Seminal and Adventitious Root Growth of Blue Grama Seedlings on the Central Plains

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Abstract

Blue grama has not established itself on abandoned farmland in the Central Plains. This study was conducted to determine the environmental conditions which limit the growth of the seminal and adventitious roots of blue grama seedlings in northeast Colorado. Field seedings of blue grama were made in both spring and late summer of 1973 and 1974. It was found that the soil surface had to remain moist for 2 to 4 days for blue grama seeds to germinate and initiate growth of the seminal root. A second moist period of 2 to 4 days was required some 2 to 8 weeks later in order for adventitious roots to initiate growth. If adventitious roots were not initiated, blue grama seedlings died during the winter. Seminal roots of blue grama grew 1 · cm · day^{-1} under favorable soil-moisture and temperature conditions, and only 0.6 cm · day^{-1} under less favorable conditions. Adventitious roots grew 2.3 cm · day^{-1} under favorable soil-moisture and temperature conditions, and only 0.7 cm · day^{-1} under less favorable conditions.

A warm-season forage grass is needed to take full advantage of 80% of the annual precipitation which occurs during April through September on the Central Plains. Cool-season grasses, such as crested wheatgrass (*Agropyron desertorum*), are needed for early spring grazing; but precipitation in the spring is too undependable and temperatures during the summer are too high for consistent, long-term production. In many situations, warm-season grasses would be the best species to revegetate denuded areas on the Central Plains. Blue grama (*Bouteloua gracilis*) appears to be the most promising warm-season grass for use in revegetation of the drier areas of the Central Plains because, once established, it is persistent, productive, and of high forage value.

The use of blue grama for revegetation in the Central Plains is limited because of difficulties in its establishment from seed. Blue grama has not re-established itself in areas that were plowed 40 years ago, and attempts to plant blue grama have seldom been successful (Bement et al. 1965; Hyder et al. 1971).

Low seed weight, the potential for only one seminal root (Hyder 1974), a limited capacity for water uptake by the seminal root (Wilson et al. 1976), and a seedling form that places the crown (from which adventitious roots may develop) at an average depth of only 0.2 cm (Hyder et al. 1971) contribute to the difficulties encountered in the establishment of blue grama. Consequently there is a need for improved planting methods and seedlings with improved drought resistance characteristics. The objectives of this study were to measure soil temperature and moisture conditions during the initiation and growth of seminal and adventitious roots of blue grama seedlings on the Central Plains and define the environmental requirements for root growth.

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Methods

Blue grama was seeded on May 10 and August 3, 1973, and June 11 and mid-August, 1974. Six replications were established at the Central Plains Experimental Range (CPER) in northeast Colorado on each planting date. Plot size was 2.0 by 3.0 m. Row width was 0.3 m. Average annual precipitation is 31 cm, about 80% of which falls during April through September. The soil is a sandy loam. Blue grama is the dominant species on adjacent native rangeland.

The soil was rototilled to a depth of about 15 cm, leveled, and packed with a roller (60 cm long by 45 cm diameter) filled with water. The soil was leveled before and after planting with a leveling bar on a wood frame surrounding each plot. Seeds were planted at a rate of 0.1 g/m of row (about 200 seeds/m) and covered with 1 cm of loose soil. In 1974, the plots were covered with a straw mulch after planting to conserve soil water and provide uniform seedling emergence. The mulch was removed after emergence so that root development could be studied under natural conditions of water loss from the soil surface.

Root growth was determined at frequent intervals after emergence by removing soil cores over two seedlings per plot during the early part of the season and one seedling per plot during the latter part of the season. The starting point for sampling along a row was randomly selected and then later samples were collected sequentially at 30 cm intervals. The largest seedling within ±5 cm of the sampling point was collected for the measurement of root and shoot growth. Seedlings were removed with a steel sampling tube (12 cm in diameter) which was driven to a depth of 60 cm down over the seedling. The seedling and soil core were removed without damage to the root system. The soil was washed from the root system through a slot (7.5 cm wide) that extended along the length of one side of the tube. The seminal root of blue grama is delicate and easily broken. If a root was broken during the washing procedure, the entire seedling was discarded and a new seedling was sampled.

Root depth was determined by measuring the length of the main axis of the seminal root; total length of the seminal root (main axis and all branches) was estimated by suspending the root in a shallow tray of water and counting the number of times roots intersected grid lines (Newman 1966). A 0.5-cm grid was used for small root systems and a 1-cm grid was used for large root systems. Roots of known length were randomly placed on the grid to determine the accuracy of the measurement. The standard deviation was ±3.3% of total root length when the number of intersections of roots with grid lines ranged from 50 to 150. The number of intersections multiplied by 0.397 for the 0.5-cm grid and 0.794 for the 1.0-cm grid estimated total cm of root length. The average depth to which roots had penetrated at various times during the study was estimated by polynomial regression of seedling age (t) on root depth (Y).

In 1974 we counted number of tillers and adventitious roots, determined shoot and root dry weight, and estimated leaf blade area. Total leaf blade area of seedlings was estimated by covering leaves with a 1-mm grid overlay and counting the number of grid intersections within the perimeter of the flattened leaves. Integral mean net assimiliation rates (mg biomass $\cdot$ cm^{-2} leaf area $\cdot$ day^{-1}) were calculated by the method of Ondok and Kvet (1971) for only 1974 data. Separate estimates of net assimilation rate were made for each replication and the mean and standard deviation were calculated.

Soil water content was determined by collecting soil samples twice weekly between blue grama rows. Soil in the 2.5-cm diameter sampling tube was separated into sections representing depths of 0 to 2, 2 to 4, 4 to 6, 6 to 10, 10 to 20, 20 to 30, and 30 to 40 cm. Gravimetric soil water content was determined by drying the soil at 100°C for 24 hr; it was then multiplied by the bulk density of soil at each depth to obtain the volumetric water content (g H_2O $\cdot$ cm^{-3} soil). A desorption curve, prepared with a pressure membrane apparatus, was used for determining relationships between soil moisture and soil water potential. Water potential in zones of root elongation were estimated with the use of rooting depth, average soil water content in the soil zone through which the root tip had penetrated during a given time, and the desorption curve.

The amount of water that potentially could move to root surfaces as a result of penetration of the seminal root tip into deeper layers of the soil profile was estimated by assuming that water could move a horizontal distance of 4 cm through the soil to the main axis of the seminal root (Slatyer 1967). Analysis of variance and Duncan's multiple range test were used to determine significant differences among sampling dates in total amount of water in the soil zone through which the seminal root had extended during a 1-day period.

Soil temperatures, recorded at 2.5, 5.7, 10.2, 20.3, and 50.8 cm depths at CPER by the Natural Resource Ecology Laboratory, Colorado State University, were interpolated to obtain an estimate of temperature in the zone of root elongation. Precipitation amounts were obtained at CPER headquarters.

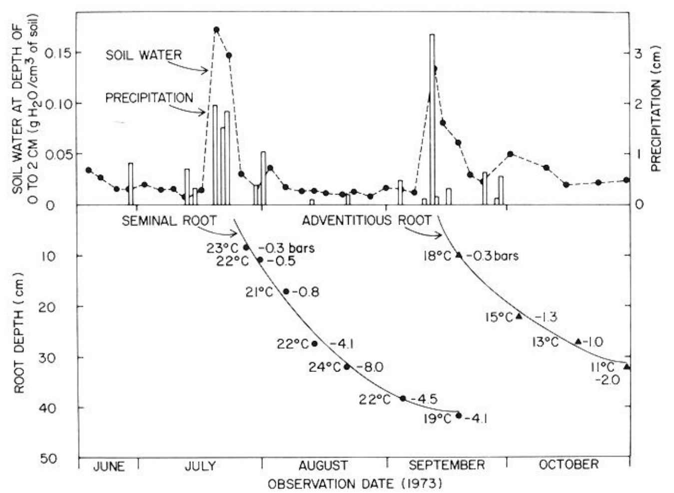

Fig. 1. *Precipitation, soil water content in the 0- to 2-cm zone of the soil profile, temperature and water potential in the zone of root elongation, and average depth of penetration of seminal primary roots and adventitious roots of blue grama seedlings that emerged July 23, 1973, from a spring planting.*

Results

Spring Planting—1973

Seminal Root Growth

Blue grama seeds were planted on May 10; however, because of inadequate precipitation, seedling emergence was delayed until July 23 (Fig. 1). Total rainfall during the 4 days preceding July 23 was 5.3 cm. At the time of emergence, total water in the 0- to 40-cm zone of the soil profile was 5.8 cm. This was 0.3 cm more than the amount required to moisten the 40-cm profile to a water potential of -0.3 bars.

During the initial stages of growth, the rate of seminal root elongation was 1.1 cm$\cdot$day^{-1}. The rate then decreased until elongation had essentially ceased in 56-day-old seedlings (Fig. 1). Soil water potential in the zone of seminal root elongation varied from -0.3 to -8.0 bars, and temperature in the zone of root elongation varied from 24 to 19°C. Although the average depth attained by seminal roots was about 40 cm, the seminal root of one exceptional seedling extended to a depth of 54 cm (Fig. 2). Seminal roots attained average total lengths (main axis and all branches) of 195 cm.

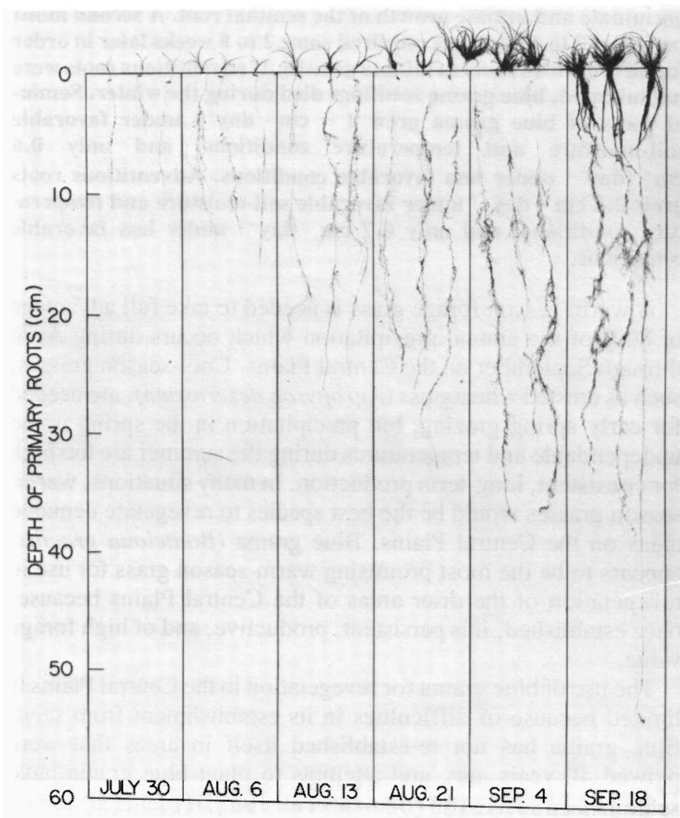

Fig. 2. *Growth of seminal primary roots and adventitious roots of blue grama seedlings that emerged July 23, 1973.*

Because of a deficiency of precipitation and high rates of evaporation, the 10- to 20-cm zone dried to a water potential of -15 bars within 3 weeks after emergence (Fig. 3). Thus, seedlings depended on the extension of the seminal root into deeper soil layers. Slatyer (1967) suggested that under natural conditions water can be expected to move a radial distance of about 4 cm to a root surface. On this basis, the amount of water that potentially could move to root surfaces (as a result of penetration of the seminal root tip into successively deeper layers each day) decreased from about 7.7 g in 7-day-old seedlings to less than 3.0 g in 35-day-old seedlings (Table 1).

Table 1. Total amount of water (g) in the soil zone through which the seminal root tip of blue grama penetrated during a 1-day period in 1973 as influenced by seedling age (days) and predicted root depth (cm).

Interval for determining soil H_2O	Seedling age[1]	Predicted root depth[2]	H_2O in soil zone[3]
July 26	3	6.4	–
July 26 to 30	7	11.3	7.7 a[4]
July 30 to Aug 2	10	14.7	7.4 a
Aug 2 to 6	14	19.0	6.1 b
Aug 6 to 10	18	22.8	5.1 c
Aug 10 to 13	21	25.5	4.6 d
Aug 13 to 16	24	27.9	3.7 e
Aug 16 to 20	28	30.8	3.3 f
Aug 20 to 23	31	32.7	3.2 f
Aug 23 to 27	35	35.0	3.0 f
Aug 27 to 31	39	36.8	2.6 g
Aug 31 to Sep 4	43	38.3	2.0 h
Sep 4 to 7	46	39.1	1.4 i

[1] Seedling age at the end of the sampling interval.
[2] Root depth (Y) was predicted from the equation: $Y=2.413 + 1.350t - 0.012t^2$, where t is days after emergence. $r^2=0.90$; standard error of estimate=4.1 cm.
[3] We assumed that water could move a horizontal distance of 4 cm (Slatyer 1967).
[4] Values labeled with the same letter are not significantly different at the 0.05 level according to Duncan's multiple range test.

The decrease resulted from both the drying of the soil profile and the decreasing rate of root elongation.

Adventitious Root Growth

Rainfall of 0.4 and 1.0 cm fell on July 30 and August 1, respectively (Fig. 1). Only two of the twelve seedlings sampled on August 6 had developed an adventitious root. Seedlings were only 9 days old on August 1, and most of them apparently were not yet physiologically ready to develop adventitious roots. On later sampling dates, we observed that adventitious roots formed in early August had died, probably because of lack of soil water. The 3.8 cm of rain that fell from September 11 to 18 maintained a moist soil surface for about 7 days (Fig. 1), and seedlings developed an average of ten adventitious roots. During the months of September and October, soil water potential in the zone of adventitious root elongation decreased from -0.3 to -2.0 bars; temperature in the zone of elongation decreased from 18 to 11°C. Adventitious roots elongated at an average rate of 0.67 cm $\cdot$ day^{-1}, and reached an average depth of 32 cm by the end of October 1973. These seedlings survived through the 1973-1974 winter and developed into vigorous plants.

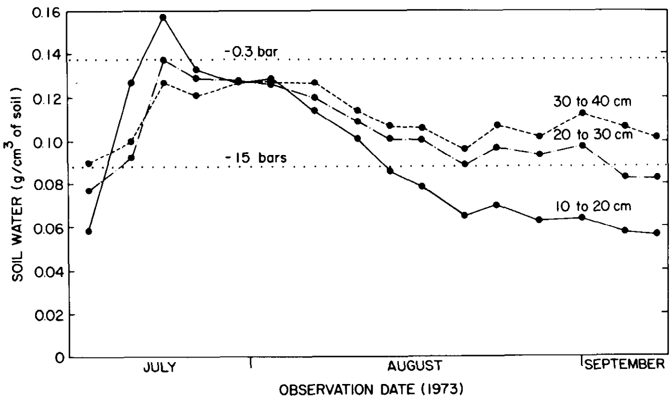

Fig. 3. *Depletion of soil water in the 10- to 20-, 20 to 30-, and 30-to 40-cm zones of the soil profile in plots in which blue grama seedlings emerged July 23, 1973.*

Thus seedlings from the spring 1973 planting were supported by only the seminal root from July 23 to September 11, a period of 50 days during which there was little effective precipitation (Fig. 1). Survival for such a long dry period would have been improbable if the soil profile had not been at a water potential of about -0.3 bars at the time of emergence. Although precipitation during the 50-day interval was not effective for development of adventitious roots, it apparently reduced water loss from the soil profile (Fig. 3) and thus contributed to the survival of seedlings.

Late Summer Planting—1973

Seminal Root Growth

Although blue grama was planted on August 3, 1973, the lack of effective precipitation delayed the emergence of seedlings until September 15. Seedlings emerged following a 7-day period of damp, cloudy weather during which total rainfall was 3.8 cm (Fig. 1). Total soil water in the 0- to 40-cm zone on September 18 was 4.6 cm, which was 0.9 cm less than the amount required to moisten the 40-cm profile to a water potential of -0.3 bars.

Seminal roots of blue grama elongated an average of 0.64 cm $\cdot$ day^{-1} from mid-September to mid-October. Temperature in the zone of root elongation decreased from 18 to 5°C (Fig. 4). Water potential in the zone of elongation decreased from -0.5 to -8.1 bars. Root elongation had ceased at the end of October. Seminal roots reached an average depth of 18 cm and attained total lengths (main axis and all branches) of 45 cm.

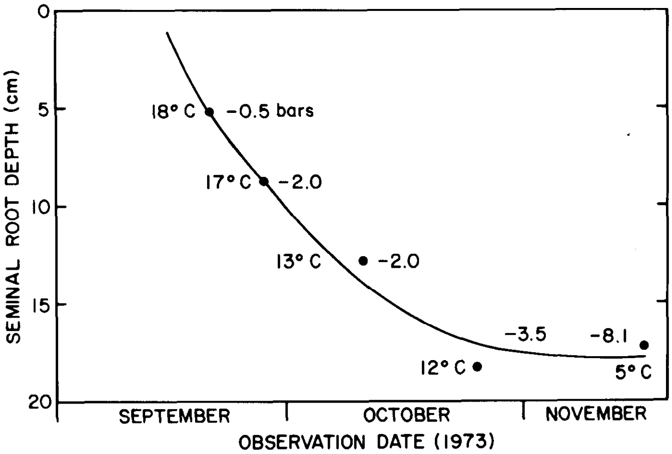

Fig. 4. *Temperature and water potential in the zone of root elongation, and depth of penetration of seminal primary roots of blue grama seedlings that emerged September 15, 1973, from a late summer planting.*

Failure to Develop Adventitious Roots

These seedlings did not develop adventitious roots because of either low temperatures or dryness of the soil surface. We considered the possibility that seedlings did not develop adventitious roots because they had not reached the required morphological and physiological stage. When six seedlings from the October 25 sampling date were placed on moist blotter paper in dishes to test for the capacity to develop adventitious roots, they all developed one 0.5-cm long adventitious root during the 24-hour test. Therefore, the failure to develop adventitious roots in the field was related mainly to environmental rather than physiological limitations.

About 10% of the seedlings from the late summer planting survived for 60 days, but none of them survived through the 1973-1974 winter.

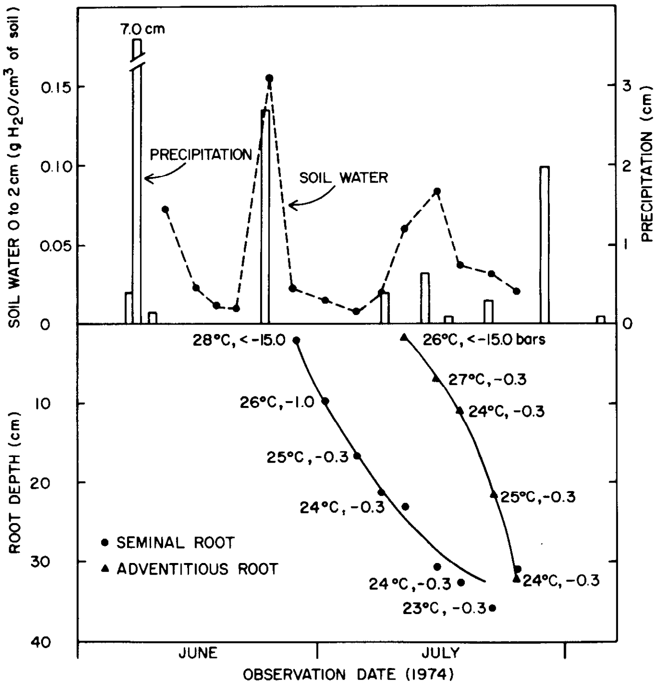

Fig. 5. *Precipitation, soil water content in the 0- to 2-cm zone, temperature and water potential in the zone of root elongation, and average depth of penetration of seminal primary roots and adventitious roots of blue grama seedlings that emerged June 26, 1974, from a late spring planting.*

Late Spring Planting—1974

Seminal Root Growth

Blue grama was seeded on June 11, 1974, 3 days after a 7.0 cm rain. Seedlings emerged on June 26 following a 2.7 cm rainfall on June 24, which provided favorable moisture conditions at the soil surface (Fig. 5). Total water in the 0- to 40-cm zone at time of emergence was 5.2 cm, indicating that this part of the profile was near -0.3 bars. Seedlings emerged after a single rainstorm because a straw mulch had been applied after planting to conserve water at the soil surface. The mulch was removed from plots after emergence.

An average water potential of less than -15 bars in the zone of seminal root elongation on June 27 indicated the need for rapid extension of the root during early stages of seedling growth (Fig. 5). The method we used did not permit the determination of water potential at the root tip, but only indicated the average water potential of the zone through which the root had elongated during the observation period. Therefore, part of the drying of soil occurred after the root had extended through the sampling zone. Nevertheless, the data suggested that during initial stages of growth the soil surface dried almost as rapidly as the root penetrated the soil. At later stages of growth, water potential in the zone of seminal root elongation remained at about -0.3 bars. Temperature in the zone of root elongation varied from 28 to 23°C. Seminal roots elongated at an average rate of 1.2 cm $\cdot$ day^{-1}. They reached an average depth of 33 cm during the period of study and attained average total lengths (main axis and all branches) of 155 cm. About 80% of the total length occurred in the upper 20 cm of soil.

Adventitious Root Growth

Seedlings initiated adventitious roots following rainfall of 0.4 cm on July 10 and 0.7 cm on July 14, which was accompanied by a period of cloudy weather (Fig. 5). Thus adventitious roots were initiated 15 days after emergence when average number of tillers per seedling was 0.4 and leaf blade area was 0.43 cm^2. The average number of adventitious roots per seedling increased from 0.7 on July 11 to 2.0 on July 15. Only July 11, the average water potential in the zone of adventitious root elongation was less than -15 bars. On subsequent sampling dates, the water potential in zones of adventitious root elongation was -0.3 bars and the temperature in zones of elongation varied from 26 to 23°C. Adventitious roots elongated at an average rate of 2.3 cm $\cdot$ day^{-1}.

Analysis of Seedling Growth

High rates of adventitious root elongation in 1974 were associated with high net assimilation rates, which were calculated from values of leaf area and total seedling weight. These rates were 3.0±0.6 and 2.6±0.7 mg biomass $\cdot$ cm^{-2} leaf area $\cdot$ day^{-1} during the first 2-week period and second 2-week period of seedling growth, respectively.

Vigorous stands developed from the late spring planting in 1974.

Late Summer Planting—1974

Seminal Root Growth

Blue grama seeds were again planted in mid-August. The single rainfall event of 1.2 cm on August 22 caused emergence 2 days later because a straw mulch covering the plots conserved water at the soil surface. The mulch was removed after seedlings had emerged. Total water in the 0- to 40-cm zone of the profile at time of emergence was 3.8 cm, which was 1.7 cm less than the amount needed to moisten that part of the profile to a water potential of -0.3 bars.

On August 29, an average water potential of -7.6 bars in the zone of root elongation indicated that the soil had dried at a rate almost equal to the rate of root extension (Fig. not shown). On subsequent sampling dates, water potential in zones of seminal root elongation varied from -1.8 to -3.4 bars and temperature varied from 25 to 17°C. Seminal roots penetrated to an average depth of 17 cm in 30 days, with an average rate of elongation of 0.56 cm $\cdot$ day^{-1}. Seedlings attained total seminal root lengths (main axis and all branches) of 37 cm.

Analysis of Seedling Growth

Net assimilation rates were calculated from values of leaf area and seedling dry weight. The rates were 1.6±0.6 and 1.1±0.6 mg biomass $\cdot$ cm^{-2} leaf area $\cdot$ day^{-1} during the first 2-week period and second 2-week period of seedling growth, respectively. Limited water in the soil profile probably contributed to low net assimilation rates.

Failure to Develop Adventitious Roots

Rainfall of 0.6 cm on September 2, 0.9 cm on September 12, and 1.7 cm on October 12 did not promote the development of adventitious roots. Rapid drying of the soil surface and decreasing temperatures during September and October probably accounted for the failure to develop adventitious roots. These seedlings developed 1.2 tillers and a leaf area of only 0.4 cm^2; therefore, it is probable that seedlings had attained only a limited physiological capacity for adventitious root development. None of the seedlings survived through the 1974-1975 winter.

Discussion

Rates of blue grama seminal root elongation (1.1 to 1.2 cm $\cdot$ day^{-1}) under favorable soil moisture and temperature conditions on the Central Plains were similar to the rate observed in the greenhouse (1.0 cm $\cdot$ day^{-1}) under similar conditions (Wilson and Briske 1978). However, seedlings attained total seminal root lengths (main axis and all branches) of only 195 cm on the Central Plains as compared with 840 cm in the greenhouse.

Under favorable conditions of soil moisture (about -0.3 bars) and temperature (24 to 27°C) on the Central Plains, adventitious roots of blue grama elongated at an average rate of 2.3 cm $\cdot$ day^{-1} (Fig. 5), which is the same rate observed in a plant growth chamber at 25°C (Briske and Wilson 1977).

A controlled environment study indicated that a soil water potential of -50 bars, or greater, was required for adequate growth of adventitious roots when the seminal root was maintained in moist soil (-0.3 bars) and the soil surrounding the seedling crown was independently controlled at various water potentials (Briske and Wilson 1978). These results agree with observations on the Central Plains indicating that adventitious roots fail to develop when the soil surface is dry (Fig. 1 and 5).

Brown and Trlica (1977) found rates of net photosynthesis of 3.7 and 1.4 mg carbohydrate $\cdot$ cm^{-2} leaf area $\cdot$ day^{-1} in June and September 1972, respectively, in native blue grama swards at CPER. These investigators concluded that productivity was relatively low in September because of low irradiance and shortened day length. In comparison, our estimates of net assimilation rate were 2.6 to 3.0 and 1.1 to 1.6 mg biomass $\cdot$ cm^{-2} leaf area $\cdot$ day^{-1} in early and late summer of 1974, respectively. We concluded that limited soil moisture, as well as low irradiance and short day length, reduced net assimilation rates in late summer.

Observations on the Central Plains indicate that blue grama seedlings may experience four critical periods for survival when they depend entirely on water stored in the soil profile. The first critical period is during initial growth of the seminal root. During this period the soil may dry almost as rapidly as the seminal root extends. When the seminal root is killed by drought, there is little opportunity for survival, because blue grama seedlings lack seminal lateral roots (Hyder 1974). During the period, seedlings do not have the capacity to develop adventitious roots.

The second critical period begins about 6 weeks after emergence when the seminal root stops elongating and the drying soil front gets close to the maximum depth of rooting. The maximum capacity for water uptake by the average seedling when the entire seminal root is growing in moist soil is about 3 to 4 g per day (Wilson and Sarles 1978). In that situation, water uptake is probably limited by the small size and number of xylem vessels in the subcoleoptile internode as well as the total extension of the root (Wilson et al. 1976). However, when seedlings on the Central Plains depend entirely on water stored in the profile, uptake probably is limited also by the water content of soil and the volume of soil into which the seminal root extends during each day (Table 1).

Blue grama seedlings may die during a third critical period even though the entire seminal root is growing in moist soil (approximately -0.3 bars). This study suggests that death under these conditions does not result from an inherent inability of the seminal root to extend into the soil profile. Neither does death result from an inherent limit to the longevity of the seminal root (van der Sluijs and Hyder 1974). However, death may result from the desiccation of seedlings during a rapid increase in transpirational stress (Wilson et al. 1976; Wilson and Sarles 1978). Because the *Gramineae* lack secondary growth of vascular tissues, the seminal root of the blue grama reaches the upper limit of its capacity for water uptake soon after emergence. With a given capacity for water uptake and a given transpirational stress, there is an upper limit to the amount of leaf tissue that can be kept alive. When seedlings reach these limits, hot, dry winds may cause either seedling death or a reduction in green leaf area because the rate of water loss from leaves exceeds the rate of water uptake by the seminal root.

The fourth critical period occurs when adventitious roots begin to develop. Unless a moist soil surface is maintained for 2 to 4 days, the soil surface may dry more rapidly than roots extend. Adequate moisture is more critical for adventitious root development, in some respects, than for germination, because seedling crowns (from which adventitious roots arise) are located at or very near the soil surface rather than at the depth of planting.

This study, along with controlled environment studies (Briske and Wilson 1977; Briske and Wilson 1978), suggests minimum requirements for the consistent establishment of blue grama on the Central Plains. These requirements include average soil temperatures above 15°C, two properly spaced 2- to 4-day periods with a continuously moist soil surface (one for emergence and one for adventitious root development), and a soil water potential of about -0.3 bars in the 0 to 40- cm zone at the time of emergence. Fults (1944) also emphasized the need for available water in the soil profile (0 to 60 cm) at planting time to ensure establishment of warm-season grasses on the Central Plains.

Improving drought resistance of seedlings might also reduce planting failures. Important drought resistance characteristics that may contribute to growth and survival of blue grama seedlings are as follows: (1) rapid extension of the seminal root, (2) deep penetration of the seminal root into the soil profile, (3) high capacity for water uptake by the seminal root, (4) high resistance to water loss from leaves (Wilson and Sarles 1978), and (5) high capacity for development of adventitious roots (Briske and Wilson 1977).

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