Leaf Area, Nonstructural Carbohydrates, and Root Growth Characteristics of Blue Grama Seedlings

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Abstract

Establishment of blue grama [*Bouteloua gracilis* (H.B.K.) Lag ex Steud.] seedlings requires extension of adventitious roots into the soil profile. The objectives of this study were to determine the effects of leaf area and total nonstructural carbohydrates (TNC) on root growth characteristics of blue grama. Seedlings supported by the seminal root only were treated with 3 days of reduced light and then with 0, 1, 2, and 3 days of full sunlight to alter TNC percentage in crowns. Seedlings within each of these treatments were then clipped at a height of 3, 6, 9, and 12 cm, or left unclipped to alter leaf area. Adventitious root growth was studied during a 3-day test. Path coefficients indicating the effects of leaf area on number of roots per seedling, depth of roots, and root weight per unit length (diameter) were 0.72, 0.47, and 0.77, respectively. The TNC had smaller effects on root growth than did seedling leaf area. Clipping treatments probably reduced root growth because of a deficiency of photosynthetic products. But, the reduction was explained by an adjustment in all components of growth rather than in root depth only. Thus, blue grama seedlings maintained a reasonable rate of root elongation even under severe clipping treatments.

Establishment of blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.] seedlings requires the initiation and the extension of adventitious roots (Wilson and Briske 1979). That process depends on seedling leaf area (Wilson 1981), total nonstructural carbohydrates (TNC), tolerance of dehydration (Briske and Wilson 1980, Khan 1980), and favorable environmental conditions (Hyder et al. 1971).

The relationships among clipping treatments, TNC, rate of root elongation, and total dry weight of roots have been studied by several investigators (Booysen and Nelson 1975, Buwai and Trlica 1977, Crider 1955, Hansen 1978, Smith 1974, Youngner and Nudge 1976). Little information is available, however, on the possible effects of clipping and TNC on other components of root growth (Parker and Sampson 1930). The objectives of this study were to determine effects of seedling leaf area (clipping treatments) and crown TNC percentage (light treatments) on 3 components of root growth in blue grama seedlings: number of roots, root length (depth), and root weight per unit length (diameter). Information on root growth characteristics associated with clipping and environmental stress will aid in seedling establishment and in managing blue grama stands.

Materials and Methods

The effects of light and clipping treatments on the components of adventitious root growth were investigated on blue grama seedlings under greenhouse conditions during June through September. Air temperatures in the greenhouse varied from 25 to 35°C. Maximum midday photosynthetic photon flux density (PPFD) was 1,650 μmole m^{-2} sec^{-1} in early summer and 850 μmole m^{-2} sec^{-1} in late summer.

Plastic pots (15 cm diameter by 15 cm deep) were filled with 1,800 g of sterilized (100°C dry heat for 2 days) sandy loam soil (fine-loamy, mixed, mesic Aridic Argiustoll). The soil was surface irrigated with 250 ml of water, and 25 'Lovington' blue grama seeds were planted at a depth of 2 mm in the moist soil. Seeds were then covered with 2.5 cm of air-dry soil. Seedlings emerged through the dry soil layer within about 5 days.

Pots were weighed on alternate days and the amount of water needed to bring the lower 1,800-g of soil to field capacity was placed in a petri dish. Water moved into the soil through holes in the bottom of the pot. The subirrigation procedure maintained a moist subsoil and a dry soil surface which promoted seedling growth but prevented growth of adventitious roots. Thus, seedlings were supported by the seminal root only during this phase of the study.

At 3 weeks after planting, pots were thinned to 8 vigorous, well-spaced seedlings. At 5 weeks, seedlings were exposed to 3 days of shade and then to 0, 1, 2, or 3 days of sunlight to create various levels of total nonstructural carbohydrates in seedling crowns. Average midday PPFD in shade was 240 μmole m^{-2} sec.$^{-1}$. After shade and light treatments, the pots were separated into 5 groups and seedlings were clipped at heights of 3, 6, 9, or 12 cm. The fifth group of seedlings was left unclipped. Four seedlings in each pot were randomly sampled to determine the weight of shoot removed by clipping and the weight of shoot remaining after clipping. Leaf-blade area remaining after clipping was also determined. The lower 3-cm portion of stem base was dried at 60°C and used for determination of percent TNC (Association of Official Agricultural Chemists 1965, Heinze and Murneek 1940, Smith et al. 1964). Measurements before the root growth test were based on a composite sample of 12 seedlings harvested from 3 pots.

Immediately after clipping, the remaining seedlings in each pot were surface irrigated to promote growth of adventitious roots during a 3-day test. Shade, light, and clipping treatments were scheduled so that the root growth test could be started on the same day for all treatments. After 3 days with a moist soil surface, seedlings in each pot were harvested, adventitious roots were counted, the length of each root (main axis) was measured, and roots were oven-dried and weighed. Root weight per unit length was estimated from the total length of the main axis of all roots in a sample divided by the dry weight of the sample. There was little or no branching of adventitious roots at this stage of development. Leaf blades were removed and leaf area was measured. Measurements after the root growth test were based on a composite sample of 6 seedlings harvested from 3 pots.

The study was conducted as a randomized complete-block. Factor 1 represented 4 light treatments and factor 2 represented 5 clipping treatments. The study included 6 replications which represented different dates of growth in the greenhouse. Analysis of variance was used to test for differences among treatments. Path

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Table 1. Effects of days of sunlight after shade and height of clipping on leaf area per seedling (cm^2) before and after the 3-day root growth test.

	Clipping height (cm)					
Days of sunlight	3	6	9	12	Unclipped control	Mean
Before root growth test						
0	1.55	4.57	6.86	8.52	10.95	6.49[1]
1	1.34	4.15	6.64	8.82	11.58	6.51
2	1.59	4.23	6.61	8.49	11.43	6.46
3	1.31	4.04	6.48	8.72	11.32	6.37
Mean	1.45[2]	4.25	6.65	8.63	11.32	
Pooled standard error ($s_{\bar{x}}$) = 0.59						
After root growth test						
0	3.32	6.83	10.20	10.95	13.07	8.87[1]
1	3.73	6.08	10.17	11.32	12.24	8.71
2	3.74	7.00	9.30	13.06	12.58	9.13
3	3.94	7.57	9.40	12.18	12.24	9.06
Mean	3.69[2]	6.87	9.77	11.88	12.53	
Pooled standard error ($s_{\bar{x}}$) = 0.67						

[1]Within each sampling period (before or after root growth test), differences among light treatments were not significant ($P<0.05$).
[2]Within each sampling period (before or after root growth test), differences among clipping treatments were significant ($P<0.01$).

Table 2. Effects of days of sunlight after shade and height of clipping on the average number of adventitious roots and the length of longest adventitious root (cm) produced per seedling during the 3-day test.

	Clipping height (cm)					
Days of sunlight	3	6	9	12	Unclipped control	Mean
Number of roots per seedling						
0	11.3	18.4	21.4	24.0	27.3	20.5[1]
1	13.0	18.3	21.2	23.2	25.0	20.1
2	13.9	20.6	22.2	27.4	26.6	22.2
3	14.8	22.2	24.3	27.4	30.2	23.8
Mean	13.2[2]	19.9	22.3	25.5	27.3	
Pooled standard error ($s_{\bar{x}}$) = 1.3						
Length of longest root per seedling						
0	5.63	7.48	8.97	8.90	9.85	8.17[1]
1	5.80	7.72	8.83	9.92	9.83	8.42
2	6.67	8.20	9.22	9.62	9.98	8.74
3	6.40	8.53	9.13	9.65	9.87	8.72
Mean	6.12[2]	7.98	9.04	9.52	9.88	
Pooled standard error ($s_{\bar{x}}$) = 0.25						

[1]Differences among light treatments in number of roots and length of longest root per seedling were significant ($P<0.01$).
[2]Differences among clipping treatments in number of roots and length of longest root per seeding were significant ($P<0.01$).

Table 3. Effects of days of sunlight after shade and height of clipping on the weight per unit length of adventitious roots ($\mu g/cm$) and the total weight of adventitious roots (mg/seedling) produced during the 3-day test.

	Clipping height (cm)					
Days of sunlight	3	6	9	12	Unclipped control	Mean
Weight per unit length of adventitious roots						
0	145	137	160	164	187	159[1]
1	124	144	159	181	197	161
2	137	149	189	184	216	175
3	136	152	176	172	208	169
Mean	136[2]	146	171	175	202	
Pooled standard error ($s_{\bar{x}}$) = 7						
Total weight of adventitious roots per seedling						
0	6.2	12.9	20.5	22.6	34.8	19.4[1]
1	6.4	13.6	20.3	28.3	34.6	20.6
2	8.0	17.1	26.5	32.2	40.4	24.8
3	9.1	20.2	27.2	32.8	42.1	26.3
Mean	7.4[2]	16.0	23.6	29.0	38.0	
Pooled standard error ($s_{\bar{x}}$) = 2.2						

[1]Differences among light treatments in weight per unit length of adventitious roots and total weight of adventitious roots per seedling were significant ($P<0.01$).
[2]Differences among clipping treatments in weight per unit length of adventitious roots and total weight of adventitious roots per seedling were significant ($P<0.01$).

coefficient analysis was used for evaluating possible cause and effect relationships among variables associated with adventitious root growth (Nie et al. 1975).

Results and Discussion

The relative shoot weight removed by clipping at a height of 3, 6, 9, and 12 cm was 51, 36, 25, and 16%, respectively. The relative shoot weight removed by clipping seedlings in the 0-, 1-, 2-, and 3-day light treatments was 25, 25, 26, and 27%. Before the root growth test, leaf-blade area in the 3-, 6-, 9-, and 12-cm clipping treatments, and in the unclipped treatment, was 1.4, 4.2, 6.6, 8.6, and 11.3 cm^2 per seedling (Table 1). Days of sunlight after shade did not affect the leaf-blade area remaining when clipping treatments were imposed. The increases in leaf-blade area (during the root growth test) in the 3-, 6-, 9-, and 12-cm clipping treatments, and in the unclipped treatment, were 2.24, 2.62, 3.12, 3.25, and 1.21 cm^2 per seedling. Apparently leaf-blade area of unclipped seedlings had approached the maximum that could be supported by the seminal root. Therefore, leaf area expansion began slowly as new adventitious roots developed. Days of sunlight after shade had little or no effect on the increase in leaf area during the root growth test.

Average crown TNC values in the 0-, 1-, 2-, and 3-day light treatments were 11.07, 12.26, 12.75, and 12.98%, respectively. All of the TNC levels were considered favorable for the development of adventitious roots (Wilson 1984).

A decrease in leaf-blade area (11.3 vs 1.4 cm^2) resulted in a decrease of 52% in number of adventitious roots per seedling (Table 2), 38% in length of longest adventitious root per seedling, 33% in root length per unit length (Table 3), and 81% in total adventitious root weight per seedling ($P<0.01$). A decrease in days of sunlight after shade (3 vs 0) resulted in a decrease of 14% in number of roots per seedling (Table 2), 6.3% in length of longest root per seedling, 5.9% in root weight per unit length (Table 3), and 26% in total adventitious root weight per seedling ($P<0.01$).

Path coefficient analysis showed possible cause and effect relationships among variables associated with root growth (Fig. 1). Leaf area (before the root growth test) affected number of roots per seedling (p_{53} = 0.724), length of longest root per seedling (p_{52} = 0.474), and root weight per unit length (p_{51} = 0.766). Crown TNC percentage, to a lesser degree than leaf area, affected number of roots per seedling (p_{43} = 0.132) and root weight per unit length (p_{41} = 0.212). The effect of TNC on length of longest root was not significant (p_{42} = 0.026). In a related study, TNC varied widely among treatments and was significantly associated with root length (Wilson, in press).

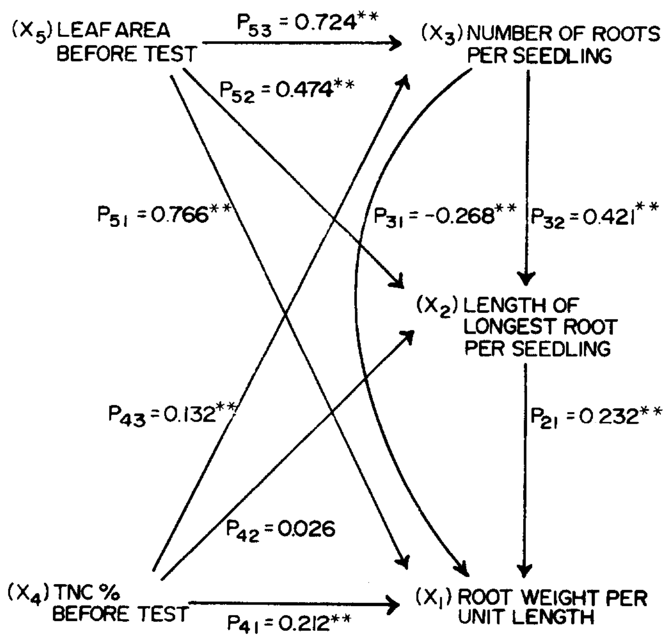

Fig. 1. *Path coefficient analysis of factors associated with root growth in blue grama seedlings. **Path coefficients were significant (P<0.01).*

There was a positive association between number of roots and length of longest root per seedling (p_{32} = 0.421) and between length of roots and root weight per unit length (p_{21} = 0.232). Those associations probably do not have a genetic basis because each sample represented 6 seedlings. Rather, they are explained by differences in environmental conditions during growth of seedlings in replications that represented different dates of growth. Favorable light conditions in the greenhouse early in the summer resulted in seedlings with a high number of roots, rapid elongation of roots, and a high root weight per unit length.

The positive association in this study between length of roots and root weight per unit length differs from the results found in a previous study in which increasing soil temperatures (10 to 30° C) caused a substantial increase in root length but a decrease in root weight per unit length (Wilson 1981). Temperature affected the 2 components of growth in a different way. The negative effect of number of roots (p_{31} = −0.268) on root weight per unit length is consistent with the results of the earlier study. Thus, seedlings that produced many roots tended to have roots that were small in diameter.

The possible reasons that TNC exerted smaller effects on root growth than did leaf area are as follows: (1) shade treatments did not cause TNC to fall below critical levels, (2) amounts of TNC in seedling shoots generally are lower than the amounts of current net assimilate produced in leaves during the 3-day root growth test, and (3) current assimilate is more readily utilized for root growth than is the TNC accumulated in crowns before the root growth test (Wilson 1984). There were similarities in the effects of TNC and leaf area on the components of root growth notwithstanding differences in the magnitude of the effects.

The results suggest that blue grama seedlings possess morphological and physiological characteristics which favor survival during stress. Plant survival under grazing and drought stress apparently is favored by the effective allocation of photosynthetic products into the various components of root growth. Clipping treatments probably reduced root growth because of a deficiency of photosynthetic products. But the reduction was explained by an adjustment in all components of root growth rather than in root length or depth only. Thus, blue grama seedlings maintained a reasonable rate of root elongation even under severe clipping treatments. A deep root system may be more critical than diameter of roots or number of roots in the survival of seedlings under long-term drought conditions. It is not known whether mature stands of blue grama make similar adjustments in the components of root growth in response to clipping, grazing, or changes in TNC.

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