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TOTAL NET PRODUCTIVITY AND TURNOVER ON AN ENERGY BASIS FOR TALLGRASS PRAIRIE[1]

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(Accepted for publication February 27, 1967)

Abstract. The energy equivalent of total net productivity including foliage and roots on unburned prairie in 1962 was 4.351×10^6 cal/m^2, representing 992 g of biomass. The root system provided slightly over 50% of the annual increment. For 1963 the total growth was 1,133 g/m^2. The average energy for these years was equivalent to 1.21% of the incident radiation received during the growing season for the 400–700 mμ portion of the light spectrum. The maximum energy budget including current increment, roots of previous years, and litter was equal to 2.6 turnovers. In years with favorable rainfall, fire approximately doubled the aboveground yield. During drought, productivity increases of fire plots over control plots were curtailed sharply. On a dry matter basis, the total aboveground biomass at the end of the growing season was approximately twice that of the standing crop. During the April–September period for 3 years of observation, the loss in dry weight of the aboveground material ranged from 57% to 65%. For the remainder of the year the decrease was 31–39%. These values indicate a fluctuating but generally balanced annual system of growth and decay. For aboveground biomass, the turnover estimate was 2 years, and for root biomass, 4 years. The decay time of a standing crop or root increment as determined from isolated litter samples and carbon–14-labeled roots in the field indicated that the annual turnover was comprised of a series of increments of different ages, decreasing in caloric content with time on a dry weight basis (uncorrected for ash). On an ash-free basis, litter 4 years old showed some increase in caloric content, suggesting changing composition of the residual fraction. The tallgrass prairie is seen as a relatively efficient ecosystem when compared to the worldwide terrestrial average. The stimulus of fire to dry matter production in the humid prairie indicates a more efficient use of solar energy; however, the long-term effects of sustained burning require observation.

Introduction

Various aspects of primary production and turnover have been studied in an unbroken tallgrass prairie in Missouri for the past several years. Information dealing with seasonal increments and biomass accumulation of the total vegetation is pertinent to our understanding of organic turnover, mineral cycling, and energy flow. These functions in the maintenance of community diversity and equilibrium are critical to all trophic levels whose existence depends ultimately on the primary producer. To appraise the plant function in the ecosystem completely, quantitative data are required for both above- and belowground components. Often data are incomplete or lacking for biomass and turnover characteristics of the root system, probably because of inherent difficulties involved in sampling, particularly in the measurement of annual growth. The purpose of this paper is to integrate data for both top growth and root system and thereby assess total net productivity, biomass, and energy relationships in a tallgrass prairie.

[1] These studies were supported by NSF Grants 16156 and 702.

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Location and Description of Study Area

The study area is a 145-acre tract of unbroken tallgrass prairie in central Missouri, located 17 miles east of Columbia on Interstate Highway 70. The principal grasses are big bluestem, *Andropogon gerardi* Vitman; little bluestem, *A. scopa-*

rius L.; Indian grass, *Sorghastrum nutans* (L.) Nash; and prairie dropseed, *Sporobolus heterolepis* A. Gray. Junegrass, *Koeleria cristata* (L.) Pers.; fescue, *Festuca paradoxa* Desv.; and hairgrass, *Agrostis hiemalis* (Walt.) B.S.P., are lesser grasses, and in local swales switchgrass, *Panicum virgatum* L., forms almost pure stands. On flat terrain of the prairie, a well-developed claypan, B_2 horizon, begins at approximately 16 inches in the profile and extends to 28–30 inches. These flat areas are designated in the Putnam soil series and during late winter and early spring are generally water-logged. On sloping ground of the Mexico soil series the zone of clay accumulation in the subsoil is less developed. Retardation of internal drainage is not as critical and runoff is greater. On this sloping phase of the prairie an invasion zone of shrubs and small trees occurs, grading toward the forested drainage. In fire plots, however, woody plants are scarce or absent, with increasing frequency of burning resulting in purer stands of grass on both flat and sloping terrain. The mean annual rainfall for a station nearest the study area is approximately 39 inches, with 51% of this amount occurring from April through August. The actual annual rainfall in inches and the amount received during this major period of growth, the latter in parentheses, are as follows: 1960, 28.3 (15.3); 1961, 41.4 (20.8); 1962, 25.4 (10.4); 1963, 25.5 (16.4); 1964, 31.4 (17.6); and 1965, 37.5 (18.9). Throughout the study no large herbivores were present in the prairie tract. The only sources of consumption or attrition other than microbial processes and fire were rodents and insects.

Methods

The study plots selected for biomass measurements were representative of the flat terrain in which the aforementioned grass species provided the dominant cover. Methods employed in field sampling and washing procedures for measuring annual root growth and total belowground biomass in 1962 have been described in detail (Dahlman and Kucera 1965). In 1963 roots and rhizomes in the current growth were separated by visual inspection from plant material older than 1 year. For this purpose young rhizomes and associated roots were collected in July at the time of active development. Only structures which appeared fresh, light-colored, and with intact cortical layer were selected. Older rhizomes and roots, which were sampled in December, showed discoloration and partial sloughing of the cortex. Simulated litter samples were prepared previously for field observation on dry matter losses as a function of age (Koelling and Kucera 1965). Two additional years of weathering have been recorded in the present paper. Total net productivity, including standing crop and root increment, was also measured in 1963. In 1964 and 1965 only gross biomass measurements of standing crop and root system were made. Additional determinations included calorimetric measurements of current standing crop, litter of different age to a maximum of 4 years, and root and rhizome fractions described above. All plant materials were ovendried and ground in a Wiley mill to pass a 0.5-mm mesh. An Emerson fuel calorimeter was used in measuring caloric content, based on duplicate samples of 500 mg each. Total ash content was also determined so that caloric equivalents could be expressed on an ash-free basis. After each run the bomb was rinsed with a methyl orange wash which was then titrated with Na_2CO_3 solution to correct for unconsumed acid residues. These data expressed as calories per gram were applied to biomass values to determine the component and total energy budget of the living vegetation and its by-products.

Results

Caloric values for above- and belowground biomass comprising different ages decreased with weathering time on an actual dry weight basis (Table 1). Belowground material in general had greater energy content than tops, and rhizomes exceeded roots. The greatest decline in caloric content of the litter occurred in the oldest material, which was 4 years. Values on an ash-free basis indicate an increasing energy content of residual organic material with increasing age. The highest value on an ash-free basis was 5,095 cal/g for litter 4 years old. The relative ash content on a dry weight basis of this material had risen to 40%, suggesting considerable leaching and breakdown of the original dry matter.

Since aging materials varied in energy content, the proportionate part of the whole litter biomass assigned to a particular standing crop was determined by the following method. Using litter samples isolated in screened containers and placed in the field 4 years earlier, dry matter losses were assessed with increasing decay time. Approximately 60% of the dry weight was lost after 2 years, and nearly 91% at the end of 4 years, suggesting an exponential decay relationship. With this information estimates of residual material after selected periods of decomposition were made from the following:

$$\frac{X_t}{X_o} = e^{-\frac{0.693}{T_{1/2}}}$$

TABLE 1. Caloric equivalents (cal/g) for bluestem standing crop, root increment, old roots, and litter of different weathering ages; gross biomass energy; and total net annual energy production (cal/biomass/m²) for 1962

Plant material	I Actual value	II Ash-free basis	III Gross energy (column I x biomass) Beginning of growing season	III Gross energy (column I x biomass) End of growing season	IV Annual energy production
Standing crop[1]					
Foliage	4,071.7	4,459.6	—	1.962×10^6	1.962×10^6
Flower stalks[2]	4,287.1	4,596.9	—	—	—
Total annual aboveground				1.962×10^6	1.962×10^6
Belowground					
Roots (new)	4,291.3	4,684.8	—	1.583×10^6	1.583×10^6
Rhizomes (new)	4,514.0	4,682.5	—	0.806×10^6	0.806×10^6
Total annual belowground				2.389×10^6	2.389×10^6
Belowground > 1 yr old					
Roots	4,067.6	4,489.7	3.909×10^6	3.358×10^6	—
Rhizomes	4,226.1	4,623.7	2.012×10^6	1.801×10^6	—
Total belowground > 1 yr			5.921×10^6	5.159×10^6	—
Litter[1]					
1 yr old	4,007.6	4,492.8	1.632×10^6	0.840×10^6	—
2 and 3 yr old	3,871.2	4,624.9	1.419×10^6	0.824×10^6	—
4 yr old or more	3,032.4	5,095.7	0.344×10^6	0.150×10^6	—
Total aboveground 1 yr or more			3.395×10^6	1.814×10^6	—
Total biomass equivalent			9.316×10^6	11.324×10^6	4.351×10^6
Efficiency of vegetation[3] = 1.21%					

[1]Based on big bluestem dry matter, the principal component in the study area.
[2]No flower stalks produced on control plots; determinations based on fire plot samples.
[3]Calculation based on accumulated radiant energy in the 400–700 mμ range for the frost-free season, April 20–October 18, and mean of 1962 and 1963 dry matter production.

where X_t = material remaining at time t; X_o = material at the beginning of the decay period; $T_{1/2}$ = observed half-life in years; t = decay period in years; —0.693 = natural log of 0.5; and e = base of natural log. By this approach, using the exponential decay curve, a proportionate part of the total litter comprising different ages was assigned to a particular standing crop. Employing the litter values at the beginning and at the end of the growing season, energy equivalents of the different-age components were determined (Table 1). The sum of these determinations was an estimate of the total litter energy for that time of the year.

Energy conversions for the 1962 standing crop and root system were also calculated to determine values for annual production and gross biomass at the beginning and at the end of the growing season. The energy equivalent of the total net productivity including tops and roots for 1962 was 4.351×10^6 cal/biomass/m². This amount added to the energy inventory of the system at the beginning of the growing season (9.316×10^6 cal/biomass/m²) produced the sum of 13.667×10^6 cal/biomass/m². The actual energy equivalent at the end of the season, including the annual increment, was 11.324×10^6 cal/biomass/m². The difference between these values represented a loss during the April–September period of 2.008×10^6 cal/biomass/m², 54% of the net annual energy production. An efficiency value of 0.48% was calculated for the total net production, using as a basis solar radiation values for the growing season recorded at the nearest station. The energy equivalent of the 1963 yield for above- and belowground parts was 0.55% of the radiant energy. On the basis of the spectral energy of the 400–700 mμ range, an average efficiency value for these 2 years was 1.21%.

DISCUSSION

During the present study and previous years (1960–1962) annual top growth averaged 0.55 of the total maximum aboveground biomass, which occurs with the addition of the standing crop at cessation of growth. This value suggests a replacement time of about 2 years for the bulk of the biomass under present equilibrium conditions. The complete disappearance of any given standing crop, however, does not occur within this period of time. Observation of simulated litter samples under natural conditions from 1962 to

1965 showed that 9% of the initial dry matter remained after 4 years. The extended longevity is attributed to the increasingly slower decay of residual products in the later stages of decomposition. The disappearance of 50% of the initial material occurred in about 20 months, indicating a non-linear decay rate. Hopkins (1954) noted also that nearly one-half of the mulch in Kansas grassland was lost in the first year and most of the remainder in 2 additional years of weathering. The rate of loss in the present study would seem low, especially for the initial decay period; however, the isolation of plant material in screens for the purpose of age identification may have retarded breakdown. Also, the first summer of decay observation (1962) was extremely dry with rainfall 10 inches below normal. The lack of moisture may have been a factor in slower breakdown. Despite these variations in weather conditions from year to year, attrition rates for litter during the growing season ranged from 57% to 65% of annual growth and from 31% to 39% for the remainder of the year, thus indicating a fluctuating but generally balanced system of growth and decay on an annual basis.

The observation of retarded spring development and lower annual yields on control plots with natural litter than on fire plots (Table 2) is similar to results of other studies dealing with the effect of litter removal on growth. Penfound (1964) found that litter removal in Oklahoma prairie resulted in larger standing crops. Favorable responses to burning in terms of more growth have been observed mainly in eastern parts of the prairie region. The similarity of results between litter removal by mechanical means and by fire suggests that the beneficial effects of burning are related to the elimination of the physical hindrance to new growth and to improved light and temperature conditions at the soil surface.

Exceptions to favorable responses to prairie burning or denudation have been reported in North Dakota (Dix 1960) where fire caused decreased yields. Similar results were observed by Anderson (1953) in Kansas and by Larsen and Whitman (1942) in South Dakota. In the present study the large increases in productivity noted on fire plots in 1960 and 1961 did not occur in 1962 (Table 2). Less rainfall during 1962 may have curtailed growth to a greater degree on denuded fire plots than on controls with litter. Thus the beneficial effect of litter removal by fire may be offset by greater water losses and more critical moisture conditions on denuded prairie in time of drought. Higher soil moisture values on mulched plots in the mixed prairie of central Kansas was shown by Hopkins (1954) to result in more growth than on denuded prairie. Considering the regional implications of rainfall and evaporation potentials, and the negating effects of periodic drought on fire plots, the beneficial effects of fire are implied only for those regions where rainfall is generally dependable and exceeds a certain minimum. An attempt to correlate normal rainfall patterns with regional reports concerning ecologic advantages of fire on prairie stability would suggest a minimum summer value of 15–18 inches in most cases.

Table 2. Total aboveground biomass (standing crop + litter) at the end of current growing season on control plots and fire plots with single burn (g/m²—ovendry weight) for 1960, 1961, and 1962

Year	Control plots	Fire plots
1960	980 (570[1] + 410[2])	1,250[1] (119%)[3]
1961	938 (509 + 429)	933 (83%)
1962	956 (482 + 474)	522 (15%)

[1]Current year's standing crop.
[2]Litter of previous years (removed on fire plots).
[3]Increase in annual production on fire plots compared to controls.

The seasonal development of standing crop, cessation of growth, and transfer to the litter stage are complex phenomena. In a multispecies community the time of maximum biomass may not be coincident with phenological development of all components. Net productivities would tend to be minimum estimates (Ovington, Heitkamp, and Lawrence 1963). The functional aspect of the root system bearing on initiation and termination of growth, productivity, and turnover is even less clear. The inclusion of root-increment estimates in the total net productivity evaluation of control plots in Missouri prairie indicates approximately 50% of the dry matter yield is belowground. Productivity or growth per unit of time in a stable ecosystem is difficult to evaluate, and such data appear limited. Weaver and Zink (1946) studied several native grasses, including big bluestem, under controlled conditions for 3 years from the seedling stage. While increases in dry matter reflect new growth from year to year, the increments obtained under these conditions would not be comparable to those estimated for well-established prairie. Root-top growth ratios were also different, with maximum values for big bluestem less than 0.50, compared to near 1:1 in the present study. A partial explanation for the lower ratio may be ample watering resulting in stimulated top growth. Bray (1963) compiled root-shoot ratio data from a large number of sources and showed that the ratio of belowground to aboveground production for certain grasses increased as xeric conditions increased. No data on prairie grasses were given other than those by Weaver and Zink cited above.

The annual root increment in a 30-inch profile was one-fourth of the total underground biomass, indicating an average replacement time of 4 years under present conditions. As in the case of litter disappearance, there is tentative evidence that the time requirement for essentially complete removal of a given root mass is somewhat longer. Preliminary data from carbon–14-labeled plots indicate a root "half-life" of approximately 1.5–2 years, based on declining activity in root samples taken over a 2-year period following the initial label. Assuming an exponential decay scheme for underground parts, the time estimated for 90% disappearance would be approximately 5 years. Additional data are needed to verify these early measurements. Total biomass, combining standing crop and root system, varied from year to year, probably reflecting differences in growing season conditions. Biomass values ranged from a low of 2,320 g/m^2 in 1962 to 3,015 g/m^2 in 1964 for the 1962–65 period. Despite the range of variation, the values permit comparison with other prairie studies. For example, data from Minnesota prairie (Ovington, Keitkamp, and Lawrence 1963) show considerable less biomass based on similar seasonal development. Maximum standing crop was approximately one-fifth that in the present study, and total root mass about 40%. These differences in productivity probably relate to climatic variation, mainly length of the growing season and rainfall, both of which are less in the northern locality. Another factor is the sandy nature of the parent material on which the soil had developed. In Illinois, with more nearly comparable growing season and rainfall as well as soil development, the combined root-top biomass for unburned bluestem prairie was similar to that in Missouri (Hadley and Kieckhefer 1963).

The weathering and decay of dry matter was accompanied by general decreases in energy content, with the largest change occurring in aging litter (Table 1). These decreases are due to the faster loss of organic material relative to the mineral content, and are seen most markedly in 4-year litter for which 40% ash on a dry weight basis was measured. The original ash content of prairie foliage in the standing crop was 8.7%. Thus each gram of dry matter, while losing approximately 900 mg of its original weight or 90% in 4 years, showed during the same period a reduction in mineral content from 87 mg to 40 mg, or a 54% loss. Conversion to the ash-free basis, however, showed increasing heat values of the residual organic product in litter with age. The absence of such an increase in roots and rhizomes suggests that the age separation of roots on a visual basis was not as effective as the use of screens for litter. The caloric values of underground materials of big bluestem on an ash-free basis were similar to those obtained by Hadley and Kieckhefer (1963).

For old field vegetation in Michigan, Golley (1960) observed slight changes in energy content on a seasonal basis. In a later paper (1961) he reports significant differences for Georgia broomsedge between current growth and litter, the latter with lower heat values uncorrected for ash. In this respect the data show trends similar to those in the present study; however, on an ash-free basis, the older material did not show a rising trend as in the current data. Studying forest materials, Ovington and Heitkamp (1960) also noticed a general decrease in energy of older material; however, a conversion to the ash-free basis also showed lower energy content of the organic fraction. Lack of agreement in these reports may result from differences in the materials being studied as well as from differences in the degree of weathering of the litter. In a study of peat materials in Finland, however, increase in heat values on an ash-free basis was noted with increasing humification (Salmi 1954). Possibly the rise in caloric content of the residual ash-free organic material is due to change in organic composition. As the more easily leached and weathered compounds are removed, the residual product consists to an increasing degree of resistant carbon complexes with higher heat of combustion. Bondi and Meyer (1948) observed that grass flower stalks had more lignin than the foliage, which may relate to their higher heat content compared to leaves (Table 1). The larger energy values on an ash-free basis for aging materials reported in this study may result from a relative build-up of lignin or lignin-like substances. Changes in organic composition may also include a narrowing C/N ratio as the material is weathered. In an earlier study (Koelling and Kucera 1965), the total nitrogen in litter doubled over 2 years, from 0.41% to 0.80% on a dry weight basis, thus suggesting a build-up through retention as humification is advanced.

The total energy produced by bluestem prairie was 4.351×10^6 cal/biomass/m^2 or 0.48% of total solar radiation for the 1962 growing season. The root system provided approximately 55% of this amount. The accumulation of gross energy of total biomass reached a peak value of 11.324×10^6 cal/biomass/m^2 and represented 2.6 turnovers. For 1963, net productivity, including both top and root estimates, was 0.55% of the total radiant energy received during the growing season, April to September. Observations of prairie phenology and maximum development over several years would suggest that the season is probably shorter for at least the bulk of biomass synthesis. If incident radiation were adjusted to the actual growing time, the resulting efficiency values would be somewhat larger. Several workers have calculated efficiencies for net plant production on the basis of only light energy within the 400–700 mμ range of the spectrum, resulting in comparatively higher values (Blackman and Black 1959, Bray 1961). In an early paper on the subject of efficiency, Transeau (1926) lucidly outlined the energy budget of a maize ecosystem, basing estimates on this range of spectral energy. Considering only wavelengths in the photosynthetic range, Wassink (1959) reported average efficiencies for best agricultural yields to range from 0.5% to 2.5%. On a worldwide basis an average efficiency of 0.2% was estimated for all aspects of terrestrial production. In order to compare prairie values with these estimates, the radiant energy of the 400–700 mμ spectrum was determined from conversion tables (Gast 1961). On this basis the energy equivalent for average net productivity for 1962 and 1963 was 1.21% of the spectral energy received. The tallgrass prairie in this section of the grassland region is seen as a relatively efficient ecosystem, for which the belowground part contributes over 50% of the energy produced on a sustained basis. The stimulus of fire in dry matter production reported here and elsewhere in the humid grassland would indicate a more efficient use of solar energy. Applying similar procedures to fire plot data for years with favorable moisture, and assuming concomitant increases in root productivity as shown by Hadley and Kieckhefer (1963) for similar prairie, efficiency values approaching 3.00% are feasible. However, the long-term effects of sustained burning of prairie are not known, particularly in relation to vegetational equilibrium and humic levels in the soil.

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