

Seasonal Nitrogen Translocation in Big Bluestem During Drought Conditions

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Abstract

This study, conducted during a severe drought in 1980, assesses the effects of burned and unburned treatments in tallgrass prairie on nitrogen content of big bluestem, *Andropogon gerardii* Vitman. Seasonal total nitrogen and amino-nitrogen translocations in big bluestem in the tallgrass prairie were studied on burned and unburned treatments within Konza Prairie Research Natural Area, Manhattan, Kans. Leaf total nitrogen dropped from .71% in June 1980 to .21% in November with no significant difference between treatments. Rhizome total nitrogen was significantly different between treatments with a June to November increase of .46% to .86% in unburned and .41% to .82% in burned treatments. Roots averaged 72% of rhizome total nitrogen, indicating that roots are also used as storage organs for nitrogen. Comparisons with other studies conducted in 1980 and 1971–1972 indicate that drought stress may reduce the total nitrogen content of big bluestem. In April 1980, emerging leaves on the unburned plots were significantly higher in amino acid concentration than those on the burned plots. Although leaf amino acid concentration was constant after July, the percent of total nitrogen as amino acids increased 3 to 4 fold from mid-August to October. Rhizome amino acid concentration was significantly higher on the unburned than on burned plots. The September 1980 increase in leaf amino acid concentration and percent of total nitrogen as amino acids indicate a breakdown of protein in aboveground tissue. The concurrent increase in rhizome amino acid concentration and percent of total nitrogen as amino acids supports the concept of fall translocation of nitrogen to the belowground parts which serve as storage organs.

Fall translocation of nitrogen from foliage to storage organs has been suggested as the explanation for nitrogen losses from living aboveground material of grasses during late summer (Weinmann 1940, 1942, 1948; Clark 1977, 1981). Pate (1971), Perry and Moser (1974), and Trlica and Singh (1979) discussed the possibility of nitrogen movement out of senescing plant parts and into storage organs for use in the spring. Amino acids are hypothesized to be the form of late season nitrogen movement (Weinmann 1942). Total amino acids decrease in leaves and increase in stems of grasses and trees as the amino acids move out of the senescing plant parts (Koretskaya and Zholkevich 1966, Trlica and Singh 1979, Chapin and Kedrowski 1983). Concurrently, the total nitrogen content in leaves decreases as the total nitrogen levels in stems, rhizomes and roots increases. The storage of nitrogen in perennial plant parts may be in the form of amino acids (Weinmann 1942, Perry and Moser 1974) or as protein (Thimann et al. 1974, Chapin and Kedrowski 1983).

Internal conservation of nitrogen could be critical for survival in a nitrogen limited system (Pate 1971, Switzer and Nelson 1972, Woodmansee et al. 1978). As Bormann et al. (1977) stated, fall translocation would maintain a mobile pool of nitrogen unaffected by outside losses and serve to guard against short-term shortages in soil nitrogen availability. Trlica and Singh (1979) projected that

with internal nitrogen recycling the plant would be protected from reduced availability of soil nitrogen under drought conditions.

Some reported estimates of internal nitrogen conservation in grasses are 75% for *Molinia* (Morton 1977); 33% (Clark 1977) and 25% (Woodmansee et al. 1978) for the shortgrass prairie; and 18% (McKendrick et al. 1975) and 40% (Adams 1982) for big bluestem in the tallgrass prairie. These estimates describe an important system of nitrogen conservation in perennial grasses; however, Clark (1977) and Woodmansee et al. (1978) state that these values are only assumptions of fall translocation and the mechanisms for nitrogen losses from living aboveground plant material have not been established.

The objective of this study was to follow the movement of total nitrogen in leaves, rhizomes, and roots of big bluestem, *Andropogon gerardii* Vitman, a dominant grass of the tallgrass prairie. Specific attention was given to the fall decrease in leaf total nitrogen and concurrent increase in rhizome total nitrogen which has been hypothesized to be fall translocation of nitrogen to the perennial plant parts for storage. In this paper fall translocation is used to refer to the movement of nitrogen from the annual to the perennial parts during senescence. This may be a method for internal conservation of nitrogen to reduce losses and maintain a reliable nitrogen supply for the plant. Amino acid levels in the various plant parts were measured to test the hypothesis that nitrogen is transported to the storage organs as amino acids. Burned and unburned treatments were followed to assess the effect of burning on total nitrogen and amino acid content in grasses.

Study Site and Methods

The study was conducted at Konza Prairie Research Natural Area (KPRNA), 12 km south of Manhattan, Kans. Two sites were used, referred to as north and south sites, respectively. The north site is on Reading silt loam, a fine mixed, mesic Typic Argiudoll, formed in alluvial sediments. The south site is on Tully silty clay loam, a fine mixed mesic Pachic Argiustoll, formed in colluvial and alluvial sediments.

In April 1980, eight 5 × 2-m plots were set up at each site providing 4 replicates of burned and unburned treatments. At the north site burned and unburned treatments were paired, with 1 plot randomly selected to be burned and its paired plot left unburned. The north site, and thus the unburned treatment, was last burned in 1978. The south site design conformed to a previously designed KPRNA management plan, which had been in effect for 8 years. Plots were established on opposite sides of the 3-m fireguard between an area burned that spring (annually burned) and one burned 1 year earlier (a 2-year burn) referred to hereafter as burned and unburned, respectively. Statistical analysis at the end of 1980 indicated no significant difference in plant total nitrogen between sites for each treatment. The north site was abandoned in 1981 due to logistical problems and the replicates on the south site increased to 8 for each treatment to reduce variance for leaf total nitrogen.

On the average, 75% of the yearly precipitation comes from April through September, the big bluestem growing period. In 1980, only 46% of the average for this period was received. In McKendrick's (1975) study of big bluestem on a nearby area, the leaves gained weight until mid-September and began to turn

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reddish brown, a sign of senescence, in early October. In this study, growth appeared to have stopped in mid-June 1980 and browning of mature leaf tips was observed in mid-July, indicating early senescence. This drought was taken into account in interpreting the results of this study. In 1981, 107% of the average precipitation from April to September was received.

Field Sampling

A soil core (30 cm dia by 20 cm deep) with roots and plant tops intact was collected from each plot at approximately 2-week intervals from 19 May 1980 to 2 November 1980 and 4 April 1981 to 18 June 1981. The cores were chosen to contain a majority of big bluestem. Soil samples from 0–10 cm and 10–20 cm depths were also collected for gravimetric soil moisture determinations. The soil cores with intact plants were soaked in cold water for 1 hour before washing the soil from the roots and rhizomes by spraying water from a garden hose. Only belowground parts attached to a live big bluestem leaf or a recently dead leaf (that year) were retained. After washing, the samples were frozen until further processing. Total elapsed time from field sampling to freezing was 4 hours.

The samples were thawed and separated into 3 categories: (1) leaves, (2) crowns and rhizomes, and (3) roots. Due to the drought, stems and seedheads did not develop on the study plots and very few were observed anywhere on KPRNA in 1980. The samples were dried at 60°C to a constant weight, ground to 40 mesh in a Wiley mill, and stored in the dark in air-tight bottles.

Analytical Procedure

Plant total nitrogen was analyzed by the standard micro-Kjeldahl procedure (Bremner 1960) using a Pro-Pak catalyst and an Aminco distillation apparatus, then titrated with weak sulfuric acid. Random samples of each tissue type over several dates were run on a Technicon autoanalyzer, and a U.S. Bureau of Standards orchard leaves standard was used to assess the accuracy of the micro-Kjeldahl method and to correct for incomplete recovery of nitrogen. Data are expressed on a dry matter basis.

Samples of 0.25 g oven-dry tissue for the amino acid analysis were extracted by incubating overnight in a water bath shaker at 65°C in 25 ml of 80% ethanol. The solution was filtered, dried to a powder with a roto-evaporator and rehydrated to standard volume with glass double distilled deionized water. Test analysis determined that extraneous compounds such as organic sugars, etc., did not interfere with the Yemm and Cocking (1955) ninhydrin reaction for total amino acids; therefore a resin column purification was not needed (Hayes 1982). The method detects glutamine and asparagine but not tryptophan. Glycine was used for a standard curve and all chemicals were fresh for each assay run. Data are reported as $\mu\text{g amino N} \cdot \text{g}^{-1}$ oven dry plant tissue for amino acid concentrations. Percent of total nitrogen as amino acids was calculated by dividing total amino acid concentrations by total nitrogen concentrations. Percent of total nitrogen as amino acids shall be referred to as percent amino acids throughout. (Only leaf and rhizome samples collected during the first 2 weeks of each month were analyzed).

A two-way analysis of variance for site-time, treatment-time, and site-treatment and interactions using SAS procedures was run on all 1980 data. Two-way analysis of variance for treatment-time and the interactions was run on 1981 data. Due to no statistical difference between sites for any parameters, data presented graphically for 1980 are an average of both sites. All statistical differences reported are significant at the $p < 0.05$ level.

Results

Total Nitrogen

The leaf total nitrogen concentration peaked in May (1.64%), declined rapidly until July (0.60%) and decreased slowly throughout the summer and fall (Fig. 1). Rhizome total nitrogen concentration declined slightly through June but subsequently increased

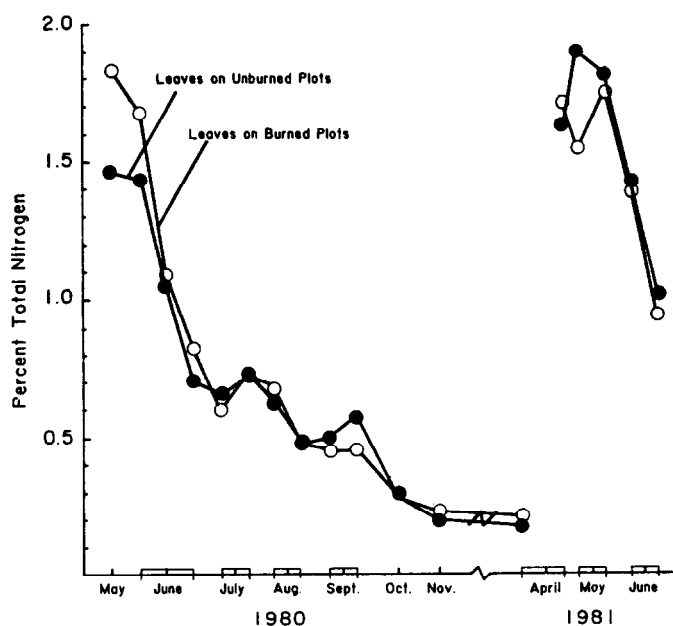


Fig. 1. Total nitrogen content in big bluestem leaves on burned and unburned treatments. The first data point in April 1981 is standing dead leaves from the previous year's production.

to an average October high of 0.94% (Fig. 2). The root and rhizome total nitrogen patterns were markedly similar with concentrations of total nitrogen in roots averaging 72% (57% to 95%) of that in rhizomes (Fig. 2). Both root and rhizome total nitrogen concentration were significantly lower in the burned than in the unburned

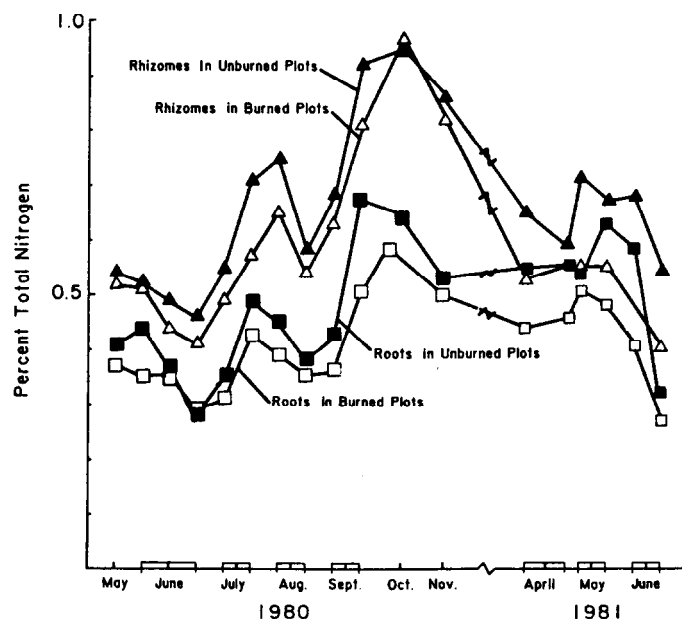


Fig. 2. Total nitrogen content in big bluestem rhizomes and roots in burned and unburned treatments.

treatment. Leaf total nitrogen was not significantly different between treatments.

The soil moisture at the 10 to 20-cm soil depth was significantly lower in burned plots than in unburned with a low in August 1980 of 11% and 15.4%, respectively. The soil moisture in the 0–10 cm soil depth was erratic due to light rainfalls and evaporation to the 10 cm depth. Burned plots were significantly lower in soil moisture at the 0–10 cm depth between rain events. Rainfall events increased

soil moisture levels slightly in September and dramatically in October of 1980. Soil moisture remained relatively high (37%) through June 1981 (Fig. 3).

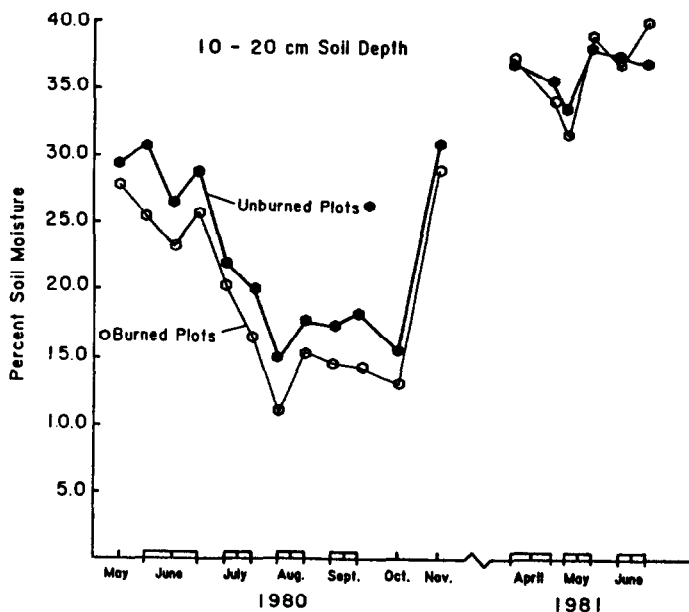


Fig. 3. Soil moisture at 10-20 cm soil depth in burned and unburned treatments.

Amino Acids

Rhizome amino acid concentration in August 1980 was significantly higher in unburned than in burned plots (Fig. 4). The sharp decline of rhizome amino acid concentration coincided with the end of the drought in September. The subsequent increase in both treatments was during the period of high precipitation. Rhizome amino acid levels increased only slightly over the winter but rhizome amino acids as a percentage of total nitrogen significantly increased over the winter of 1980-1981 (Fig. 4).

Leaf amino acid concentration was not significantly different between treatments and changed little after June 1980. However, the leaf amino acids as a percentage of total nitrogen increased slowly throughout the growing season with a dramatic increase in late August and September 1980.

Nitrogen Conservation

The percentage of nitrogen conserved by fall translocation cannot be obtained from concentrations without also having measures of total production. Aboveground biomass was obtained in this study, but root and rhizome production were not. Adams made his original data on above- and belowground production of big bluestem available from a 1980-1981 study in Osage County, Oklahoma (Adams 1982). Assuming that the ratio of above- to belowground biomass was the same in the 2 studies, concentrations were converted to amounts per unit area, which allowed the following percentage calculations to be made.

Clark (1977) and Woodmansee et al. (1978) express fall translocation in aboveground tissue as the percent of nitrogen exported from leaves during the latter part of the growing season. By this method, this study estimates 58% of the nitrogen in big bluestem leaves exported during senescence. This calculation does not consider the addition of inorganic nitrogen from precipitation, or leaching and volatilization losses. The leaves of dominant tallgrasses act as a nitrogen sink for inorganic nitrogen from precipitation while leaves were growing, but leaching losses of organic nitrogen occur during senescence (T.R. Seastedt, KSU, personal communication).

McKendrick (1975) estimated nitrogen conservation by the

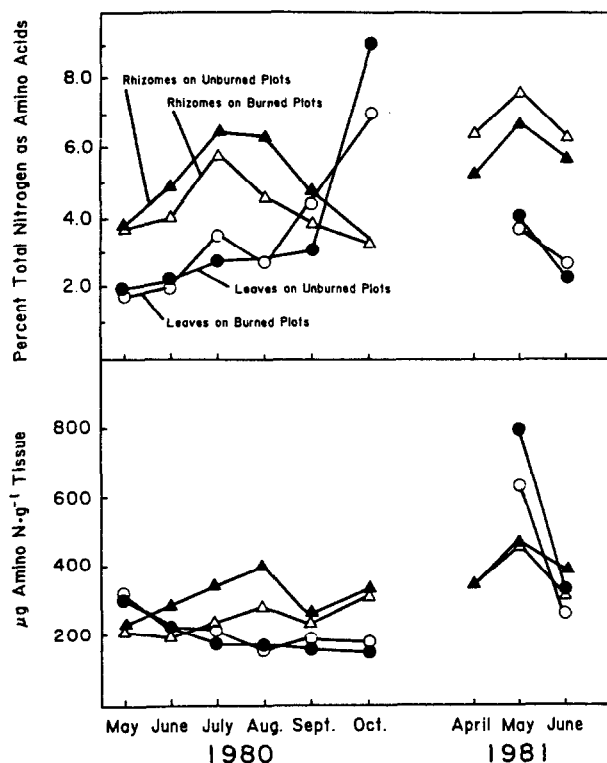


Fig. 4. Percent of total nitrogen and amino acids and total free amino acid concentrations in big bluestem leaves and rhizomes in burned and unburned treatments.

export of nitrogen from big bluestem rhizomes or roots during spring growth. In 1980, 46% and 58% of the nitrogen in rhizomes and roots, respectively, was estimated to be exported in the first half of the growing season. This calculation does not exclude nitrogen uptake from the soil entering rapidly growing rhizomes and roots, nor does it include the nitrogen losses from root exudates. Because the above methods measure only part of the several processes involved, the above calculations are only a first approximation for the tallgrass prairie.

Discussion

The findings of this study support the concept of internal conservation of nitrogen within big bluestem. The rhizome and root total nitrogen increased slightly prior to spring leaf growth, the period Nooden (1980) believes root uptake of soil nitrogen is the greatest. During the period of rapid stem and leaf growth (June), rhizome and root nitrogen reserves were depleted as would be expected due to translocation to growing tissue. In June leaf amino acid amounts declined as leaf total nitrogen concentrations increased due to rapid synthesis of amino acids into proteins. During senescence the percent of total leaf nitrogen as amino acids, hereafter referred to as percent amino acids, increased as total nitrogen concentrations declined.

Nitrogen absorbed by roots would be converted into amino acids while storage proteins were broken down for translocation to the leaves as described by Beevers (1976). Water stress can cause a decrease in spring translocation and protein synthesis (Beevers 1976, Nooden 1980), thus amino acids would accumulate in the rhizomes. Rhizome amino acid concentration and percent amino acids increased during the first half of the growing season (Fig. 4).

After July leaf percent amino acids increased as protein was broken down into amino acids. As Weinmann (1942) suggests leaf amino acid concentrations remained constant as total nitrogen declined due to rapid fall translocation of amino acids to perennial

organs for storage. The marked similarity in total nitrogen patterns of rhizomes and roots (Fig. 2) strongly indicates that big bluestem roots play an important role in nitrogen storage and conservation. Fall translocation is also indicated by the increase in rhizome amino acid concentration. Rhizome and root total nitrogen reached a peak in mid-October when 80% of the aboveground parts had died. Nitrogen in storage organs can be stored as a water soluble compound (Weinmann 1942, Perry and Moser 1974) or as protein (Thimann et al. 1974, Chapin and Kedrowski 1983). The decrease in percent amino acid in rhizomes in conjunction with the increase in root and rhizome total nitrogen would indicate storage as protein.

In early April 1981, the rhizome amino acid levels increased dramatically, suggesting remobilization of stored nitrogen from protein into amino acid (Beever 1976, Chapin and Kedrowski 1983). The May-June decline in rhizome amino acid concentration and rhizome total nitrogen indicates that translocation of nitrogen out of the rhizome to the leaves is greater than rhizome nitrogen uptake from the soil. The leaf total nitrogen concentration decreases rapidly with cell maturity as cell walls thicken and cellulose "dilutes" the plant nitrogen. Leaf amino acid concentrations also decrease as amino acids are converted into protein (Beever 1976).

Leaf total nitrogen was similar for both the burned and unburned treatments (Fig. 1). Leaf percent amino acids increased dramatically in late summer as leaf total nitrogen was declining. The earlier increase on burned plots of leaf percent as amino acids may indicate earlier senescence than on unburned plots.

The unburned treatment had overall significantly higher total nitrogen concentrations in belowground components than burned (Fig. 2). Rhizome amino acid concentrations and percent amino acids were higher in the unburned plots than in the burned plots in both summer 1980 and spring 1981. In this study, soil moisture values were significantly lower in the burned plots, implying that the plants in the burned plots were more stressed due to greater evapotranspiration than in the unburned plots. Thus the decreased amino acid concentration on burned plots was unexpected since others report that amino acid levels increased in water stressed plants (Barnett and Naylor 1966, Thimann et al. 1974, Beever 1976). The plants in burned plots seem to have decreased their production and initiated early senescence due to water stress. Russell (1973) suggests that as the upper soil layers dry out, the rate of nitrogen mineralization decreases with a corresponding decrease in available soil nitrogen. Garwood and Williams (1967) reported that nitrogen fertilization of lower soil depths during a drought increased grass production aboveground. Hake et al. (1984) suggests that big bluestem draws on its deep root system to avoid dehydration. The plants on burned plots may have shifted their root activity to lower soil depths to reach enough moisture to function at a low level. However, soil water below .5 m is low in nitrogen so the plants may not have had an adequate nitrogen supply. The plants on unburned plots had enough water and nitrogen at upper soil depths to continue functioning.

McKendrick's (1975) nitrogen values for big bluestem rhizomes on a similar site in the Flint Hills during 1971 were significantly higher than those of this study. Adams' (1982) Osage data collected in 1980 and 1981 are not significantly higher than those of this study. Although Adams did not find a significant difference between nitrogen concentrations in 1980 and 1981, his 1980 values (during a drought) were generally lower than those obtained in 1981 (a wet year). Adams' big bluestem September leaf nitrogen concentration was 0.32% compared to 0.80% reported by Risser and Parton (1982). The 1980 peak leaf nitrogen concentration (1.30%) in May was lower than the 2.00% reported for 1971 and 1972 by Risser and Parton (1982). Thus Adams' work and the overall findings of this study show reduced nitrogen concentration during a drought.

Mineralization and movement of soil nitrogen decreases under

drought conditions (Russell 1973). It is possible that root uptake of nitrogen in this study was reduced in early summer 1980, thus lowering the overall nitrogen content of the plant as suggested by McKendrick (1975). Root uptake of minerals decreases during the reproductive stage according to Nooden (1980), so plants may have been unable to respond to the rains in September and October 1980. Another interpretation is that the lower nitrogen concentration in drought years may result from leaves being partially senescent through the summer.

Drought stress may increase nitrogen conservation efficiency. McKendrick (1975) found only 18% efficiency in spring transport of nitrogen from rhizomes to leaves while Adams (1982) and this study found 35% and 46%, respectively. Adams found a 50% export of nitrogen from leaves in 1980 compared to 36% in 1981. This study estimated 58% export of leaf nitrogen during senescence in 1980. Risser and Parton (1982) suggested a 36% reduction in leaf nitrogen during a senescence ($0.8 \text{ g} \cdot \text{m}^{-2}$ retranslocated vs. $2.27 \text{ g} \cdot \text{m}^{-2}$ left in leaves in August). A higher efficiency of nitrogen conservation would indicate a response to drought conditions. Gosz (1981) hypothesized that a greater amount of nitrogen is recycled in nitrogen-stressed systems than for the same species in a nitrogen rich system. However, Chapin and Kedrowski (1983) concluded that taiga trees on low nitrogen sites do not have increased nitrogen fall translocation over those trees in high nitrogen sites.

We know of no other field studies of amino acid nitrogen dynamics in grasses on the Central United States grasslands. The total nitrogen and amino acid findings of this study strongly support the concept of fall translocation of nitrogen to storage organs for reuse the next year. Results also show that storage occurs in roots as well as in rhizomes. Burning during a drought year was found to lower the nitrogen concentration of roots and rhizomes but not of leaves of big bluestem. A higher efficiency of nitrogen conservation than previously reported was found in above- and belowground parts. Additional study will be necessary to ascertain whether this higher efficiency is a result of the drought conditions or a normal trait of the Flint Hills tallgrass prairie.

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