Effect of Plant Moisture Stress on Carbohydrate and Nitrogen Content of Big Sagebrush

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Highlight: *Delineation of the effects of plant moisture stress on carbohydrate and nitrogen content of important range species is needed for proper intensity of range use of summer ranges when high plant water stress conditions exist. Water potential of big sagebrush shows great seasonal variation, ranging from a low of −70.3 bars in September to a high of −8.3 bars in April. Starch content did not significantly change in water stressed plants, but sugar content significantly increased in leaves, stem, and roots. Leaf nitrogen content significantly decreased in water stressed plants, while stem nitrogen content significantly increased. Sugar increases in the leaves, stem, and roots and nitrogen accumulation in the stem of water stressed plants may be of adaptive significance.*

Big sagebrush (*Artemisia tridentata* Nutt.) is an important browse plant on western ranges. Since moisture is an important environmental factor on desert ranges, a clearer understanding of the effects of plant moisture stress on carbohydrate and nitrogen reserves of range species such as big sagebrush is useful in range management.

Although the seasonal carbohydrate reserve cycle of big sagebrush has been studied (Coyne and Cook, 1970), and carbohydrate and nitrogen content determined during winter and summer range conditions (Cook and Harris, 1950; Esplin et al., 1937), little attention has been given to the effect of plant water stress on carbohydrate and nitrogen bal-

ance.

Despite much work showing that water stress alters both the carbohydrate and nitrogen balance of plants, generalizations from the literature do not fulfill the need for specific knowledge. This study provides some basic information on the effect of plant water stress on carbohydrate and nitrogen balance of big sagebrush.

Methods and Materials

To assess the range of moisture stress experienced by big sagebrush in the field, plant water potential (WP) measurements were obtained from plants growing on a south-facing slope (1,640 m elevation) in Red Butte Canyon, east of Salt Lake City, Utah. Field WP measurements were made at weekly intervals from late August to early November, 1969, and during April and May, 1970. All WP measurements were made using the pressure bomb technique (Scholander et al., 1965; Waring and Cleary, 1967). Determinations were obtained from more or less uniformly sized plants, generally about 0.5 m tall, between 12:00 noon and 5:00 pm. Measurements were obtained from three to eight individual plants on each sampling date.

The effect of plant water stress on

carbohydrate and nitrogen balance of big sagebrush was studied under controlled laboratory conditions to separate seasonal and other effects on carbohydrate and nitrogen content from those due to water stress.

Entire plants approximately 2 to 4 dm tall were collected at the field study site during late summer and early fall, 1969. Plants were packed in wet peat and transported to a greenhouse, where root systems were washed with tap water and dipped into Rootone. They were then potted in a uniform loam soil and kept in a greenhouse for at least 2 months prior to use. Plants were well watered and periodically fertilized with a commercial liquid mixture during this time.

Healthy plants were randomly selected from those growing in the greenhouse, placed into a Sherer-Gillett environmental chamber, and acclimated for at least 2 weeks prior to use. During acclimation all plants were well watered. Moisture stress was gradually imposed by withholding water following acclimation, and time elapsing before plants attained the lowest WP values was 15 days. The environmental chamber regime was based on data obtained at the field study site during August through September (the most arid months). Maximum temperature was 29 °C and minimum 13 °C. Temperature was gradually changed in increments of 1 to 3 units per hour. The chamber was lit with fluorescent lamps supplemented by incandescent bulbs and kept on a 14 hr light/10 hr dark photoperiod.

All plants used were randomly selected and removed from the growth chamber at the same light phase cycle time ± one hour. Upon removal from the chamber, plant WP was measured with the pressure bomb method. All leaves were removed and dropped whole into boiling 80% ethyl alcohol (ETOH). The entire stem system was then sectioned and dropped into boiling ETOH, and lastly the entire root system was washed with tap water, blotted nearly dry, sectioned, and dropped into boiling ETOH. All organs were in boiling ETOH within 10 to 15 minutes following removal from the chamber.

Subsequent extraction of reducing sugars, including hydrolysis of oligosaccharides to monosaccharides, was done following the procedures of the Official Methods of Analysis of the Association of Official Agricultural Chemists (ninth edition, 1960). Total reducing sugars were analyzed using the method of Somogyi (1952). The alcohol-soluble nitrogen extraction procedure followed that of Saunier et al. (1968). Total alcohol-soluble nitrogen was determined using a micro-kjeldahl method and includes chlorophyll nitrogen of chlorophyllous organs in addition to other alcohol-soluble nitrogenous compounds.

Starch extraction and hydrolysis followed the procedure of Hassid et al. (1940), but maltose produced after amylase hydrolysis was determined by the method of Somogyi (1952). Total alcohol-insoluble nitrogen was determined with a microkjeldahl technique, following the procedures of Chen et al. (1964).

Since virtually all nitrogen of the alcohol extracted material is alcohol-insoluble protein nitrogen (Chen et al., 1964), alcohol-insoluble nitrogen values are reported as alcohol-insoluble protein nitrogen. All reducing sugar, starch, alcohol-soluble nitrogen, and alcohol-insoluble protein nitrogen data are expressed as milligrams per gram of the alcohol-insoluble dry weight for leaf, stem, and root material.

Results and Discussion

Big sagebrush shows great seasonal variation in WP, ranging from a high of −8.3 bars in April to a low of −70.3 bars in September (Table 1). Both August and

Table 1. Water potential (bars) of big sagebrush in Red Butte Canyon at 1,640 m elevation.

Month	Range	Mean
August	−36.5 to −49.1	−42.1
September	−42.7 to −70.3	−54.6
October	−22.7 to −43.4	−30.9
November	−12.4 to −33.8	−24.3
April	− 8.3 to −11.0	− 9.8
May	− 9.7 to −16.5	−12.8

September, 1969, were unusually arid months with precipitation being 38% and 23%, respectively, of the long term (18 year) monthly mean (Dina, 1970). Thus the lowest WP values found in the field were probably lower than in most years. Carbohydrate and nitrogen balance was examined over the WP range of −8.3 to −38.9 bars. This range includes WP's experienced by plants in the field during all months except September.

Figure 1 shows the effect of decreasing plant WP (increasing water stress) on the sugar and starch content of leaves, stems, and roots and total carbohydrate (sugar plus starch) of the entire plant (leaves, stem, plus roots). Analysis of variance indicates a curvilinear regression is significantly different (0.05 level) from a linear regression in some cases. In those instances where there is significant curvilinearity in the regression, the parabolic regression line is plotted. Regressions of leaf, stem, and root starch are not significant (from zero) at the 0.05 level. In contrast, regressions of total carbohydrate, leaf, and stem sugar are significant at the 0.01 level. The regression for root sugar is significant at the 0.05 level. Coefficients of determination of significant regressions range from 0.54 to 0.82, indicating that a substantial amount of variation in carbohydrate content is accounted for by variation in plant WP.

Starch content did not significantly change with water stress in any organs of big sagebrush. However, there is a significant increase in sugar content and total carbohydrate of the entire plant (Fig. 1).

In big sagebrush plants subjected to water stress, cellular growth is probably reduced, and thus sugars accumulate in the sugar pool. Hodges and Lorio (1969) found a marked increase in sugars and total carbohydrate in the bark of water stressed loblolly pines, but no difference in the degree of starch degradation in stressed versus non-stressed controls. They attributed this to the reduced growth of stressed trees. Iljin (1957) has suggested that reduced growth with water stress may result in sugar accumulation.

Coyne and Cook (1970) reported that growth rate in eight desert range species, including big sagebrush, was inversely related to carbohydrate content.

Figure 2 shows the effect of water stress on alcohol-soluble nitrogen (soluble N) and alcohol-insoluble protein nitrogen (protein N) content of leaves, stem, and roots and total N (soluble plus protein N) of the entire plant (leaves, stem, plus roots). Regressions of protein N of leaves and roots, and soluble N of the stem are significant at the 0.01 level. The regression for stem protein N is significant at the 0.05 level. Regressions of total N and soluble N of the leaves and roots are not significant at the 0.05 level. Coefficients of determination of significant regressions range from 0.52 to 0.68.

Soluble N in the stem increases significantly with decreasing plant WP. Protein N of the stem and roots did not decrease with decreasing plant WP, but there is a significant decrease in leaf protein N (Fig. 2). These relationships indicate that the
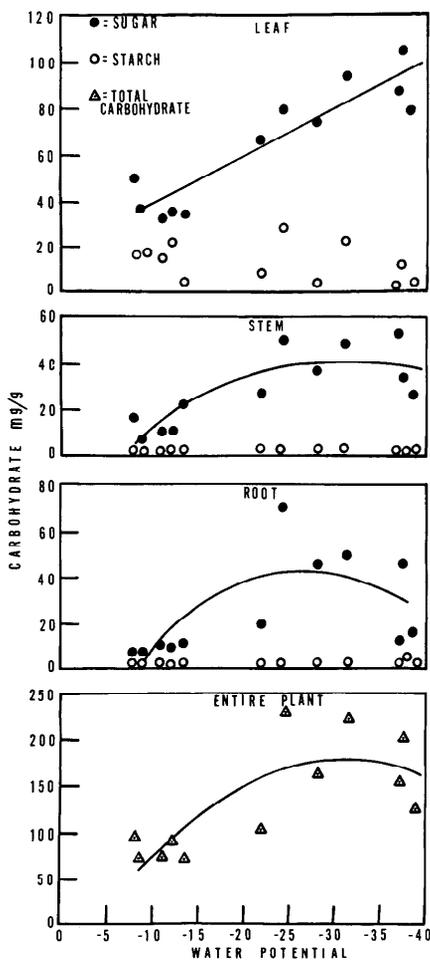
Fig. 1. *Carbohydrate content of leaf, stem, root, and total carbohydrate content of the entire plant (sugar plus starch of leaves, stems, plus roots) at various plant water potentials (bars).*
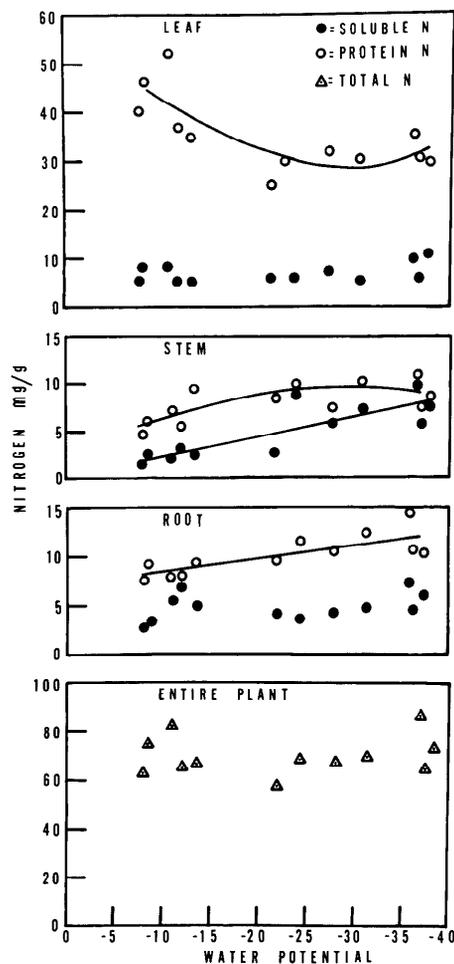
Fig. 2. *Nitrogen content of leaf, stem, root, and total nitrogen content of the entire plant (soluble plus protein nitrogen of leaves, stems, plus roots) at various plant water potentials (bars).*

increase in stem soluble N with water stress is not due to nitrogen shifts within the root or stem, and since total N of the plant does not change significantly with water stress, the increase in stem soluble N must be a result of translocation of protein hydrolysis products from the leaves.

Bonner (1950) states that water stress may induce proteolysis in leaves and translocation of soluble N products from the leaves. Protein hydrolysis, coupled with an increase in soluble nitrogen compounds, is not uncommon in plants subjected to water stress (Petri and Wood, 1938; Chibnall, 1954; Kemble and Macpherson, 1954; Parker, 1969). Gates (1957) found that in water stressed tomato plants, leaf nitrogen decreased and stem nitrogen increased due to translocation of nitrogen from leaves to the stem.

The significant increase in protein N in both the stem and roots of big sagebrush with decreasing plant WP, but a decrease in leaf protein N (Fig. 2), indicates that protein synthesis is occuring in the stem and roots while protein hydrolysis is occurring in the leaves. Since there is no significant change in total N of the plant (Fig. 2), these relationships represent quantitative nitrogen shifts within the plant.

The stem of big sagebrush has corky layers which occur between the annual rings of xylem (Diettert, 1938 cited in Parker, 1968) and this may help to retain stem moisture (Parker, 1968). Water stress, as measured with the pressure bomb, measures xylem sap tension (Scholander et al., 1965; Waring and Cleary, 1967). Thus water stress in the leaves may well have been more severe than in either roots or the stem at a given pressure bomb WP determination. Bordeau (1954) found that when leaves of oak seedlings had died of drought, roots were still alive. Actual water deficits in the stem and roots were apparently not severe enough to preclude protein synthesis, over the range of WP's measured in this study, whereas in leaves protein synthesis was impaired and a net decrease in protein N occurred.

Conclusions

Parker (1956) suggests that increasing sugar content may result in a decrease in transpiration water loss. Sugar increases found for big sagebrush subjected to water stress may be significant to the water relations under conditions of high plant water stress. During water stress sugars may protect the RNA-DNA com-plex, as well as enzymes; and when sugars do not increase with drought, cellular injury may rapidly occur (Parker, 1969). Thus sugar increases in all organs of sagebrush with decreasing plant WP may be of adaptive significance.

Gates (1968) has described the response of plants during moisture stress as a senescent decline, and the response upon cessation of moisture stress as a physiologically young state. The senescence of leaves of woody plants is accompanied by a decline in ability to synthesize protein and by liberation of soluble nitrogenous compounds that move into stems or roots for storage (Luckwill, 1968). Nitrogen shifts reported for big sagebrush suggest an adaptation, similar to a senescent decline associated with the onset of dormancy, for conservation of nitrogen during periods of water stress via storage in the stem. As water stress becomes less severe, the nitrogen pool within the stem may be mobilized and utilized in renewed cellular growth.

As reported by Coyne and Cook (1970), the twigs of big sagebrush are an important reserve storage site for carbohydrate. As shown in this study, the twigs and stem are also an important reserve storage site for nitrogen, especially during conditions of plant water stress. Overgrazing during summer range conditions, when plant water stress is likely high, could be detrimental, since much of the stored nitrogen and carbohydrate would be removed and range quality could therefore be adversely affected. This study indicates a need for further examination of the relationships among WP and carbohydrate and nitrogen content under simulated and actual browsing conditions over several years. Such studies would provide a better understanding of grazing effects under various plant water stress conditions.

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