

# Carbohydrate Reserve, Phenology, and Growth Cycles of Nine Colorado Range Species

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## Abstract

Nine Colorado range species were studied for two consecutive years to relate the carbohydrate reserve status with phenological stage of development and current annual growth, including leaf, twig, or seedstalk length, or plant height. The species were fourwing saltbush (*Atriplex canescens*), antelope bitterbrush (*Purshia tridentata*), little rabbitbrush (*Chrysothamnus vicidiflorus*), fringed sagewort (*Artemisia frigida*), scarlet globemallow (*Sphaeralcea coccinea*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), James' cryptantha (*Cryptantha jamesii*), and pricklypear cactus (*Opuntia polyacantha* and *rhodantha* in a mixed stand). Seasonal total nonstructural carbohydrate (TNC) reserve cycles were related to phenological stages of development. Growth of all species appeared to be stimulated by late-summer or fall precipitation. Growth was found to be related inversely to carbohydrate reserve storage. Fourwing saltbush and antelope bitterbrush had typical V-shaped annual carbohydrate reserve cycles, and little rabbitbrush had a somewhat flat or extended V-shaped cycle. Fringed sagewort, scarlet globemallow, and western wheatgrass had flat or extended V-shaped cycles and maintained low reserves for more of the growing season than any of the species with typical reserve cycles. Blue grama was the only species that exhibited a narrow V-shaped cycle. The shape of the seasonal TNC cycle appeared to be a good screening tool for assessing the relative effects of defoliation on different plant species. Plants that replenished reserves rapidly after spring draw-down and regrowth periods, and minimized the part of the growing season with low reserve status, were least affected by defoliation and recovered rapidly from severe defoliation.

An index to proper frequency, intensity, and season of range use must ultimately depend upon the physiological state or condition of the plants within the various communities of the range vegetation. The total environment of the plant, including defoliation effects of grazing herbivores, is reflected in variations in plant morphological characteristics commonly used as indices of plant vigor, such as twig length, number and leafiness of reproductive culms and basal area (Cook et al. 1958), herbage yield, leaf and seedstalk heights (Vogel and Van Dyne 1966, Mueggler 1967, Buwai and Trlica 1977, Trlica et al. 1977), and number and length of new sprouts or regrowth after defoliation (Willard and McKell 1973, Trlica et al. 1977). Alteration of individual plant physiological status, concurrent with these morphological changes, often results in community change including declines in productivity and undesirable botanical composition changes that lead to depressions in range condition.

Numerous comprehensive reviews have been written on the carbohydrate reserves of plants in relation to phenological development, vigor, production, and defoliation (Graber 1931, Weinman 1948 and 1961, Troughton 1957, May 1960, Priestly 1962, Jameson 1963, Cook 1966, Menke 1973, White 1973, Trlica and Singh 1979). The depletion of stored reserves caused by excessive defoliation results in reduced vigor and herbage growth, and in extreme cases can result in death of plants (Weinman 1948). The responses differ with the plant species, however. A decrease in vegetative cover and growth can result in soil deterioration and accelerated erosion. Secondary succession and range recovery, therefore, can be slowed.

The level of carbohydrate reserves in the storage organs of plants varies during the annual growth cycle. Establishment of relationships between the carbohydrate reserve cycle and phenological stages of growth and development allows physiological changes within the plant to be related to phenological stages. The seasonal cycle of carbohydrate reserves should, therefore, be studied in relation to stages of development in plants protected from defolia-

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tion so that seasonal cycle changes can be separated from changes caused by defoliation or grazing.

This investigation was undertaken to determine relationships among carbohydrate reserves, plant phenology, and current annual growth cycles of nine important range species. Selected as representatives of important shrub browse plants for livestock and wildlife were fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.), antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), and little rabbitbrush (*Chrysothamnus vicidiflorus* (Hook.) Nutt.). Fringed sagewort (*Artemisia frigida* (Willd.) was selected as an important suffrutescent species. Scarlet globemallow (*Sphaeralcea coccinea* (Pursh) Rydb.) and James' cryptantha (*Cryptantha jamesii* (Torr.) Payson) were chosen as representatives of herbaceous perennial forbs. Blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) and western wheatgrass (*Agropyron smithii* Rydb.) were selected as desirable grass species. And finally, pricklypear cactus (*Opuntia polyacantha* Haw. and *O. rhodantha* Schumann in a mixed-species stand) was chosen as representative of important undesirable succulent perennial plants on rangelands.

### Study Areas

The studies were conducted at three enclosure sites at each of two locations in northern Colorado. The first location, referred to as the Pawnee study area, was on the Central Plains Experimental Range administered by the USDA-Science and Education Administration. The Pawnee study area is typical undulating grassland of the Central Great Plains shortgrass type. It is characterized, in general, by level and rolling plains interrupted by occasional ephemeral creeks and floodplains. The elevation is about 1,645 m.

Climate of the Pawnee study area is semiarid, with warm summers and cold winters. The frost-free period averages about 120 days, from May 25 through September 25. Annual precipitation is highly variable but generally ranges from 25 to 38 cm with about 74% of the precipitation occurring from May through September. Precipitation in late fall, winter, and early spring is usually in the form of snow. On the basis of a 34-year average (1939-1972), 1971 weather was dry and 1972 was wet. The wind blows almost continually (average 10.3 km/hr, Jameson 1969), especially in the afternoons and during the months of March and April.

Soils at the Pawnee study area, representative of dark-brown and brown soils of semiarid grasslands of the Central Great Plains region (Klippel and Costello 1960), belong to the lithosol group of azonal soils. Most of the soils are loams, ranging from clay loams to sandy loams. Soil textures were sandy clay loam at one enclosure site and silty clays and silty clay loams at the other two enclosure sites.

The second location, the Maybell study area, was in the intermountain sandhills region in Moffat County of western Colorado at an elevation of 1,920 m. Relief is characterized by gently rolling hills with occasional steeper slopes. The area is representative of the intermountain shrubland, locally dominated by antelope bitterbrush. Big sagebrush (*Artemisia tridentata*) is the dominant shrub in many of the lowland draws, while silver sagebrush (*Artemisia cana*) occurs over most of the area with antelope bitterbrush.

Climate of the Maybell area is semiarid, with warm summers and very cold winters. The frost-free period averages about 95 days, from June 10 through September 15. Average annual precipitation is about 28 cm, with only about 42% of that falling from May through September. Most precipitation from October through April is snow, and the ground is normally covered with snow during January and February. Precipitation totals for the years 1970, 1971, and 1972 were each near the 14-year average (1959-1972), although seasonal distributions were quite variable.

Soils at the Maybell study area are brown to dark brown, grading with depth into shades of yellowish brown or gray. The soils belong to the regosol group of azonal soils and are generally light-textured, low in organic matter, and without significant profile development.

Three 0.4-ha enclosures were constructed in July and August of 1970 at each of the Pawnee and Maybell locations to exclude livestock grazing. Sites were 1 to 2 m apart and were chosen to include adequate numbers of plants of each species and to be representative of the variability in soils and exposures at each location. All data presented are means of the monitored variables at the locations. The following four species were studied at the Pawnee location: fourwing saltbush, scarlet globemallow, blue grama, and western wheatgrass. Studied at the Maybell location were five other species: antelope bitterbrush, little rabbitbrush, fringed sagewort, James' cryptantha and pricklypear cactus.

Since the type of carbohydrates stored varies among plant species (Weinmann and Reinhold 1946, Weinmann 1952, Smith and Grotelueschen 1966), and since reserve carbohydrates are frequently converted from one form to another both diurnally (Holt and Hilt 1969, Lechtenberg et al. 1971) and seasonally (McCarty 1938, Weinmann 1952, Dodd and Hopkins 1958), total available carbohydrates (TAC) or similarly, total nonstructural carbohydrates (TNC) were considered to be of more practical significance than individual constituents for the management of range vegetation. TNC concentration was studied rather than absolute TNC content, which requires estimation of total storage organ biomass (George and McKell 1978). Absolute TNC content analyses are not practical because of the great cost of obtaining biomass data. The number of plant samples or size of plot needed to provide an adequate sample for TNC determinations varied among species. Collected within each enclosure at each sampling date were three plants each of fourwing saltbush and antelope bitterbrush, six plants of little rabbitbrush, and eight plants of fringed sagewort. Plants of blue grama, western wheatgrass, and scarlet globemallow were collected from plots of 1.0 to 1.5 m<sup>2</sup>. About ten plants of James' cryptantha and pricklypear cactus were sampled at each collection.

For two consecutive years (fall 1970 through fall 1972), samples of all species except James' cryptantha and pricklypear cactus were collected at 2-week intervals during early and rapid vegetative growth, and at monthly intervals or even less frequently during maturation and quiescence. James' cryptantha was studied only in the first year, and pricklypear cactus only in the second year. Clearly defined phenological stages and current annual growth measurements were recorded at the time of each collection.

Table 1 describes the phenological stages of development for each species. Decimal subdivisions of these phenological stages were used when a finer resolution clarified or described plant status more accurately. Since most phenological stages overlap, the beginning of a new stage does not necessarily mean the end of a preceding stage for the population as a whole.

Current annual growth measured for antelope bitterbrush was average new leaf length before twig elongation and was average twig length for the rest of the year. Current annual growth for fourwing saltbush, little rabbitbrush, and fringed sagewort was average new leaf length before seedstalk elongation and was average seedstalk length for the rest of the year. Current annual growth for the forbs (scarlet globemallow and James' cryptantha) and grasses (blue grama and western wheatgrass) was average plant height. Growth of pricklypear cactus was not measured.

One aboveground and one belowground storage organ were collected for TNC analysis for all species except pricklypear cactus, for which roots were the only organ sampled. The belowground plant parts studied were defined precisely: the taproot section between 5 and 15 cm below the soil surface for fourwing saltbush and antelope bitterbrush; lateral roots less than 0.5 cm in diameter for little rabbitbrush; the whole fibrous root system to a depth of 30 cm for fringed sagewort, blue grama, and cactus; all roots and rhizomes to a depth of 30 cm for scarlet globemallow and western wheatgrass; and the taproot and all lateral roots to a depth of 30 cm for James' cryptantha.

The aboveground plant parts sampled were basal stems or the

**Table 1. Phenological stages of development for nine range plants in Colorado.**

Fourwing saltbush	Antelope bitterbrush	Little rabbitbrush
1. Winter quiescence	1. Winter quiescence	1. Winter quiescence
2. Leaves regreening and apical buds swelling	2. Leaves regreening and apical buds swelling	2. Leaf buds swelling on twigs
3. Twigs elongating	3. Twigs elongating	3. Leaves elongating
4. Floral buds developing	4. Floral buds developing	4. Stems elongating
5. Flowers opening	5. Flowers opening	5. Nonreproductive stem length exceeded by flower stalk length
6. Fruit developing (male flowers dying)	6. Fruit developing	6. Flower stalks elongating
7. Seed shatter (male flowers falling)	7. Seed shatter	7. Floral buds developing
8. Fall quiescence	8. Some leaves falling and most leaves brown	8. Flowers developing
	9. Fall regrowth	9. Fruit developing
	10. Fall quiescence	10. Seed shatter
		11. Some leaves falling and most leaves brown
		12. Fall regrowth
		13. Fall quiescence
Fringed sagewort	Forbs <sup>1</sup>	Grasses <sup>2</sup>
1. Winter quiescence	1. Winter quiescence	1. Winter quiescence
2. Buds swelling on crown	2. Buds swelling on crown	2. Growth initiation
3. Stems elongating	3. Leaves elongating	3. 2nd-leaf stage
4. Nonreproductive stem length exceeded by flower stalk length	4. Stems elongating	4. 3rd-leaf stage
5. Floral stems elongating	5. Floral buds developing	5. 4th-leaf stage
6. Floral buds developing	6. Flowering	6. Head first detected in boot
7. Flowers developing	7. Fruit developing	7. Boot
8. Fruit developing	8. Seed shatter	8. Head
9. Seed shatter	9. Some leaves turning brown	9. Hard seed
10. Summer dormancy	10. Fall regrowth	10. Seed shatter
11. Fall regrowth	11. Fall quiescence	11. Summer dormancy
12. Fall quiescence		12. Fall regrowth
		13. Fall quiescence
Pricklypear cactus		
1. Winter quiescence		
2. Pads regreening		
3. Pads enlarging		
4. Floral buds developing		
5. Flowering		
6. Fruit developing		
7. Fruit drop		
8. Pads turning brown		
9. Dormancy		

<sup>1</sup>Scarlet globemallow and James' cryptantha.<sup>2</sup>Blue grama and western wheatgrass.

0.5 to 1.0 cm diameter branches growing above the root crown and containing green plant pigments in the cambium for fourwing saltbush and antelope bitterbrush; a 6-cm section of the crown or primary stem above lateral root branches and below lateral stem branches for little rabbitbrush; a 3 to 4-cm section of the plant crown remaining after all branching stems and all roots had been removed for fringed sagewort; a 2 to 3-cm section of the crown at the soil surface where stems originated for scarlet globemallow and James' cryptantha; and a 3 to 4-cm stem base or crown section near the soil surface but above the roots for blue grama and western wheatgrass.

All plant parts were washed briefly with cold water at the collection site immediately after collection. This sample material was then placed in pint jars, covered with 95% ethanol to reduce enzyme activity, and sealed tightly. Samples were dried at 70°C for about 10 days (taking about 4 days to evaporate the ethanol and an additional 6 days to dry the larger woody samples). The dried samples were ground in a Wiley mill to pass a 40-mesh screen. Total nonstructural carbohydrates were extracted from a 0.5-g plant sample with 0.2 N sulfuric acid (Smith et al. 1964). The extracts were then used to determine TNC concentration on a glucose equivalent basis (Heinze and Murneek 1940, Association of Official Analytical Chemists 1975, Trlica and Cook 1971).

### Results and Discussion

To make any generalizations about growth and carbohydrate

reserve cycles, three analyses of variance were conducted on TNC concentration data for aboveground and belowground storage organs and current annual growth for seven of the species that were studied in both years. All species at the Maybell location grew significantly more ( $p < 0.01$ ) in length of current annual growth during the first year. Both fourwing saltbush and blue grama grew more ( $p < 0.01$ ) in the second year at the Pawnee location, while western wheatgrass grew less ( $p < 0.01$ .) There was no difference ( $p > 0.10$ ) between the 2 years in growth of scarlet globemallow.

In relating current annual growth to belowground storage organ TNC level, five of the seven species had lower levels of TNC in the year of greater aboveground growth. Only fourwing saltbush had higher belowground storage organ TNC in the year of more growth and there were no differences between years in TNC levels for western wheatgrass.

The relationship between growth and TNC level was similar in aboveground storage organs and belowground storage organs. All species studied at the Maybell location had lower aboveground storage organ TNC levels during the first year as compared with data for the next year, although the difference was significant ( $p < 0.05$ ) only for fringed sagewort. Fourwing saltbush, blue grama, and western wheatgrass all had lower TNC levels in aboveground storage organs in the second year, the same year when more aboveground growth was produced at the Pawnee location. There were no differences ( $p > 0.10$ ) between years in aboveground storage organ TNC levels or growth for scarlet globemallow.

These results tend to support the hypothesis that carbohydrate reserve storage is inversely related to growth. Numerous other investigators have suggested that carbohydrate reserve storage is inversely related to growth (Aldous 1930, Sampson and McCarty 1930, McCarty 1935, Weinmann 1940, McIlvanic 1942, Alberda 1957, Dodd and Hopkins 1958, Hyder and Sneva 1959, Mooney and Billings 1960, Coyne and Cook 1970, Trlica and Cook 1972, Trlica 1977). The inverse relation between carbohydrate storage and growth is thought to apply on a seasonal basis only in situations where plant regrowth is frequent. This includes both grazed and ungrazed arid and semiarid rangelands, and grazed rangelands in humid climates. We suspect that in humid environments, where ungrazed plants can carry on nearly uninterrupted growth throughout the season, carbohydrate stores may not be drawn upon enough to cause an inverse relationship to occur, therefore growth and carbohydrate storage might be directly related.

Figures 1 and 2 show carbohydrate reserve and current annual growth cycles as related to phenological stage of development for nine species. Mean monthly maximum and minimum temperatures and monthly precipitation are included for the two study sites to help explain between-year differences in plant growth responses. Similar TNC plot scaling was used for all species, so that relative amplitudes of TNC cycles among species are apparent.

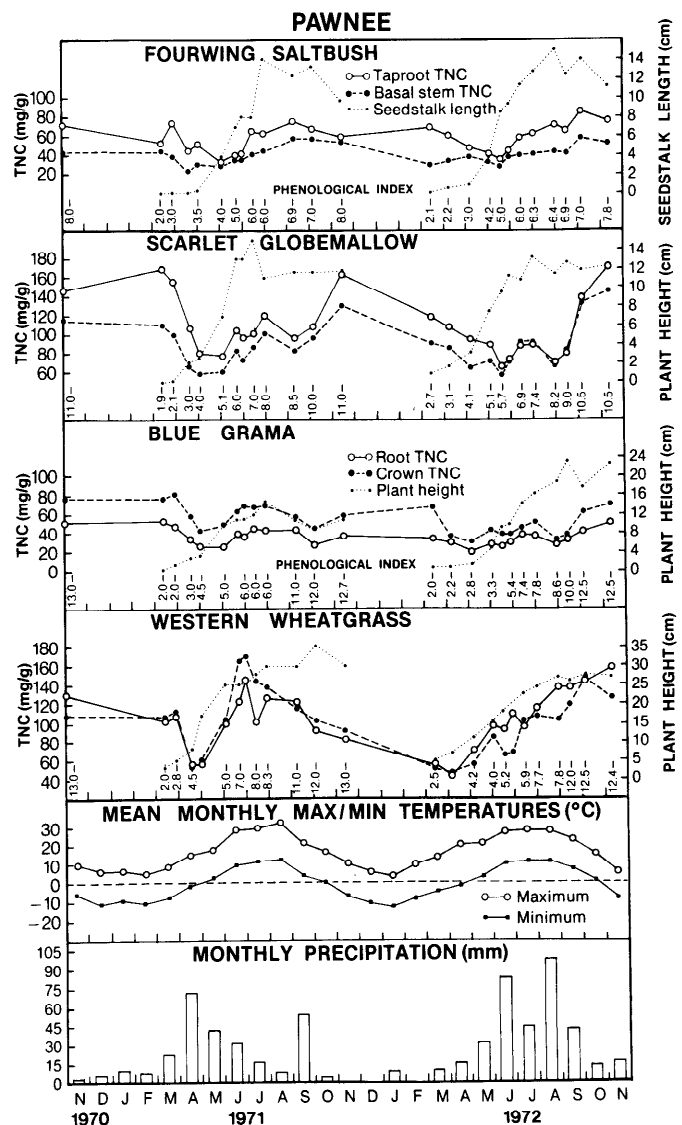


Fig. 1. Total nonstructural carbohydrates (TNC) in above- and below-ground storage organs and current annual growth of fourwing saltbush, scarlet globemallow, blue grama, and western wheatgrass as related to stage of phenological development and monthly temperature and precipitation at the Pawnee study site.

## Fourwing Saltbush

Taproots and basal stems of fourwing saltbush showed similar TNC cycles when related to phenological stage, although season differences were greater in taproots (Fig. 1). Taproots also had higher concentrations of TNC than did basal stems at all phenological stages during both years. Coyne and Cook (1970) obtained similar results for two other *Atriplex* species in Utah. The taproot may be considered as the more important storage organ provided that the total mass of the taproot is at least equal to that of basal stems.

Seasonal lows for TNC reserves of fourwing saltbush were reached earlier in basal stems than in taproots (Fig. 1). Most of the initial meristematic growth in spring originate from basal stems and might account for this differential use of reserves. The low point in basal stem TNC was reached during the bud-swelling stage (in mid-April) during the first year, but not until twig elongation (in mid-June) in the second year. The low basal stem TNC levels were respectively about 24 and 28 mg/g. The low point in taproot TNC was reached during twig elongation in both years (first week of June in the first year, and third week of June during the second year). The low taproot TNC levels were respectively 32 and 36 mg/g in 1971 and 1972. Higher April rainfall in the first year at the Pawnee site probably caused earlier initial spring growth, resulting

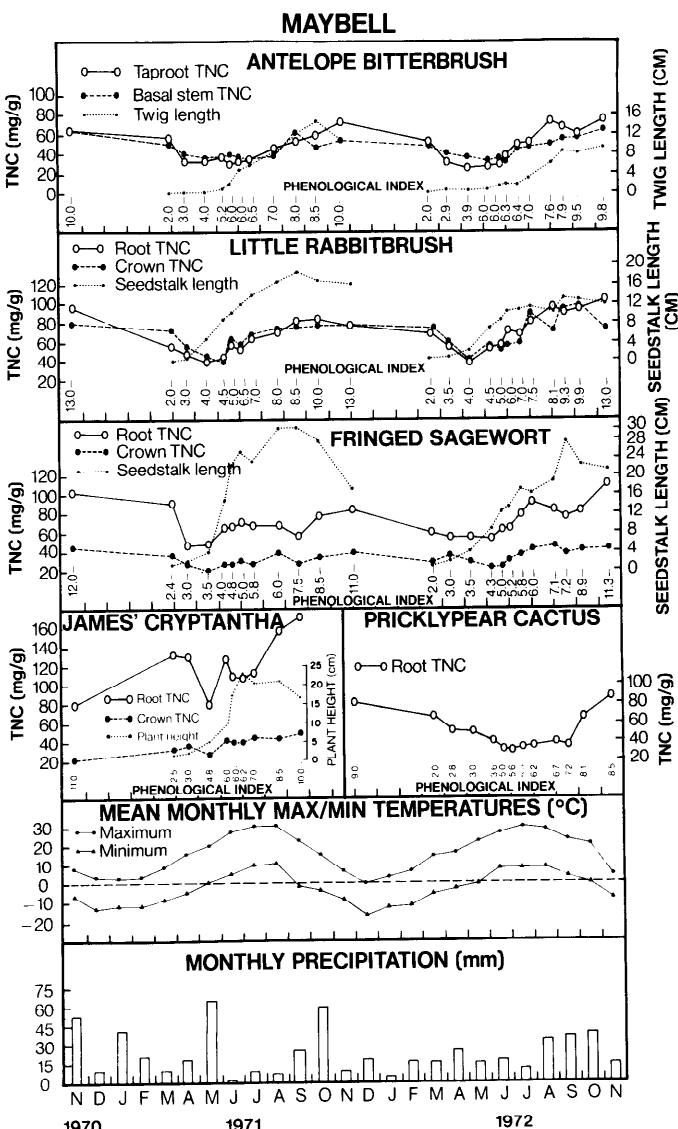


Fig. 2. Total nonstructural carbohydrates (TNC) in above- and below-ground storage organs and current annual growth of antelope bitterbrush, little rabbitbrush, fringed sagewort, James' cryptantha, and pricklypear cactus as related to stage of phenological development and monthly temperature and precipitation at the Maybell study site.

in an earlier drawdown of TNC. An over-winter (1971-72) reduction in basal stem TNC appeared to be resupplied by the taproot during early spring. Higher maximum temperatures in March and April 1972 may have caused the mid-spring rise in basal stem TNC prior to further reductions in late spring.

Levels of TNC in taproots and basal stems were maximum at the late fruit-development stage (September) in 1971, and during the early seed-shatter stage (October) in 1972. Maximum taproot TNC was about 75 mg/g in the dry year of 1971, and about 85 mg/g in the wet year of 1972. Basal stem TNC levels (about 58 mg/g in both years) were at a maximum about the same time as they were in taproots.

Spring drawdown of taproot reserves in fourwing saltbush occurred rapidly over about a 3-month period from mid-March through early to mid-June. Reserve replenishment in taproots began immediately after the low point in storage was reached and occurred at about the same rate over a 3½-month period through mid-September or early October. For categorizing species TNC and growth cycles and the comparison of species responses to their environment, fourwing saltbush is classed as having a V-shaped carbohydrate reserve storage pattern. That is, the plant spends about equal time in drawdown and replenishment phases of the TNC cycle, and rates of depletion and storage of reserves are similar.

The growth of fourwing saltbush, expressed as seedstalk length, began in March in both years (Fig. 1). Twig elongation was not rapid until May. Maximum seedstalk lengths were respectively 14 and 15 cm during the fruit-development stage (August in 1971 and early September in 1972).

Fall regrowth, concurrent with the seed-shatter stage, resulted in TNC drawdown in taproots and basal stems during both years. TNC in taproots and basal stems were respectively reduced about 16 and 3 mg/g in 1971 and 10 and 6 mg/g in 1972. Early severe frosts following this drawdown and preceding replenishment might have detrimental effects on the carbohydrate balance for the year, and on spring greenup and early growth the following year.

### Antelope Bitterbrush

Both taproot and basal stem levels of TNC in antelope bitterbrush were related similarly to phenological stage, although the drawdown in spring was slightly greater in taproots than in basal stems (Fig. 2). During the rest of the year, taproot TNC was generally higher than basal stem TNC. Changes in seasonal TNC levels were greater in taproots, which appeared to be a more important storage organ.

Spring TNC drawdown was much more abrupt in taproots than in basal stems, and the low point was reached about a month to 6 weeks earlier. The low points in taproot TNC (about 31 and 27 mg/g) occurred in June in 1971 and May in 1972, whereas the low points in basal stem TNC (37 and 35 mg/g) occurred in mid-July in 1971 and late June in 1972. The delay in low points in 1971 may have been caused by higher rainfall in May and continued vigorous spring vegetative growth.

Levels of TNC in taproots and basal stems were maximum at the end of the growing season at fall quiescence. McConnel and Garrison (1966) reported the low point and maximum storage of TNC in antelope bitterbrush in Washington occurred at the same phenological stages as found in this study. Maximum taproot TNC levels were 75 mg/g in both years whereas maximum basal stem TNC was about 56 mg/g in 1971 and 67 mg/g in 1972. The lower maximum basal stem TNC in 1971 may have resulted from reserve utilization for fall regrowth. The TNC pool used for fall regrowth each year appeared to be supplied by the plant part that had attained the greater level of TNC reserves at the time of regrowth (Fig. 2).

Seasonal curves of TNC reserves in taproots and basal stems of antelope bitterbrush possessed the classical U-shaped curve of carbohydrate reserve depletion and replenishment described by Cook (1966). Carbohydrate reserve stores were used at a relatively low rate during winter quiescence, and replenishment took place

only after the fruit was almost fully developed. In both years TNC levels were restored in taproots before basal stems were replenished. An almost even distribution of rainfall at the Maybell location in the 1972 growing season provided for nearly continuous growth and progression of phenological development in antelope bitterbrush. The TNC curves illustrate an even progression in drawdown and replenishment of reserves from growth initiation in March through seed shatter in early September.

Growth of antelope bitterbrush, expressed as twig length, began in March in both years of the study, but twig elongation did not become rapid until late May or early June. Maximum twig lengths (15 cm in October 1971 and 9 cm in November 1972) were respectively reached during fall regrowth or at fall quiescence stages. Antelope bitterbrush plants produced significantly ( $p < 0.01$ ) more growth in 1971 than in 1972. Since rainfall was only slightly less in 1972 than in 1971, a possible explanation for the growth depression is that annual grasses and forbs produced in high density in 1972 used a large amount of the available soil water.

### Little Rabbitbrush

TNC seasonal trends for little rabbitbrush were similar in both years at the Maybell location (Fig. 2). Roots and crowns had similar cycles and, in contrast to the other species studied, roots and crowns differed very little in concentrations of TNC. Spring drawdown occurred from March through May, reaching a low point of about 40 mg/g at the stem-elongation stage, in May. Donart (1969) found a low point in root TNC reserves of 56 mg/g on May 18 in the little rabbitbrush plants in Utah. Drawdown in root TNC slightly preceded drawdown in crown TNC during both years of the present study.

After the low point in TNC reserves was reached in May, reserves were rapidly replenished over the rest of the growing season. Root TNC reserves were maximum and about 85 mg/g at seed shatter in 1971 and about 104 mg/g at fall quiescence in 1972. In Utah, Donart (1969) found maximum root TNC levels of about 163 mg/g in little rabbitbrush. At Maybell, the maximum levels of crown TNC were about 79 mg/g in 1971 and about 96 mg/g in 1972.

The concentration of TNC in roots was significantly higher ( $p < 0.01$ ) in 1972 than in 1971. Higher rainfall in August and September of 1972 may have provided for higher amounts of carbohydrate production and storage in late summer and fall of 1972. There were no differences ( $p > 0.10$ ) between years in little rabbitbrush crown of TNC levels.

Seasonal TNC cycles in both roots and crowns were strongly V-shaped, and concentrations of TNC in roots and crowns changed rapidly throughout the growing season. In general, TNC drawdown was rapid during a period of 2½ to 3 months in spring, and replenishment occurred during 4 to 4½ months in late spring and summer. In contrast to fourwing saltbush, little rabbitbrush took considerably longer to replenish reserves than to draw them down.

Fall regrowth was concurrent with seed shatter in both years. The reduction of TNC levels in roots was about 6 to 8 mg/g in both years but occurred earlier in 1972 and was rapidly replenished. TNC levels in crowns were not reduced during fall regrowth in 1971, but were reduced 22 mg/g in 1972.

Growth of little rabbitbrush, expressed as seedstalk length, began in mid-March in both years (Fig. 2). Stem elongation became rapid by mid-April and continued through mid-September. Seedstalk lengths were maximum (about 18 cm in 1971 and about 13 cm in 1972) during the flowers-developing stage. Little rabbitbrush produced significantly more growth ( $p < 0.01$ ) in 1971 than in 1972. Seedstalk growth stopped during July and early August of 1972 but resumed during the last week of August and the first 2 weeks of September. In 1971, however, seedstalk growth was continuous during July, August, and the first part of September, causing a significant interaction ( $p < 0.05$ ) among years and time of year. As with the other species at the Maybell location in 1972, reduced growth by little rabbitbrush may have resulted from com-

petition by annual grasses and forbs for soil water.

### Fringed Sagewort

Both root and crown levels of TNC in fringed sagewort showed similar patterns in relation to phenological stage, although the magnitude of the change over the growing season was greater in roots (Fig. 2). Roots had higher TNC concentrations than crowns at all phenological stages in both years. Results were similar to those for fourwing saltbush and antelope bitterbrush. The mass of roots was greater than the mass of crowns, so the roots are considered to be the more important storage organ.

Spring drawdown of TNC in roots was much more abrupt in 1971 than in 1972 and reached a lower point (about 47 mg/g, vs. 54 mg/g). Drawdown in crowns was gradual in both years. Both root and crown TNC levels reached a low point during stem elongation (early May in 1971, and early June in 1972). Concentrations of crown TNC at the low points in the cycles were about 20 mg/g in 1971 and 23 in mg/g in 1972.

In both years, TNC levels in roots and crowns of fringed sagewort were maximum at the late-seed-shatter or fall-quiescence stage. Maximum root TNC levels were only about 85 mg/g in 1971 and about 110 mg/g in 1972. Maximum crown TNC levels were about 40 mg/g in 1971 and 43 mg/g in 1972.

Seasonal TNC curves in roots and crowns of fringed sagewort indicated that spring drawdown involved relatively short periods, whereas replenishment took relatively long periods (Fig. 2). Drawdowns were completed by the first week in June in each year, after which the reserves were gradually replenished until November. These results, characterized by a flat V-shaped carbohydrate reserve cycle, may indicate that fringed sagewort might be susceptible to damage from grazing during the extended period when reserve stores are low. Any interruption in the replenishment process might be detrimental to the growth and survival of fringed sagewort plants.

In 1971, no fall regrowth occurred until October, although TNC reserves appeared to be drawn upon from both roots and crowns in August and September. In 1972, fall regrowth was concurrent with drawdown of TNC in both roots and crowns in August and September. TNC in roots were reduced during fall regrowth by about 12 mg/g in 1971 and 15 mg/g in 1972, whereas TNC levels in crowns were reduced by about 12 mg/g in 1971 and 6 mg/g in 1972.

Growth of fringed sagewort, expressed as seedstalk length, began in March in both years (Fig. 2). Stem elongation was more rapid in 1971 than in 1972, and growth was significantly greater ( $p < 0.01$ ). A significant growth interaction ( $p < 0.01$ ) among years and time of year (sampling date) was a result of declining average seedstalk lengths caused by shattering in September, October, and November of 1971. Also, many of the longer seedstalks were broken in the fall of 1971 by wind, rain, and snow.

TNC levels in crowns of fringed sagewort were significantly higher ( $p < 0.05$ ) in 1972 than in 1971. There were no significant differences ( $p > 0.10$ ) between years in root TNC levels, but there was a significant interaction ( $p < 0.10$ ) among years and time of year because root TNC levels from July through November were generally higher in 1972 than in 1971. Since growth was greater in 1971 than in 1972, carbohydrate storage was, again, found to be inversely related to growth.

### Scarlet Globemallow

Roots of the forb scarlet globemallow had higher seasonal TNC levels than any aboveground or belowground storage organs of all other species studied. The average level of root TNC over 2 years was about 107 mg/g. The average crown TNC level of about 88 mg/g was higher than the average aboveground storage organ TNC level for all other species studied except western wheatgrass.

Definite seasonal trends in TNC were obtained for scarlet globemallow in both years at the Pawnee location (Fig. 1). Both root and crown TNC cycles showed similar patterns in relation to phenological stage, although the TNC levels were generally higher in roots. The mass of roots and rhizomes was many times that of crowns, so

roots and rhizomes are considered to be the more important storage site.

Spring drawdown of TNC was more abrupt in 1971 than in 1972, and the low point occurred earlier (Fig. 1). Seasonal lows in root TNC were about 77 mg/g in late May of 1971 and 64 mg/g in mid-June of 1972. Seasonal lows in crown TNC were about 58 mg/g in early May of 1971 and about 54 mg/g in mid-June of 1972. All low points in TNC were reached during stem elongation.

TNC in roots and crowns of scarlet globemallow were maximum in November (the beginning of fall quiescence) in both years. Maximum root TNC was about 164 mg/g in the dry year of 1971 and about 171 mg/g in the wet year of 1972. Maximum crown levels were about 131 mg/g in 1971 and about 145 mg/g in 1972.

The outstanding characteristic of the seasonal cycles of TNC in roots and crowns of scarlet globemallow was the relatively short period required for reserve replenishment. In 1972, root TNC increased from about 96 mg/g to 164 mg/g within a 2-month period from mid-September through mid-November, while crown TNC increased from about 82 mg/g to 131 mg/g. With the higher rainfall in 1972, root TNC increased from about 70 mg/g to 171 mg/g within 2½ months (first of September through mid-November), while crown TNC increased from about 70 mg/g to 145 mg/g.

The seasonal carbohydrate reserve cycle for scarlet globemallow is characterized as an extended V-shape. Reserves are maintained at a relatively low level for most of the growing season, making the plant highly dependent on leaf area for replenishment during a short period in the fall. Defoliation at moderate or high intensities could have serious effects on this replenishment phase of the cycle.

Carbohydrate reserves declined during the fruit development and early seed shatter stages in August of both years, while some regrowth in upper leaf axils was observed. Crown regrowth occurred in the fall of both years, although no concurrent drawdown in reserves was observed. Either the TNC drawdown occurred earlier or the depression of reserves was masked by a rapid replenishment of reserves during this period.

Growth of scarlet globemallow, expressed by plant height, began in March and rapid stem elongation began almost immediately in both years (Fig. 1). Plant height was maximum during the fruit development stage both years. Maximum height was slightly greater in 1971 than in 1972, although there was no significant difference ( $p > 0.10$ ) in seasonal growth between years. A significant growth interaction ( $p < 0.01$ ) among years and time of year resulted from declining plant heights during July of 1971 and different periods of increases and decreases in plant height in the two years.

### Blue Grama

Seasonal trends in root and crown TNC were quite similar for blue grama in both years at the Pawnee location (Fig. 1). Crowns accumulated and maintained higher concentrations of TNC than roots throughout the growing season, as has been reported for other perennial grasses (Weinmann 1949, Sprague and Sullivan 1950, Coyne and Cook 1970).

Spring drawdown of TNC reserves was very abrupt in both years, reaching the low point in both roots and crowns at the second leaf stage on about May 1. Seasonal lows in root reserves were about 25 mg/g in 1971 and 20 mg/g in 1972, while seasonal lows of crown TNC were about 42 mg/g in 1971 and 31 mg/g in 1972.

Under normal growing conditions, TNC in roots and crowns of blue grama is probably maximum at the end of the growing season. In 1971, however, fall regrowth reduced reserves so that maximum seasonal levels were not attained at the end of the growing season (Fig. 1). TNC in roots and crowns were significantly lower ( $p < 0.05$ ) at the end of the 1971 growing season than at the end of the 1970 growing season. Root and crown TNC were respectively about 50 mg/g and 78 mg/g at the end of the growing season in 1970, and only 36 mg/g and 59 mg/g at the end of the dry growing season in 1971. Low reserves at the end of 1971 probably resulted

from insufficient time for replenishment after fall regrowth. At the end of the relatively wet 1972 growing season, the level of root TNC was again about 50 mg/g and the level of crown reserves was about 70 mg/g, and reserves in both plant parts were nearly replenished.

Weaver (1958) stated that blue grama was the most drought-resistant of all the plains grasses in the Nebraska-Kansas-Colorado region. In both years of the present study, seasonal carbohydrate cycles for blue grama gave physiological indications as to why blue grama is so drought-resistant. It has the capacity to regrow rapidly during short favorable moisture conditions and rapidly replenish TNC reserves used in regrowth. Because of this capacity and the tendency for blue grama to maintain relatively high reserve stores (Fisher 1966), except during rapid spring drawdown and fall regrowth periods, the carbohydrate cycle is characterized as a narrow V-shaped cycle. Plants with such cycles should tend to be resilient to moderate or even heavy grazing.

Spring growth, expressed by plant height, had nearly ceased by the end of June 1971 but resumed rapidly after a short period of adequate rainfall (Fig. 1). TNC reserves were drawn upon and then replenished rapidly. After droughty conditions in July and August 1971, regrowth was stimulated by above-average September rainfall and TNC reserves were again drawn upon and nearly replenished to August levels.

Heavy June rainfall in 1972 speeded growth, resulting in additional TNC drawdown (Fig. 1). Above-normal rainfall in August and September of 1972 again caused regrowth and a large drawdown in reserves. Reserves in both roots and crowns were replenished very rapidly, and TNC levels were maximum by fall quiescence. Thus, blue grama has an outstanding ability to mobilize, utilize, and replenish TNC during short periods of favorable growing conditions.

Seasonal growth of blue grama was significantly greater ( $p < 0.01$ ) during the wet year of 1972, and seasonal root and crown TNC levels were significantly lower ( $p < 0.05$ ). Thus, there was a significant inverse relation between carbohydrate reserve storage and growth.

Significant interactions ( $p < 0.01$ ) among years and time of year were detected for current annual growth and TNC in roots and crowns. The growth interaction was a result of earlier growth in 1971 and reductions in plant height caused by droughty conditions in the summer of 1971. Most blue grama plants remained in the vegetative state and did not flower in the dry year of 1971 but flowered and set seed in 1972. The TNC reserve interactions observed among years and time of year were probably caused by later drawdown of TNC for fall regrowth in 1971 than in 1972.

### Western Wheatgrass

Root and crown TNC reserve cycles for western wheatgrass had similar patterns in relation to phenological stage (Fig. 1). Levels of reserves were usually slightly higher in crowns than in roots in 1971, but the opposite was true in 1972. Both phenological development and TNC reserve cycles distinctly differed between the 2 years. Most plants remained in a vegetative state during the dry year of 1971, but many became reproductive in 1972 when soil water conditions were more favorable. Even then many plants remained in a vegetative state in both years.

Root and crown TNC levels were reduced nearly 50% from about 110 mg/g to about 55 mg/g in an abrupt spring drawdown during initial spring growth in 1971. The low point was reached during the third-leaf stage. In contrast, root and crown TNC levels were reduced very gradually during spring drawdown in 1972, and more reserves appeared to be used during winter quiescence in 1971-1972 than the previous year.

Under more favorable rainfall in 1972, western wheatgrass showed a flat V-shaped carbohydrate cycle, taking considerable time for reserve replenishment. Under poor moisture conditions in 1971, reserves were replenished rapidly in early summer. Kinsinger and Hopkins (1961) had similar results with their nondefoliated western wheatgrass plants. From an ecological perspective, west-

ern wheatgrass appears to be quite drought tolerant and rather grazing intolerant relative to blue grama (Kinsinger and Hopkins 1961).

At the first collection in March of 1972, western wheatgrass already had 4.5 cm of leaf growth. Either growth had started much earlier or TNC reserves were utilized in regreening the already existing leaf growth produced the previous fall. The low point in TNC level was reached during the third-leaf stage in April of 1972.

Root and crown TNC levels were maximum during the fifth-leaf stage in late June in 1971 and at the end of the growing season at fall quiescence in 1972 (Fig. 1). After reserve storage levels reached maximum in 1971, they appeared to be drawn on continually for the rest of the growing season. The TNC levels were reduced about 45 mg/g or 35% during regrowth in late summer and fall of 1971, while TNC drawdown for fall regrowth in 1972 was only about 20 mg/g or 13% in crowns and was not observed in roots.

Seasonal growth of western wheatgrass, as indicated by plant height, was significantly greater ( $p < 0.01$ ) in 1971 than in 1972. Plant height was maximum in October in both years. However, the last 10 cm of growth in plant height in 1971 was produced during two periods of renewed growth activity. The growth rate in April and May was also greater in 1971 than in 1972 and was probably due to more rainfall in March, April, and May in 1971. Although plant heights were greater in 1971, western wheatgrass remained in a vegetative stage due to droughty conditions in the summer.

### James' Cryptantha

TNC in roots and crowns of the forb James' cryptantha showed a typical TNC seasonal cycle except for the increased TNC level from November to April. Lack of sampling during late fall did not allow detection of possible TNC buildup in the fall prior to quiescence in a one-year study in 1970-1971 at the Maybell location (Fig. 2). Root TNC levels were higher than crown TNC levels and showed greater fluctuations over the year. Since the root mass was greater than the crown mass, roots are considered to be a more important storage organ.

Spring drawdown was in May, after initial growth was over. Elongation of stems bearing floral buds may have accounted for the observed drawdown in TNC prior to flowering. Levels of TNC were maximum during fall regrowth in September. At the time of the last collection in September TNC levels were still increasing. Maximum TNC levels observed were about 171 mg/g in roots and about 48 mg/g in crowns.

Growth, expressed by plant height, began in March, and stem elongation was rapid through May and June. Plant heights were maximum at the end of June. Many seedstalks were broken after the flowering stage and during seed shatter, and plant height decreased significantly ( $p < 0.05$ ) by the time of the last collection, in September. At that time a rosette of leaves had sprouted from the crown as a result of fall regrowth.

### Pricklypear Cactus

Analysis of variance for root TNC data indicated significant changes ( $p < 0.01$ ) in TNC levels during the growing season at the Maybell location (Fig. 2). Respiration requirements during winter quiescence probably resulted in TNC decline of about 15 mg/g. Spring drawdown extended from March through June, corresponding with the phenological stage of regreening pads and flowering. TNC reserves were at a low point (about 30 mg/g) at the end of the flowering stage on about July 1. Root TNC reserves were rapidly replenished after fruit drop in September, reaching a maximum of about 87 mg/g at fall quiescence. Pricklypear cactus exhibited a typical U-shaped TNC cycle.

### Comparison Among Species

In six of eight species that were analyzed for TNC concentrations in two storage organs, TNC were higher in belowground than in aboveground storage organs. Blue grama maintained higher TNC levels in aboveground storage organs, and little rabbitbrush showed no difference in TNC between belowground and above-

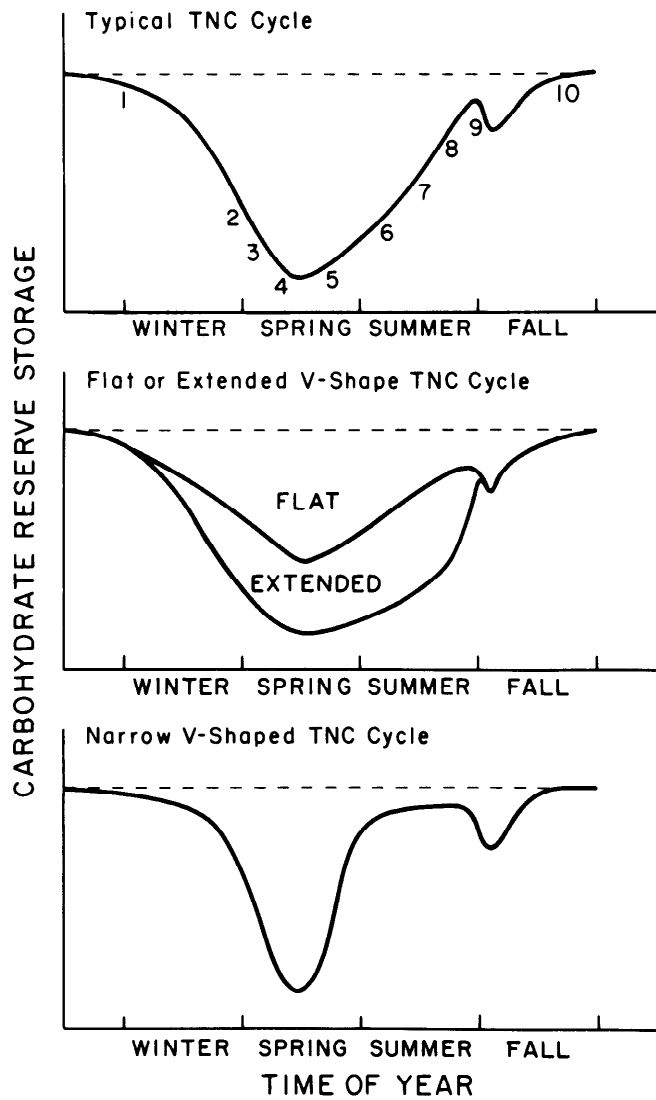


Fig. 3. Generalized annual carbohydrate reserve (TNC) storage cycles for plants exhibiting typical, flat or extended V-shaped, and narrow V-shaped conditions. Numbers on the typical cycle correspond to phenological stages listed for antelope bitterbrush in Table 1.

ground storage organs. Seasonal trends in TNC were similar in aboveground and belowground storage organs for all species, however, there were differences in the magnitude of fluctuations. In all species, the storage organ with the higher concentration of reserves also had greater fluctuations over the growing season and was identified as the more important organ for reserve storage.

Eight of the nine species studied showed the classical U- or V-shaped TNC reserve cycles (Fig. 3). All species showed the expected spring depletion of TNC in both aboveground and belowground storage organs for initiation of spring growth. Replenishment of TNC after depletion was generally completed after the seed-shatter stage except for antelope bitterbrush and scarlet globemallow. These two species completed their reproductive cycle early in the year and replenished reserves later in the year, at fall quiescence.

Fourwing saltbush and antelope bitterbrush had typical annual carbohydrate reserve cycles, and little rabbitbrush had a somewhat flattened cycle (Fig. 3). Fringed sagewort, scarlet globemallow, and western wheatgrass had definite flattened or extended V-shaped cycles and maintained low reserves for more of the growing season than did other species. Blue grama was the only species that had a narrow V-shaped cycle. It appeared to maximize the portion of the year that it maintained a high carbohydrate reserve.

Buwai and Trlica (1977) found western wheatgrass to be severely affected, fourwing saltbush considerably less affected, and blue grama not severely affected by multiple defoliation at moderate and heavy intensities. They found fringed sagewort detrimentally affected and antelope bitterbrush somewhat less affected by two defoliation treatments of moderate intensity. This ranking of defoliation effects—from some effect to a severe effect to a detrimental effect, corresponded closely with narrow V-shaped, typical V- or U-shaped, and flat or extended V-shaped annual carbohydrate reserve cycles in this study. The shape of the seasonal TNC cycle (Fig. 3) appears to be a good screening tool for predicting the relative effects of defoliation on different plant species. Least affected by defoliation are plants that replenish reserves rapidly after spring drawdown and regrowth periods (narrow V-shaped TNC cycles), thereby minimizing the part of the growing season with a low reserve status.

Except for scarlet globemallow, plants that benefitted most from a rest period following severe defoliation (Trlica et al. 1977) were those with narrow V-shaped TNC cycles, followed by typical V- or U-shaped cycles. The exception may be explained by the root morphology of scarlet globemallow and the difficulty of imposing defoliation treatments on this plant. Thick rhizomes may channel carbohydrates from undefoliated plants outside the bounds of a defoliated plot to treated plants within the plot (Menke 1973). However, additional studies are needed to confirm or refute this.

Growth of all species appeared to be stimulated by late summer or fall precipitation. Increased growth activity was accompanied by TNC reductions in all species except scarlet globemallow. Rapid TNC replenishment in scarlet globemallow at the time of fall regrowth may have masked the use of reserves for regrowth. The rate of TNC drawdown during fall regrowth was greatest in blue grama, but the rate of TNC replenishment was correspondingly greatest.

The amounts and distribution of precipitation, by affecting growth, greatly modified the characteristics of the seasonal TNC cycles. At each location, distributions of rainfall that caused increased seasonal growth resulted in lower seasonal TNC levels. Growth was found to be inversely related to storage of carbohydrate reserves.

Higher rainfall in April of 1971 resulted in increased early spring growth of all species studied at the Pawnee location and a corresponding reduction in TNC reserves. Higher rainfall in June, July, and August of 1972 resulted in increased growth and regrowth and a corresponding reduction in TNC reserves in all species at this location.

Annual precipitation at the Maybell location was only slightly greater in 1971 than in 1972, but early spring precipitation caused more soil water to be available for plant use in that year. Therefore, all species studied at this location grew more in 1971 and all maintained lower seasonal TNC levels in belowground and aboveground storage organs.

## Conclusions

Shrubs, forbs, and grasses have characteristic cycles of phenological development, storage, and depletion of carbohydrate reserves, and growth response to their environment. These cycles can be categorized on the basis of the shape of the annual TNC cycle, to help the range manager predict the likely response of a plant species to defoliation. Plants with narrow V-shaped drawdown and replenishment TNC cycles appear to be affected the least by defoliation. Plants with flat or extended V-shaped carbohydrate drawdown and replenishment cycles are more affected by defoliation than plants having either the narrow or typical V- or U-shaped TNC cycles.

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