserves in the period from head emergence to flowering was of paramount importance in slender wheatgrass. However, it is recognized that there is sufficient opportunity for controversy.

Early accumulation of carbohydrates may be illustrated with data regarding orchardgrass *(Dactylis glomerata)*. Concentrations of food reserves (sugars and fructosan) in the stubble decreased to about 12 percent shortly after clipping and increased to about 26 percent in 35 days after clipping (Sullivan and Sprague, 1953). Reserve levels in the roots were lower than in the stubble, but followed a similar trend of increase from about 10 percent to 19 percent in 35 days after cutting.

A number of factors other than the duration of pre-flowering vegetative growth may contribute to differences in the pattern of carbohydrate accumulation in grasses. Morphological differences in the origin of photosynthetic tissue may be of special interest in range management. Branson (1953) discussed the importance of vegetative: reproductive stem ratio and the height of the growing points. The occurrence of basal leafiness in many species is easily recognized in the field. Species having vegetative stems, in which the internodes are very short and produce only leaves, appear to have good structure for early development of abundant photosynthetic tissue as well as for the replacement of photosynthetic tissue removed by grazing. Species having a high proportion of reproductive stems appear to develop abundant photosynthetic tissue more slowly, and to replace it with greater difficulty after grazing or clipping than those with vegetative stems. In reproductive stems short basal internodes may permit more rapid development of photosynthetic tissue than long basal internodes, because a leaf arises at each node. Also, as emphasized by Branson (1953), short basal internodes delay the rise of growth primordia to a grazable height.

Table 2. Pre- and post-flowering trends in herbage dry-matter yields by untreated and deheaded crested wheatgrass plants grown in the field.

Removal date (1957)	Herbage dry-matter yields (lb/A) by plants:		
	Untreated	Deheaded*	Average
June 5	701	626	664†
June 12	902	862	882
June 19	829	786	808
June 26	970	1006	988
July 3	1316	976	1146
July 10	1057	952	1005
July 17	1268	981	1124
July 24	1160	1084	1122
Aug. 1	1160	1058	1109
Aug. 8	1076	1112	1094
Aug. 14	1074	924	1000
Aug. 21	966	994	980
Average	1040††	947	993

* Heads were removed from the culms June 12-17. This removed an average of 53 lb/A.
† 5% L.S.D. for date means: 192 lb/A.
†† 5% L.S.D. for treatment means: 80 lb/A.

Early growth in crested wheatgrass was characterized by abundant leafiness, delay in stem elongation, and opportunity for the accumulation of carbohydrates. The abundant leafiness at an early stage of growth was attributed to short basal internodes, because each stem produced a reproductive culm. Crested wheatgrass produced 2 or more short internodes below the soil surface as described by Cook and Stoddart (1953). For contrast we may consider bluebunch wheatgrass *(Agropyron spicatum)*. This species apparently has relatively low storage concentrations, relatively long basal internodes of 1½ to 2 inches in length, and slow development of abundant photosynthetic tissue (McIlvanie, 1942; and Branson, 1956). As compared with crested wheatgrass, it seems reasonable that bluebunch wheatgrass would require greater depletion of stored reserves during initial growth and require more time for its restoration.

After the early basal leafiness was produced by crested wheatgrass, the clums arose rapidly and uniformly. The culms terminated growth by flowering time.

In the consideration of carbohydrate accumulation it is also important to recognize environmental factors. Nitrogen fertilization and other factors that stimulate growth activity tend to mobilize carbohydrates. Graber (1931) reported that nitrogen fertilization may hasten the decline of reserves under close grazing or clipping. Benedict and Brown (1944) reported similar results regarding the effects of nitrogen fertilization. Several workers have found the rate of carbohydrate accumulation to be inversely related to the rate of growth. The inferences are that patterns of carbohydrate depletion and accumulation may be quite variable from year to year and site to site; although related to morphological and phenological features that characterize different species.

In brief, a plant's demand for carbohydrates in respiration, growth, and reproduction must be met by carbohydrates from stored reserves and current photosynthetic production. Production in excess of demand promotes active storage, and vice versa. Crested wheatgrass, with relatively high storage levels, short basal internodes, and early abundant leafiness, developed high photosynthetic production rapidly while demands in stem elongation remained low. Somewhat later, when reserves and photosynthetic production were high, the additional burdens in growth and reproduction were not especially serious. Within this framework of carbohydrate supply and demand there is opportunity to recognize species and environmental differences that are important in grazing management.

The decrease in carbohydrate concentrations at about flowering time was intriguing because data on other species sometimes indicate similar decreases. It seemed logical to assume that the energy expended in flowering was directly involved in the requirement for utilization of stored carbohydrates. However, deheading did not affect carbohydrate trends, and it must be concluded that flowering was not the direct cause of the temporary decrease in food reserves. The requirements in very fast stem elongation after head emergence were likely dominant in producing the imbalance between carbohydrate production and utilization.

The data presented on the growth and carbohydrate trends in crested wheatgrass support the contentions of early range readiness and high tolerance to grazing often attributed to this species.

Summary

Herbage yields and root-carbohydrate concentrations in crested wheatgrass *(Agropyron desertorum)* were obtained in 1956 and 1957. In 1956 mature potted plants were used. Four plants were removed every 2 weeks to obtain herbage yields, root yields, and root-carbohydrate concentrations. In 1957 plants were taken directly from the field on 2 sites. On site I herbage and roots were removed every 2 weeks to obtain herbage yields and root-carbohydrate concentrations. On site II, trends in herbage yields and root-carbohydrate concentrations were taken at weekly intervals on untreated and on deheaded plants. Deheading was accomplished by cutting the culms at the base of the heads shortly after emergence from the boot.

Growing-season trends in the carbohydrate content of roots (with stem bases) were characterized by: (a) An early accumulation of carbohydrates to a level near 27 percent by the time of head emergence, (b) a moderate decrease at or just before flowering that was not altered by deheading, and (c) a final recovery during or just following seed formation to a level approximately the same as that attained by head emergence.

Within the framework of carbohydrate supply and demand there is opportunity to recognize species and environmental differences that are important in grazing management. Some phenological and morphological characteristics of crested wheatgrass were discussed as a basis for the appreciation of species differences in carbohydrate depletion and accumulation. The data presented on the growth and carbohydrate trends in crested wheatgrass support the contentions of early range readiness and high tolerance to grazing often attributed to this species.

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