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# ROOT PRODUCTIVITY AND TURNOVER IN NATIVE PRAIRIE<sup>1</sup>

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**Abstract.** Quantitative measurements of root systems on a seasonal basis for a 34-inch profile in Central Missouri Prairie ranged from 1,449 g/m<sup>2</sup> prior to resumption of growth in the spring to 1,901 g/m<sup>2</sup> at the end of the growing season. Underground parts in the upper 2 in. of the profile varied from 48% of the total quantity in April to 60% in July. Over 80% of the root mass occurred in the A<sub>1</sub> horizon, or the top 10 in. of the profile. Annual increment in the A<sub>1</sub> horizon or surface 10 in. was 429 g/m<sup>2</sup>. In the A<sub>2</sub> horizon, 10-18 in., the measurement was 40 g/m<sup>2</sup> and in the B<sub>2</sub> horizon, 18-30 in., 41 g/m<sup>2</sup>. These values were approximately 25% of the maximum dry matter measurement for each profile level, suggesting a turnover for the root system as a whole every 4 years. Variations in turnover for different parts of the root system were indicated, however, as shown by an annual loss of 22.8% for rhizomes, and 40.8% for roots in the 0- to 2-in. zone. Decomposition constants showed a marked decrease with depth, ranging from 4.3% in the A<sub>1</sub> horizon to 0.8% in the B<sub>2</sub> horizon. Estimated time required to reach 99% organic matter equilibrium under present conditions of production and breakdown was 110, 420, and 590 years for the A<sub>1</sub>, A<sub>2</sub>, and B<sub>2</sub> horizons respectively. Increasing time values would be expected with increasing depth as the reduction in annual increment was proportionately greater at lower levels in the profile than that for the total root-humus product.

## INTRODUCTION

Since Lindeman's early work (1942) on the energy structure of ecosystems, numerous studies have dealt with dynamic community analysis. In terrestrial communities, however, the annual production of underground parts is difficult to evaluate and, compared to productivity values for aerial components, only limited information of a precise nature is available. Furthermore, little is known about the periods of greatest root development and breakdown. Studies in prairie conducted by Weaver and Zink (1946a) showed that banded roots remained functional for 1 to 3 years, and possibly longer. In another study (1946b) these authors concluded that maximum root growth of little bluestem under controlled conditions occurred after 2 years, and after 3 years for big bluestem. Total organic production and turnover for old fields were studied by Odum (1960); however, separate values for roots were not determined. Ovington, Heitkamp, and Lawrence (1963) reported productivity values for several ecosystems, including a maize field. Only for the latter was annual root production given. Despite the apparent significance of root systems in organic matter development of prairie soils, the cyclic processes associated with root growth and decay are poorly understood.

The purpose of the present study was to evaluate the dynamic aspect of root systems in stable prairie. Annual increment, total organic matter, and the time factor required for the humus level to reach equilibrium under present conditions of

primary production and mineralization were evaluated.

## LOCATION AND DESCRIPTION OF STUDY AREA

The site for root studies was the University of Missouri Prairie Research Station,<sup>2</sup> located in the east-central part of the state at the southern limits of Kansan glaciation. The 145-acre tract has never been plowed and is representative of the flat, poorly-drained prairies with planosol soils which formerly were extensive in the peninsular region of the Middle West. The undisturbed profile is derived from fine loess and is slowly permeable with a claypan subsoil. Physiographically, the tract is in a broad tension zone between the flat prairies of the drift region and the forested drainages and hill topography to the south. The mean annual rainfall is approximately 40 in. Drew (1947) provided a detailed floristic list for this area, in which *Andropogon gerardi*, big bluestem, and *A. scoparius*, little bluestem, are the principal components. Whiteside and Marshall (1944) studied mineralogical and chemical characteristics of the soil profile in the prairie. Productivity and nutrient composition of the foliage were described by Kucera and Ehrenreich (1962).

## METHODS AND MATERIALS

A core sampling method was used to make quantitative determinations of root systems and total organic accumulation (all roots plus humus) as a function of profile depth. Bulk densities

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were also measured for continuous increments in the profile. Intact soil cores 1.65 in. in diameter and approximately 36 in. long were collected with a hydraulically operated probe mounted on a pick-up truck loaned by the Soils Department of the University. As the probe was forced into the soil, the resulting core was retained in a pipe with a diameter slightly larger than that of the cutting bit. The probe was pulled from the soil and removed from the hydraulic unit. By forcing a rod into the bit end of the probe, the intact core was pushed through the top of the pipe into prepared cartons. Generally the lowermost 2 in. retained within the bit were compressed and therefore discarded, leaving a usable core of about 34 in. Ten to 15 cores per hour were collected by this method.

Core samples were collected in the first week of July and October 1962 and January and April 1963. Based on phenological observations extending over several years, these periods were selected to sample: (1) rapid growth of mid-summer when vegetative development is nearing a peak; (2) cessation of all top growth, with normal curing or drying of foliage and flower stalks; (3) a midwinter condition; and (4) conditions just prior to resumption of growth in spring. On each occasion, 60 cores were collected making a total of 240 for the study. Ten composite samples of five cores each were used for determining dry matter of washed roots and for measuring bulk density. The replications were treated statistically to determine the significance of difference between sampling dates. The remaining ten cores were used for determination of total organic matter. The fewer cores for organic matter measurements were justified on the basis of less variability of data, compared to root values. In the laboratory, the top 6 in. of the core were divided into 2-in. increments. The remainder of the core was cut into 4-in. units.

Soil cores for bulk-density determinations were oven-dried and weighed. Bulk-density values were calculated as grams of dry soil per cubic centimeter and served as a check on uniformity of sampling between individual cores as well as between seasonal collections. In addition, bulk densities were used to convert the percentage organic matter determinations to absolute weight values per unit area for each increment of the profile. To measure the quantity of roots in core samples, the cores were grouped in lots of five and treated in a 1% solution of sodium hexametaphosphate (Calgon) for 1 hour to disperse the soil and aid in the separation of roots.

After soaking, the roots, including rhizomes, and soil suspension were transferred to a bank of sieves immersed in a solution of 0.8% sodium hypochlorite. The oxidizing agent aided in further dissolving any additional clay and humus fractions from the roots and rhizomes. A mechanical agitator moved the sieves at the rate of 60 cycles per minute. After a washing time of 1 hour, the roots were gathered from the screens, rinsed in tap water, dried at 70° C for 24 hours, and weighed to 0.01 g. Dry-matter values were expressed as grams per square meter for each profile level and represented an average of ten lots of five cores each for a total of 50 cores. Most of the roots and rhizomes were retained on the top mesh of 10 squares per inch, although some very fine material passed through 35 squares into the washing solution. These roots were collected after the washing operation by draining the solution through a 60-mesh sieve. A new solution was prepared for each core lot.

Total organic matter combining both the root system and soil humus was determined. For the July collection, intact soil cores were oven-dried, weighed, and oxidized in an electric furnace at 600° C for 24 hours. The loss on ignition was evaluated as the total organic matter complex in the soil. The procedure resulted in abnormally high values, probably due to combined water, and was considered unreliable. For the other seasonal collections, wet combustion was employed to determine organic matter. In this method (Graham 1949), for which reproducible results were obtained, chromic acid is reduced to chromous acid resulting in a color change of the solution. The transmittance of light measured in a spectrophotometer was inversely related to the amount of reduced acid and in turn to the quantity of oxidized organic matter. Known standards were used to establish calibration curves by wet oxidation against which the results of the unknown sample were compared and calculated as percentage organic matter. These values were converted to grams per square meter for each increment of the profile by multiplying percentage organic matter by bulk density (grams per cubic centimeter) by cubic centimeters of soil per square meter of given thickness. Decay constants for each level of the profile were calculated, based on the following formula employed by Jenny, Gessel, and Bingham (1949) in a study of renewal and breakdown of forest litter:  $k = A/F + A$  where  $A$  = annual increment,  $F$  = litter accumulation, and  $k$  = decay constant.

## RESULTS

The greatest concentration of roots and rhizomes occurred in the top 2 in., ranging from 48% of the 34-in. profiles in January to 60% in July (Table I). Roots and rhizomes in the

TABLE I. Oven-dry weight ( $\text{g}/\text{m}^2$ ) of total roots in tall-grass prairie by sampling increments and soil horizons

Depth (inches)	Sampling period			
	April	July	October	January
0-2	766	1,107	1,025	839
2-4	188	255	238	291
4-6	115	130	151	170
6-10	119	125	161	170
10-14	74	65	79	97
14-18	52	52	70	60
18-22	49	45	65	49
22-26	38	37	45	38
26-30	36	31	44	32
30-34	12	13	23	9
Total	1,449	1,860	1,901	1,755
0-10 ( $A_1$ horizon)	1,188	1,617	1,575	1,470
10-18 ( $A_2$ horizon)	126	117	149	157
18-30 ( $B_2$ horizon)	123	113	154	119

top 10 in. of the soil, comprising the  $A_1$  horizon, varied from 81% to 87% of the observed profile during the year. Thus, the distribution of underground parts showed a sharp decrease immediately below the 2-in. level and a more gradual decrease to 10 in. Below 10 in. the attenuation was even less marked, with approximately 6.5-9.0% of the root system in the 10 to 18-in. zone,  $A_2$  horizon, and 6.0-8.5% in the 18- to 30-in. level, or  $B_2$  horizon.

The data for the 2- to 10-in. level indicated a logarithmic function with depth when plotted on semi-log coordinates (Fig. 1). Although the slopes of the seasonal collections varied, a straight-line relationship was apparent for all seasons. Since rhizomatous material is largely concentrated in the 0- to 2-in. zone, a projection of the 2- to 10-in. slope to the surface level provided a basis for estimating both root and rhizome fractions. The difference between the intercept taken at the midpoint of the upper 2 in. and the total root-plus-rhizome determination based on soil washing was an evaluation of the quantity of rhizomes. Taking values of roots plus rhizomes in the upper 2 in. (Table I) for July and the following April, which were the high and low values respectively, extrapolated data for root-rhizome fractions showed the same seasonal trends. Peak July values for roots and rhizomes were 490 and 617  $\text{g}/\text{m}^2$ . For April the values were 290 and

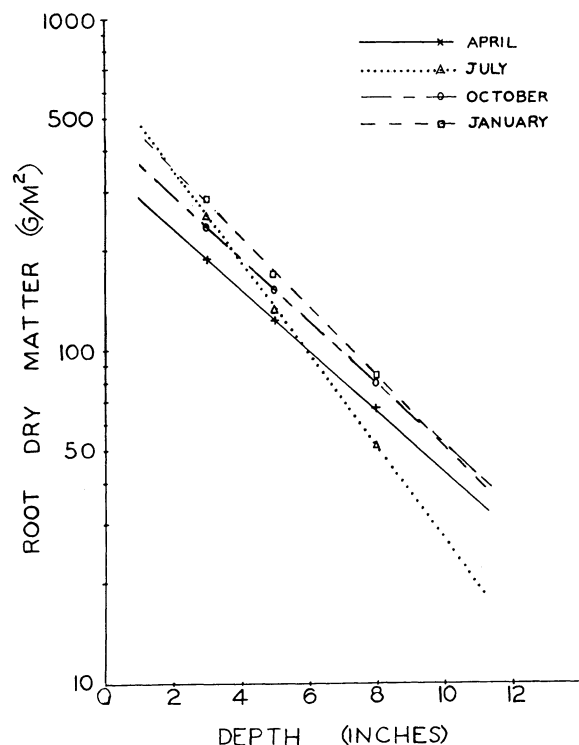


FIG. 1. Seasonal determinations of root dry matter as a logarithmic function of depth for the upper profile.

476  $\text{g}/\text{m}^2$ . During this period the net decrease in roots was 40.8% compared to 22.8% for rhizomes. For the April-July period of active growth, roots increased 69.8% while rhizomes increased only 29.6%.

Net annual increment by  $A_1$ ,  $A_2$ , and  $B_2$  horizons represents the difference between the high and low seasonal totals of the entire root mass in each horizon (Table II). Although amount of root dry matter varied from one profile level to another, the ratios of annual production to the total root mass, or turnover values, were similar

TABLE II. Relation of annual increment to the maximum total root mass ( $\text{g}/\text{m}^2$ ), by soil horizons

Depth (inches)	Period of greatest difference	Maximum root mass	Annual increment	Turnover <sup>1</sup> value
0-10 ( $A_1$ )	April to July**	1,617	429	0.26
10-18 ( $A_2$ )	July to January**	157	40	0.25
18-30 ( $B_2$ )	July to October**	154	41	0.27

<sup>1</sup>Ratio of annual growth to total root mass.

\*\*Difference between high and low extremes of accumulation significant at the 1% level.

(Table II). On this basis it was estimated that approximately 25% of the root system as a whole would be replaced each year. Certain segments of the system, however, may be exchanged more or less rapidly. As shown above, for example,

the turnover of the root fraction in the top soil apparently occurs at a faster rate than that for rhizomes at the same level.

Total volatile matter (including all roots and rhizomes plus soil humus) as determined by wet oxidation is shown by soil horizons (Table III). Decay constants for each level are also shown. The annual production of roots, based on a washing method, includes both volatile and mineral matter. This value was corrected to volatile material only, in order to be comparable to wet oxidation data. Whereas both annual increment and total residue decreased with depth, the relatively smaller change in the latter compared to the amount being added annually resulted in decreasing  $k$  values at lower depths (Table III).

TABLE III. Volatile material for total dry matter (roots plus humus), and annual increment ( $\text{g/m}^2$ ), decomposition constants ( $k$ ), and equilibrium time in years ( $t$ ) by soil horizons

Depth (inches)	Total dry matter	Annual increment	$k$	$t$
0-10 ( $A_1$ )	8,910	382	0.043	110
10-18 ( $A_2$ )	3,230	34	0.010	420
18-30 ( $B_2$ )	4,370	36	0.008	590

A log-phase of humus accumulation was assumed during which period of time there is a net annual increase in organic matter until an equilibrium between addition and loss is reached. The following formula was applied in estimating the time required for 99% equilibrium in each horizon in the profile, under present conditions of growth and decay:

$$t \text{ (yrs)} = \frac{-\ln \left( \frac{100 - 99}{100} \right)}{k \text{ (decay constant)}}$$

These estimates of time in terms of spatial relationships in the profile (Table III) varied inversely with corresponding  $k$  values. As the relative magnitude of the total stable residue to annual additions increased, time values also increased, irrespective of the absolute replacement rate (Table II). If the total plant product was relatively less, in comparison to the annual product, equilibrium time would also be lessened.

#### DISCUSSION

An analysis of root productivity and turnover in a tallgrass prairie ecosystem showed that root mass reached its peak in July for the top 2 in. of the profile (Table I). Below this level high values occurred later in the year. A general decline occurred during the winter months at all

levels. Mueller (1941), studying several prairie grasses under experimental conditions, noted that rhizomes made the most growth in the spring. Rhizomes were more numerous at cool temperatures according to Darrow (1939). In the present study, cooler and more constant temperatures at lower levels in the profile may account for a later root maximum, compared to the upper zones where high and perhaps inhibiting temperatures would occur at an earlier date. Furthermore, with more moderate temperatures, respiration losses would be lessened providing surplus carbohydrates for new roots at lower levels subsequent to maximum growth of rhizomes. Brown (1943) noted that both roots and rhizomes of blue grass usually lost weight during the summer at mean temperatures near or above  $80^\circ\text{F}$ . Similarly, it was observed by Stuckey (1941) that grasses ceased root growth at high temperatures.

Lack of marked progressive changes through the year in roots and rhizomes in Minnesota prairie was attributed to possible inadequacy of sampling (Ovington et al. 1963). It was also suggested that values for rhizomes may not change greatly since new organs are formed as old ones are being exhausted. Comparing the July measurements in the Minnesota and Missouri studies, mass of total underground parts for the top 20 in. was over two times as great for Missouri prairie. Regional influences as effected by higher latitude and decreased rainfall are suggested as the basis for lower production in Minnesota. Similarly, a comparison of Missouri data with those for one prairie station in Iowa and two in Nebraska (Shiveley and Weaver 1939) showed a functional relationship of greater productivity with increasing precipitation. For the latter stations with annual precipitation means of 26, 29, and 32 in., the values on the basis of summer sampling for the top 4 in. of the profile were 3.14, 3.54, and 4.54 tons/acre, respectively. At the Missouri site with 40 in. average rainfall, the converted root value for the same level was 6.06 tons/acre for July, followed successively with 5.62, 5.03, and 4.25 tons/acre for the other seasonal determinations. In a study of Illinois prairie, Sperry (1935) observed that root systems were less extensive than those in western prairies. No weight determinations were made in these comparisons, however. In the present study, root distribution in the profile showed a concentration at the upper level with approximately 85% of the total mass in the  $A_1$  horizon (Table I). Weaver (1958) discussed a similar

pattern derived from several earlier studies, stating that root weights decreased rapidly in the lower profile.

For communities with perennial root systems, the problem of separating current growth from increment of preceding seasons presents some difficulties. By making seasonal measurements, at times when high and low accumulations might most likely occur, the difference in extremes is proposed as an estimate of net growth under field conditions. These estimates of net production are considered minimal since additional growth may still occur after the period of greatest recorded measurement. Subsequently, decay processes may reduce the next measurement below that of the preceding one, so that the peak of the growth curve would be omitted. More frequent measurements would increase the probability of assessing the greatest actual root and rhizome mass, although Ovington et al. (1963) proposed that sampling can rarely be frequent enough so that no possibility exists to miss peak values. Little seems to be known about the amount of annual production of underground parts in prairie vegetation. Weaver and Zink (1946a) reported root increases based on quantity of dry matter produced as grasses grew from seedlings to maturity. However, these increases would not seem applicable to a stable prairie community. Odum (1960) reported annual net production for old field succession, but root and shoot values were combined in the tabulation. No mention is made of the method of determining root increment for perennial species. Ovington et al. (1963) reported net productivity for aerial parts of a prairie ecosystem and total root quantity for different periods of the year, but not annual production. Annual production (Table II) followed total root mass in the several profile horizons, as indicated by the close similarity of ratios between the two quantities. The ratios suggested a turnover of 4 years for the root system as a whole, although certain parts may persist for a longer or shorter period. Weaver (1947) observed that decomposition proceeded at about the same rate for all levels and that rhizomes, compared to roots, were neither more nor less resistant. Based on extrapolation of present data (Fig. 1), estimates of rhizome values would indicate an attrition rate almost one-half that for roots. Carbohydrate storage in rhizomes, however, may be a factor in this difference. When the percentage decreases are applied to absolute values, the losses of rhizomes and roots are more nearly comparable. Over a year's time from the July maximum to the April minimum, root loss was 200

g/m<sup>2</sup> in the upper 2 in., compared to 141 g/m<sup>2</sup> for rhizomes.

Humus accumulation at various levels of the profile for Missouri prairie fits into a regional pattern based on other portions of the grassland formation. Thorpe (1948) reported 20 to 25 tons of humus per acre in the upper 6 in. of the profile for Kansas and Nebraska prairies, 40-100 tons/acre in North Dakota and Canadian prairies, and 10-20 tons/acre in warmer, southern areas with Reddish-Prairie and Rendzina soils. For comparative purposes, a humus value expressed in the same equivalents exceeded 25 tons/acre in the top 6 in. of the Missouri study site. This value was determined by subtracting total root mass in April from the wet combustion measurement for the same period. Under cooler climates, humus development is greater, even though root production is less as cited earlier (Ovington et al. 1963). Woodruff (1949) determined an original nitrogen content of 3,400 lbs/acre for the plow layer in Putnam silt loam, compared to an equilibrium value under corn of 1,000 lbs/acre. This pre-cropping value was larger than the equivalent nitrogen value for the present study with the same soil type. Assuming 5% nitrogen in organic matter, a value of 2,500 lbs/acre was determined. A possible cause for the difference may be the long mowing history of the prairie and its effect on root development. Russell (1962), studying humus stabilization in forage pastures, showed a negative relationship between decay constants and "half life" of soil organic matter. Equilibrium was more rapid in warm, moist climates and well-aerated soils, in contrast to cooler climates and anaerobic conditions. Longer equilibrium periods resulting from slower decay rates in cooler climates, compared to tropical conditions, were determined by Jenny et al. (1949) for different forest floor types. Thorpe (1948) estimated 200 to 300 years would be required for organic matter to reach an equilibrium level in prairie soils. In the present study, comparable values were determined (Table III). These show a marked increase with profile depth. As both productivity and rate of mineralization of humus lessen with increasing depth, this trend would be expected. Decreased microbial activity, less aeration, and lower temperatures are contributing factors to smaller *k* values, and hence longer equilibrium periods.

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