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BIG BLUESTEM AND INDIANGRASS VEGETATIVE REPRODUCTION AND ANNUAL RESERVE CARBOHYDRATE AND NITROGEN CYCLES

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ABSTRACT

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Vegetational development of big bluestem (*Andropogon gerardi* Vitman) and indiangrass (*Sorghastrum nutans* (L.) Nash) was studied during 19 consecutive months. All big bluestem tillers arose extravaginally (penetrated the sheath of the subtending leaf) during late April and early May. Each tiller lived only during one growing season. Vegetatively reproductive tillers consisted of a rhizome, four to six adventitious roots, and an aerial shoot, and developed mature buds in leaf axils on their rhizomes. Reproductive tillers averaged two tiller offspring each during the succeeding growing season. About half of all big bluestem tillers were vegetatively non-reproductive, produced no mature buds on their rhizome, and were rootless. Indiangrass tillers arose extra- and intravaginally (the shoot remained within the subtending leaf's sheath) during late spring, early summer and autumn. Most tillers were biennial. Extravaginal tillers were vegetatively reproductive and each produced three to five adventitious roots from the rhizome portion of the tiller. By autumn, about half of all indiangrass shoots were first-year tillers that had emerged from parent-tiller buds during that growing season. Intravaginal indiangrass tillers were vegetatively non-reproductive, rootless, and usually short-lived. Total non-structural carbohydrates (TNC) in rhizomes of both species reached maximum concentrations during winter and were depleted during late spring. TNC levels recovered partially during the summer, and declined slightly for a short time during late August. Total Kjeldahl nitrogen (N) concentrations in rhizomes of both species was highest during winter, declined during late spring, remained low through mid-summer and began to recover during late summer.

INTRODUCTION

Life history descriptions of important range grasses are necessary to understand and to properly manage rangelands for producing domestic livestock and to preserve native ecosystems. Information concerning the normal cycles

of root, rhizome and shoot growth, and the formation and utilization of reserve substances will improve management practices. The need for life history studies has long been recognized (Sampson, 1914; Love and Hanson, 1932; Etter, 1951), but life histories of many important range species remain unknown.

In the True Prairie, big bluestem (*Andropogon gerardi* Vitman) and indiangrass (*Sorghastrum nutans* (L.) Nash) are abundant and highly productive forage grasses (Weaver, 1931) that persist by vegetative reproduction. Except for root system studies (Weaver and Zink, 1946; Weaver, 1958), brief life history descriptions (Weaver and Fitzpatrick, 1932; Nieland and Curtis, 1956) and fragmentary information in other reports (Aldous, 1930, 1934, 1935; Anderson, 1953), no comprehensive study outlines the normal vegetative life cycle of those species. For that reason, we studied the normal vegetative life-history of big bluestem and indiangrass from mid-June, 1969, through December, 1970, in a native prairie near Manhattan, Kans.

METHODS OF STUDY

The area studied was in a loamy upland range site, equivalent to "ordinary upland" (Anderson and Fly, 1955), in an excellent condition stand (Dyksterhuis, 1949) of True Prairie in the Kansas Flint Hills. The area fenced for the study had been lightly grazed for several years, but was not grazed during the study or in the preceding year.

From mid-June through mid-October, 1969, tiller samples (rhizomes and shoots) were collected on a weekly basis by removing approx. 0.1 to 0.2 m^2 areas of sod 4—8 cm thick. The samples were taken to the laboratory and washed with cold-water under pressure to remove soil, cataphylls, and other debris. All plant material was oven-dried for 24 h at 65—70°C to kill the tissues. Total leaf lengths and rhizome lengths were measured. Green leaves, expanded green leaves, and roots per tiller were counted on 45 tillers selected randomly from each sample. All rhizomes with roots and shoots were separated into current-year's (1969) and all prior-year's (pre-1969) age-classes. Each rhizome sample was oven-dried again, weighed to the nearest 0.0001 g, ground to 40 mesh in a Wiley mill, and then analyzed for total Kjeldahl nitrogen (N) and total non-structural carbohydrates (TNC) (Smith, 1969) by extracting with 0.2 N H_2SO_4 (Smith et al., 1964) and titrating reducing sugars by the Shaffer-Somogyi technique outlined by Heinze and Murneek (1940) and reported as glucose-equivalents.

Sampling in 1970 began in January and ended in December, and three big bluestem rhizome age-classes (current year's, 1970, previous year's, 1969, and older than 2 years, pre-1969) were separated. Aerial shoots were analyzed for Kjeldahl N and TNC during 1970. Root numbers and leaf and rhizome length data were not collected in 1970, but average shoot and rhizome weights were determined on each sample.

The number of 1969 tillers produced by each 1968 big bluestem rhizome

collected during 1969 was recorded for an estimate of the vegetative reproduction rate. Similar data were not recorded for indiangrass because identifying tillers by their year-of-initiation was questionable. All indiangrass rhizomes collected were separated into live and dead age-classes.

RESULTS

Big bluestem vegetative reproduction

The mature big bluestem tiller had an aerial shoot of leaves and sometimes an elongated culm. A rhizome and sometimes a root system comprised the underground portions of those tillers. Tillers began as buds on the rhizomes of their parent tillers. Buds grew horizontally from their parents before emerging through the soil surface. The axis that developed underground was the rhizome. Leaves were then produced, after which roots initiated from the rhizome portion of the tiller.

Big bluestem tillers arose extravaginally from parent tillers' rhizomes. Some tillers developed root systems and leaves and were usually vegetatively reproductive. Vegetatively reproductive tillers developing during 1968 initially produced about two 1969 tillers each, but only about half of the 1969 offspring survived the entire growing season (Table I). Tillers that died prematurely failed to produce mature buds or new tillers and developed no roots. Since rhizomes remained in the soil for several years following the death of the tillers' shoots, they were used to evaluate previous growth history. Data from rhizomes collected at the end of the 1970 growing season indicated about 50% of all shoots initiated during 1968, 1969, and 1970 were vegetatively non-reproductive (Table II). Reliable estimates of vegetatively reproductive to vegetatively non-reproductive ratios could not be ascertained for years before 1968.

TABLE I

Average numbers of live-1969 tillers attached to 1968 big bluestem rhizomes in weekly collections from June to October, 1969

Collection date	1969 tillers/ 1968 rhizome	Collection date	1969 tillers/ 1968 rhizome
June 16th	2.2	August 11th	1.4
June 23rd	1.8	August 18th	1.3
June 30th	1.8	August 25th	1.2
July 8th	1.6	Sept. 1st	1.2
July 14th	1.9	Sept. 9th	1.1
July 21st	1.4	Sept. 15th	1.1
July 28th	1.7	Sept. 22nd	1.2
August 4th	1.5	Oct. 7th	1.1

TABLE II

Number of vegetatively reproductive (R) and vegetatively non-reproductive (N) rhizomes among six rhizome age-classes (1965—1970) collected November, 1970

	Year produced:											
	1970		1969		1968		1967		1966		1965	
Rhizome type	*R*	*N*	*R*	*N*	*R*	*N*	*R*	*N*	*R*	*N*	*R*	*N*
Rhizome number	70	36	57	22	43	24	18	1	10	0	2	0

After remaining dormant during the winter season, rhizome buds commenced to grow early the next spring around March 20th. Bud swelling (Fig.1) was the first visible sign that growth was beginning. By about April 10th, buds that elongated had tips oriented horizontally and produced vegetatively reproductive tillers, while non-elongating buds' tips were

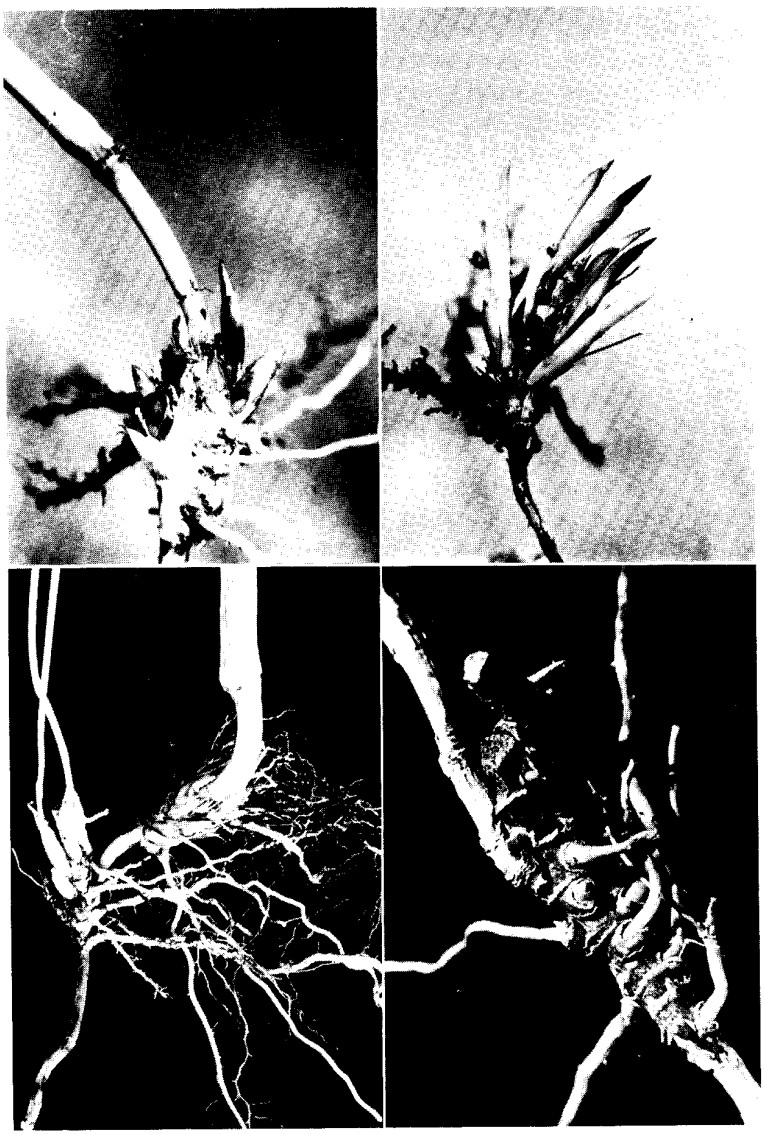

Fig.1. Four stages in the life cycle of big bluestem tiller.

oriented vertically (Fig.1) and usually produced no vegetatively reproductive tillers.

Vegetatively reproductive tillers were composed of a rhizome, leaves, roots and mature buds. As the tiller's 9 to 18 rhizome internodes elongated, cataphylls developed, encasing the rhizome. The first two to four rhizome internodes usually did not elongate; the next two to four elongated (4—10 mm each) and remained at maturity as a narrow stalk-like structure (Fig.1). The next six to eleven internodes elongated slightly less (2—7 mm each) and was the major storage and bud producing portion of the rhizome. Rhizome growth after shoots emerged was restricted to diameter enlargement (cell growth), bud development, and uppermost internode elongation above the expanded leaves' insertion. Rhizome lengthening ceased as jointing (aerial culm development) began in mid-July (Table IV).

Current-year rhizomes (1970) constituted the largest age-class (about 45% by weight) of rhizomes at the end of the growing season indicating decomposition of rhizomes produced the previous year (Table III). Approximately half of the rhizomes produced during each of the years, 1968, 1969, and 1970, were vegetatively non-reproductive and contributed little to the total sod rhizome weight. Only a few vegetatively reproductive rhizomes older than 3 years were found, and none older than 6 years could be identified. Vegetatively non-reproductive rhizomes older than 4 years were not found in the sample.

The first one to three leaves emerging from the soil were morphologically intermediate between the cataphylls and the cauline leaves; their sheath-blade separation was lacking as in cataphylls, but they had a photosynthetically active blade as did cauline leaves. A total of 6 to 18 aerial leaves developed per tiller. Tillers producing an inflorescence had the maximum number of leaves. Between two and three fully expanded green leaves were displayed per tiller from May through August (Table IV). Maximum leaf height was as jointing ceased in August.

Leaf production and death occurred continuously throughout the tillers' lives. Leaves normally died acropetally on the shoot; however, after a tiller produced an inflorescence, leaf death occurred both acropetally and basipetally, with an intermediate culm leaf usually the last to die (mid-October). Leaf death on tillers without an inflorescence proceeded acropetally until the last leaf exerted senesced.

Each vegetatively reproductive big bluestem tiller averaged three to six adventitious roots per rhizome (Table IV) and were confined to the bud producing and storage portion of rhizomes. Usually one or two (sometimes four) roots emerged per internode with only a few rhizome internodes producing roots. Roots emerged after at least one aerial leaf was fully exerted (about May 11th—15th) from the upper and lower surfaces, in a plane generally perpendicular to the insertions of the cataphylls and buds. A flush of adventitious roots was initiated with late summer rains in August (Table IV). During the mid-summer drought (July) and autumn senescing periods

TABLE III

Oven-dry rhizome weight by age-class, rhizome age-class composition by year and by vegetatively reproductive (*R*) and vegetative non-reproductive rhizomes (*N*) within years, and average oven-dry rhizome weight from big bluestem rhizomes collected in a 0.3m² area of prairie soil. November 6th, 1970

	Year rhizome developed											
	1970		1969		1968		1967		1966		1965	
Weight (g)	15.38		9.38		6.02		1.77		1.34		0.14	
% by weight	45.2		27.6		17.7		5.2		3.9		0.4	
	R	*N*	*R*	*N*	*R*	*N*	*R*	*N*	*R*	*N*	*R*	*N*
Weight (g)	14.7	0.7	8.9	0.5	5.7	0.3	1.8	0.0	1.3	0.0	0.1	0.0
Average weight (mg)/rhizome	210	19	155	23	133	13	98	5	134	0	141	0

TABLE IV

Average tallest leaf height, number of expanded green leaves/tiller, roots/rhizome, rhizome length, and percentage of vegetatively reproductive tillers in big bluestem during 1969

1969 date	Average total leaf height (cm)	Number of expanded green leaves/ tiller	Number of roots/ rhizome	Rhizome length (mm)	% of 1969 tillers reproductive
June 16th	47.7	2.2	0.8	15.1	39
June 23rd	52.9	2.2	0.7	13.7	43
June 30th	59.3	2.1	1.9	13.0	42
July 8th	78.1	2.4	2.0	23.7	67
July 14th	83.4	2.3	2.6	17.0	44
July 21st	73.0	2.8	2.9	33.1	62
July 28th	73.8	2.5	3.3	26.5	64
August 4th	68.8	2.3	2.7	22.5	73
August 11th	81.1	2.6	4.6	30.6	75
August 18th	91.3	2.7	4.6	23.4	55
August 25th	85.4	3.0	5.2	29.6	71
Sept. 1st	77.7	2.7	5.3	33.0	67
Sept. 9th	77.3	1.7	5.2	28.6	49
Sept. 15th	61.5	1.4	4.3	28.2	54
Sept. 22nd	69.5	1.1	5.8	34.1	71
Sept. 29th	72.9	0.9	6.9	37.3	82
Oct. 7th	80.4	0.5	6.3	36.3	87

(October) no adventitious roots were produced. Rhizomes ceased initiating roots at the end of the tiller's growing period; rhizomes that lived into a second growing season initiated no new roots. As big bluestem rhizome roots aged, their cortex loosened and decomposed, leaving a tough, woody core with a suberized surface and contained many reserve starch granules during autumn (Fig.2). Root cores persisted in the upper soil horizon 3 to 5 years, though not functional after the first year. Year-old roots must have temporarily served the next season's reproductive tillers until those tillers developed their own root systems.

Each mature vegetatively reproductive tiller had 6 to 14 buds in an alternating arrangement along both sides of its rhizome between the stalk structure and the culm (Fig.1). Buds were inserted in the cataphyll and true leaf axils. Buds near the rhizome extremities (stalk and aerial culm) were usually poorly developed. Normally, all buds remained quiescent during their parent tiller's growing season unless the parent's growing point died; thereafter, usually one sufficiently matured lateral bud developed into a secondary tiller. A few latent buds as old as three years were observed (Fig.3).

Vegetatively non-reproductive tillers usually developed from among buds

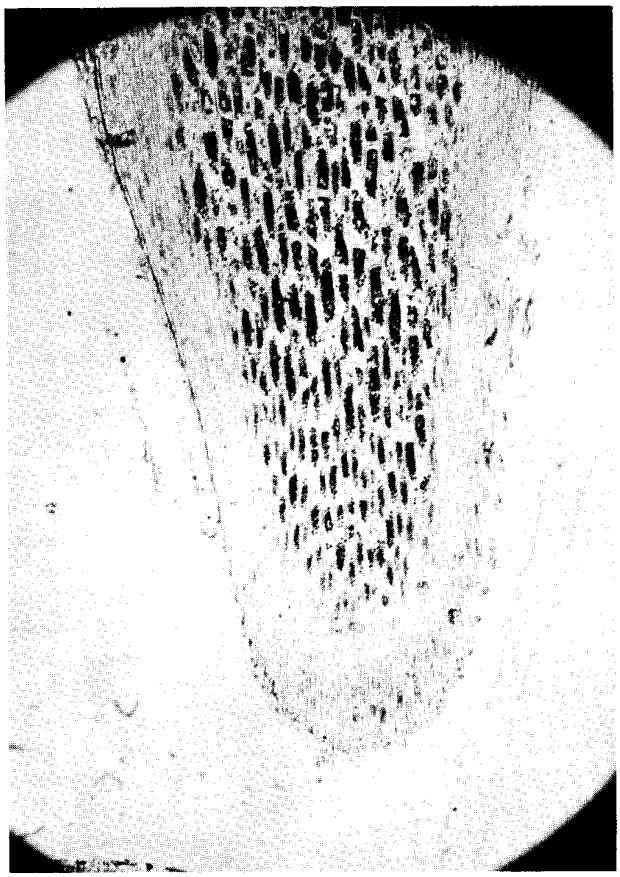

Fig.2. Diagonally sectioned root tissue from big bluestem.

near the aerial culm-base and produced leaves and rudimentary buds, but not mature buds or aerial culms (Fig.1). Such tillers began dying midway into the growing season, often concurrently with drought stress about mid-July.

Big bluestem rhizome TNC and nitrogen content

Big bluestem aerial shoots gained weight from May to mid-September to an annual maximum of 680 mg per shoot, and then began losing weight rapidly (Fig.4). Average TNC per aerial shoot increased from about 10 mg during May to 70 mg in late August and then declined in weight. Nitrogen content (mg N) per shoot increased from 0.73 in early May to 2.64 in early June, then declined to a mid-season low of 2.1 mg, and remained low until

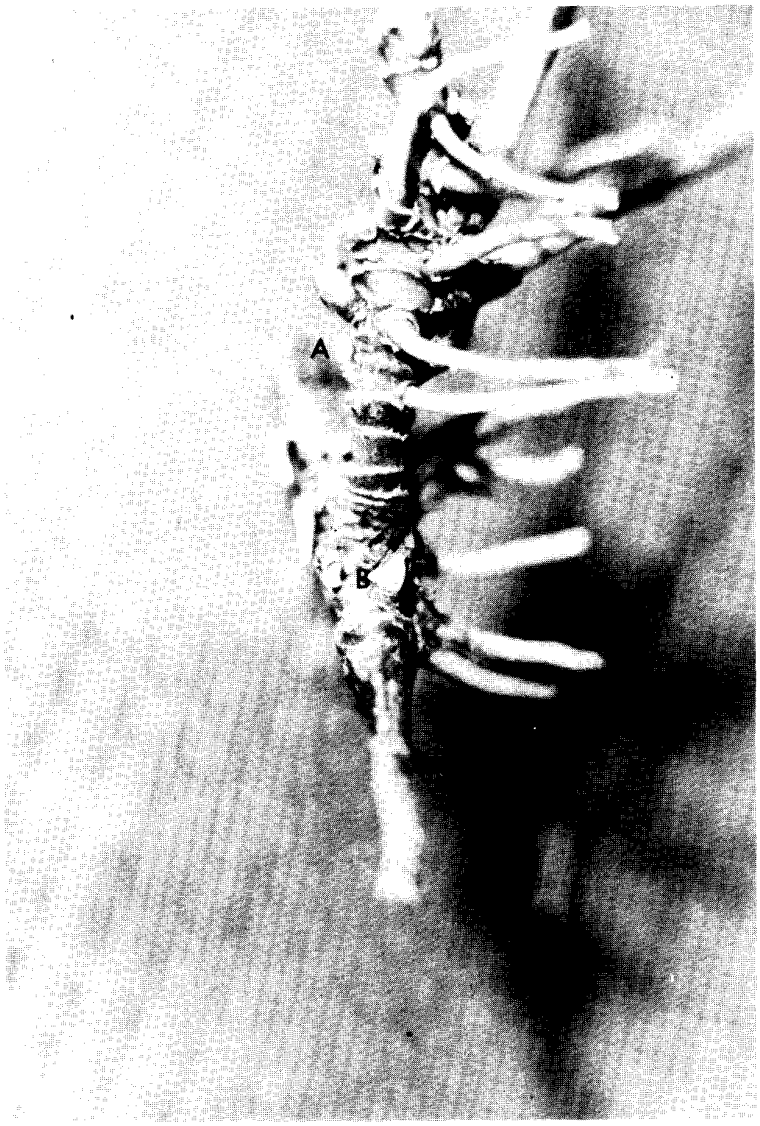

Fig.3. Dormant rhizome buds two and three growing seasons old on big bluestem rhizomes.

August. Then N content increased again, to an annual maximum (about 3 mg per shoot) by mid-September.

TNC concentration in aerial shoots was at its maximum, 13% in early May, declined to 8% during mid-May, then gradually increased during early June to its former maximum by July and finally decreased from August through September. Nitrogen concentrations in shoots, at their annual maximum

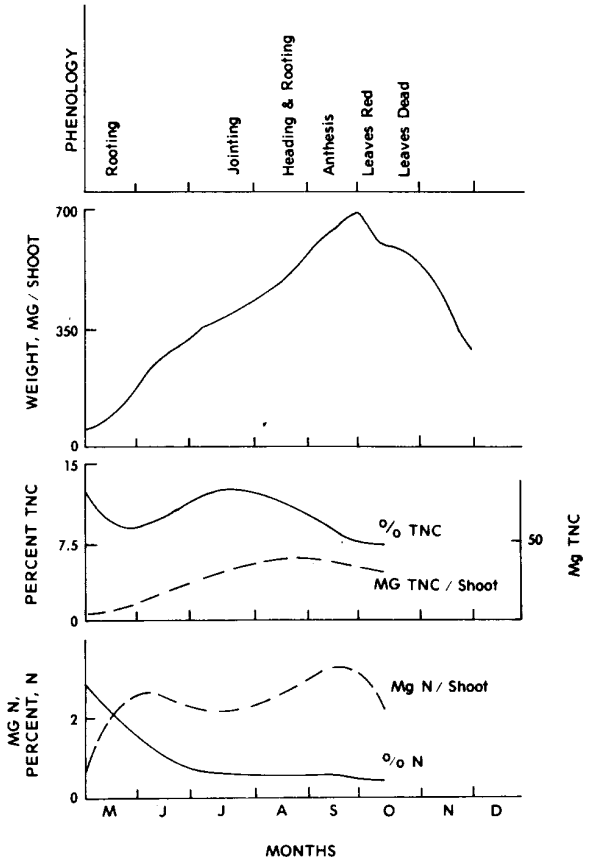

Fig.4. Average oven-dry shoot weight, N concentration and amount per shoot, TNC concentration and amount per shoot in 1970 big bluestem shoots.

(2.7%) as shoots emerged in the spring, fell continuously thereafter. The largest and most rapid decline in N concentration (from 2.7 to 0.6%) occurred between emergence and the beginning of jointing, after which N concentration declined only slightly.

Pre-1969 rhizomes generally declined from their maximum of 80 mg per rhizome in June, 1969, to a minimum of 39 mg per rhizome in December, 1970. Mid-growing season lows, and partial recoveries each autumn occurred during 1969 and 1970. The 1969 rhizomes increased in weight during the 1969 growing season, reaching a maximum of 100 mg per rhizome that year. The 1969 rhizomes lost weight in mid-season and recovered partially during autumn, 1970. Average weight of 1970 rhizomes reached maximum (76 mg per rhizome) by September.

Cyclic TNC fluctuations were similar to that typically described in grasses,

reached a low as spring growth began, partially recovered, dropped again with inflorescence development and new rhizome rooting (Fig.5). During leaf senescence rhizome TNC concentrations increased again, peaked during winter both years. Mid-season declines in TNC coincided with rooting and were most evident in the current-year rhizome age-class. Generally, old rhizomes had less TNC than young ones, and similar TNC concentrations among age-classes.

Nitrogen concentrations reached maximum during winter; minimum, during summer with recovery in late July or early August. All rhizome age-classes had similar N fluctuations in both 1969 and 1970.

INDIANGRASS VEGETATIVE REPRODUCTION

Vegetatively reproductive indiangrass tillers arose extravaginally from

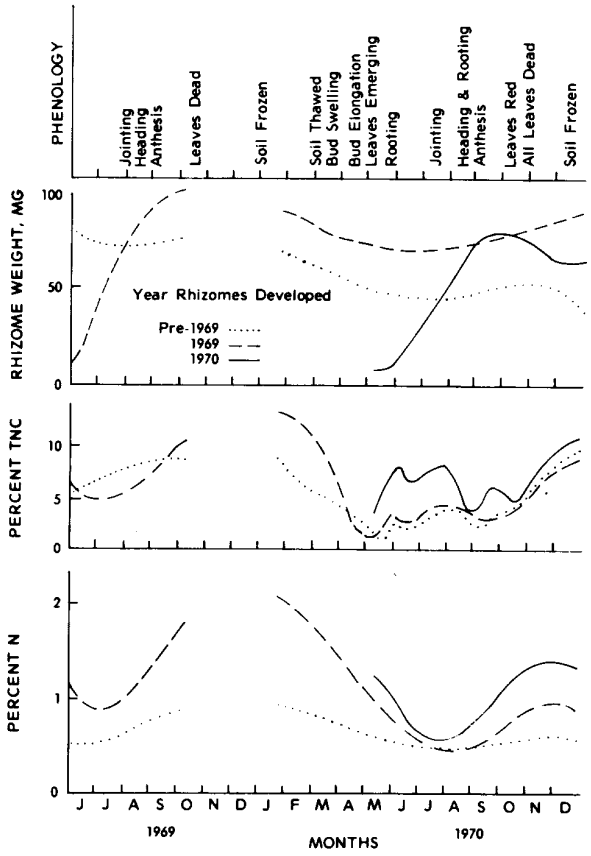

Fig.5. Average oven-dry weight per rhizome, average percentage of TNC and N and phenological data for three big bluestem rhizome age-classes.

parent rhizomes, spanning two growing seasons. Those biennial tillers produced a rhizome, root system, and aerial leaves during the first growing season. During their second they produced leaves, roots, and sometimes an aerial culm terminating in an inflorescence.

Vegetatively non-reproductive indiangrass tillers arose intravaginally as well as extravaginally. They had no root system and failed to develop either mature rhizome buds or inflorescences and failed to elongate from their parent tillers.

As the tiller population consisted of both first- and second-year tiller age-classes, results depicted averages between age-classes instead of averages within a single age-class. From mid-July until the growing season ended, 40—50% of all indiangrass shoots were from first-year tillers. The number of fully expanded, green leaves per tiller reached maximum, 2.3, during August, after inflorescences had emerged, and declined sharply after anthesis in September (Table V). Cauline leaves on second-year indiangrass tillers persisted well, since only eight to ten leaves were produced during the 5-month growing season.

Rhizome lengths ranged from 10 to 114 mm and averaged between 19 and 34 mm (Table V). Rhizomes were uniform in diameter throughout, hollow and slightly flattened laterally. Internodes' lengths ranged from 1 to 8 mm. Internode numbers per rhizome ranged between 10 and 24 and averaged 14 on vegetatively reproductive tillers.

Buds grew outward from rhizome internodes and were mainly confined to the region root initiation. One to ten buds matured on each vegetatively reproductive tiller's rhizome, and only a few (one to five per tiller) developed into another tiller.

Lateral buds initiated growth during early to mid-March and grew most actively during mid-May. Growth continued until late September stopping only during a mid-summer drought. As growing points moved laterally from their parent rhizome, they developed new rhizomes that initiated adventitious root systems before cauline leaves emerged from the soil. By then parent tillers had fully expanded leaves. First aerial leaves appeared about June 20th during the tiller's first growing season. Aerial shoots continued growing until frost, and other adventitious roots were continually being initiated except when soil around the rhizomes was dry. Newly emerged tillers usually produced leaves during their first growing season (shoots emerging in late autumn often produced cataphyll-like leaves), but their growing points remained below the soil surface. Aerial leaves died usually by November; although, partially emerged leaves' intercalary meristems remained alive over winter and resumed growing the next spring. Green leaves found during mid-April, grew rapidly during early May, overtopping other warm-season grasses emerging in the stand. Other adventitious roots were initiated beginning about mid-May, but relatively few roots emerged from rhizomes during the tiller's second growing season. The next generation of tillers was initiated from rhizome buds during the second growing season, completing the life cycle.

Jointing began during mid- to late July and inflorescences began emerging by late July to mid-August. Anthesis began the last week in August, reached maximum during the first week of September, and ended by September 15th. Aerial portions of second year tillers began dying in late September and by mid-October appeared dead. Indiangrass aerial leaves died basipetally during vegetative growth and acropetally and basipetally after anthesis. If inflorescences were produced, an intermediate culm leaf was the last to die.

Indiangrass oven-dry shoot weight increased from emergence to an annual maximum (420 mg) near the end of jointing early in August, then declined gradually (Fig.6). TNC content per shoot (mg) increased with early-season shoot growth, reached annual maximum (53 mg) by early August, and declined gradually during anthesis and seed developmental stages. Unlike big bluestem, annual indiangrass TNC percentage changes were relatively slight, ranging between 8% during late May and mid-October to 13% in late July.

Nitrogen content per shoot (mg) in indiangrass showed no mid-season depression as in big bluestem. Nitrogen content per shoot (mg) declined during anthesis, seed development, and shoot senescing stages. Average N concentration in indiangrass shoots (Fig.6) was at its seasonal maximum, 3%, during emergence, and declined rapidly to 0.5% before jointing. After jointing, N percentage remained relatively constant.

TABLE V

Average tallest leaf height (cm) and number of expanded green leaves/tiller, number of roots/rhizome, rhizome length (mm), and percentage of live indiangrass tillers, during 1969

1969 date	Average total leaf height (cm)	Number of expanded green leaves/ tiller	Number of roots/ rhizome	Rhizome length (mm)	% first year tillers
June 16th	40.3	1.4	4.1	20.3	
June 23rd	60.5	1.4	3.9	24.5	
June 30th	53.1	1.5	4.7	21.2	
July 8th	61.1	1.6	3.8	25.1	11
July 14th	59.8	1.9	5.2	18.9	22
July 21st	65.6	2.2	6.4	34.0	16
July 28th	50.9	1.9	4.0	32.3	51
August 4th	45.0	2.0	5.2	23.1	49
August 11th	52.1	2.3	5.8	30.2	44
August 18th	54.3	2.3	3.8	23.7	40
August 25th	54.4	1.9	4.5	27.3	36
Sept. 1st	58.7	1.8	4.5	27.5	40
Sept. 9th	57.9	1.6	6.2	24.9	47
Sept. 15th	47.7	1.6	4.1	25.3	38
Sept. 22nd	50.5	1.2	4.2	26.8	47
Sept. 29th	45.0	0.4	5.1	27.7	51
Oct. 7th	54.3	0.3	5.3	29.6	49

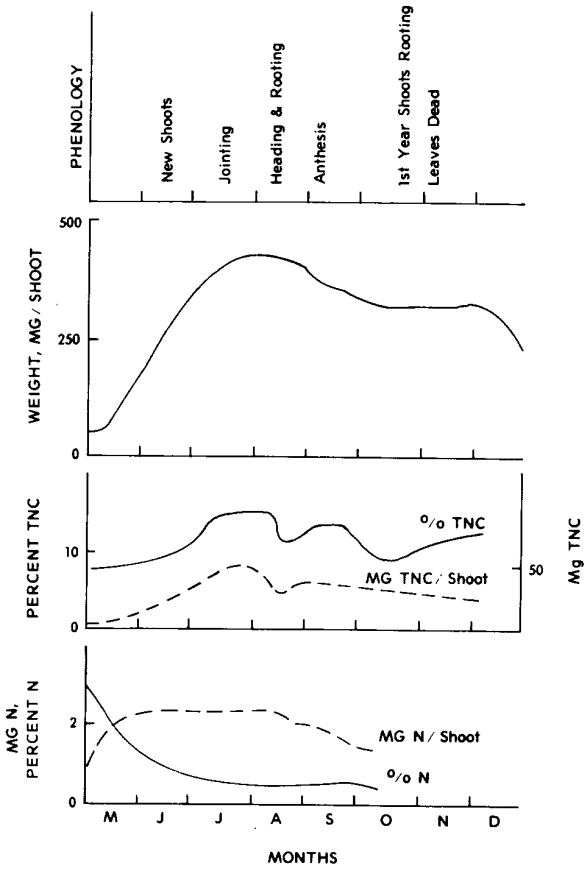

Fig.6. Average oven-dry shoot weight, N concentration and amount per shoot, TNC concentration, and amount per shoot in indiangrass.

Indiangrass rhizome TNC and nitrogen content

Indiangrass rhizomes on first- and second-year tillers, followed a pattern of high weights in winter and low in summer, but dead age-class rhizomes had highs in summer and lows in winter (Fig.7).

Minimum TNC concentration in both age-classes of indiangrass rhizomes was concurrent with spring emergence with a second seasonal decline in rhizome reserves as plants jointed. Annual TNC concentration reached maximum during winter. Younger rhizomes always had higher TNC averages than did older ones.

Rhizome N percentages in both indiangrass rhizome age-classes fluctuated

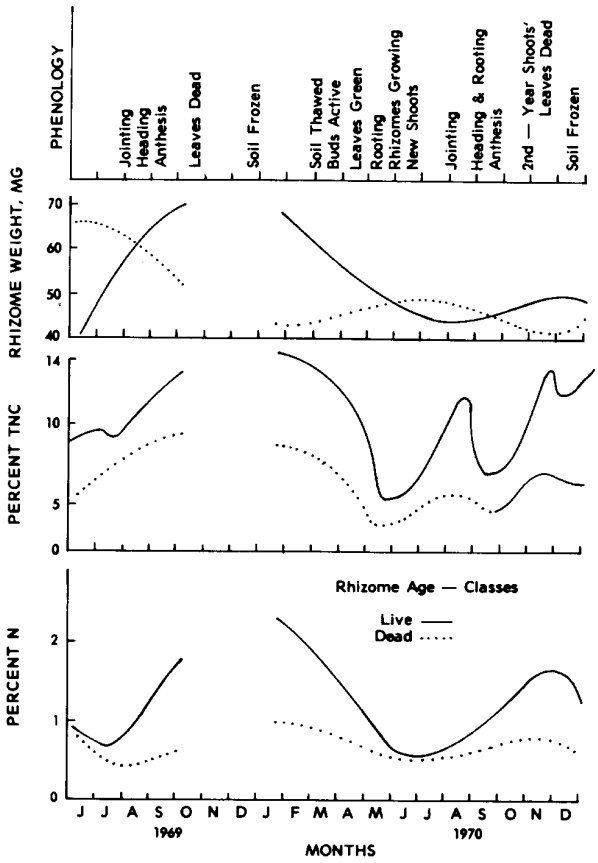

Fig.7. Average weight per rhizome, average percentage of TNC and N, and phenological data for two indiangrass rhizome age-classes.

in annual patterns similar to those in big bluestem, although the absolute N concentrations tended to be higher in indiangrass than in big bluestem. Maximum N was in winter; and minimum, during summer. Younger rhizomes maintained more N with larger fluctuations than did older rhizomes.

DISCUSSION AND CONCLUSIONS

Big bluestem tillers were comparable to annual tillers. Buds on rhizomes over-wintered and developed into tillers the next year, then lived only one growing season. Tillering in big bluestem was clearly determinant, i.e., under protection a definite number of shoots emerged as a spring flush during May, and no other shoots emerged the remainder of the season. If the growing

point on those shoots was removed by grazing, trampling, or insect damage, the current-year rhizomes' buds stimulated secondary shoots. But tertiary shoots were never found on secondary shoots, even when secondaries were severely grazed. Secondary tillers also failed to joint.

Indiangrass had indeterminant tillering and biennial tillers establishing progeny tillers throughout most of the growing season. Vegetative reproduction while the parent tiller was still photosynthetically active was believed to have a definite survival advantage over vegetative reproduction after the parent tiller had senesced because initial growth in the latter instance would depend wholly on stored reserves. Carbohydrate reserves were depleted in indiangrass rhizomes while second-year tillers were resuming growth and rhizomes of first-year tillers were developing during late spring.

New roots appeared on big bluestem and indiangrass tillers only when green leaves were present. Therefore, initial root growth probably depended on current photosynthate rather than stored food reserves.

Big bluestem vegetative reproduction rate may be largely controlled by changes in the vegetatively reproductive to non-reproductive tiller ratio which was consistently about 1 : 1 during 1968 through 1970. However, observations in a poor condition prairie where big bluestem was increasing in density during a protection period indicated that ratio to be larger than 1 : 1.

Range scientists have recommended mowing prairie areas in Kansas used for hay production only once a year, July 1st—15th (Hyde and Owensby, 1970), to obtain a maximum yield of good quality hay and stand persistence. Shoot growth, TNC, and N data, as indices of yield and forage quality, supported the July 1st—15th recommendation. Earlier mowing would produce less hay with higher N content; later mowing, poorer quality hay with no increase in herbage yield (Owensby and Anderson, 1969). TNC in forage reached maximum during the recommended harvest period, indicating readily digestible carbohydrates were relatively high then.

Indiangrass tillers were of two age-classes, so first-year tillers, mostly below cutting height, escape harvest in a haying operation, while all big bluestem tillers were of a single age-class subjected to harvest. Big bluestem's regrowth (from rhizome buds) would depend on reserves for carbohydrate supplies. In contrast, indiangrass regrowth came primarily from the release of already established and photosynthetically active tillers after the overstory was removed by mowing. Owensby and Anderson (1969) reported July and August clipping reduced big bluestem basal cover without changing indiangrass basal cover.

Nitrogen accumulation in big bluestem shoots suggests that N uptake is related to soil moisture availability and root activity. Nitrogen content in shoots increased during early spring and again in August when new roots were being initiated into moist soil.

Big bluestem and indiangrass accumulated about 85 and 95%, respectively, of their annual herbage N-requirement between May 15th and June 15th.

Earlier N demands of the herbage were met by using N reserves. Moisture was depleted in the upper soil horizons by July 1st; therefore, further N uptake after July 1st could have been by new actively growing roots then being initiated on new rhizomes. Irrigating in conjunction with late-season N applications reportedly has stimulated warm-season herbage growth and N accumulations (Owensby et al., 1970). Light N applications between May 1st and May 15th most likely would favor big bluestem and indiangrass.

Based on our N content data for big bluestem and indiangrass shoots, a prairie yielding 2802 kg/ha (2500 lb/acre) of big bluestem and indiangrass forage required about 17 kg N for herbage production. Habitat must have supplied 14 kg N, while 3 kg came from N reserves in parent rhizomes. If annual root system yields could be estimated as equivalent to or less than top growth, and N concentrations in roots were similar to those in aerial portions of the plants, maximum N requirement per year for big bluestem and indiangrass yielding 2802 kg/ha was approx. 34 kg/ha.

Carbohydrate and N reserves in big bluestem and indiangrass were increasing during September and later when above-ground plant parts appeared to be dead. Such late season accumulations, in the absence of photosynthesis, probably resulted from carbohydrate and N-compounds migrating from dying culms and roots. Herbage removal during late fall and early winter could affect food reserves.

Nitrogen migration from shoots to rhizomes previously has been described (Richardson et al., 1932; Weinmann, 1940, 1942). However, the amplitude in the N concentration cycle discovered for big bluestem and indiangrass rhizomes was unexpected. Big bluestem rhizomes more than doubled in N concentration, increasing from 0.90% during July, 1969, to 2.00% during January, 1970, a calculated increase of 1.43 mg N per rhizome. During the next spring, N concentration in rhizomes of that age-class decreased to 0.49%, a calculated loss of 1.43 mg N per rhizome. Presumably, N lost from rhizomes during the spring went into developing shoots.

Utilization of the phenological and physiological data found here to manipulate plant communities is possible. Better management decisions with respect to haying and N fertilization are now possible.

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