Nitrogen and Carbohydrate Partitioning in 'Caucasian' and 'WW-Spar' Old World Bluestems

B.I. COYNE AND J.A. BRADFORD

Abstract

Total nonstructural carbohydrates (TNC) and nitrogen (N) in 'WW-Spar' *(Bothriochloa ischaemum)* and 'Caucasian' *(B. caucasica)* Old World bluestems were monitored in field experiments during spring-summer and summer-fall growth cycles. The objectives were to determine seasonal partitioning of TNC and N among biomass compartments and to determine relationships between concentrations and pool sizes of TNC and N in the perennating storage organs (stem bases and roots). Average TNC concentrations during the growing season were highest in the leaf sheaths and enclosed stems followed by leaf blades>stem bases >roots. Total TNC was highest in the roots>stem bases>stem plus sheaths>leaf blades. Average N concentrations were highest in the leaf blades> roots>stems plus sheaths>stem bases while the rank for total N was root>stem base>leaf blade>stems plus sheaths. Thus, the perennating organs (stem bases, roots) represented the largest reservoirs for both TNC and N reserves. Reserve cycles were similar in both grass species. Differences were primarily in the perennating organs as WW-Spar bluestem stored more TNC and N in stem bases and Caucasian bluestem stored more of both constituents in roots

It is often assumed that plant vigor is related to TNC and N reserves and that management of forage-based livestock production systems can be keyed to reserve cycles. Therefore, we sought to answer the question of whether concentrations alone could adequately predict relative vigor or whether pool sizes must be known. Our analysis showed that concentrations tracked pool sizes of TNC extremely well in the roots, but that the relationship was not as strong in the stem bases. The relationship for N concentration and total N was highly significant for roots, but not as good as for TNC. Concentrations of N were not good predictors of total N in stem bases. Fluctuations in total N were much greater than for concentration. Although nitrogen-use efficiency increased linearly with season, N investment per unit leaf blade area declined. This suggested that nitrogen limitation was the main cause for reduced rates of increase in TNC-use efficiency during the last third of the first growing cycle. This was a time when TNC investment per unit leaf blade area was increasing. In these Old World bluestems, management decisions related to plant vigor can apparently be keyed to TNC concentrations thereby eliminating the more laborious tasks required to determine TNC pool sizes. Further study is necessary to determine the feasibility and economics of using nitrogen fertilizer applications in the final third of a growing cycle to reverse the loss in leaf TNC-use efficiency observed in this study.

Key Words: *Bothriochloa caucasica, B. ischaemum,* total nonstructural carbohydrates, nitrogen and carbohydrate reserves, specific leaf weight

Reserve constituents [primarily total nonstructural carbohydrates (TNC), but also nitrogen (N)] of both desirable and undesirable perennial plant species have long been considered important indices to guide the application vegetation management alternatives with respect to timing, frequency, and rate. A voluminous literature that details annual cycles in TNC concentrations and the interpretation of these cycles in the context of grazing management (range readiness, season and intensity of use, etc.) and improvement of the vegetative cover (weed and brush control, changes in botanical composition) dates from the 1920s. Concentrations of TNC or N can be misleading because changes in their values can result from gains or losses in biomass of the storage compartment, while absolute quantities of these constituents remain fairly constant and vice versa. For example, Santos and Trlica (1978) reported concentrations of TNC in the crowns and roots of blue grama *(Bouteloua gracilis)* were minimally affected by clipping treatments but were reduced in western wheatgrass *(Agropyron smithii).* However, TNC pool sizes were reduced in both species because crown and root biomass responded negatively to clipping.

Because of shortcomings associated with interpretations of concentration data, Priestly (1962), and more recently Caldwell (1984), have properly emphasized the importance of measuring total quantities of reserve constituents rather than just concentrations. In addition, Caldwell (1984) has demonstrated that the importance of reserve pools has perhaps been overstated. Not only can large changes in concentration show little correlation to changes in pool size, the actual size of a reserve pool may be quite small compared with the daily production of photosynthate. For example, the entire carbon pool in the shoots of winterfat *(Ceratoides lanata),* a suffrutescent desert species, was calculated to represent 1 day of photosynthetic fixation in the spring. The total net change of this pool during the spring cycle of depletion and replenishment was equivalent to only 3 to 4 hours of maximum photosynthesis during the spring. Data such as these led Caldwell to propose that reserve pools might better be perceived as buffers rather than reservoirs.

The objectives of this study were to document the seasonal partitioning of TNC and N among the various above- and belowground tissues of 'WW-Spar' *(Bothriochloa ischaemum)* and 'Caucasian' *(B. caucasica)* Old World bluestems and to determine the relationships between concentrations and pool sizes of TNC and N in the perennating storage organs (stem bases, roots).

Materials and Methods

Plant Materials and Culture

Above- and belowground biomass of Caucasian (Accession WW-758) and WW-Spar (WW-573) bluestems growing as monocultures in the field (randomized complete block design with 8 blocks) were sampled repetitively during the 1983 growing season. Plant culture and biomass sampling methods and soil moisture levels were previously described by Coyne and Bradford (1986). Five biomass or tissue fractions (leaf blade, leaf sheath plus enclosed stem, exposed stem plus inflorescence, stem base, and roots to a depth of 1.2 m) were analyzed to determine the concentrations of total nonstructural carbohydrates (TNC) and nitrogen (N). Pool sizes of these nutrients were calculated as a product of the concentrations and the quantity of biomass in each fraction (from Coyne and Bradford 1986) and expressed on a per plant basis. Per plant values divided by 0.0929 m^2 $plant^{-1}$ converts the data to a unit land area basis. Root and stem base values were converted to an ash-free basis.

Field Sampling Scheme

The growing season was divided into spring-summer and summer-fall growth cycles (hereafter cycle 1 and cycle 2, respectively). Blocks 1 through 4 were used for cycle 1 and blocks 5 through 8 (which grew undisturbed during cycle 1) were used for

Authors are plant physiologists, Fort Hays Experiment Station, Kansas State University, Hays 67601 and Southern Plains Range Research Station, USDA/ARS, 2000-18th Street, Woodward, Oklahoma 73801, respectively.

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cycle 2. After spring growth initiation (11 April 1983), plants were sampled 12 times during cycle 1: 18 April; 2, 9, 16, 23 May; 1, 6, 13, 20, 27 June; and 5, 11 July. Cycle 2 was initiated by mowing the plots to a uniform stubble height of 50 mm on 14 July 1983 and plants were subsequently sampled 9 times: 14 July; 1, 15, 22, 30 August; 9, 19, 29 September; and 10 October. Two plants per plot (block) were sampled for each grass at each sample date.

Laboratory Analyses

Lyophilized biomass samples were ground in a cyclone sample mill (0.5-mm screen) and stored in plastic vials until analyzed further. TNC was digested by a dual enzyme (glucoamylase and mycolase) method and the reducing power of the digest was determined by copperiodometric titration (Khaleeluddin and Bradford 1986). Nitrogen was determined by Hach's Digesdahl H_2O_2-H_2SO_4 digestion method (Hach Agricultural Division, P.O. Box 907, Ames, Iowa 50010) using bovine serum albumin and NBS standard reference material (No. 1573, tomato leaves) for calibration.

Data Analysis

Measured and calculated parameter differences between Caucasian and WW-Spar bluestems were determined by analysis of variance within a growth cycle using a split plot in time model (Steel and Torrie 1960). Unit leaf, unit nitrogen, and unit TNC rates were derived using the methods of Hunt and Parsons (1974) as previously described (Coyne and Bradford 1985). Basically, the unit rates measure the rate of biomass production per unit leaf area, nitrogen, and TNC, respectively.

Results and Discussion

Total Nonstructural Carbohydrates (TNC)

Seasonal trends in TNC concentrations (Fig. 1) were similar in both WW-Spar and Caucasian bluestems. Across dates, WW-Spar bluestem had higher concentrations of TNC in the stem plus leaf sheath fraction in cycle 1 and in all fractions except leaf blades in cycle 2 than did Caucasian bluestem (Table 1). TNC concentration cycles in the storage organs (stem bases, roots) exhibited a pattern that is commonly described (Trlica 1977) as "U" shaped in which concentrations declined concurrently with the initiation of spring growth and remained low until about half way through cycle 1 when inflorescences were beginning to appear. Conversely, a "V" shaped cycle was observed in cycle 2, which probably resulted from precipitation-irrigation events (Coyne and Bradford 1986). Reserves declined rapidly during cycle 2 after the grasses had been clipped to a 50 mm stubble height. Then TNC immediately increased rapidly, eventually leveled off, but retained a positive slope throughout the rest of the cycle. The vertex of the "V" (Fig. 1d,e, day 227) and the late season increase in TNC of stem bases and roots (day 262) coincided with soil moisture recharge following dry periods.

The relative rank in mean TNC concentrations (Table 1) among the 5 biomass compartments was stem plus sheath>leaf blade> stem base>root>stem plus inflorescence for both species and cycles. High TNC concentrations were retained in nonperennating organs (stems, blades, sheaths) until the final sample date (10 October) when the plants were becoming quiescent. Translocation of TNC to stem bases and roots evidently occurred well after frost in WW-Spar and Caucasian bluestems as found in other grasses (Dewald and Sims 1981, McKendrick et al. 1975, Rains et al. 1975) and fall grazing practices must recognize the potential for removing reserve resources prior to their transfer to storage sites.

Although TNC concentrations in the leaf blades and stems plus sheath peaked early in cycle 1 (Fig. 1a, b), absolute quantities of TNC continued to increase throughout the cycle (Fig. 2a,b) because concurrent increases in biomass allocation to these compartments more than offset the dilution of TNC. Conversely, trends in TNC pool size for roots and stem bases (Fig. 2d, e) were quite similar to those for TNC concentration (Fig. 1d,e). In general, species differences in TNC pool sizes (Table 2) paralleled

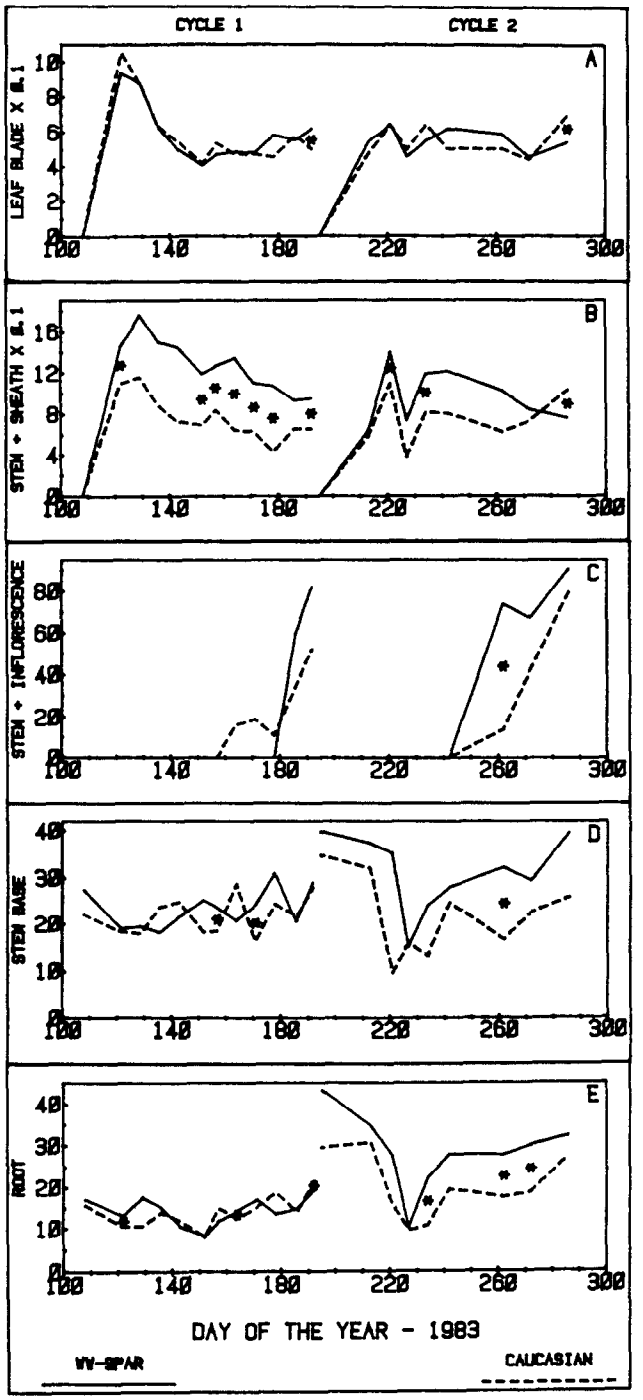

Fig. 1. *Total nonstructural carbohydrate concentrations (mg g^{-1}) in five tissue compartments in WW-Spar and Caucasian bluestems during two growing cycles. Asterisks denote significant differences ($P<0.05$) between species within dates. Note that Subfigs. A and B are scaled.*

those in concentration (Table 1).

A discontinuity can be noted in both concentration (Fig. 1d, e) and total (Fig. 2d, e) TNC in stem bases and roots in the transition from cycle 1 to cycle 2. Biomass also showed this same pattern (Coyne and Bradford 1986), which explains the discontinuity in pool size but not concentration. None of the parameters measured suggested an explanation for this aberration in concentration and it may be due to physical differences between blocks 1–4 used for cycle 1 and blocks 5–8 used for cycle 2.

If we assume that plant vigor is related to TNC, a practical

Table 1. Mean concentrations of total nonstructural carbohydrates (TNC) and nitrogen (N) in five tissue compartments in WW-Spar and Caucasian bluestems during two growth cycles.[1]

Parameter	Cycle 1			Cycle 2		
	WW-Spar	Caucasian	P>F	WW-Spar	Caucasian	P>F
TNC concentrations (mg g^{-1}):						
Leaf blade	55.48	56.82	0.78	46.95	47.92	0.73
Stem + sheath	112.08	70.23	0.01	81.75	63.87	0.05
Stem + inflorescence	7.28	11.18	0.31	28.37	15.27	0.02
Stem base	23.17	21.78	0.70	30.94	22.47	0.03
Root	14.10	13.89	0.72	28.94	20.35	0.16
N concentrations (mg g^{-1}):						
Leaf blade	15.00	15.60	0.51	12.37	13.76	0.25
Stem + sheath	7.34	8.52	0.30	5.29	6.20	0.14
Stem + inflorescence	1.10	2.24	0.07	4.28	2.31	0.07
Stem base	4.93	5.13	0.66	4.31	3.98	0.35
Root	8.61	10.35	0.04	7.39	7.55	0.24

[1]Sample size ranged from 38 to 45 in cycle 1 and 29 to 31 in cycle 2 depending on the presence of a compartment in the early years of growth or regrowth. To compare species for a particular parameter within cycles, P>F is the probability of a type I error.

Table 2. Mean pool sizes of total nonstructural carbohydrates (TNC) and nitrogen (N) in five tissue compartments in WW-Spar and Caucasian bluestems during two growth cycles.[1]

Parameter	Cycle 1			Cycle 2		
	WW-Spar	Caucasian	P>F	WW-Spar	Caucasian	P>F
TNC (g $plant^{-1}$):						
Leaf blade (TNCb)	0.69	0.78	0.04	0.40	0.30	0.03
Stem + sheath (TNCss)	0.75	0.74	0.85	0.73	0.32	0.01
Stem + inflorescence (TNCsi)	0.01	0.01	0.44	0.06	0.03	0.29
Stem base (TNCsb)	0.94	0.54	0.01	1.20	0.53	0.03
Total aboveground (TNCag)	2.42	2.09	0.01	2.35	1.22	0.02
Total root (TNCr)	1.84	1.73	0.19	4.39	3.05	0.16
Total plant (TNCp)	4.21	3.80	0.05	6.79	4.25	0.09
TNC partitioning ratios (g g^{-1}):						
TNCb/TNCp	0.17	0.21	0.16	0.07	0.08	0.23
TNCss/TNCp	0.13	0.14	0.36	0.11	0.08	0.02
TNCsi/TNCp	0.00	0.00	0.39	0.01	0.01	0.36
TNCsb/TNCp	0.24	0.16	0.03	0.18	0.12	0.00
TNCag/TNCp	0.54	0.51	0.14	0.36	0.29	0.02
TNCr/TNCp	0.46	0.49	0.14	0.64	0.72	0.02
N (g $plant^{-1}$):						
Leaf blade (Nb)	0.17	0.20	0.02	0.10	0.07	0.05
Stem + sheath (Nss)	0.04	0.06	0.01	0.05	0.02	0.17
Stem + inflorescence (Nsi)	0.00	0.00	0.97	0.01	0.00	0.03
Stem base (Nsb)	0.19	0.13	0.02	0.16	0.09	0.02
Total aboveground (Nag)	0.42	0.39	0.10	0.32	0.18	0.02
Total root (Nr)	1.11	1.29	0.03	1.13	1.16	0.13
Total plant (Np)	1.54	1.67	0.02	1.47	1.32	0.01
N partitioning ratios (g g^{-1}):						
Nb/Np	0.12	0.13	0.63	0.07	0.06	0.23
Nss/Np	0.02	0.03	0.05	0.03	0.02	0.37
Nsi/Np	0.00	0.00	0.66	0.01	0.00	0.01
Nsb/Np	0.13	0.08	0.01	0.11	0.07	0.07
Nag/Np	0.28	0.24	0.05	0.22	0.15	0.05
Nr/Np	0.72	0.76	0.05	0.78	0.85	0.05
Investment per unit leaf blade area (g m^{-2}):						
Specific leaf nitrogen	0.73	0.74	0.73	0.64	0.67	0.69
Specific leaf TNC	2.75	2.77	0.94	2.50	2.46	1.00
Specific leaf weight	46.53	47.61	0.64	45.79	42.27	0.18

[1]Sample size ranged from 34 to 45 in cycle 1 and 28 to 31 in cycle 2 depending on the presence of a particular compartment in the early stages of growth or regrowth. To compare species for a particular parameter within cycles, P>F is the probability of a type I error.

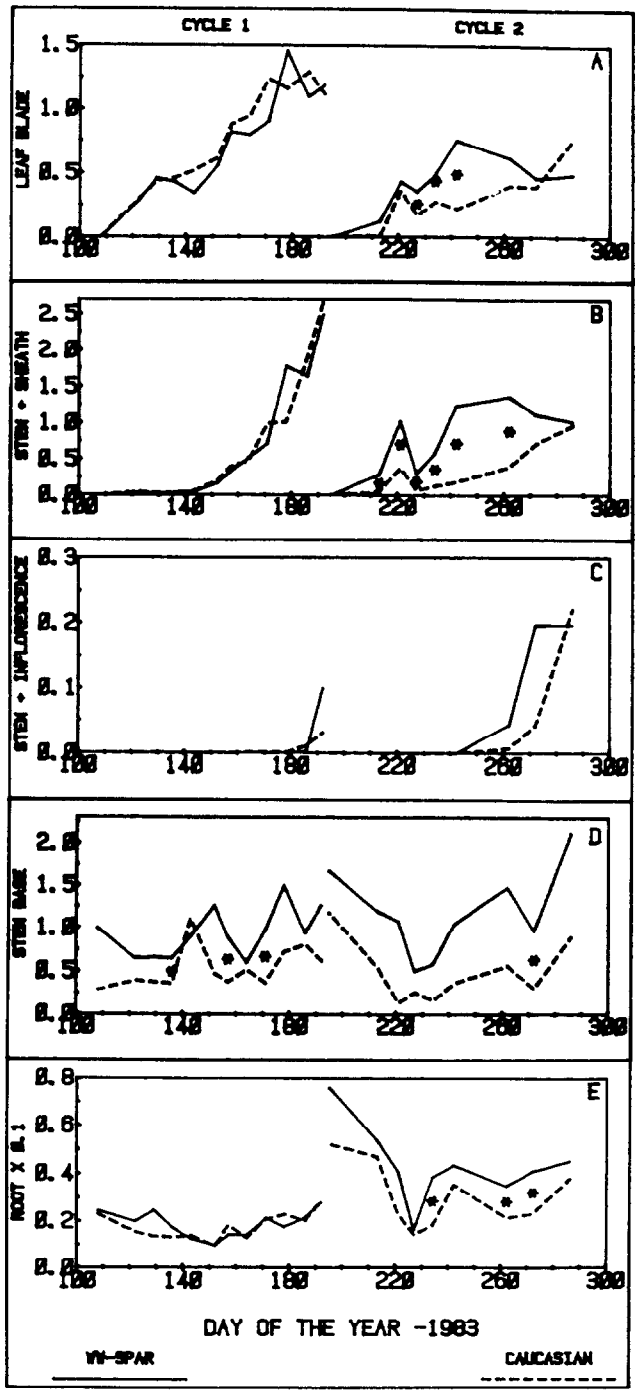

Fig. 2. *Total nonstructural carbohydrate pool sizes (g plant^{-1}) in 5 tissue compartments in WW-Spar and Caucasian bluestems during 2 growing cycles. Asterisks denote significant differences (P<0.05) between species within dates. Note that Subfig. E is scaled.*

question is whether TNC concentration could predict plant vigor any differently than would TNC pool size. We attempted to answer this question by calculation of the relative change in either concentration or pool size between high and low points of a growth cycle, but this was not entirely satisfactory because variability made it difficult to determine cycle extrema precisely in some instances. Nevertheless, when averaged across species, cycles, stem bases, and roots, the relative amplitude of change was slightly greater (0.52 versus 0.60) for pool size than for concentration. However, as would be expected, the coefficient of variation for pool size (which included the covariance of its components, biomass and concentration) was 20 to 40 and 15 to 60% higher than for concentration alone for WW-Spar and Caucasian bluestems, respectively.

Perhaps a better way to compare the ability of concentration and pool size to predict the same trends in vigor is to plot normalized values (divide all values by maximum value) against each other as in Figure 3. These graphs, along with the corresponding high and positive simple correlation coefficients, clearly show that TNC concentration followed trends in total TNC quite well in the roots. Except for Caucasian bluestem in cycle 1, TNC concentration also followed the trends in total TNC of stem bases as well. The relationships for the roots were linear and the points fell very close to the 1:1 line, but a curvilinear pattern can be detected in the stem bases which caused departure from the 1:1 line for mid-level concentrations.

These grasses partitioned only slightly more TNC belowground than aboveground during cycle 2 (Table 2). The drier second cycle limited forage production and resulted in 60 to 70% of total TNC being allocated to roots. Across species and cycles, the partition of total TNC among the sampled tissues was greatest in roots>stem bases>leaf blades>stems plus sheaths>stems plus inflorescences. The primary differences between species reflected morphological differences in that WW-Spar bluestem had a significantly larger stem base biomass compartment than did Caucasian bluestem (Coyne and Bradford 1986). TNC concentration was also greater for stem bases in WW-Spar bluestem than in Caucasian bluestem. Therefore, a greater portion of WW-Spar's total TNC reservoir was allocated to stem bases and less to roots as compared with Caucasian bluestem.

WW-Spar bluestem has repeatedly demonstrated superior drought performance with respect to forage production compared to Caucasian bluestem. While differences between the grasses in leaf water-use efficiency (Coyne et al. 1982) and rooting patterns appear to correlate with their drought performance, the partitioning of the TNC pool, as noted for WW-Spar bluestem above, may also be conducive to better forage regrowth following defoliation, particularly under limited soil water conditions. There is evidence (White 1973) that TNC in the roots of grasses are probably not used directly in the support of new herbage growth following defoliation. If this is generally true, the higher partitioning coefficient for TNC in stem bases of WW-Spar bluestem may confer a competitive advantage to this cultivar in grazing situations over Caucasian bluestem.

Nitrogen

While carbohydrates are generally considered to be the major carbon storage compounds in plants, nitrogenous compounds also show cyclical patterns that indicate periods of storage and depletion commensurate with demands of the plant. In addition, the uptake and partitioning of N by forage plants is of particular importance to grazing management to meet nutritional needs of livestock.

Nitrogen concentrations were most variable in the nonperennating organs (Fig. 4a,b,c) and relatively stable in the stem bases and roots (Fig. 4d,e). Although there is a barely detectable replenishment phase in the storage organs during cycle 1 (Fig. 4d,e), which parallels the trend in TNC (Fig. 1d,e), the N concentration trend in cycle 2 was totally different from that of TNC. The slight increase in root N after day 220 (Fig. 4e) corresponded with soil water recharge from irrigation (Coyne and Bradford 1986). Species differences across cycles were minimal and were limited primarily to Caucasian bluestem having higher root N concentrations than WW-Spar bluestem in cycle 1 (Table 1). The highest root N concentration for Caucasian bluestem was observed at spring growth initiation, but for WW-Spar bluestem, this point occurred late in cycle 1.

Nitrogen concentrations of forage necessary to meet the requirements of a 250 kg steer gaining 0.7 kg d^{-1} are about 10.7 mg g^{-1} (NRC 1976). Both WW-Spar and Caucasian bluestems maintained adequate levels of N in leaf blade tissue (Fig. 4a) throughout the growing season. However, concentrations of N in stems plus

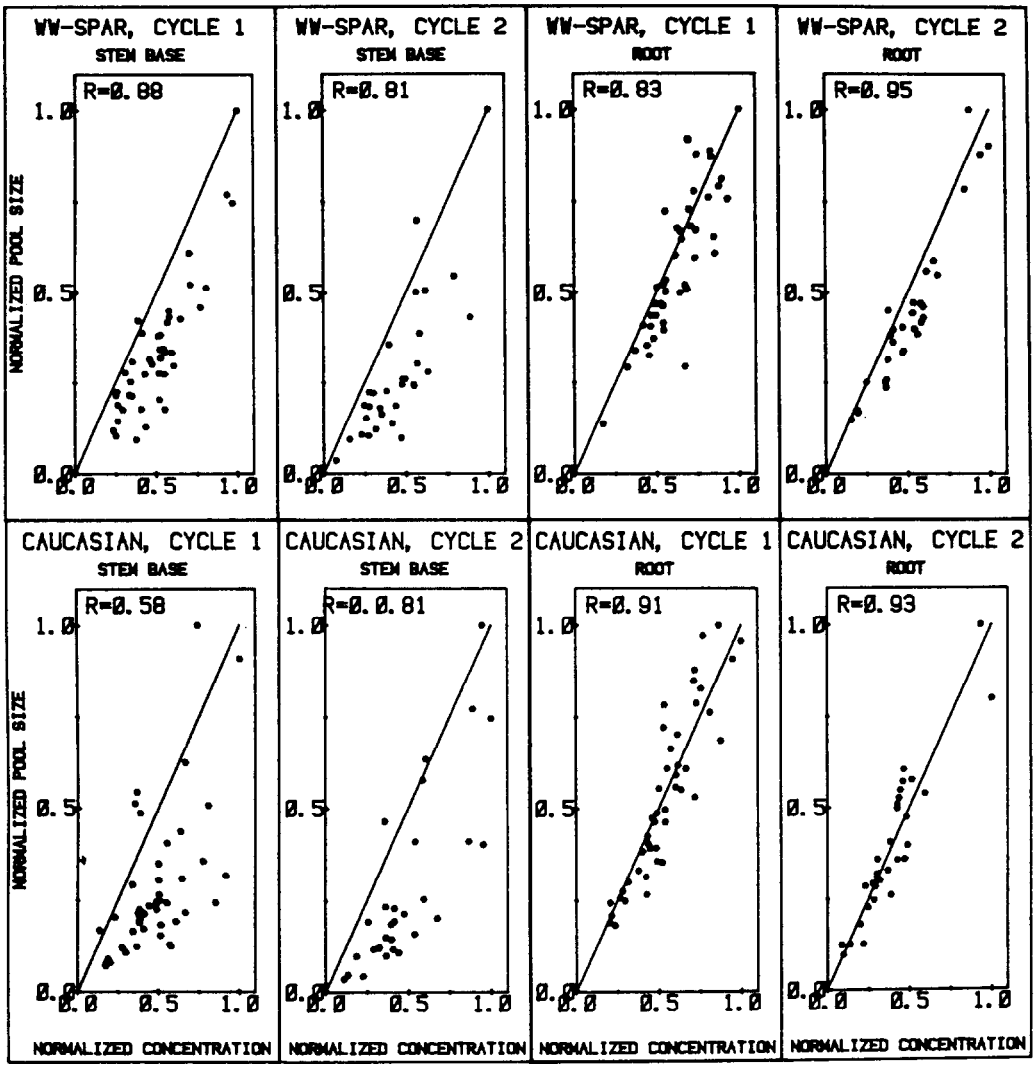

Fig. 3. *Relationship between total nonstructural carbohydrate concentration and pool size in stem bases and roots of WW-Spar and Caucasian bluestem during 2 growing cycles. Data were normalized by dividing each value by the maximum value in the dataset and the line delineates the 1:1 relationship. Simple correlation coefficients for the untransformed variates are shown for each subfigure. All coefficients were significant ($P<0.01$).*

sheaths (Fig. 4b) were marginal to low.

Like TNC, N pool sizes followed trends similar to concentrations in stem bases and roots, but with predictably higher variation (coefficients of variation for total N were 35 to 40 and 30 to 100% higher than for concentration in WW-Spar and Caucasian bluestems, respectively). Also like TNC, concentrations of N in the leaves and stems peaked much earlier than did total N in these compartments, which indicates the necessity for herbivores to gradually increase their daily intake of forage to meet protein requirements.

Two points were erratic in the stem plus sheath nitrogen data that are likely sampling artifacts. The very high initial N concentration (Fig. 4b) in Caucasian bluestem reflects a very limited quantity of leaf sheath tissue available for collection at this point in the growth cycle. Since biomass was so small, this outlying concentration had little effect on pool size (Fig. 5b). Secondly, the abnormally high total N recorded for WW-Spar bluestem in the middle of cycle 2 (Fig. 5b) was entirely due to its biomass component since concentration (Fig. 4b) did not show departure from trend.

Roots were by far the most important reservoir of N in these grasses. Some 70 to 80% of total plant N was located in the roots across growing cycles (Table 2) and this partitioning ratio exceeded 0.6 even at the lowest point of the cycle. Stem bases accounted for 15 to 30% of total N. Leaf blades contained only 15 to 20% of total N even at their peak standing crop of N. Between species, Caucasian bluestem generally had more total N associated with its roots, whereas, WW-Spar bluestem had more in the stem bases.

The relationship between N concentration and total N was not as well defined as it was for TNC. Like TNC, N values were better correlated in the roots than in the stem bases (Fig. 6). Root N values did not conform to a 1:1 relationship as well as did root TNC values. For stem bases, a relationship between concentration and total N was nonexistent in two cases (Fig. 6: Caucasian, cycle 1 and WW-Spar, cycle 2) and weak in the other 2 cases. Thus, variations in N concentrations were not good predictors of variations in total N in these 2 grasses, especially in the stem bases.

Investments in Leaf Biomass, Nitrogen, and TNC

Investment costs per unit leaf blade area with respect to biomass, N, and TNC, were calculated (ratios of biomass, N, TNC to corresponding leaf area) and expressed as specific leaf weight, specific leaf nitrogen, and specific leaf TNC, respectively (Fig. 7). Among these parameters, there were no differences between species for the growing cycle means (Table 2) and only a few within date comparisons were significant (Fig. 7).

These grasses continued to increase in biomass invested per unit

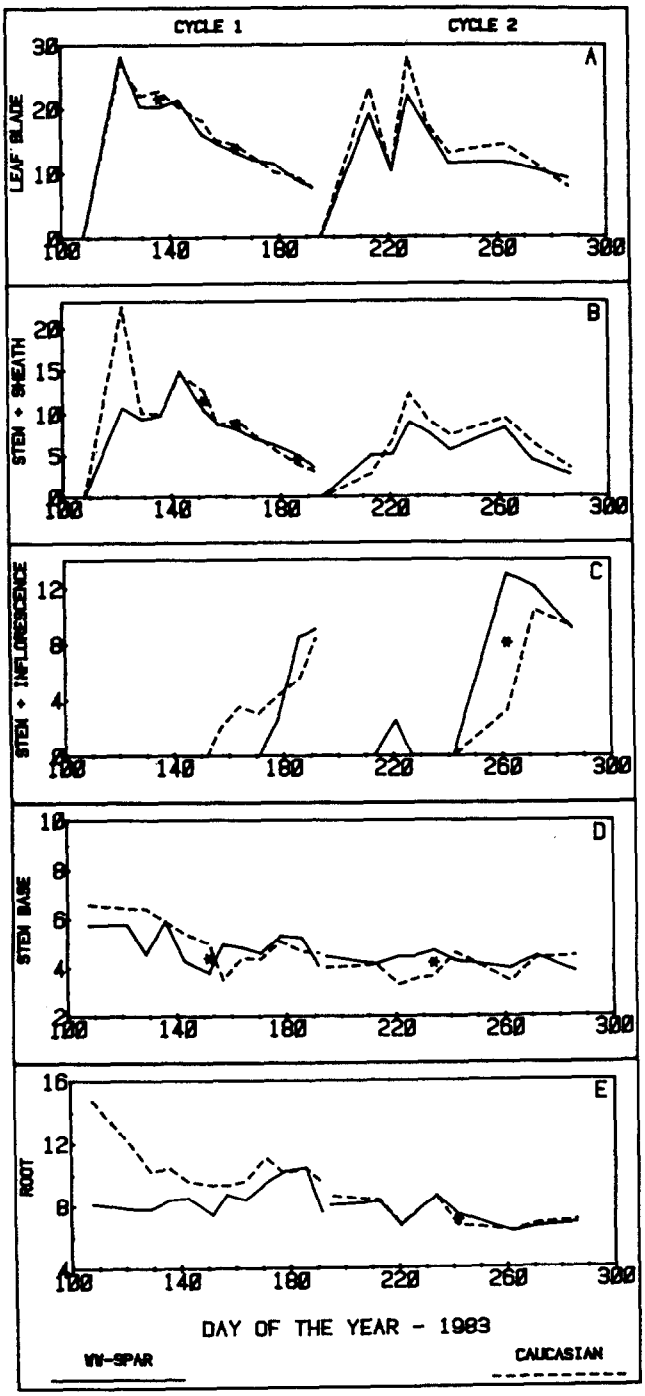

Fig. 4. *Nitrogen concentrations (mg g^{-1}) in 5 tissue compartments in WW-Spar and Caucasian bluestems during 2 growing cycles. Asterisks denote significant differences (P<0.05) between species within dates.*

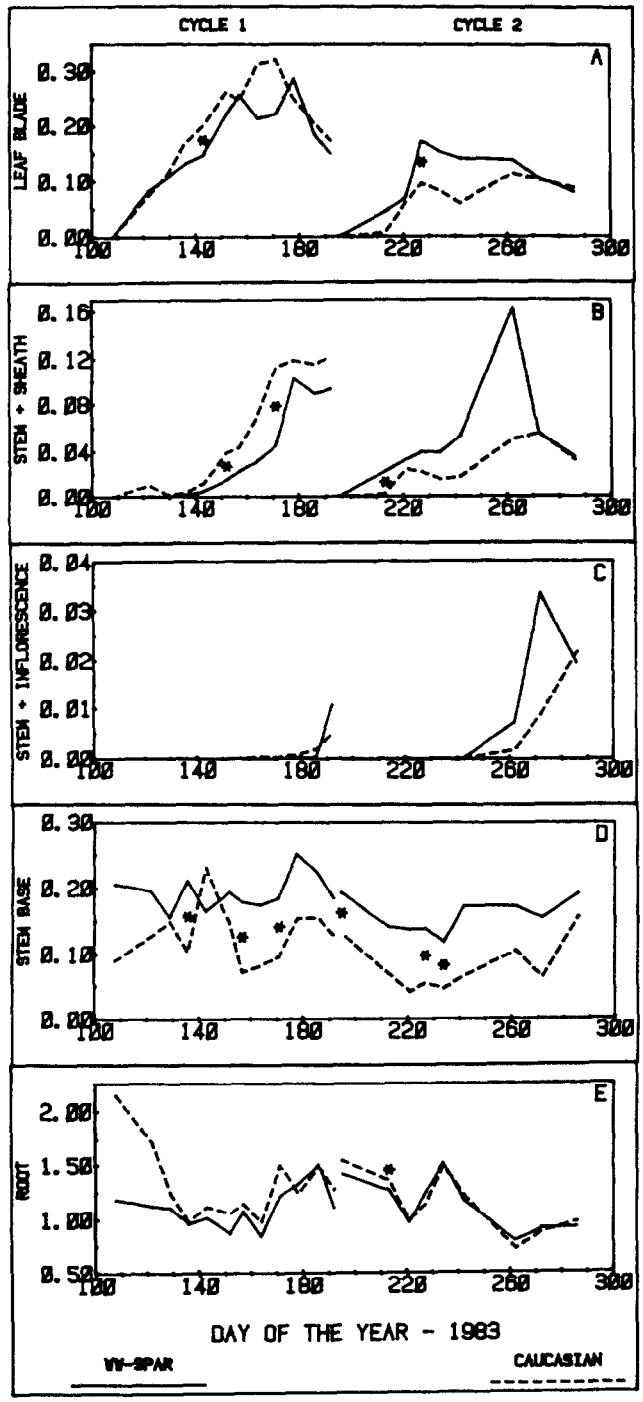

Fig. 5. *Nitrogen pool sizes (g plant^{-1}) in 5 tissue compartments in WW-Spar and Caucasian bluestems during 2 growing cycles. Asterisks denote significant differences (P<0.05) between species within dates.*

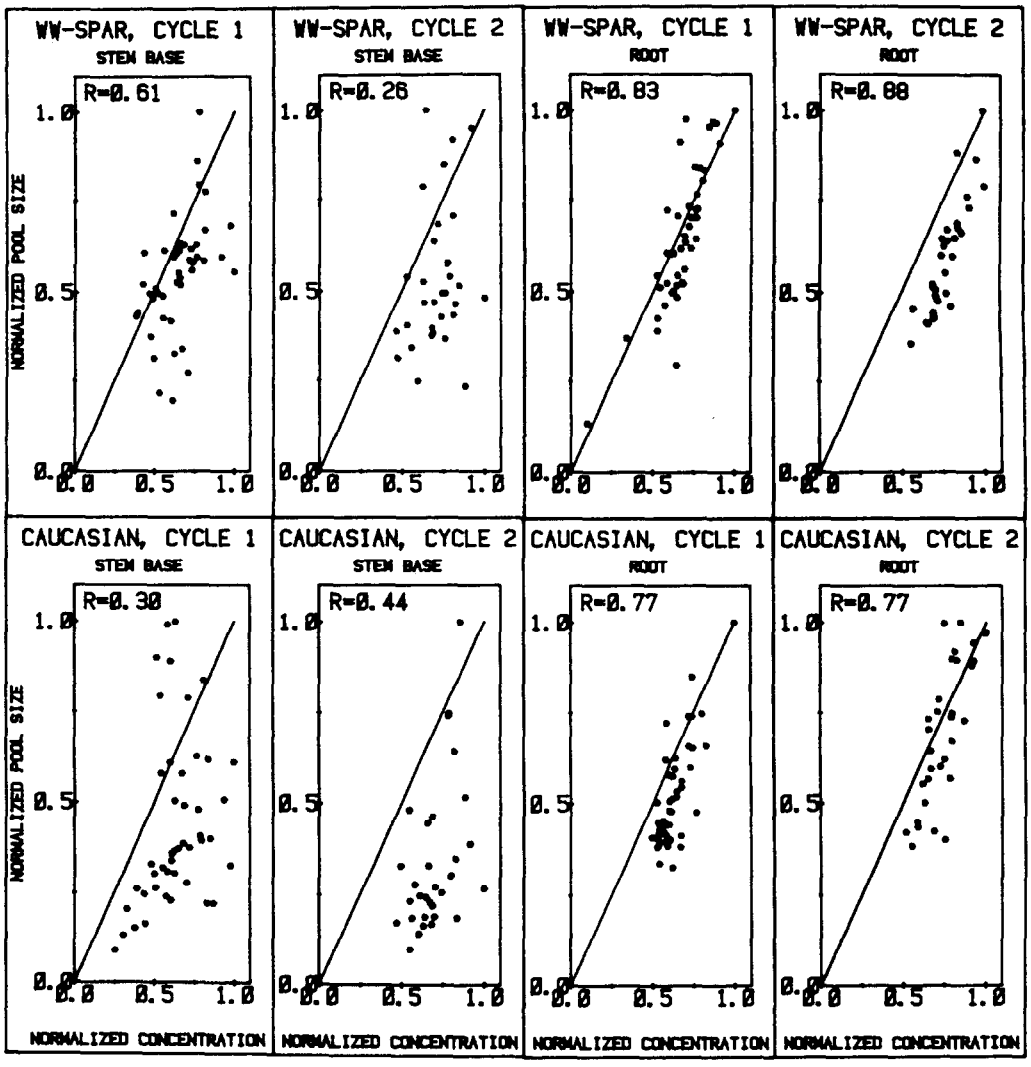

Fig. 6. *Relationship between nitrogen concentration and pool size in stem bases and roots of WW-Spar and Caucasian bluestems during 2 growing cycles. Data were normalized by dividing each value by the maximum value in the dataset and the line delineates the 1:1 relationship. Simple correlation coefficients for the untransformed variates are shown for each subfigure. Values for* R = *0.26 and 0.30 are not significant.* R = *0.44 is significant at* $P<0.05$ *and all other coefficients at* $P<0.01$.

area of leaf from spring growth to the end of cycle 1 (Fig. 7a). Nitrogen investment, however, was highest in the first leaves produced and N was diluted linearly with time (Fig. 7b). The "U" shaped curve for specific leaf TNC (Fig. 7c), in conjunction with those for total TNC (Fig. 2a), confirm conclusions based on leaf area ratio (Coyne and Bradford 1986) that these grasses were expanding leaf area more rapidly than leaf biomass to about day 150, after which the reverse was true.

Drought stress and the alleviation of this stress affected the shapes of the cycle 2 curves. Reversals in trend on days 227 and near the end of cycle 2 corresponded with periods of soil moisture recharge.

The question that is raised, but not answered, from these data is: why do leaf investments in labile carbohydrates increase from about day 150 in cycle 1 (Fig. 7c)? We can speculate that TNC was being accumulated to support seedstalk and seed production which began about the same time, but no subsequent dilution of TNC to signal its use in reproduction was observed. Perhaps nitrogen levels were limiting the use of this resource in the production of new leaf biomass. Unit growth rates for leaf area, nitrogen, and TNC.

Unit Growth Rates for Leaf Area, Nitrogen, and TNC

These parameters were calculated according to the methods of Hunt and Parsons (1974) and represent the efficiencies with which biomass, N, and TNC resources were used to increase total plant biomass (Fig. 8). As leaf area expanded early in cycle 1, its efficiency in the production of new plant biomass increased exponentially, thereby increasing the autotrophic capacity of these grasses and decreasing their dependence upon reserves. However, this increase in efficiency leveled off at the same time as root biomass ceased to decline (Coyne and Bradford 1986), but before TNC (Fig. 2e) and N (Fig. 5e) reached the low points of their cycles, and remained flat until late in the cycle. Cycle 2 patterns were similar. Throughout both cycles, nitrogen-use efficiency (Fig. 8b) increased and evidently compensated for the decreases in nitrogen investment (Fig. 7b) with time. The leveling off of TNC-use efficiency in the leaf blades (Fig. 8c) is the predictable result of increased investments in leaf TNC (Fig. 7c) concurrent with reduced investments in leaf N (Fig. 7b).

The challenge in managing forage-based livestock production systems has always included the maintenance of forage quality (protein) longer into the season. Grazing practices such as intensive early-stocking (Launchbaugh et al. 1978) are attempts to utilize forage more intensively in the period when quality meets or

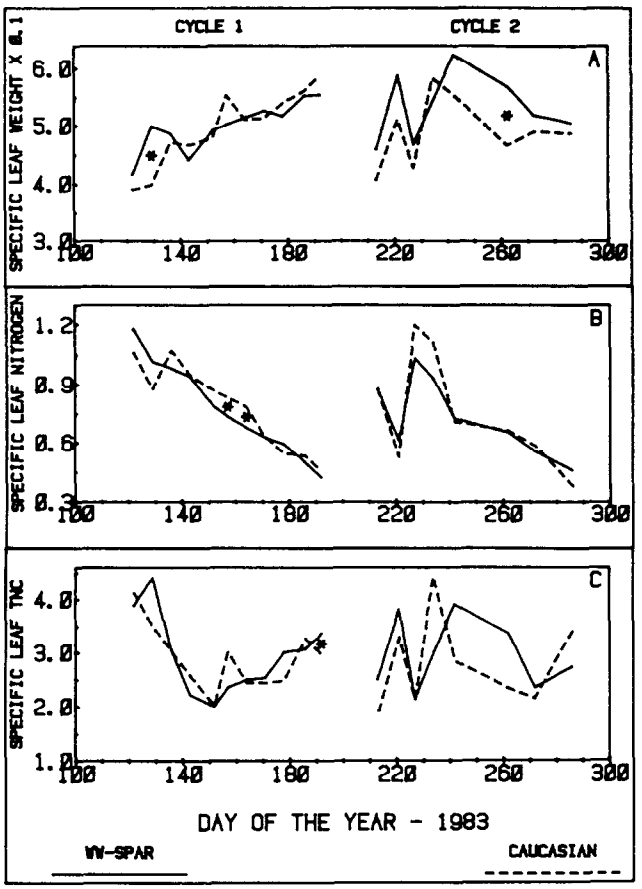

Fig. 7. *Investments of biomass, nitrogen, and total nonstructural carbohydrates per unit leaf blade area (g m^{-2} in WW-Spar and Caucasian bluestems during 2 growing cycles. Asterisks denote significant differences (P<0.05) between species within dates. Note that Subfig. A is scaled.*

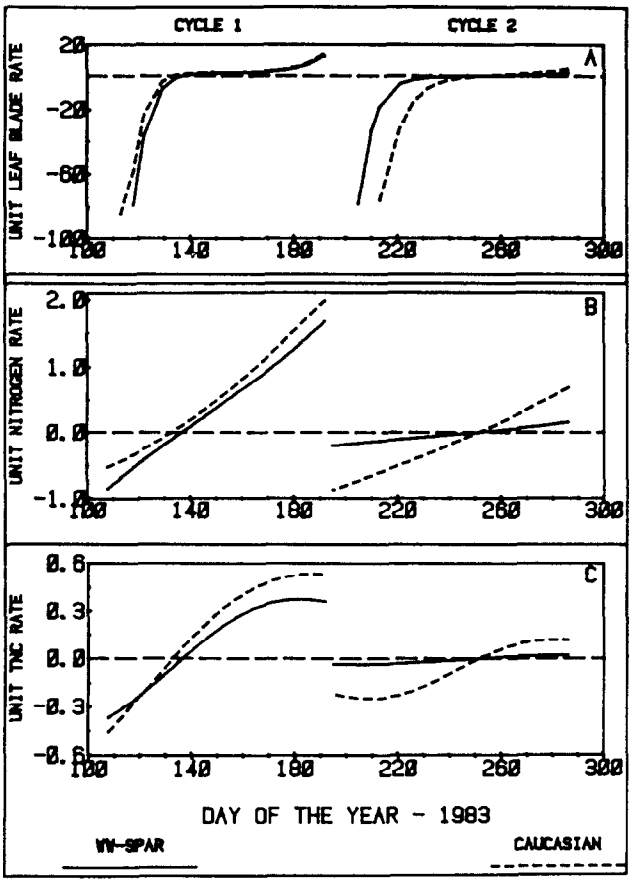

Fig. 8. *Relative rates of biomass production per unit leaf blade area (unit leaf rate in g $d^{-1}m^{-2}$), per unit nitrogen (unit nitrogen rate in g $d^{-1}g^{-1}$), and per unit total nonstructural carbohydrate (unit TNC rate in g $d^{-1}g^{-1}$). The general form of the relationship plotted on the ordinate is [(1/Y)(dWp/dt)] where Y = either leaf blade area, nitrogen, or TNC, Wp = total plant (roots + shoots) biomass, and t = time.*

exceeds demands of growing animals followed by rest during periods of low forage quality. Because nitrogen-use efficiency in these Old World bluestems apparently continued to increase throughout the season (Fig. 8b), the problem reduces to one of maintaining the photosynthetic apparatus per se. This is the age-old problem of delaying the biochemical changes associated with senescence, and growth regulator research as well as genetic engineering may one day provide a solution. In the meantime, further work is needed to determine how nitrogen fertility might be better managed in the latter part of a growing cycle to maintain the efficiency of TNC use in the production of leaf biomass when these species are used in intensively managed situations.

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