Total Nonstructural Carbohydrates in the Vegetation Components of a Shortgrass Prairie Ecosystem Under Stress Conditions

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Highlight: Total nonstructural carbohydrate (TNC) contents and its distribution in five above- and belowground compartments of the producer subsystem were studied under control, water, nitrogen, and water + nitrogen treatments on the native shortgrass prairie ecosystem. Results indicated that water and water + nitrogen treated plants accumulated significantly greater amounts of TNC (g • m^{-2}) in both the aboveground and belowground compartments than the control and nitrogen fertilized plants. Greater amounts of TNC in the water and water + nitrogen treatments were accumulated primarily because of greater biomass production and not as a result of greater TNC concentration (percent dry weight). Significantly greater amounts of TNc (50% and 80%) were channeled below ground than above ground in all four treatments. Stepwise multiple regression analysis indicated positive relationship between TNC (g • m^{-2}), TNC concentration (percent dry weight), and certain abiotic variables that appear to limit growth and TNC accumulation in different treatments.

The major source of energy for growth, maintenance, and regrowth in perennial grasses is considered to be residing in the carbohydrate fraction of the organic compounds. Many review articles and reports have emphasized the function of carbohydrate reserves during regrowth in the spring or following defoliation at different phenological stages and under different environmental conditions (Graber et al. 1927; May 1960; Cook 1966; Trlica and Cook 1971, 1972; White 1973; Menke 1973; Bokhari and Dyer 1974). However this subject is still controversial. Substances other than carbohydrates, such as proteins and fats, are also believed to be involved in the regrowth of grasses (Sullivan and Sprague 1943; Davidson and Milthorpe 1965). How long perennial grasses remain dependent on reserve food substances following defoliation or at the onset of spring is not fully understand. Recent studies using labeled carbon-14 (Pearce et al. 1969; Smith and Marten 1970; Bokhari 1977) have provided direct evidence of the role of carbohydrate reserves in the regrowth of many plants.

Many environmental factors such as nutrients, temperature, water, solar radiation, and photoperiod influence the magnitude of photosynthates available for current growth and for regrowth. The effect of water stress and nitrogen fertilization on carbohydrate reserves depends upon the species involved, the growth stage, and the environmental factors (Brown and Blaser 1965; Adegbola and McKell 1966; Murata 1969; Bokhari and Dyer 1974). This study was undertaken to investigate the effect of perturbed conditions, in this case, additional water and nitrogen on the distribution of carbohydrate in the above- and belowground biomass.[1]

Methods and Materials

Site Description

This study was conducted at a native shortgrass prairie site dominated by blue grama (*Bouteloua gracilis* [H.B.K.] Lag.). The site is the field research facility of the Natural Resource Ecology Laboratory, Colorado State University, located on the USDA Agricultural Research Service Central Plains Experimental Range in northeastern Colorado.

The Ecosystem Stress Area[2] (ESA) consists of four treatments of two replicates each on a 1-ha plot. These treatments include a control, a nitrogen treatment at the rate of 150 kg N · ha^{-1} as ammonium nitrate to maintain a difference of at least 50 kg · ha^{-1} of mineral nitrogen (NO_3^- + NH_4^+) between the nitrogen and the control plots, a water treatment to maintain at least -0.8 bars soil water potential at a depth of approximately 10 cm, and a water + nitrogen treatment at the rate stated above. The nitrogen treatment was initiated in the spring of 1970 and the water treatment using a sprinkler irrigation system in 1971. The water + nitrogen treatment received applications of nitrogen in the spring of 1972, 1973, and 1974 at the rate of 150, 100, and 100 kg · ha^{-1}, respectively. An additional 100 kg · ha^{-1} of nitrogen was applied to the nitrogen only treatment in 1973 and 1974.

Sampling of Biomass and TNC Determination

The aboveground herbage of each species for biomass estimation and total nonstructural carbohydrates (TNC) determination was taken every other week by clipping six 0.5 m^2 circular quadrats within each replicate of each treatment. Each species from each quadrat was separated into current live, perennial live, recent dead, and old dead compartments. Each of these compartments were pooled across the same replicate, oven dried at 60°C to a constant weight, and an aliquot was taken for TNC determination. Litter was collected from each quadrat by vacuum cleaner and recovered by water flotation and oven dried to a constant weight. Belowground plant parts were sampled by removing soil cores (10 cm deep and 7.5 cm diameter) from each of the clipped quadrats. These were separated into roots (0-5 cm and 5-10 cm) and crowns. Cores were oven dried, crushed, and separated by a cyclone seed

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[1]Data on primary production, species composition, and diversity are available in the central data library of the Natural Resource Ecology Laboratory, Colorado State University, Fort Collins.

[2]Stress is defined as "the manipulations of environmental variables to produce inputs beyond the range of normal variations that the system would encounter" (Lauenroth and Sims 1973).

cleaner, oven dried, and an aliquot was taken for TNC determination.

Total nonstructural carbohydrates were extracted by the method of Smith (1969) and their reducing power was determined by the method of Shaffer-Somogyi as outlined by Smith (1969). In the case of aboveground compartments, the TNC content for each species was weighted for the biomass it represented to calculate total TNC $\cdot$ m^{-2}). Root and crown TNC on m^2 basis were calculated by multiplying the percent TNC with their respective biomass on each sampling date. Average monthly maximum and minimum temperatures (°C), total precipitation (mm), evaporation (mm), solar radiation (ly $\cdot$ m^{-2}), and soil temperature (0-10 cm) during the 1973-1974 growing season were obtained daily at the native shortgrass prairie site. Data were analyzed statistically using a model of repeated analysis of variance testing for treatment differences and by Tukey's Q test. All results mentioning significant differences are at $P < 0.01$.

Results

TNC in the Aboveground-Live and Dead Compartments

Grasses Only

The water + nitrogen treatment accumulated significantly greater amounts of TNC in the aboveground components (live + dead) than the other treatments during 1973-1974 growing season (Table 1). Major contribution to the aboveground component from water + nitrogen treatment during 1973 was made by aboveground live materials, while in 1974 it was from the aboveground recent dead materials. The control treatment during both the study years recorded significantly lower amounts of TNC in the aboveground recent dead or the old dead materials.

Table 1. Peak standing state of TNC (g • m^{-2}) in aboveground compartments of the shortgrass prairie (grasses only) under stress conditions during 1973 and 1974 growing seasons.

Year	Treatment	Live	Recent dead	Old dead	Live + dead	Litter
1973	Control	3.0	1.7	0.6	5.3	5.1
	Water	10.3	5.3	2.5	10.1	4.1
	Nitrogen	5.2	4.6	5.0	14.8	9.2
	Water + nitrogen	30.5	16.4	8.7	55.7	10.2
1974	Control	3.4	2.3	0.9	6.6	8.5
	Water	3.9	5.0	4.6	13.5	10.7
	Nitrogen	3.1	3.9	2.9	9.1	11.3
	Water + nitrogen	12.6	20.8	5.1	38.5	23.3

Figure 1 gives the seasonal dynamics of TNC in the aboveground-live compartment from the four treatments during the 1973 growing season. At the final harvest the control treatment exhibited about 300% increase in its TNC contents over the initial values. The water treatment had about 20 times more TNC at the end of growing season than at the beginning of the growing season. The TNC of the nitrogen treatment increased from the initial value of 0.9 g $\cdot$ m^{-2} to a maximum of 5.2 g • m^{-2} at the end of the growing season. The water + nitrogen treatment indicated over a 300% increase in TNC toward the end of the growing season over that of the early growing season. The average contents of TNC were 2.0, 7.1, 3.0, and 18.6 g • m^{-2} from the control, water, nitrogen, and water + nitrogen treatments, respectively.

The average seasonal TNC in the standing dead compartment from the control, water, nitrogen, and water + nitrogen treatments were 0.6, 2.5, 1.2, and 9.0 g $\cdot$ m^{-2} respectively

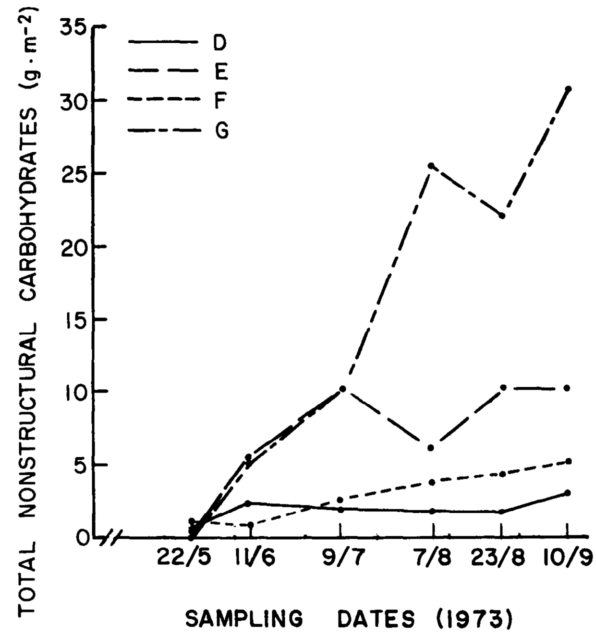

Fig. 1. *Total nonstructural carbohydrates (TNC, g · m^{-2}) in the aboveground-live compartment of grasses from the control —, water — —, nitrogen ----, and water + nitrogen —-— treatments during 1973 growing season.*

(Fig. 2). The control treatment at the end of growing season had about 190% more TNC in standing dead compartments than at the beginning of the growing season. The water treatment indicated about 110% increase in TNC between the beginning and the end of the growing season. The nitrogen treatment had about 10 times more TNC in the standing dead compartment at the end of the growing season than at the beginning. The water + nitrogen treatment contained greater amounts of TNC at the beginning and end of the growing season than the rest of the three treatments. The TNC of both the water and water + nitrogen treatments exhibited two distinctive peaks during the growing season.

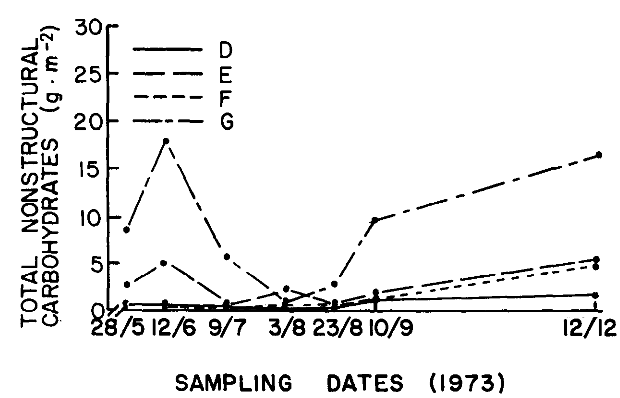

Fig. 2. *Total nonstructural carbohydrates (TNC, g · m^{-2}) in the aboveground-standing dead compartment of grasses from the control —, water — —, nitrogen ----, and water + nitrogen —-— treatments during 1973 growing season.*

Grasses + Forbs + Shrubs

In the preceding section, the distributional pattern of TNC was presented only through the grasses because in terms of biomass and energy flow, grasses are the most important constituents of shortgrass prairie ecosystem. Forbs and shrubs along with grasses are discussed in this section to investigate their contribution to the total TNC pool and compartmentalization in a shortgrass prairie ecosystem. Forbs and shrubs are usually not considered very important in an otherwise dominant grass community, but in terms of energy flow (TNC distribution) or nutrient cycling, they may be playing an important role because their wood structure may be prolonging the residence time of TNC in these structures.

Table 2. Peak standing state of TNC (g • m^{-2}) in the aboveground compartments (grasses + forbs + shrubs) under stress conditions during 1973 and 1974 growing seasons.

Year	Treatment	Current live	Perennial live	Recent dead	Old dead	Live + dead
1973	Control	14.6	9.7	9.3	2.8	36.4
	Water	15.7	9.1	8.7	5.8	39.3
	Nitrogen	23.5	5.9	7.1	1.4	37.9
	Water + nitrogen	33.8	5.3	20.3	20.6	80.0
1974	Control	4.5	11.3	3.8	3.3	23.0
	Water	8.8	7.3	7.3	5.1	28.4
	Nitrogen	4.9	8.6	4.9	3.6	21.9
	Water + nitrogen	21.1	6.8	27.0	7.8	62.7

The control and water treatments during 1973 exhibited identical amounts of peak TNC in the current and perennial live compartments (Table 2). Peak TNC in the current live compartment from nitrogen and water + nitrogen treatments were significantly greater than from the control or the water treatments. During 1974 the water + nitrogen treatment accumulated significantly greater amounts of TNC in the current live compartment than did the rest of the three treatments. On the other hand, the control treatment during the same year had slightly greater contents of TNC in its perennial live compartments than did the other treatments. The peak TNC in the recent dead compartments from the water + nitrogen treatment during both the study years had significantly greater amounts of TNC than the rest of the three treatments. The old dead compartment from the water + nitrogen treatment during 1973 contained significantly more TNC than that from the other three treatments, but in 1974 the TNC from the same treatment were slightly greater than that from the rest of the treatments during the same year.

The seasonal average contents of TNC in the aboveground-live (current live + perennial live) compartment of grasses + forbs + shrubs from the control, water, nitrogen, and water + nitrogen treatments (Fig. 3) were 9.7, 15.2, 11.3, and 24.7 g · m^{-2}, respectively.

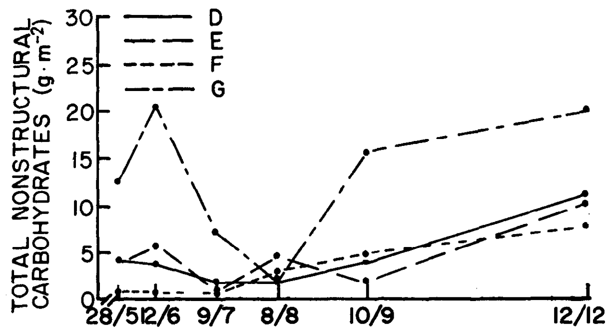

Fig. 4. *Total nonstructural carbohydrates (TNC, g · m^{-2}) in the aboveground-standing dead compartment of grasses + forbs + shrubs from the control —, water — —, nitrogen ----, and water + nitrogen —— treatments during 1973 growing season.*

At the beginning of the growing season, there were greater contents of TNC in the standing dead (recent + old) from the control and water treatments than at the mid-growing season (Fig. 4). The TNC contents of standing dead from nitrogen treatment increased from a minimum of 0.7 g · m^{-2} at the start of the growing season to a maximum of 7.8 g ·m^{-2} at the end of the growing season. The water + nitrogen treatment had 12.4 g · m^{-2} TNC in its standing dead at the onset of the growing season, which increased to 20.5 g · m^{-2} during the next sampling date, followed by a decline during the mid-growing season (1.9 g · m^{-2}). Average seasonal contents of TNC in standing dead from the control, water, nitrogen, and water + nitrogen treatments were 4.3, 4.5, 3.0, and 13.0 g · m^{-2}, respectively (Fig. 4).

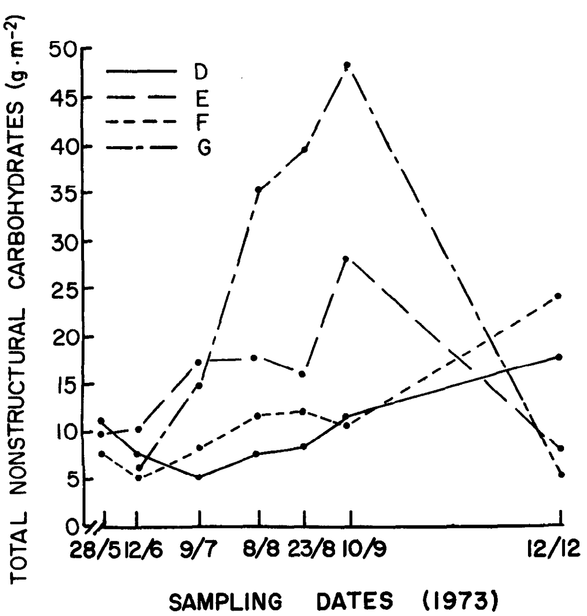

Fig. 3. *Total nonstructural carbohydrates (TNC, g · m^{-2}) in the aboveground-live compartment of grasses + forbs + shrubs from the control—, water——, nitrogen----, and water + nitrogen——— treatments during 1973 growing season.*

TNC in the Aboveground-Litter Compartments

Peak TNC contents in the litter compartments from the four treatments represent contributions by grasses + forbs + shrubs. No distinction could be made between the percent contribution to litter compartment by species or by functional groups. During 1973 the control and water treatments had almost identical peak content of TNC but significantly less than the water + nitrogen or the nitrogen (Table 1) treatments. The latter two treatments contained similar amounts of TNC in their respective litter compartment. During the 1974 growing season there was no difference in TNC of litter from the control, nitrogen, and water treatments but the water + nitrogen treatment accumulated significantly greater amounts of TNC than the rest of the three treatments.

Peak TNC contents in litter from different treatments did not occur at the same time (Fig. 5). The nitrogen and water + nitrogen treatments had greater amounts of TNC in their litter compartments at the beginning and end of

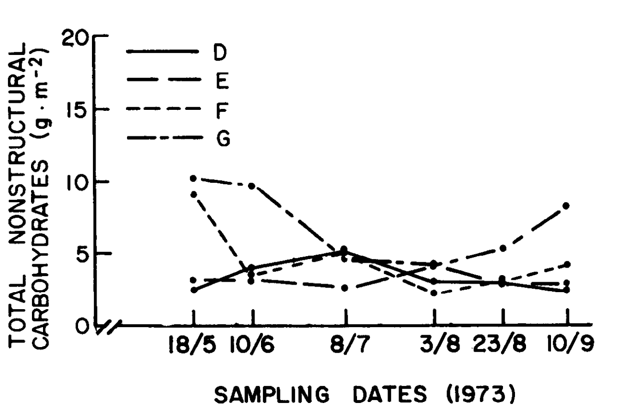

Fig. 5. *Total nonstructural carbohydrates (TNC, g · m^{-2}) in the litter compartment from the control —, water — —, nitrogen- - - -, and water + nitrogen — - — treatments during 1973 growing season.*

the growing season than that of the mid-growing season with 4.4 and 7.0 g $\cdot m^{-2}$ as the seasonal average content of TNC, respectively. On the other hand the litter from control and water treatments had minimum contents of TNC at the beginning and end of growing season with 3.2 and 3.1 g $\cdot$ m^{-2} as the seasonal average content of TNC, respectively.

TNC in the Belowground Compartments

The TNC in the belowground compartments represent contributions by all plant species, i.e., grasses + forbs + shrubs, because it was not possible to separate the crowns or root biomass by species.

Generally, there was no difference between the amounts of TNC in the belowground compartments from different treatments during 1973, except for the water treatment which exhibited slightly greater amounts (Table 3). During

Table 3. Peak standing state of TNC (g • m^{-2}) in the belowground compartments of shortgrass prairie under stress conditions during 1973 and 1974 growing seasons.

Year	Treatment	Root	Crown	Root+ crown
1973	Control	20.7	25.9	46.6
	Water	22.4	33.6	56.0
	Nitrogen	27.3	19.2	46.5
	Water + nitrogen	27.6	21.0	48.6
1974	Control	24.2	20.4	44.6
	Water	23.4	27.5	50.9
	Nitrogen	27.1	24.8	51.9
	Water + nitrogen	32.4	24.8	57.2

1973 growing season, the control and water treatments accumulated almost identical amounts of TNC in roots. Similarly, the nitrogen and water + nitrogen treatments recorded identical amounts of TNC in their roots during 1973 growing season. There was no significant difference between the TNC contents of crowns from all the treatments during the 1974 growing season. The TNC in roots (Fig. 6) for control, water, nitrogen, and water + nitrogen treatments indicated about 120%, 30%, 100%, and 195% increases respectively between the beginning and end of the growing season.

TNC in crown (Fig. 7) recorded increases of 116%, 110%, 111%, and 162% from the control, water, nitrogen, and water + nitrogen treatments respectively during the 1973 growing season. Seasonal average contents of TNC in roots

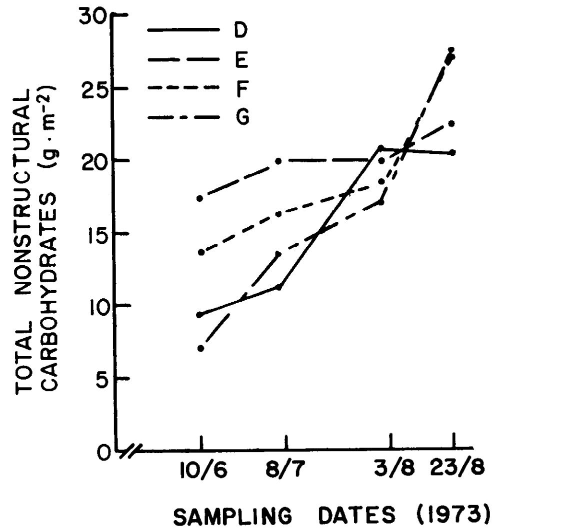

Fig. 6. *Total nonstructural carbohydrates (TNC, g · m^{-2}) in the below-ground-root compartment from control —, water — —, nitrogen - - - -, and water + nitrogen — - — treatments during 1973 growing season.*

from the control, water, nitrogen, and water + nitrogen treatments were 15.5, 19.8, 18.9, and 16.3 g $\cdot m^{-2}$, and in the crowns these amounted to 20.6, 26.0, 13.5, and 16.2 g $\cdot m^{-2}$, respectively.

Contribution to TNC by Different Compartments

Grasses

The contribution by belowground compartments to total TNC varied between treatments. Generally there was a greater contribution by the belowground compartments from the control (70%-80%), water (60%-70%), and nitrogen (70%) treatments than that from the water + nitrogen (40%-50%) treatment during 1973 and 1974 growing season. The contribution by aboveground compartments to total TNC ranged from a minimum of 9% (control in 1973) to a maximum of 48% (water + nitrogen in 1973). The contribution to total TNC by the aboveground compart-

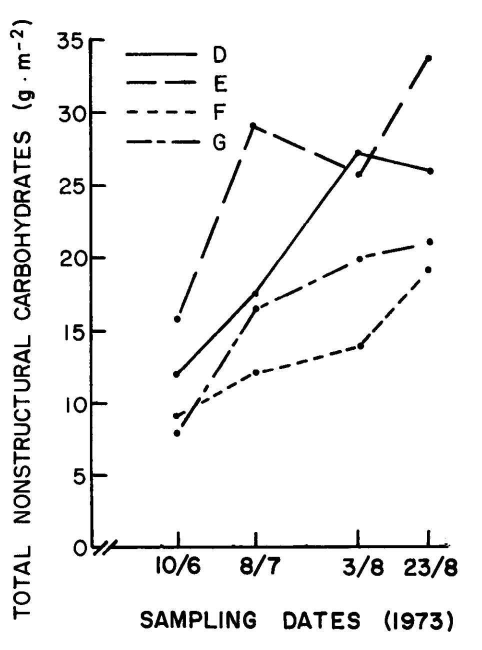

Fig. 7. *Total nonstructural carbohydrates (TNC, g · m^{-2}) in the below-ground-crown compartment from control —, water — —, nitrogen - - - -, and water + nitrogen — - — treatments during 1973 growing season.*

ment from control treatment was almost identical during both the study years. The contribution by aboveground compartments from water and water + nitrogen treatments ($g \cdot m^{-2}$) was significantly greater during both the study years than the rest of the treatments.

Contribution by litter compartment to total TNC varied from 5% (water in 1973) to 20% (water + nitrogen in 1974).

Grasses + Forbs + Shrubs

The major contribution by forbs and shrubs to the TNC contents of aboveground live compartments was from the control and nitrogen treatments in 1973 and from the water + nitrogen treatment in 1974. Their contribution to the live compartment in these treatments ranged from 11.0 $g \cdot m^{-2}$ (control to 18.3 $g \cdot m^{-2}$ (nitrogen in 1973 and about 8.5 $g \cdot m^{-3}$ (water + nitrogen) in 1974.

The perennial live compartment represented additional TNC contribution by forbs and shrubs which ranged from 5.3 $g \cdot m^{-2}$ (water + nitrogen, 1973) to 11.3 $g \cdot m^{-2}$ (control, 1974). There was also significant contribution by forbs and shrubs to the TNC in recent dead and old dead compartments. The overall contribution by forbs and shrubs to the aboveground compartment from the different treatments ranged from 21.3 $g \cdot m^{-2}$ (water) to 31.1 $g \cdot m^{-2}$ (control) in 1973 and from 12.7 $g \cdot m^{-2}$ (nitrogen) to 24.2 $g \cdot m^{-2}$ (water + nitrogen) in 1974. During 1973 growing season forbs and shrubs contributed from 9% (water + nitrogen) to 32% (control) TNC to the aboveground biomass and from 11% (water + nitrogen) to 19% (control) during 1974 growing season. The greater contribution by the belowground compartments to the total TNC from grasses alone (Table 1) was slightly upset (Table 2) because of the contribution by forbs and shrubs to the TNC in the aboveground compartments.

Discussion

The total nonstructural carbohydrate content in several above- and belowground compartments of grasses and grasses + forbs + shrubs indicated significant intertreatment and interseasonal variations. The belowground compartments always stored greater amounts of TNC ($g \cdot m^{-2}$) than the aboveground compartments. Belowground net production of TNC in grasses varied from 40% (water + nitrogen) to 75% (control) in 1974. The water + nitrogen treatment stored comparatively smaller amounts of TNC in belowground compartments and greater amounts in aboveground compartments than did the other three treatments. The greater amounts of TNC ($g \cdot m^{-2}$) in the aboveground compartments of water + nitrogen treatments could be attributed to the greater biomass production, not to greater concentration of TNC (per gram dry weight basis). For example, during the 1973 growing season the average weight percent TNC (per gram dry weight basis) in the aboveground-live compartment from the control, water, nitrogen, and water + nitrogen treatments was 8.2, 7.0, 8.0, and 6.5, respectively. The smaller amounts of TNC ($g \cdot m^{-2}$) in the belowground compartments of water + nitrogen treatments (42%-48%) as compared to the other three treatments (60%-80%) could also be caused by greater utilization of TNC by the excessive growth rate of aboveground parts resulting in excessive accumulation of aboveground biomass. For example, the aboveground net production (ANP) of grasses in the water + nitrogen treatment was 475 and 387 $g \cdot m^{-2}$) in 1973 and 1974, respectively. At the same time, the ANP in the control treatment was 58 $g \cdot m^{-2}$ in 1973 and 40 $g \cdot m^{-2}$ in 1974.

Interseasonal variations between the control and the nitrogen treatments as well as between the water and the water + nitrogen treatments could be attributed to seasonal variations in the abiotic factors. For example, the TNC in the aboveground live compartment from the control treatment is expressed by a linear combination of annual precipitation, actual evaptranspiration, and mean annual solar radiation according to the following regression:

$$\hat{Y} = -7.166 + 0.058\ X_1 - 1.802\ X_2 + 0.044\ X_3$$

where $\hat{Y}$ is the peak TNC content in aboveground live ($g \cdot m^{-2}$), X_1 is the annual precipitation (mm), X_2 is the annual actual evapotranspiration (mm), and X_3 is the mean annual solar radiation ($ly \cdot m^{-2}$). A total of 67% variability ($R = 0.823$, $P < 0.01$, *SE* of estimate 0.97) in TNC of aboveground live compartment is explained by the above three factors. On the other hand, more than 53% variability ($R = 0.725$, $P = 0.01$, *SE* of estimate 4.28) in the TNC content of aboveground live compartment of water treatment is explained by a combination of minimum air temperature (°C) and mean annual solar radiation ($ly \cdot m^{-2}$), according to the following regression:

$$\hat{Y} = 284.243 + 10.412\ X_1 + 0.021\ X_2$$

where $\hat{Y}$ is TNC ($g \cdot m^{-2}$) in aboveground live, X_1 is air temperature, and X_2 is mean annual solar radiation.

The example of the control treatment indicates that water, solar radiation, and evapotranspiration are important factors for biomass and TNC production in a shortgrass prairie ecosystem. When water is nonlimiting, other factors, such as temperature and solar radiation as in the case of the water treatment, become important factors.

In the case of the nitrogen only treatment, about 60% variability ($R = 0.768$, $P < 0.01$, *SE* of estimate 2.07) in TNC content of aboveground live materials is explained according to the following regression.

$$\hat{Y} = 2.905 - 1.475\ X_1 + 0.005\ X_2 + 0.254\ X_3$$

where $\hat{Y}$ is TNC ($g \cdot m^{-2}$), X_1 is annual actual evapotranspiration, X_2 is annual solar radiation ($ly \cdot m^{-2}$), and X_3 is mean annual soil temperature (°C).

In the case of the water + nitrogen treatment about 68% variability ($R = 0.829$, $P < 0.001$, *SE* of estimate 8.49) is explained only by solar radiation according to the following regression:

$$\hat{Y} = 116.577 - 0.172\ X_1$$

where $\hat{Y}$ is TNC ($g \cdot m^{-2}$) and X_1 is solar radiation ($ly \cdot m^{-2}$). The last two examples indicate the importance of water (in the case of nitrogen treatment) and solar radiation (in the case of water + nitrogen treatment). When water and nutrients (in this case, nitrogen) are not limiting, other factors such as solar radiation or soil temperature appear to play an important role in the production of dry matter (e.g., TNC) in a shortgrass prairie ecosystem.

Many investigators (Viets 1962; Wight and Black 1972; Lauenroth and Sims 1973) have reported that fertilization frequently increases water use-efficiency of native and cultivated plants when water is nonlimiting. Positive correlations between rainfall and forage production have been reported in a number of plant communities (Thomas and Osenberg 1964; Wight and Black 1972). Seasonal variations in yield of blue grama and other shortgrass prairie species have been attributed mainly to rainfall patterns (Rogler and Haas 1947; Noller 1968; Hyder et al. 1975).

In the native shortgrass prairie, production is usually limited by water and nutrient availability (Klipple and Retzer 1959; Lauenroth and Sims 1973). Decreasing soil or leaf water potentials generally result in reduced photosynthetic rates, largely as a result of stomatal closure (Boyer 1971; Hsiao 1973). Additional amounts of water and nutrients increase photosynthetic capacity (leaf area) and thus provide an effective sink for utilization of TNC. The native shortgrass prairie site where this study was conducted is dominated by blue grama, a C_4-species which is usually considered an efficient water utilizer (Downes 1969; Slatyer 1970; Black 1971). Plants with C_4-photosynthetic pathway are generally considered to maintain higher rates of net photosynthesis (Black 1973) than those with C_3-pathway.

In the present study, the increase in TNC of water and water + nitrogen treatments was believed to be caused by greater biomass production and not by greater concentrations of TNC, because TNC concentrations in the above- or belowground parts of these plants were either lower or similar to those of other treatments. Drought or water-stressed conditions were believed to increase carbohydrate reserves in many grass species (Brown and Blaser 1965; Blaser et al. 1966) while others reported that drought decreased carbohydrate reserves (Bukey and Weaver 1939; Dina and Klikoff 1973). Similarly, many reports (Prianishnikov 1951; Drake et al. 1963; Colby et al. 1965) indicated that nitrogen fertilization reduced the carbohydrate concentration of a number of plants, a fact that had been attributed to increased utilization of the carbon skeleton for amino acid and protein synthesis. On the other hand, Adegbola and McKell (1966), Murata (1969), and Bokhari and Dyer (1974) reported that nitrogen fertilization increased carbohydrate reserves in many grasses.

The results of this study indicate that generally a significant amount of photosynthates is channeled below ground because of greater accumulation of belowground biomass and not necessarily because of greater concentrations of TNC. For example, the percent TNC (per gram dry weight basis) during 1973 was 2.2, 3.0, 2.8, and 2.3 in the roots from the control, water, nitrogen, and water + nitrogen treatments, respectively. The difference between the control and nitrogen treatments and the water and water + nitrogen treatments is that, in the case of water and water + nitrogen treatments, most of the available carbohydrates are utilized above ground for support of aboveground biomass and proportionately a smaller amount of assimilates (TNC) are translocated below ground.

The relationship between TNC concentration (percent dry weight) in aboveground live materials and abiotic factors was evaluated using stepwise multiple regression analysis. This relationship for the control treatment is expressed according to the following regression:

$$\hat{Y} = 76.82 + 4.24\ X_1 + 0.03\ X_2 - 2.55\ X_3$$

where $\hat{Y}$ is TNC (percent dry weight), X_1 is mean annual maximum temperature (°C), X_2 is mean annual precipitation (mm), and X_3 is soil temperature (°C). About 82% variability ($R = 0.907$, $P < 0.001$, SE of estimate 1.35) in TNC of aboveground live materials of control treatment can be explained by the above three factors.

On the other hand, about 66% variability ($R = 0.81$, $P < 0.001$, SE of estimate 0.91) in TNC (percent dry weight) of aboveground live materials from the water + nitrogen treatment is explained by mean annual maximum temperature and evapotranspiration according to the following regression:

$$\hat{Y} = 19.35 - 0.32\ X_1 - 0.29\ X_2$$

where $\hat{Y}$ is TNC (percent dry weight), X_1 is mean annual temperature (°C), and X_2 is evapotranspiration (mm).

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