Root dynamics of *Bouteloua gracilis* during short-term recovery from drought

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Abstract

1 The ability of drought-stressed *Bouteloua gracilis* H.B.K. Lag. ex Steud. to respond rapidly to a small rainfall event with increases in leaf water potential and leaf conductance directed our attention to the role of the roots in these responses. Our first objective was to determine whether new root growth was required to restore the water status to that of a non-stressed plant, following a small rainfall event. The results indicated that surviving roots were able to absorb water at approximately 40% of the rate of new roots, which was sufficient to restore non-stressed leaf water potentials within one day of watering.

2 The second objective was to estimate the rate and amount of new root growth following simulated rainfall events. New root growth occurred approximately 40 h after watering. New roots never accounted for more than 15% of total root length but they made possible the continued response to increased water availability.

3 The third objective was to evaluate the importance of previous water stress in the response of *Bouteloua gracilis* to watering. The response of leaf water potential was influenced by previous water stress as well as by the amount of water added. However, the response of root growth was independent of water stress when 15 mm of water was added and dependent upon water stress in the case of the addition of only 5 mm.

4 A simulation analysis of potential carbon gain, as a result of *Bouteloua gracilis* responding to a 5-mm rainfall event, suggested that the cost of producing new roots was less than the gain.
Key-words: Drought, *Bouteloua*, root growth, steppe region, C_4

Introduction

An important characteristic of plants inhabiting arid and semi-arid regions is their ability to survive dry periods yet to respond to increases in soil water (Orians & Solbrig, 1977; Westoby, 1980). Populations that have the capability to respond rapidly to an increase in soil water should have an advantage in acquiring both water and mineral nutrients.

Bouteloua gracilis H.B.K. Lag. ex Steud. is the dominant plant species throughout the shortgrass steppe region of the Great Plains of North America. The growth of this C_4 grass has been reported to follow closely changes in soil water availability (Bement, 1974). Sala & Lauenroth (1982) found that *Bouteloua gracilis* responded very rapidly to a small (5-mm) rainfall event following a period of drought. Plant water potential and leaf conductance increased during the day following the simulated rainfall. The results of this experiment raised the following questions about the role of root growth in the short-term recovery of *Bouteloua gracilis* from drought. What are the relative roles of surviving and new roots in the recovery process? How do the severity of the drought and the amount of water added control the roles of surviving and new roots in the recovery process?

We designed an experiment to provide answers to these questions. The hypothesis we wished to address was that evolution of *Bouteloua gracilis* in the semi-arid environment of the shortgrass steppe has presumably resulted in adaptations to the variability in the availability of soil water. It seems reasonable to assume that these adaptations have been constrained by a cost-benefit function (Orians & Solbrig, 1977). From this hypothesis and previous information about the response of *Bouteloua gracilis* to small rainfall events (Sala &

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Lauenroth, 1982), the following testable deductions were derived:

(1) The rapid response of leaf water potential following a small (5-mm) rainfall event will be the result of water absorption by surviving roots.

(2) The response of leaf water potential following a large (>5-mm) rainfall event will be the result of water absorbtion by both surviving and new roots.

(3) The response of *Bouteloua gracilis* to both large and small rainfall events will decrease as the severity of the drought increases.

Methods and materials

The experiment consisted of a factorial combination of two sizes of simulated rainfall events, 5 and 15 mm, and two levels of severity of drought. The 5- and 15-mm additions of water were chosen to represent a small and a large rainfall event for the shortgrass steppe (Sala & Lauenroth, 1982). The level of severity of the preceding drought was represented by $-3\cdot5$ and $-5\cdot0$ MPa midday leaf water potentials. These values were found to represent points at which the slope of the leaf water potential versus time curve changed sharply during a drought period (Sala *et al.*, 1981).

All experiments were carried out in a growth chamber that was programmed to simulate average temperature, light and humidity conditions characteristic of a shortgrass site in midsummer (Rasmussen, Bertolin & Almeyda, 1971). Daily temperatures alternated between 30 °C at midday and 18 °C at dawn, with a gradation of temperature through the day. Relative humidity ranged between 50% at dawn to 20% at midday. The daylight period was 16 h with maximum irradiance for a duration of 12 h.

Soil and sods, consisting largely of *B. gracilis*, were collected from the Central Plains Experimental Range, in north-eastern Colorado, USA. The plants were washed free of soil and planted in sieved field soil in PVC containers that were 30 cm in height and 10 cm in diameter.

Sixteen plants of *B. gracilis* were established by maintaining the soil at field capacity for 2 weeks, followed by a 4-week period with watering timed to simulate natural conditions. The soil was re-wetted only after leaf water potential decreased to midday readings of $-2\cdot0$ to $-2\cdot5$ MPa. This level of water stress corresponded to soil water potentials in the top 10 cm of soil of approximately $-3\cdot0$ to $-4\cdot0$ MPa. New adventitious roots developed in alternately dry and wet soil, which is a simulation of natural conditions intended to eliminate

possible differences in suberin formation that may result from root development in uniformly moist soil.

Selected response variables were leaf water potential, soil water potential, root length, number of new root tips and water-absorption rate. Leaf water potential was measured on one leaf per plant at dawn and midday the day before watering and each day afterwards until it decreased to $-3\cdot5$ or $-5\cdot0$ MPa. Plants were watered at 1500 h to approximate the timing of late afternoon thundershowers characteristic of the shortgrass region. Water was applied via a syringe from above the leaf level, thereby allowing canopy interception. Leaf water potential was estimated by the pressure chamber method (Scholander *et al.*, 1965).

Soil water potential was estimated from gravimetric measurements of soil water content and a function relating water potential to water content. Two samples were taken from each of the four replicates per treatment. Cores were removed from the top 12 cm of soil for treatments watered with 15 mm and from the top 5 cm of soil for the 5-mm watering teatments. These represented the depths of wetting by each of the simulated rainfall events.

Estimates of root length were made with the line intercept method of Newman (1966). A soil core was removed from each container with an 8-mm-diameter cork bore to depths of 5 and 12 cm for the 5- and 15-mm watering treatments, respectively. Roots were classified into three groups and length estimates made for each. The oldest roots were recognized by their dark brown appearance; the young roots were characterized by a white to yellow appearance; and the new roots were identifiable by their white, translucent appearance. The number of new, growing root tips present in each soil core was counted in five randomly selected microscopic fields. New tips were classified by their turgid, translucent appearance and by their lack of root hairs.

Water uptake was estimated for the surviving roots immediately before the simulated rainfall and during the following 2 days. Measurements of water uptake for new, growing root segments took place on plants that were first subjected to a drying period equivalent to $-5\cdot0$ MPa midday leaf water potential and then well watered to ensure new root growth. Plants used for the absorption measurements were grown in containers slit down their length. It was then possible to open partially the side of the container, tease free an adventitious root near the periphery and leave the remainder of the root system undisturbed. The test root was selected for the presence of lateral roots, one of

which was then used for the absorption measurement. The measurements of water absorption were performed with a micropotometer modeled after the design described by Clarkson & Sanderson (1971). The instrument consisted of a 3·5-mm-diameter polyethylene tubing connected to a 0·1-ml-capacity pipette on one end and sealed on the other end. A small slit was made transversely in the polyethylene tubing. A lateral root was then placed into the slit such that it transversed the inside diameter of the tube. The opening was sealed with a silicone compound. Deionized water was introduced with a syringe. The water level was adjusted in the pipette and the absorption of water by the sealed root segment was measured from the drop in the water level. Two root segments were sealed in the tubing. Absorption was calculated as the amount of water taken up over a known time interval. The surface area of the root segment was determined from the diameter and length of the sealed segment.

Results

The response of leaf water potential to watering was rapid regardless of severity of the drought or amount of water added (Fig. 1). The magnitude of the increase in leaf water potential the day following watering was affected by both the severity of the previous drought and the amount of water added. Plants receiving 15 mm of water or 5 mm of water and −3·5 MPa previous stress reached a similar maximum leaf water potential of approximately −1·5 MPa pre-dawn and −2·5 MPa midday. This is very similar to the response observed in the field (Sala & Lauenroth, 1982). In contrast to this, plants receiving 5 mm of water and −5·0 MPa previous stress did not recover to the same degree. An additional influence of the amount of water added is clear in the duration of the increases in leaf water potential. The plants receiving 5 mm of water returned to pre-watering conditions approximately 2 days earlier than the plants receiving 15 mm for both the −3·5 and −5·0 MPa treatments.

Soil water potential at 5 cm depth previous to watering was −5·0 MPa for the two −3·5 MPa leaf water potential groups and −9·0 and −10·0 MPa for the two −5·0 MPa leaf water potential groups (Fig. 2). Following watering, soil water potentials at 5 cm depth were zero for all treatments. No differences in soil water potentials were observed on the second day after watering, but on the third

and subsequent days, the −5·0-MPa/5-mm treatment containers had a lower average soil water potential than the other three treatments. Depth of penetration of water depends upon the previous soil water status and the amount of water added (Hanks & Ashcroft, 1980). For the treatment in which water should have penetrated the least (−5·0 MPa/5 mm), the rate of water loss was the highest. For this treatment, evaporation was likely the major pathway for water loss.

Microscopic evaluation of the number of new growing root tips indicated that none were present in any of the four treatments on the day following watering (Table 1). By the second day after watering, three of the four treatments had new root tips present. The −5·0-MPa/5-mm treatment plants showed no indication of new root growth on any of the 5 days following watering. Among the three treatments with new root growth, there were no differences in either the rate of appearance of new tips or in the total number of root tips per unit of biomass.

The percentage of the total root length contributed by new roots was in agreement with the
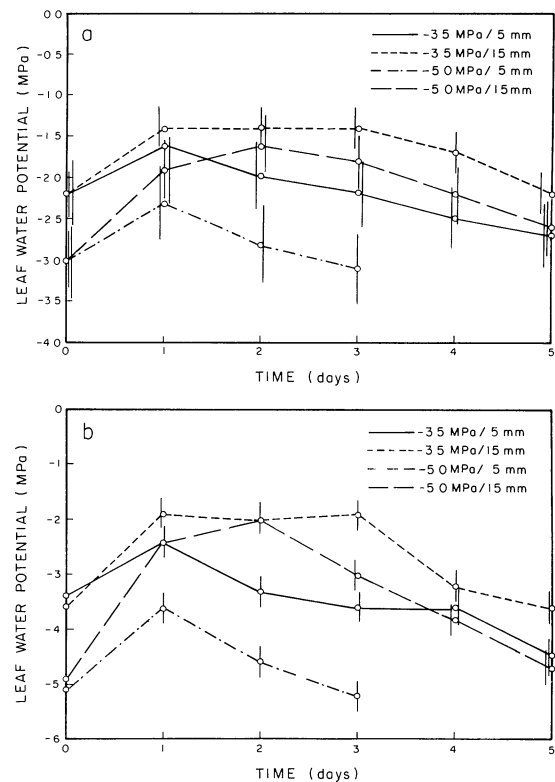

Fig. 1. Daily values of leaf water potential for two levels of previous drought and two sizes of simulated rainfall events before watering and after watering until they reached the pre-watering status (a) pre-dawn leaf water potential, (b) midday leaf water potential.

results for root tips (Table 2). The percentage of total root length contributed by new roots was zero on both the day of watering and the first day afterwards. No new root growth was detected for the $-5 \cdot 0$-MPa/5-mm treatment. New roots were observed for the other three treatments on the second day following watering and on each of the following 3 days.

The absorption of water by new roots was $2 \cdot 3$–$3 \cdot 6$ times greater than the absorption rates by the surviving root segments measured during the day following the rainfall simulation (Table 3). All surviving roots displayed the ability to absorb water both before and after the additions of water. The mean absorption rate by surviving roots was $0 \cdot 53 \, \text{ml} \, \text{cm}^{-2} \text{h}^{-1}$. The absorption of water by
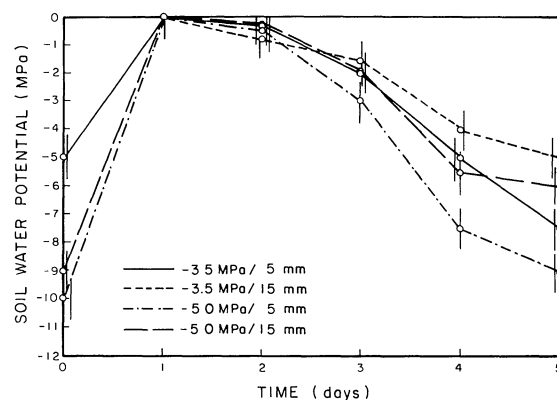

Fig. 2. Daily values of soil water potential for two levels of previous drought and two sizes of simulated rainfall events before and after watering.

Table 1. Number of new growing root tips per microscopic field ($1 \cdot 4$ cm in diameter) adjusted for differences in root biomass for two levels of drought and two sizes of rainfall events.

Days after watering	Treatment			
	$-3 \cdot 5 \, \text{MPa}/5 \, \text{mm}$	$-3 \cdot 5 \, \text{MPa}/15 \, \text{mm}$	$-5 \cdot 0 \, \text{MPa}/5 \, \text{mm}$	$-5 \cdot 0 \, \text{MPa}/15 \, \text{mm}$
1	0	0	0	0
2	4	2	0	1
3	6	5	0	8
4	7	3	0	5
5	6	5	0	6

Table 2. Percentage of root length for three root classes following simulated rainfall events. Root classes: main refers to main adventitious roots with diameters of approximately $0 \cdot 5$ mm, laterals were the fine suberized elements with diameters of approximately $0 \cdot 1$ mm and new were the new laterals initiated after watering.

Days after watering	Treatment											
	$-3 \cdot 5 \, \text{MPa}/5 \, \text{mm}$			$-3 \cdot 5 \, \text{MPa}/15 \, \text{mm}$			$-5 \cdot 0 \, \text{MPa}/5 \, \text{mm}$			$-5 \cdot 0 \, \text{MPa}/15 \, \text{mm}$		
	new	lateral	main	new	lateral	main	new	lateral	main	new	lateral	main
0	0	94	6	0	94	9	0	91	9	0	91	9
1	0	91	9	0	93	7	0	85	15	0	96	4
2	2	90	8	4	89	7	0	92	8	2	96	2
3	7	90	3	9	88	3	0	97	3	15	78	7
4	8	89	3	8	83	9	0	89	11	12	85	3
5	8	88	4	12	85	3	0	97	3	15	81	4

Table 3. Rate of water absorption (ml $\text{cm}^{-2} \text{h}^{-1}$) ($\bar{X} \pm \text{SE}$) for surviving roots subjected to two levels of drought and two sizes of rainfall events, and for new growing roots.

	Surviving roots				New roots
	$-3 \cdot 5 \, \text{MPa}/5 \, \text{mm}$	$-3 \cdot 5 \, \text{MPa}/15 \, \text{mm}$	$-5 \cdot 0 \, \text{MPa}/5 \, \text{mm}$	$-5 \cdot 0 \, \text{MPa}/15 \, \text{mm}$	
Before watering	$0 \cdot 40 \pm 0 \cdot 07$	$0 \cdot 45 \pm 0 \cdot 04$	$0 \cdot 20 \pm 0$	$0 \cdot 35 \pm 0 \cdot 04$	
After watering	$0 \cdot 60 \pm 0 \cdot 04$	$0 \cdot 64 \pm 0 \cdot 05$	$0 \cdot 47 \pm 0 \cdot 03$	$0 \cdot 41 \pm 0 \cdot 03$	$1 \cdot 47 \pm 0 \cdot 07$

surviving roots was statistically indistinguishable for the four treatments both before and after watering.

Discussion

Sala & Lauenroth (1982) reported a field experiment in which *Bouteloua gracilis*, with midday leaf water potentials as low as $-6 \cdot 0$ MPa, responded to 5-mm simulated rainfall with increased leaf water potential within 12 h. Forty-eight hours after watering, pre-dawn and midday leaf water potentials had decreased to the pre-watered values. The recovery rates of leaf water potential reported by Sala & Lauenroth (1982) agree with our measured increases in leaf water potential for container-grown *Bouteloua gracilis* for both drought severity treatments (Fig. 1).

Our results for both the appearance of new roots (Tables 1 and 2) and water absorbtion rates (Table 3) support the deduction that the rapid response of leaf water potential following a small rainfall event is the result of water uptake by surviving roots. No new roots were found before the second day following watering for any combination of previous water stress and simulated rainfall event. Ares (1976) observed that new roots of *Bouteloua gracilis* slowed their growth and died when the soil water potential decreased below $-4 \cdot 0$ MPa. The measured ratio between the absorption rate by new and surviving roots for *Bouteloua gracilis* of $2 \cdot 8$:1 closely corresponds to previous comparisons. Working with barley, Clarkson, Robards & Sanderson (1971) calculated a new:suberized ratio of $2 \cdot 2$:1, Graham, Clarkson & Sanderson (1974) found a ratio of 5:1, and Clarkson & Sanderson (1974) reported a 3:1 ratio. In each case, these results were obtained from absorption measurements made on suberized roots but not on roots subjected to low soil water potentials before measurement. The surviving laterals of *Bouteloua gracilis* were able to take up water under drought stress with a comparable capability of the non-stressed suberized barley roots.

The rate of water uptake by the surviving roots of *Bouteloua gracilis* was sufficient to increase the leaf water potential within 24 h. Absorption by surviving roots suggests that water loss from the root into dry soil is possible when a reversed gradient occurs in some portions of the soil (Dirksen & Raats, 1985). The soil and root properties that affect the flow of water into the root should also affect water movement out of the roots. Williams (1969), Huck, Klepper & Taylor (1970), Cole & Alston (1974), Hansen (1974) and Drew (1979) discussed the importance of water movement in maintaining a continuous water film between the root surface and soil particles. When the root contracts upon desiccation, the break in contact with the soil is a major limiting step in water movement into the root. Similarly, break in contact between the root surface and soil particles would retard the outward flow of water.

Cole & Alston (1974) observed a 60% reduction in wheat root diameters with a decrease in water potential. At the end of the drought period and before watering, the surviving lateral roots of *Bouteloua gracilis* were 20–40% smaller in diameter than the new root tips. The diameter of these roots did not increase after watering, suggesting that Beckel's (1956) observation on cortical collapse is applicable.

A few of the surviving roots were not contracted and these were covered with root hairs with soil particles adhering to their surfaces. By contrast, soil was easily washed from the surface of contracted roots. This indicated a break between the root surface and soil, as the root diameter shrunk in response to desiccation. The adherence of soil particles to the laterals suggests that the cortex had not collapsed and that the root hairs on these root segments were still functional in maintaining contact between the root and the soil.

Upon watering, a supply of water comes into contact with at least part of the root surface. As the water immediately in contact with the root surface is depleted by root uptake, the rate of absorption will decline. The water-absorption ability of a suberized, non-growing root network is limited. Greater root length in the rewetted soil zone and new root growth should extend the duration of absorption of the water supplied by a rainfall event.

The results for the appearance of new roots (Tables 1 and 2) and their absorptive capacity (Table 3) support our second deduction that the response following a large rainfall event will be the result of water absorption by both surviving and new roots. Additionally, they point out a difficulty associated with the deduction. Our arbitrary division between large and small rainfall events is not the best basis for explaining when new root growth should become important in the response of *B. gracilis* to an increase in soil water availability. Whether or not new root growth will be involved in the response to increased water availability will depend upon the duration of the increase in soil water rather than simply the amount of water added.

The absorptive ability of new roots and the extent of new root growth following soil water replenishment combine to suggest that the root system, shortly after a rainfall event, can potentially absorb water at rates higher than the surviving root network alone. The surviving roots will not decrease during the recovery but can be expected to supply a fixed absorptive surface. The extension of new roots will increase the surface area of functional roots and, based on the micropotometer results, will absorb water at rates higher than the suberized roots. The potential increase in water absorption by new root growth was calculated by combining information about the length of new roots (Table 2) with their absorption capacity (Table 3). These calculations indicated that new root growth contributed 10–20% of the potential water absorption over the 5 day recovery period.

Caldwell (1976) indicated that root extension was primarily a means to ensure root contact with water in a soil in which water was not homogeneously distributed. Water absorption by roots results in the development of gradients in the soil immediately surrounding the roots; therefore, the actual water absorption by new roots may have been larger than the 10–20% that we calculated. The surviving roots were capable of absorbing water to re-establish non-stressed leaf water potentials and could hypothetically maintain this level of water uptake as long as the roots were in contact with soil with high water content. A stationary root network does not maintain contact with soil with a decreasing water content.

The third deduction suggested that the severity of the drought period would have an influence on the ability of *Bouteloua gracilis* to respond to an increase in water availability. This deduction was only partially supported by our results. The response of leaf water potential to the addition of either 5 or 15 mm of water was rapid regardless of the severity of the previous water stress (Fig. 1). The magnitude of the increase in leaf water potential was influenced by the previous stress. Plants whose roots were subjected to $-10\cdot0$ MPa soil water potential and received only 5 mm of water did not recover to the same degree as plants receiving 15 mm of water or plants subjected to higher soil water potentials.

The severity of the previous water stress had no effect on root growth when 15 mm of water was added. The response in both the number of new root tips and the percentage of the total root length contributed by new roots (Tables 1 and 2) were the same for the $-3\cdot5$ MPa and $-5\cdot0$ MPa treatments.

The two 5-mm treatments provided the only support for deduction (3). The $-3\cdot5$-MPa/5-mm treatment resulted in the production of new roots by the second day following watering. The amount and timing of new root growth was similar to the 15-mm treatments (Tables 1 and 2). The $-5\cdot0$-MPa/ 5-mm treatment resulted in no root growth following watering. The explanation for the lack of root growth for this treatment is probably related to the very dry soil conditions in the top 5 cm of the containers for this treatment (Fig. 2). Roots exposed to $-9\cdot0$ to $-10\cdot0$ MPa soil water potential may have been unable to respond to increased water availability by producing new roots in only 5 days. The physiological changes induced by such dry conditions may require a much longer recovery period. If this is correct, it means that the new roots observed for the $-5\cdot0$-MPa/15-mm treatment occurred below 5 cm in the soil.

Although not an explicit part of the experiment, the analysis of this problem is not complete without considering the following question. Does the carbon gain that results from the response of *Bouteloua gracilis* to 5 mm of rainfall offset the cost of new root growth? To answer this question, carbon gain was calculated using the net photosynthesis model of Detling, Parton & Hunt (1978), which utilizes irradiance, canopy temperature and soil-water potential in the 0–10-cm layer. Simulations were run with environmental data corresponding to conditions in the growth chamber and assuming a leaf-area index of 0·4 (Knight, 1973). Assuming that in the absence of the 5 mm of simulated rainfall, net photosynthesis remains at the pre-watering level over the 6 days of the experiment (the day of watering and the subsequent 5 days), the model predicted a gain equivalent to $3\cdot8$ gC/m^2 over the 6 days. Plants receiving 5 mm of rainfall over the same time period gained the equivalent of $11\cdot6$ gC/m^2.

At the end of the experiment, root biomass in the top 5 cm of the containers was equivalent to $24\cdot8$ gC/m^2. If we assume that the 8% of root length contributed by new roots was equivalent to 8% of the root carbon, then approximately $2\cdot0$ gC/m^2 was incorporated into new root growth.

The 5 mm of simulated rainfall that was applied when midday leaf-water potential was $-3\cdot5$ MPa and soil-water potential was $-5\cdot0$ MPa resulted in a gain, over the unwatered plants, of $7\cdot8$ gC/m^2. New root growth accounted for $2\cdot0$ gC/m^2, leaving a net gain of $5\cdot8$ gC/m^2, or $12\cdot8$ g/m^2 biomass. This analysis provides evidence of the potential for carbon gain by *Bouteloua gracilis* as a result of responding to a 5-mm rainfall event, it does not

provide answers to the question of the carbon gain that would result in the absence of new root growth.

Conclusions

Bouteloua gracilis responded rapidly by increasing leaf water potential following rainfall regardless of the previous drought stress or the size of the simulated rainfall event. The initial rapid response to addition of water following a drought was entirely the result of uptake by surviving roots.

The continued response to increased water availability was made possible by the appearance of new roots on the second day following watering. This new root growth increased the absorption rate and expanded the root system, which increased contact with wet soil.

Previous drought was an important control on the response of *B. gracilis* to simulated rainfall only under the most extreme conditions. We suggested that the very low soil water potential to which the roots in the -5.0 MPa treatments were subjected prevented their rapid response to the increase in water availability. In all other cases, the responses of leaf water potential and the timing and amount of root growth were indistinguishable.

The cost, in terms of carbon, of producing new roots in response to a 5-mm rainfall event was more than compensated for by the gain over the 6-day response period.

Acknowledgments

References

Ares, J. (1976) Dynamics of the root system of blue grama. *Journal of Range Management,* **29,** 209–213.
Beckel, D.K.B. (1956) Cortical disintegration in the roots of *Bouteloua gracilis* (H.B.K.) Lag. *New Phytologist,* **55,** 183–190.
Bement, R.E. (1974) Strategies used in managing blue grama range on the Central Great Plains. In *Plant Morphogenesis for Scientific Management of Range Resources* (ed. K.W. Kreitlow & R.H. Hart), pp. 160–166. United States Department of Agriculture Miscellaneous Publication Number 1271. Washington, D.C.
Caldwell, M.M. (1976) Root extension and water absorption. In *Water and Plant Life* (ed. O.L. Lange, L. Kappen & E.D. Schulze), pp. 63–85. Springer-Verlag, Berlin.
Clarkson, D.T. & Sanderson, J. (1971) *Relationship Between the Anatomy of Cereal Roots and the Absorption of Nutrients and Water.* Agricultural Resource Council, Letcombe Laboratory, Report 1970:16–25.
Clarkson, D.T. & Sanderson, J. (1974) The endodermis and its development in barley roots as related to radial migration of ions and water. In *Structure and Function of Primary Root Tissues* (ed. J. Kolek), pp. 87–100. Slovak Academy of Sciences, Bratislava, Czechoslovakia.
Clarkson, D.T., Robards, A.W. & Sanderson, J. (1971) The tertiary endodermis in barley roots: Fine structure in relation to radial transport of ions and water. *Planta,* **96,** 292–305.
Cole, P.J. & Alston, A.M. (1974) Effects of transient dehydration on absorption of chloride by wheat roots. *Plant and Soil,* **40,** 243–247.
Detling, J.K., Parton, W.J. & Hunt, H.W. (1978) An empirical model for estimating CO_2 exchange of *Bouteloua gracilis* (H.B.K.) Lag. in the shortgrass prairie. *Oecologia,* **33,** 137–147.
Dirksen, C. & Raats, P.A.L. (1985) Water uptake and release by alfalfa roots. *Agronomy Journal,* **77,** 621–626.
Drew, M.C. (1979) Root development and activities. In *Arid-land Ecosystems: Their Structure, Functioning and Management. Vol. 1* (ed. D.W. Goodall & R.A. Perry), pp. 573–606. Cambridge University Press, Cambridge.
Graham, J., Clarkson, D.T. & Sanderson, J. (1974) *Water Uptake by the Roots of Marrow and Barley Plants.* Agricultural Resource Council, Letcombe Laboratory, Report 1937:9–12.
Hanks, R.J. & Ashcroft, E.L. (1980) *Applied Soil Physics: Soil Water and Temperature Applications.* Springer-Verlag, Berlin.
Hansen, G.K. (1974) Resistance to water transport in soil and young wheat plants. *Acta Agriculturae Scandinavica Sweden,* **24,** 37–48.
Huck, M.G., Klepper, B. & Taylor, H.M. (1970) Diurnal variations in root diameter. *Plant Physiology,* **45,** 529–530.
Knight, D.H. (1973) Leaf area dynamics of a shortgrass prairie in Colorado. *Ecology,* **54,** 891–896.
Newman, E.I. (1966) A method of estimating the total length of root in a sample. *Journal of Applied Ecology,* **3,** 139–145.
Orians, G.H. & Solbrig, O.T. (1977) A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *American Naturalist,* **111,** 677–690.
Rasmussen, J.L., Bertolin, G. & Almeyda, G.F. (1971) *Grassland Climatology of the Pawnee Grassland.* US IPB Technical Report Number 127. Fort Collins.
Sala, O.E. & Lauenroth, W.K. (1982) Small rainfall events: An ecological role in semi-arid regions. *Oecologia,* **53,** 301–304.
Sala, E.E., Lauenroth, W.K., Parton, W.J. & Trlica, M.J. (1981) Water status of soil and vegetation in a shortgrass steppe. *Oecologia,* **48,** 327–331.

Scholander, P.R., Hammel, H.T., Bradstreet, E.O. & Hemmingsen, E.A. (1965) Sap pressure in vascular plants. *Science,* **148,** 339–346.

Westoby, M. (1980) Elements of a theory of vegetation dynamics in arid rangelands. *Israel Journal of Botany,* **28,** 169–194.

Williams, T.E. (1969) Root activity of perennial grass swards. In *Root Growth* (ed. W.J. Whittington), pp. 270–277. Butterworths, London.

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