Seasonal Variation in Total Nonstructural Carbohydrate Levels in Nebraska Sedge

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Abstract

Seasonal variation in total nonstructural carbohydrate (TNC) levels in rhizomes and shoots of Nebraska sedge (*Carex nebraskensis* Dewey) suggest that grazing too early or too late or both may be detrimental. Samples were collected from a natural population of Nebraska sedge growing in Tule Meadow at 2,170 m elevation in the Sierra Nevada, Calif. TNC reserves in rhizomes decreased to 7.5% of the dry weight during early shoot growth, and reached a peak level of 17.4% in the fall. TNC levels in shoots ranged from a low of 10.6% in the spring to a high of 16% in August, after flowering. TNC levels in emerging shoots averaged 16.4% in September and 19.1% at the end of October.

Nebraska sedge (*Carex nebraskensis* Dewey) is a perennial species common in mountain meadows of the Western United States. Frequently heavily grazed by cattle and horses, it is considered a valuable late-season sedge (Hermann 1970). However, the effects of grazing on Nebraska sedge are not known. Knowledge of its seasonal fluctuations in carbohydrate levels would aid in evaluating the effects of defoliation on its energy reserves and health.

Total nonstructural carbohydrate (TNC) levels provide an estimate of the amount of energy available for plant growth (Weinmann 1947, Smith 1969). A pattern of storage and use of TNC reserves has been noted in many perennial species. Reserve carbohydrate levels in storage organs generally decline to a seasonal minimum upon initiation of spring growth. Reserves are then replenished during the summer, and a high level of TNC is attained before dormancy in the fall (Humphreys 1966).

Carbohydrate reserves in rhizomes of Bigelow sedge (*Carex bigelowii* Torr.) were high in the spring and fell sharply when early shoot growth began (Fonda and Bliss 1966). These reserves were rapidly replaced and peaked after seed dispersal. A similar trend in carbohydrate storage was noted in river sedge (*Carex lacustris* Willd.) (Roseff and Bernard 1979). Total nonstructural carbohydrate levels were low early in the growing season and were at a high level in the fall.

This paper reports a study of seasonal carbohydrate levels in Nebraska sedge in the Sierra Nevada, Calif.

Methods

A site at Tule Meadow, a wet meadow, on the Sierra National Forest, Fresno County, Calif., was selected for this study. Tule Meadow, at 2,170 m elevation, lies in a swale formed by moraines (Wood 1979). Soils of the meadow have not been classified. Generally, however, beneath a sod surface is an organically rich top soil, which extends to depths of 90 cm to 120 cm. Soil texture ranges from sand to silt loam. Inorganic, gleyed material then extends to 275 cm (the depth sampled by Wood).

The specific site selected falls into the Nebraska sedge class (Ratliff 1982) or the Nebraska sedge wet meadow association (MW19 11) of Hall (1979). Other species of some importance on the site included beaked sedge (*Carex rostrata* Stokes) and tufted hairgrass (*Deschampsia caespitosa* (L) Beauv.). Soil at the site is typical of Nebraska sedge sites in the Sierra Nevada. Such sites have a loam texture, a strongly acid reaction, and more than 20% organic matter at the 10 to 20 cm depth (Ratliff 1982).

On April 10, 1980, snow was 1.5 m deep over the site. By May 8 snow was melting and some ground could be seen. The site was fully accessible on May 22. As is usual in the Sierra Nevada, little precipitation occurred during the summer (Table 1). Minimum air temperatures were above freezing only from mid-July to about mid-August. Soil temperatures were above freezing at all times. Free surface water remained into August, and soil water content was at or near saturation level even when surface water was not present. Rain in early September caused a temporary return of free surface water and was associated with a hard freeze. Hot weather in late September and early October produced a temporary warming.

Samples were collected at 2-week intervals from May 22 through October 23, 1980. All sampling was done before noon so as to reduce any variability due to time of day. Three samples were taken from an ungrazed native population of Nebraska sedge on each date. Intact blocks of sod (about 30 cm thick and 30 cm in diameter) were removed from near the centers of randomly selected 0.5-m^2 (0.5 × 1.0 m) quadrats in a 12 × 6-m study plot. Care was taken not to disturb adjacent quadrats during block extraction. The wet sod blocks were set in plastic bags to reduce loss of soil moisture. That care and the block size should have minimized respirational degradation of TNC during transportation.

At the laboratory sod blocks were washed to remove soil and separate Nebraska sedge from any other plant material present. Established shoots, rhizomes, and new shoots (without unfolded leaves) of Nebraska sedge were then separated. New shoots began to appear in abundance in the fall and were separated from other plant parts on September 11 and 25 and on October 9 and 23 only. While rhizomes of sedges *(Carex)* are important, their roots comprise relatively small proportions of the underground biomass and are relatively unimportant as storage organs (Fonda and Bliss 1966). Root material, therefore, was not saved for analysis.

Plant parts were washed thoroughly in tap water. To facilitate drying, shoots and rhizomes were cut into short segments (4 to 6 cm). They were oven dried for 1 hour at 100° C and then dried to a constant weight at 70°C (Raguse and Smith 1965). The dried materials were ground to pass a 40-mesh (0.42-mm opening) screen and stored at room temperature in sealed bottles until TNC analysis.

To remove total nonstructural carbohydrates from the plant tissue samples, we followed the takadiastase enzyme method (Smith 1969). After digestion by takadiastase, fructosans and other sugars were hydrolyzed to monomers with 0.1 N sulfuric acid. Reducing power of the resulting solutions was measured by the Shaeffer-Somogyi copperiodometric titration method (Heinze and Murneek 1940, Smith 1969).

Sample weights used for analysis ranged from 100 to 200 mg, depending on the type of plant tissue and the date of sampling.

Data were analyzed following analysis of variance procedures for the randomized complete-block, fixed effects experimental

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Table 1. Precipitation, maximum and minimum air temperatures, soil temperatures, and surface water depths at Tule Meadow (June 19 to October 23, 1980).

Sampling date		Precipitation cm	Air temperatures Maximum	Air temperatures Minimum	Soil temperatures 0-10 cm	Soil temperatures 10-20 cm	Surface Water Depth cm
			Degrees C		Degrees C		
June	19	Note taken	Not taken		13.9	13.9	10.4
July	3	0.0	24.7	-1.1	14.2	14.4	8.8
	17	0.0	24.4	-2.2	15.6	13.6	4.4
	31	0.3	29.7	3.1	17.5	15.6	1.5
Aug.	14	0.0	26.7	5.0	15.0	14.7	0.0
	28	0.0	22.8	-4.4	12.2	12.5	0.0
Sept.	11	3.6	25.6	-11.7	10.0	9.7	1.7
	25	0.1	25.0	-4.4	11.1	10.8	0.0
Oct.	9	Trace	28.3	-2.2	11.7	10.8	0.0
	23	1.7	17.8	-12.8	6.1	5.8	0.3

design. Means were separated by Duncan's multiple-range test.

Results and Discussion

The TNC cycle of Nebraska sedge is similar to that of other species and follows closely the generalized cycle characterized by Humphreys (1966). Carbohydrate levels in the rhizomes were low at the beginning of the season and dropped sharply when shoot growth began. Levels of TNC in the rhizomes and shoots rose significantly during the short maturation period. Shoot TNC levels declined with the onset of shoot senescence.

Total nonstructural carbohydrate levels for shoots averaged 10.6% on May 22, the first sample date (Fig. 1), and were statistically constant until the period of full bloom. Anthesis began about

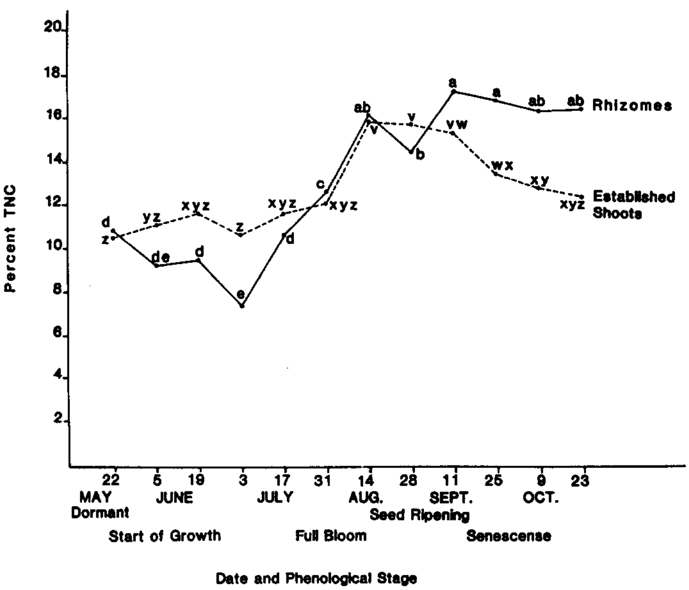

Fig. 1. *Seasonal variation in levels (expressed as percentage of dry weight) of total nonstructural carbohydrate (TNC) in established shoots and rhizomes of Nebraska sedge, as related to reproductive shoot phenology. Data points followed by the same letter within plant parts are not significantly different at the .05 level.*

July 17, and shoots were in full bloom by July 31. Shoot TNC levels reached a peak of 16% on August 14, shortly after the full bloom period, and then slowly declined to 12.5% by the final sample date (October 23).

Rhizome TNC level averaged 10.8% on May 22 (Fig. 1). It declined significantly and reached a seasonal low of 7.5% on July 3, just before the early bloom period. The rhizome TNC level rose steadily from that period until August 14, when it reached 16.1%. It reached a seasonal high of 17.4% on September 11, and then remained statistically constant. Nevertheless, a tendency of rhizome TNC levels to decline late in the growing season is seen.

Carbohydrates were transferred from rhizomes to actively growing shoots of Bigelow sedge, and rhizome reserves declined to 9.6% in the spring (Fonda and Bliss 1966). Nebraska sedge shoot TNC levels were constant, while rhizome TNC levels decreased to 7.5% during early shoot growth. Photosynthesis by the shoots was evidently insufficient for shoot growth and to replenish rhizome reserves until after the start of anthesis. Therefore, as with Bigelow sedge, depletion of rhizome TNC in Nebraska sedge early in the growing season may be due to carbohydrate translocation from rhizomes to shoots.

Total nonstructural carbohydrate levels in Nebraska sedge were lower than those reported for river sedge (Roseff and Barnard 1979), although the same analytical methods were used. While actual levels in the 2 species differed, the variations in carbohydrate levels during the growing season did not. High rhizome TNC levels (44.9%) were recorded for river sedge in the fall and low levels (29.2%) in the spring.

A significant interaction occurred between the sampling dates and the carbohydrate levels of mature shoots, rhizomes, and emerging new shoots of Nebraska sedge (Fig. 2). The new shoots

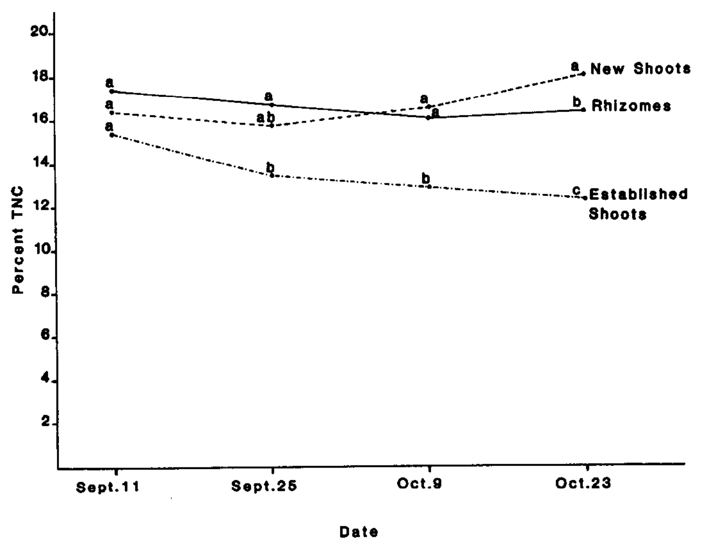

Fig. 2. *Total nonstructural carbohydrate (TNC) levels (expressed as percentage of dry weight) in new shoots, established shoots, and rhizomes of* Carex nebraskensis *from Sept. 11 through Oct. 23. Means followed by the same letter within each date are not significantly different at the .05 level.*

contained a relatively high level (16.4%) of TNC on September 11. By then, the TNC level of established shoots had begun to decline, while the rhizome TNC level was at its seasonal peak. On September 11, we found no significant differences among the TNC levels of the 3 plant parts.

On October 9, the TNC level in the new shoots was 16.6%, and that of established shoots was 12.9%, a significant difference. Rhizome TNC levels had gradually declined to 16.2%, a value similar to the level in new shoots. On October 23, TNC levels in plant parts were: new shoots—19.1% (the highest level recorded during this study), established shoots—12.5%, and rhizomes—16.3%.

The high accumulation of carbohydrates in new shoots in the late fall may account for the significant TNC decrease in established shoots. Carbohydrates appeared to be transferred to the young shoots from mature shoots and (perhaps to a lesser extent) from rhizomes. We suggest that during the fall period new shoots are carbohydrate sinks. In a concurrent study, 79 new Nebraska sedge shoots were observed September 11 through November 20, 1980. Of the new shoots 11, 27, 22, and 25% were first observed on September 11 and 25 and October 8 and 22, respectively. The other 15% were first observed on November 5 and 20. Photosynthesis by newly emerged shoots could explain their increased TNC levels, but it seems likely that such activity was minimal. The new shoots began to appear as reproductive shoots became senescent and older vegetative shoots became quiescent. Very few of those shoots (even among the earliest ones) had advanced beyond the first phenological stage by November 20. While environmental conditions following the September freeze were not prohibitive, photosynthetic activity by established shoots was clearly declining. And, there was an abundance of developing unemerged shoots.

Attaining a high concentration of TNC in the fall may be necessary for the survival of the new shoots during the winter and/or upon emergence in the spring. Data on overwinter survival of fall emerging shoots of Nebraska sedge have not yet been analyzed. However, they appear to overwinter at least as successfully as mature vegetative shoots, for which a 95% overwinter survival rate is indicated (Ratliff 1983).

Management Consideration

Based upon the results from this study we hypothesize that at Tule Meadow the optimum grazing period for maintenance of Nebraska sedge is from about mid-August to mid-September, when shoots and rhizomes attain their highest TNC levels. We suggest that it is best to not graze or defoliate Nebraska sedge until after anthesis, when seed is ripening and peak TNC levels have been reached and after the onset of senescence. Rhizome reserves are at a minimum during early shoot growth. At this point in its seasonal growth Nebraska sedge may not be able to recover from significant loss of photosynthetic tissue. This premise is supported by responses in grasses defoliated when carbohydrate reserves were low (Donart and Cook 1970). Late defoliation may adversely affect overwinter survival of fall emerging shoots by reducing TNC accumulation in those tissues.

Effects of grazing at times other than the optimum grazing period will, of course, depend upon the degree and frequency of defoliation and the regrowth opportunity for restoration of TNC reserves.

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