

Dynamics of the Root System of Blue Grama

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Highlight: *Field experiments were conducted to determine dynamics of the root system of blue grama (*Bouteloua gracilis*) during the 1973 growing season at the US/IBP Pawnee Site in northern Colorado. Differentiation and growth of blue grama roots were recorded in field conditions by means of windows in excavations. Roots began to grow and differentiate a short time before leaf growth was apparent. Desiccation of soil in the mid-growing season resulted in death and subsequent decomposition of 30% to 60% of the newly formed roots. Massive root growth occurred when soil water potential was high near the end of the growing season. Roots were separated into morphological categories by microscopic analysis of soil samples on May 15, near the beginning of the growing season, and on August 9, near the end of it. Young nonsuberized roots, so important in water absorption, were concentrated in regions of the soil profile where soil water potential was high. An empirical model of root growth and development in *B. gracilis* is derived from the data.*

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The author is grateful to Drs. J. S. Singh, J. L. Dodd, and N. R. French for their comments during the development of this project and for their revision of the manuscript. This paper reports on work supported in part by National Science Foundation Grants GB-31862X, GB-31862X2, GB-41233X, and BMS73-02027 A02 to the Grassland Biome, U.S. International Biological Program, for "Analysis of Structure, Function, and Utilization of Grassland Ecosystems." The work was done during a fellowship granted the author from the Consejo Nacional de Investigaciones Científicas y Técnicas, República Argentina. The AID (Alianza Interamericana para el Desarrollo) provided funds for the field experiments. These were carried out with the cooperation of the Central Plains Experimental Range of the Agricultural Research Service.

Manuscript received February 26, 1975.

Blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.), a dominant, perennial, warm-season grass in the prairie of western United States, is a key species on these rangelands because of its forage value. The growth of aerial and underground plant parts varies with the weather regime in the shortgrass prairie, particularly in response to the dynamics of soil water during the growing season which changes with depletion of stored winter moisture and with thunderstorm precipitation that usually occurs in midsummer (Smith, 1972). This suggests that the dynamics of the root system is an important element in the ecological mechanisms determining success of this species. Also, the root system of a perennial grass receives an important fraction of the total carbon assimilated by the green aboveground tissues (Mooney, 1972). Experimental evidence shows blue grama is not an exception (Schmer and Knieval, 1972; Singh and Coleman, 1974). These studies were undertaken to determine the timing and extent of the root growth of this species and its relation to the growth of aerial parts of the plant and to environmental factors such as soil temperature and soil water potential. This knowledge could be profitably used for the rational design of range management practices in the shortgrass prairie.

Methods

Observation of Root Growth by Glass Windows

In the fall of 1972 several excavations of 0.9 m × 0.5 m × 0.8 m (depth) were dug at the US/IBP Grassland Biome Pawnee Site, 12 miles northeast of Nunn, Colo., and 25 miles south of Cheyenne, Wyo., in an area where several stands with high abundance of blue grama occurred. The soil is a sandy

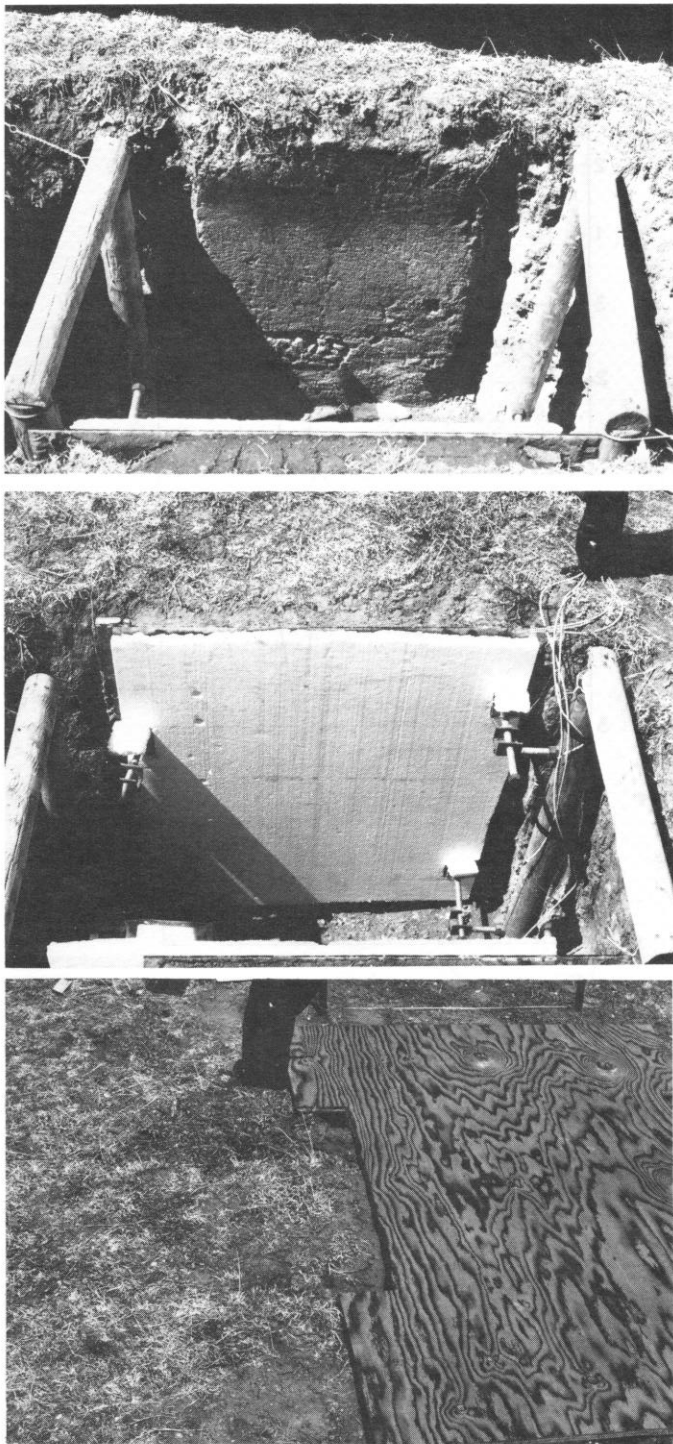


Fig. 1. Preparation of excavations to observe root growth. (upper) Aspect of the wall of excavation after smoothing. (middle) Glass window installed and covered with black plastic sheet and insulating foam. (lower) Closed excavation with terminals of temperature-monitoring elements.

loam of the Ascalon series. The observation surface, inclined approximately 10° from the vertical, resulting in the bottom of the pit being slightly wider than the top, was made as smooth as possible. A glass plate (91 cm \times 102 cm) 0.5 cm thick was fitted closely to this surface by applying a fine layer of sieved soil to the inner surface. The glass was braced against the observation surface and covered with a black plastic sheet and then a thick plastic foam sheet, which excluded light and

provided insulation but could be removed for observation. The whole excavation was then covered with a sheet of plywood to prevent possible damage by rain or snow (Fig. 1). The preparation of seven windows in four excavations was finished by February 1973. All plants other than *B. gracilis* on the 0.60 m \times 1.00 m plot adjacent to the window were clipped at that time and at regular intervals during the growing season.

At intervals of 7 to 16 days during the growing season the windows were uncovered at night or before dawn and inspected for root growth. When root growth activity was detected (April 1973), color photographs were taken at intervals of the windows from a distance of 0.4 m using a wide-angle lens. The resulting transparencies were projected on a white board upon which the roots were drawn and measured with a curvometer of the type used for map measuring.

Root Morphology, Development, and Function

Detailed observations were required to relate changing root morphology observed in the root windows to functional activity of roots. Thus, a quantitative expression of root growth and functional development could be derived for use in modeling efforts. It was also important to make an accurate estimate of total volume and biomass of root material in order to relate these results to studies of grassland productivity. For this purpose root volume and biomass were measured in small subsamples of 5-cm diameter soil cores taken to a depth of 50 cm in an almost pure blue grama sward. Three cores were taken on both May 15 and August 9 and each was subdivided into 5-cm segments.

Soil water potential was determined for these segments by storing each in a vial at 20°C with a disc of filter paper of known water potential-retention characteristics (McQueen and Miller, 1968). This method provided statistically accurate determinations in the 0 to -5 bar range, with wider confidence intervals of lower values of soil water potential. Values reported here are averages of three determinations, one from each of three different core sections.

Precise measurement of root segments and morphological classification required microscopic dissection (Head, 1971). This was performed on each of two small subsamples (≈ 0.5 g of oven-dry soil) from core sections at 0 to 5 cm, 10 to 15 cm, and 40 to 45 cm depths. All identifiable segments of roots recovered were measured according to length and diameter and classified according to degree of suberization. The categories of classification were: (1) *juvenile*: segments of roots of hyaline, translucent appearance with a diameter of < 0.05 mm; (2) *nonsuberized*: segments of roots of white-yellow color with a mean diameter of 0.115 to 0.158 mm; and (3) *suberized*: segments of roots of light to dark brown color with a mean diameter of 0.148 to 0.202 mm. The diameters of the roots diminished as depth increased and, therefore, there was no overlap of the above categories within the samples taken at the same depth.

The subcategory, "friable," was distinguished within each major category to describe root material that retained the morphological characteristics of a root segment, but disintegrated into pieces when touched by a flexible plastic needle. This material was assumed to be nonfunctional and probably dead. After the root material was separated, each subsample was weighed and the soil volume calculated on the basis of Van Haveren and Galbraith (1971) estimates of bulk density of sandy loam Ascalon soil on a site where no grazing by large herbivores had occurred for about 4 to 5 years (1.3 to 1.4 g/cm^3 soil).

Functional activity of root segments with varying degrees of suberization was tested to determine their water permeability. The resistance of root tissues to water flow and to water transfer at the soil-root interface can directly regulate flow of water through the plant (Slatyer, 1967). When

considering the soil-plant-atmosphere system, differential permeability to water diffusion of the cell walls of different roots, or different segments of the same root, might decide the pathway of water through particular regions of the root system.

Three root segments of nonsuberized and of suberized types were selected under the microscope from a soil sample of ≈ 100 g, which had been stored in a sealed vial at 5° to 7°C ; the water potential of the sample was estimated by the filter-paper technique (McQueen and Miller, 1968) and found to be -0.11 bar immediately before the experiment. The diameter and length of each root segment was measured, and the tips sealed by immersion in paraffin. Following initial weighing, the root segment was floated in distilled water at a temperature of 21.4°C . At approximately 5-second intervals the root segment was recovered, blotted to remove surface water, and weighed. Changes in segment weight were expressed per unit surface area and the results for each type of root were averaged.

Measurement of Growth and Expansion of Leaves

The amount of leaf area (leaf area index) was used as an index of leaf growth. At regular intervals during the growing season the leaf area index in a plot adjacent to the excavations, in which all species but blue grama were periodically clipped, was recorded by the inclined point quadrat technique. An inclination of 32° with respect to the horizontal plane was used for these determinations (Knight, 1973). The size of the sample was selected to obtain a reasonable confidence interval (standard error equal to 5% of the mean).

Results and Discussion

Root growth was recorded during the period April 22 to August 14 in five windows. The total length of new roots by depth increment in all windows is shown in Figure 2. Many roots were found to shrink, die, and disappear as a consequence of decomposition. A record was kept of the disappearing roots, and their length is also shown in Figure 2. The ratio of length of growing roots to dying roots indicated that 30% to 60% of the current year's roots were replaced during the growing season. The mortality of roots decreased at the end of the growing season; at this time many roots became brown, indicating the progress of suberization.

Root differentiation and growth started very early in the growing season, though at a low intensity, nearly at the same time or shortly before any leaf expansion was noticeable. Mean maximum air temperature of the 10 days before the start of growth was 8°C . Since the amount of aboveground green tissue was very low, it can be assumed that early root growth occurred at the expense of reserves in the crown and/or in older roots of the plant. Maximum root growth, however, occurs when leaf expansion is also maximum and soil water potential is high.

The young roots stopped growing when the soil water potential reached -40 to -60 bar, and died soon after. Roots decomposed most rapidly when the soil water potential was again high following rainfall events. The patterns of occurrence of mortality and growth during the midgrowing season differed from those observed in late season. During the growing season, while the plants were in vegetative stages, high mortality rates occurred in dry portions of the soil profile simultaneously with very low growth rates. At the end of the growing season, considerable mortality of deep roots (10 to 20 cm) occurred even when the soil water potential of that level was high and roots were growing in upper layers of the soil. This suggests that carbohydrate requirements of

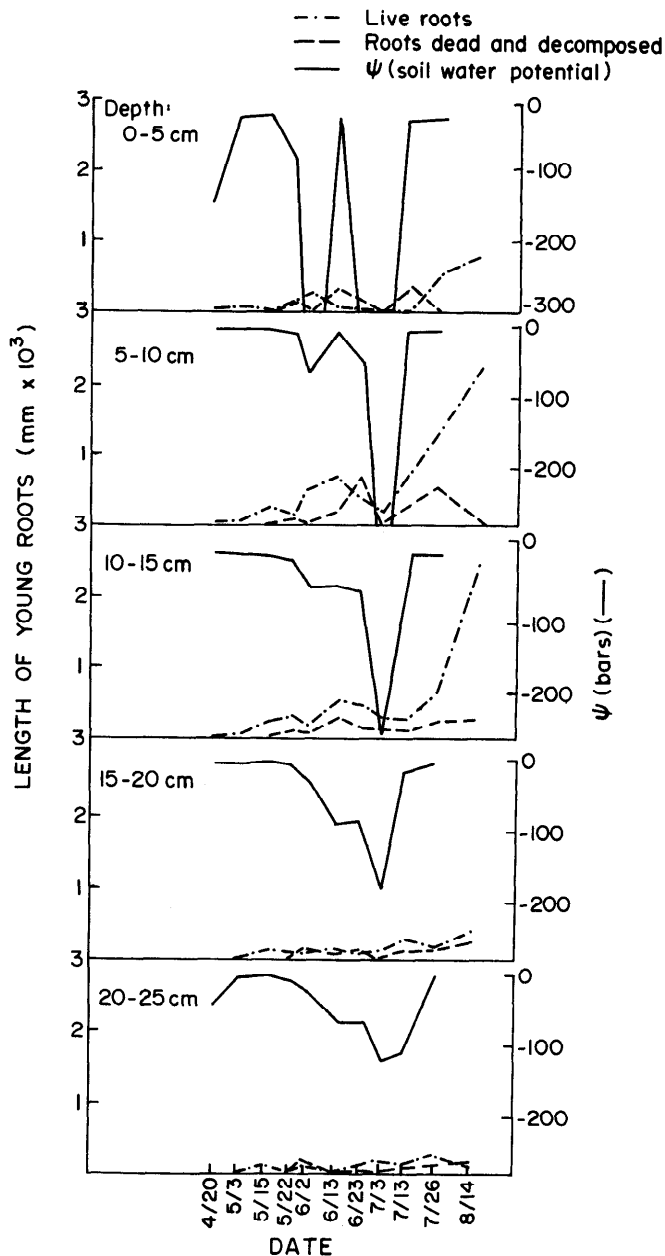


Fig. 2. Total length of young live and dead roots during the period April 22 to August 14. Values of length of live roots indicate the total length of roots at any given date in five windows. Length of dead and decomposed roots was computed by measuring the extension of roots which were found at the previous sampling date but not at the current sampling date.

developing flowers and fruits (Wardlaw, 1965) might reduce the amount of carbohydrates available for downward translocation, and that the proximal roots have priority for carbohydrates over the deeper roots.

Specific weight and ash content determinations indicate that ash content diminishes during the life of a root (Table 1). When the root dies, the decomposition of some of the organic components probably accounts for an increase in ash content on a per unit weight basis.

Results of computations of root volume, surface, and weight are shown in Tables 2 and 3 and Figure 3. The functional root biomass became concentrated at the top layers of the soil as the growing season proceeded. This is in

Table 1. Relationship between volume, dry weight, and ash content of different portions of *Bouteloua gracilis* root biomass. Sample taken on May 15.

Type of root	Sample volume (mm ³)	Sample dry weight (mg)	Ash (% of total dry weight)	Specific weight (ash free basis) mg/mm ³
Nonsuberized	0.59	0.12	47	0.19
Suberized nonfriable	8.26	2.75	20	0.33
Suberized friable	0.92	0.12	54	0.13

agreement with results reported in Singh and Coleman (1974). The values of root biomass/m² obtained suggest that the sampling procedure utilized here resulted in an underestimation of the actual value, which could be as much as 30% higher (Sims and Singh, 1971). This is probably because of either an incorrect estimation of soil bulk density or the assumption of a constant distribution of root biomass within the depth intervals at which samples were taken.

Observation of root growth in the windows under field conditions indicates that 15 to 25 days are required for a juvenile root to attain a diameter of 0.126 mm (nonsuberized root). Assuming that growth in diameter follows a sigmoidal pattern, it should be possible to reproduce a growth curve for roots knowing the average diameter of segments of roots of increasing age and the time needed to attain these diameters.

Analysis of root diameters (Table 4) was used to derive a growth curve of a single root showing the periods in which

Table 2. Total volume, lateral surface, and weight of root material per cm³ of soil at different depths as estimated by samples extracted on May 15. Confidence intervals correspond to ± 2 SE of the mean. Weight was estimated by the conversion factors in Table 1. Soil bulk density estimates were taken from Van Haveren and Galbraith (1971).

Measurement and type of root	Depth		
	0.05 m	0.15 m	0.45 m
Volume (mm³ root/cm³ soil)			
Juvenile	0.08 ± 0.06	-	0.006 ± 0.008
Nonsuberized	3.12 ± 1.80	4.57 ± 2.50	1.49 ± 0.90
Nonsuberized friable	1.84 ± 1.74	0.51 ± 0.30	0.27 ± 0.20
Suberized	2.38 ± 2.20	1.14 ± 1.30	0.27 ± 0.24
Suberized friable	4.85 ± 2.30	1.12 ± 0.74	1.50 ± 0.81
Lateral surface (mm²/cm³ soil)			
Juvenile	4.7 ± 2.3	-	0.1 ± 0.6
Nonsuberized	78.9 ± 59.6	88.4 ± 37.4	41.6 ± 21.0
Nonsuberized friable	34.9 ± 28.0	12.7 ± 7.4	7.5 ± 2.2
Suberized	40.8 ± 30.0	31.3 ± 32.0	5.6 ± 4.1
Suberized friable	80.1 ± 42.0	24.1 ± 14.8	22.2 ± 18.7
Dry weight (ash free) (mg/cm³ soil)			
Juvenile	0.01	-	0.001
Nonsuberized	0.59	1.50	0.15
Nonsuberized friable	0.35	0.09	0.05
Suberized	0.78	0.38	0.09
Suberized friable	0.63	0.15	0.20
Dry weight (ash free) (g/m² cumulative to depth indicated)			
Juvenile	0.5	0.5	0.8
Nonsuberized	29.5	179.5	224.5
Nonsuberized friable	17.0	26.0	41.0
Suberized	39.0	77.0	104.0
Suberized friable	31.5	46.5	105.0

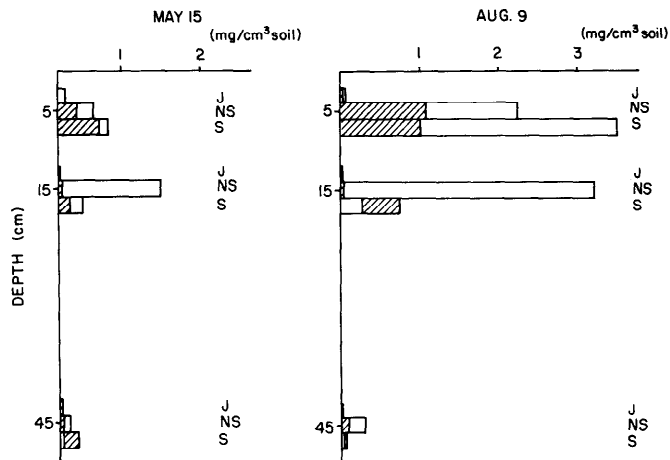


Fig. 3. Composition of the root biomass (mg/cm³ soil) as estimated by samples taken on May 15 and August 9. J = juvenile roots; NS = nonsuberized roots; S = suberized. The dark section of bars indicates the amount of friable roots found. See Tables 2 and 3 for confidence intervals of estimates.

Table 3. Total volume, lateral surface, and weight of root material per cm³ of soil at different depths as estimated by samples extracted on August 9. Data is presented in Table 2.

Measurement and type of root	Depth		
	0.05 m	0.15 m	0.45 m
Volume (mm³ root/cm³ soil)			
Juvenile	0.02 ± 0.01	0.006 ± 0.004	0.00 ± 0.00
Juvenile friable	0.001 ± 0.001	0.00 ± 0.00	0.00 ± 0.00
Nonsuberized	11.80 ± 3.39	17.12 ± 12.49	1.53 ± 0.26
Nonsuberized friable	6.01 ± 2.95	0.14 ± 0.04	0.53 ± 0.39
Suberized	13.59 ± 5.87	0.77 ± 0.39	0.05 ± 0.04
Suberized friable	10.97 ± 2.48	5.61 ± 1.62	0.51 ± 0.16
Lateral surface (mm²/cm³ soil)			
Juvenile	1.93 ± 0.84	0.58 ± 0.37	0.00 ± 0.00
Juvenile friable	0.20 ± 0.23	0.00 ± 0.00	0.00 ± 0.00
Nonsuberized	167.70 ± 23.12	126.10 ± 43.95	35.66 ± 4.87
Nonsuberized friable	60.46 ± 18.44	5.86 ± 1.76	9.41 ± 5.72
Suberized	105.41 ± 44.41	12.70 ± 4.73	1.20 ± 0.80
Suberized friable	101.11 ± 19.55	58.89 ± 12.36	7.63 ± 2.31
Dry weight (ash free) (mg/cm³ soil)			
Juvenile	0.005 ± 0.002	0.001 ± 0.008	0.00 ± 0.00
Juvenile friable	0.0002 ± 0.0002	0.00 ± 0.00	0.00 ± 0.00
Nonsuberized	2.24 ± 0.64	3.25 ± 2.37	0.29 ± 0.05
Nonsuberized friable	1.14 ± 0.56	0.03 ± 0.01	0.10 ± 0.07
Suberized	3.61 ± 1.46	0.25 ± 0.13	0.02 ± 0.01
Suberized friable	1.09 ± 0.33	0.73 ± 0.21	0.07 ± 0.02
Dry weight (ash free) (g/m² to depth indicated)			
Juvenile	0.22	0.34	0.34
Juvenile friable	0.01	0.01	0.01
Nonsuberized	112.08	437.28	524.52
Nonsuberized friable	57.09	59.85	90.27
Suberized	180.00	205.46	210.50
Suberized friable	54.30	127.19	146.96

Table 4. Mean (\bar{X}) and standard error (SE) of the estimate of diameter (mm) of root sections of different categories and at different depths as estimated by a sample obtained on May 15.

Type of root	Depth					
	0.05 m		0.15 m		0.45 m	
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE
Juvenile	<0.05	—	<0.05	—	<0.01	—
Nonsuberized	0.13	0.01	0.13	0.01	0.12	<0.01
Nonsuberized friable	0.16	0.01	0.14	0.01	0.11	0.01
Suberized	0.18	0.02	0.13	0.01	0.14	0.02
Suberized friable	0.20	0.01	0.16	0.01	0.20	0.01

major changes in root structure occurred. The equation for root growth is:

$$Y = \frac{0.182}{1 + k [e^{-\lambda \times 0.182 \times \text{time (days)}}]}$$

where

Y = root diameter (mm)

0.182 = the asymptote of the sigmoidal curve, the maximum observed average diameter of the oldest roots

k = 3 and $\lambda = 0.7$ were determined by iteration till a fit to the third significant digit was obtained.

The equation describes a curve showing the rhythm of growth of a single root and the times at which suberization of the cortical tissues occur (Fig. 4). The estimated growth curve indicates that a root may grow and become suberized in approximately 2 months. This process did not seem to be retarded by unfavorable conditions in the soil, but rather the young root was likely to die if soil water potential became too low. Observation of color of roots growing in the windows at the end of the growing season confirmed that the suberization of the root tissues may begin approximately 1 month after the root is differentiated.

Weight change after immersion in water was much greater in nonsuberized than in suberized roots (Fig. 5). This indicates a major functional role of young nonsuberized roots in the

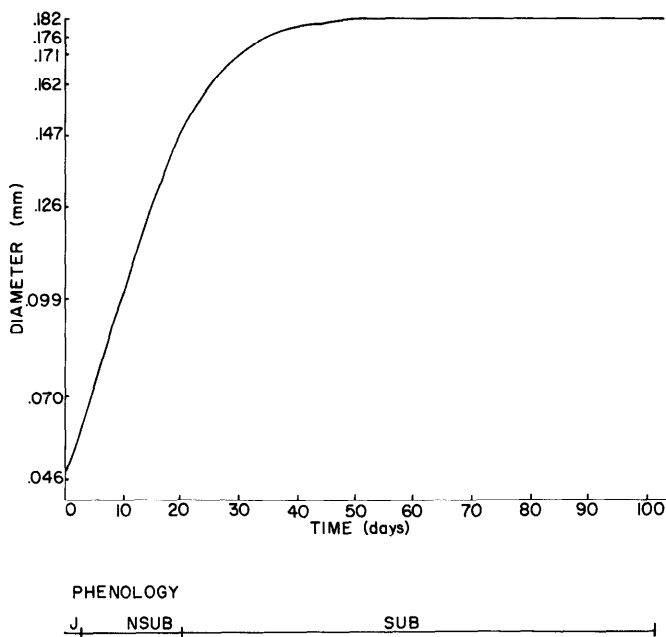


Fig. 4. Derived curve of diameter growth of a single blue grama root. Approximate lengths of growth stage identified by degree of suberization process indicated below: J = juvenile; NSUB = nonsuberized; SUB = suberized.

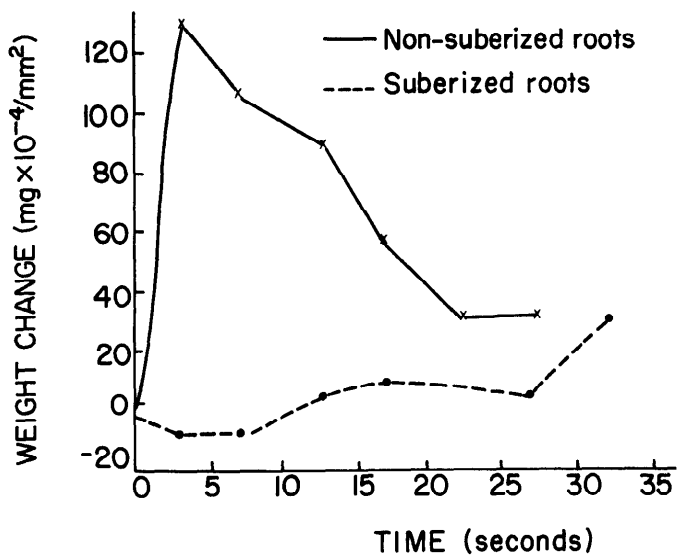


Fig. 5. Changes in weight per unit surface area of sections of roots with different degrees of suberization after immersion in distilled water. Each point is an average of three values.

uptake of water by the plant.

Data on soil water potential (ψ) and leaf area index (L) during the period April 15 to June 12 (Table 5) were analyzed to study the relation between these variables. Leaf area index during this period depended upon leaf expansion rate and also on the curling of leaf blades due to water stress. The linear correlation between specific growth rate and the \log_{10} of ψ (bars) at different depths was calculated. The correlation coefficients (r) of the regressions obtained when using ψ values

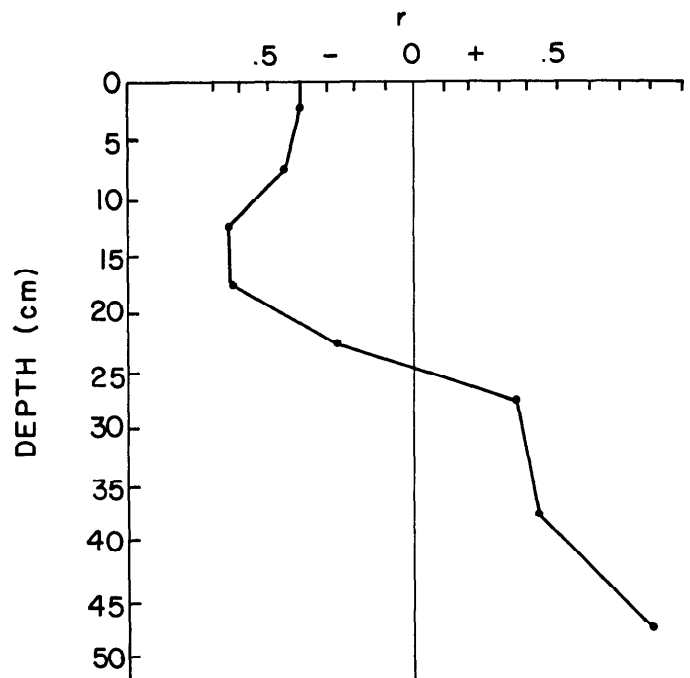


Fig. 6. Correlation coefficients (r) of the linear regressions $y = a + bx_i$, where y = specific growth rate of leaves in $\text{cm}^2 \cdot \text{day}^{-1}$ and $x_i = \log_{10}$ of soil water potential (Ψ) in bars at depths $i = -5, -10, -15, -20, -25, -30, -40,$ and -50 cm. High negative values of Ψ are associated with high water stress, which is inversely correlated with specific growth rate. Values used to compute the correlation coefficients were obtained from April 15 to June 6. Average and SE of Ψ measurements in the layer -10 to -20 cm were -0.22 and -0.18 , respectively.

Table 5. Blue grama leaf area index (L) in cm² leaf/cm² soil and soil water potential (Ψ) in bars at different depths during the 1973 growing season in the experimental field plots at Pawnee site. Initiation and progress of flowering of blue grama indicated.

Growth factors	Depth (cm)	Date											
		4/18	5/8	5/15	5/22	6/2	6/13	6/23	7/3	7/13 ^a	7/26 ^b	8/14 ^c	9/3 ^d
L *		≅0	0.07	0.40	0.90	0.68	0.65	0.72	0.64	0.68	—	1.00	
Ψ **	0-5	-143.00	-5.15	-2.43	-88.12	-891.00	-0.04	-381.00	-688.00	-4.70	-0.06	-16.00	
	5-10	-0.12	-0.13	-0.13	-9.62	-62.00	-2.33	-55.00	-514.00	-0.36	-0.02	-7.70	
	10-15	-0.13	-0.11	-0.60	-8.36	-50.00	-10.20	-57.00	-264.00	-0.95	-0.05	-13.50	
	15-20	-0.19	-0.19	-0.09	-4.76	-33.00	-75.20	-73.00	-182.00	-19.20	-0.04	-6.40	
	20-25	-42.00	-2.56	-0.16	-8.15	-26.00	-73.80	-74.00	-135.00	-115.00	-0.04	-3.40	
	25-30	-150.00	-21.97	-4.25	-6.22	-21.00	-56.50	-69.00	-137.00	-158.00	-0.04	-0.12	
	35-40	-185.00	-136.62	-21.97	-30.40	-21.00	-54.40	-59.00	-110.00	-128.00	-20.00	-24.10	
	45-50	-200.00	-174.83	-18.66	-42.69	-46.00	-68.40	-70.00	-122.00	-167.00	-76.00	-68.10	

* SE = 0.05 × \bar{L} .

** SE = 0.4 × $\bar{\Psi}$.

^aBeginning of flowering.

^bFlowering abundant.

^cFlowering and fruits abundant.

^dRipe fruit, 30% dead leaves.

for each depth are plotted as a function of depth in Figure 6. During the period of rapid leaf expansion the highest negative correlation with water potential was found at depths of 10 to 15 cm and 15 to 20 cm. Results of microscopic observations showed that a high proportion of the biomass of young nonsuberized roots was located in the upper 20 cm of soil at that time of the growing season; these young, permeable roots were the ones through which soil water was most available to the plant.

Also, the nonsuberized roots occurred in a region of the soil where water potential was high, and most of them died and disappeared when the soil dried out (Fig. 2 and Table 5). The life-span of some growing roots, therefore, was very short and many died during the growing season when soil water potential became low. The location of nonsuberized roots in the soil profile varied during the growing season as a result of both fluctuation in soil water potential and morphological changes of the root system. At the beginning of the growing season, when the top layer of soil was too dry to stimulate or sustain root differentiation and growth, they occurred at maximum concentration in the subsuperficial 10 to 20 cm region layers of the soil. At the mid or latter part of the growing season, when the soil water potential was very high even in the surface layers, the location of the growing roots was very superficial (Fig. 2 and 3 and Table 5). The occurrence of root differentiation and growth processes in the upper layer (0 to 5 cm) of the soil profile was not clearly observable through the windows because the top of the soil profile was damaged by installation of the glass panels. The roots in the top layer of the soil reached the windows only some centimeters below ground level. Results of microscopic observations reported in Tables 2 and 3, though, confirm that the amount of growing roots was high in the 0 to 5 cm depth by the end of the growing season and low at deeper levels, despite high soil water potential throughout the profile. This suggests that if soil water potential is high in a wide region of the profile, the differentiation of roots proceeds from the region nearest the crown of the plant downward and the growth of the roots already differentiated follows the same downward pattern, perhaps because translocated photosynthate is more available to roots near the crown of the plant.

Conclusions

Root observation windows can provide a precise picture of root dynamics during the growing season. Roots of *Bouteloua gracilis* are transient, with a high proportion dying and decomposing during the same season in which they were

differentiated. Functional development parallels the degree of suberization, with young nonsuberized roots performing most of the water uptake. Foliar growth rate is correlated with root development in soil layers with high water content. Late in the season root growth is greatest near the crown of the plant. This resulted in increased root biomass in upper levels of the soil profile as the season progressed.

Estimates of root biomass derived from microscopic analysis of small samples do not compare well with biomass estimates made from soil cores. Crowns are excluded by the microscopic method, but other reasons for underestimation of root biomass by this procedure are discussed. An empirical equation is presented which represents a quantitative description of root growth in *Bouteloua gracilis*, assuming exponential growth rate. It will be useful in developing models of root dynamics and can serve as an hypothesis for future experiments.

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