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Small Rainfall Events: An Ecological Role in Semiarid Regions

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Summary. Small precipitation events account for a large proportion of the precipitation received in semiarid regions, and their potential ecological importance has previously been ignored. We investigated the effect of a small rainfall event (5 mm) upon *Bouteloua gracilis*, the dominant grass species of the central and southern Great Plains of North America. An effect of a small event on leaf water potential and leaf conductance to water vapor was observed in less than 12 h and lasted for up to two days.

The remarkable short response time of *Bouteloua gracilis* to a rainfall stimulus enables this species to utilize small events and, therefore, may influence its persistence as a dominant species in the steppe region.

We proposed response times to be one of the major species characteristics determining capacity for utilizing different portions of the water resource of the region. We suggest that small precipitation events are ecologically significant and a qualitatively distinct resource for ecosystems in semiarid regions.

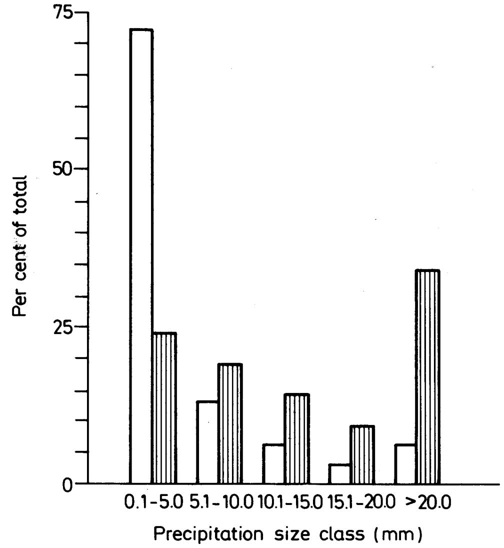

Fig. 1. Distribution of precipitation events by size class during the growing season at a shortgrass steppe site in north-central Colorado; ☐ = frequency, ▥ = amount contributed to seasonal precipitation

Introduction

Precipitation in semiarid regions is widely recognized as being low and highly variable (Noy-Meir 1973; Bailey 1979). A less clearly appreciated characteristic is the important contribution of small events to both the total incidence and total amount of precipitation. Smith and Schreiber (1974) analyzed long-term daily rainfall records from three stations in semiarid regions of Arizona and found that approximately 80% of the rainfall events were smaller than 10 mm. The analysis of 10 years of precipitation records from our study site in the semiarid Great Plains of North America (Fig. 1) illustrated that events of 10 mm or less accounted for 41% of the growing season rainfall and 83% of the rainfall events. Precipitation events of 5 mm or less contributed 25% of the total rainfall received during the growing season and comprised 70% of the events.

Traditional analyses of the behavior of semiarid grasslands has ignored the potential ecological importance of small rainfall events. Currently held ideas of "effective" precipitation in dry environments regard events of less than 8–10 mm as ecologically unimportant (Coupland 1950; Paulsen and Ares 1962; Reynolds and Martin 1968). Noy-Meir (1973) explained that an effective rain event stimulates biological processes, particularly production and reproduction, and that only a few of the total rainfall events may be sufficiently large to be considered effective. This interpretation may not hold for semiarid grasslands.

A unique characteristic of carbon and mineral nutrient cycles in semiarid grasslands is the concentration of material and activity at or very near the soil surface (Clark 1977; Cole et al. 1977; Woodmansee et al. 1981). Small precipitation events which occur with relatively high frequency wet these important surface layers. The large contribution of small events to the total growing season environment, their high frequency of occurrence together with the characteristics of the top soil layer led us to question the assumptions about the ecological significance of small events. As a first step in understanding the role of small rainfall events in semiarid ecosystems, we investigated the influence of a 5-mm event on *Bouteloua gracilis* (H.B.K.) Griffiths, the dominant perennial grass of the semiarid steppes of the central and southern Great Plains. Our objective was to test the hypothesis that small events were an important resource for ecosystems in semiarid regions and hence were ecologically significant.

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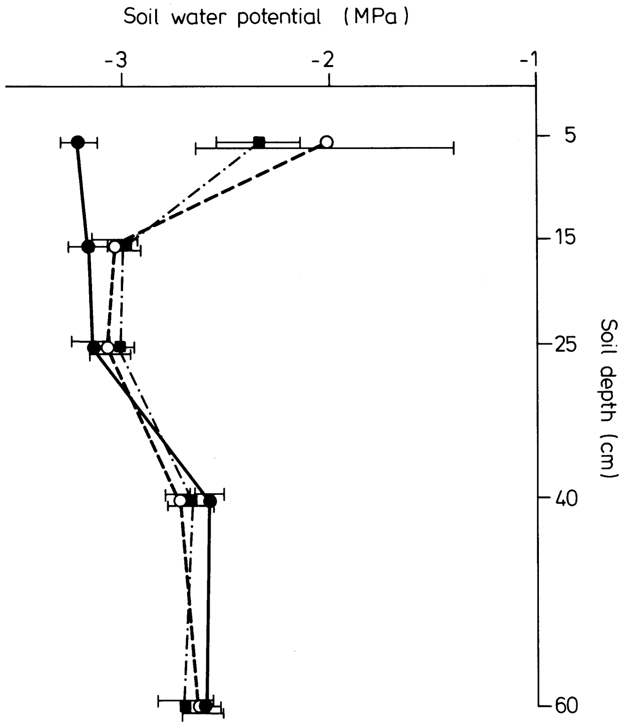

Fig. 2. Soil water potential as a function of depth (±standard error; $N=6$) before (——), the first day after (– – – –), and the second day after (–·–·–·–) addition of 5 mm of water

Methods and Materials

The experiment was conducted at a shortgrass steppe site located in the piedmont of north-central Colorado, 61 km northeast of Fort Collins, Colorado, and 40 km south of Cheyenne, Wyoming (40°49' N latitude, 104°47' W longitude), at an elevation of 1,650 m. The climate is typical of midcontinental areas, except for the strong influence of the Rocky Mountains approximately 60 km to the west. Mean annual precipitation is 311 mm, 70% of which occurs during the May-through-August growing season. The range of annual precipitation measured over the past 30 years was from a low of 110 to a high of 580 mm. The dominant plant species are *Bouteloua gracilis*, *Artemisia frigida* Willd., and *Opuntia polyacantha* Haw. *B. gracilis* accounts for 90% of the aboveground biomass of grasses and 30% of total aboveground biomass (Lauenroth et al. 1978).

On August 19, a 5-mm rainfall event was simulated by applying water with a hand-held sprayer in the late afternoon, the most common time for the occurrence of small rainfall events. The experimental area was a 3-m diameter × 1.5-m depth lysimeter (Armijo et al. 1972) dominated by *B. gracilis*. The lysimeter provided an accurate measurement of the water applied and prevented lateral movements of water in the soil. Leaf water potential, soil water potential and leaf conductance to water vapor were measured during the day water was applied and during the subsequent two days.

Leaf conductance to water vapor was measured on *B. gracilis* by means of a diffusion porometer (Kanemasu et al. 1969). Data were collected from before dawn until 13:00 h at two-hour intervals. Ten replications were used in each case. Leaf water potential was measured using the pressure chamber technique (Scholander et al. 1965) and by utilizing the same number of replications. Data collection ended at 13:00 h because our experience indicated that ghe status of these two variables remained constant from shortly after midday until dusk.

Soil water potential was measured with thermocouple hygrometers (Spanner 1951) placed at depths of 5, 15, 25, 40 and 60 cm. Six replications were installed at each level. These measurements allowed us to evaluate the water availability conditions previous to the experiment and the effect on soil water of the simulated rainfall.

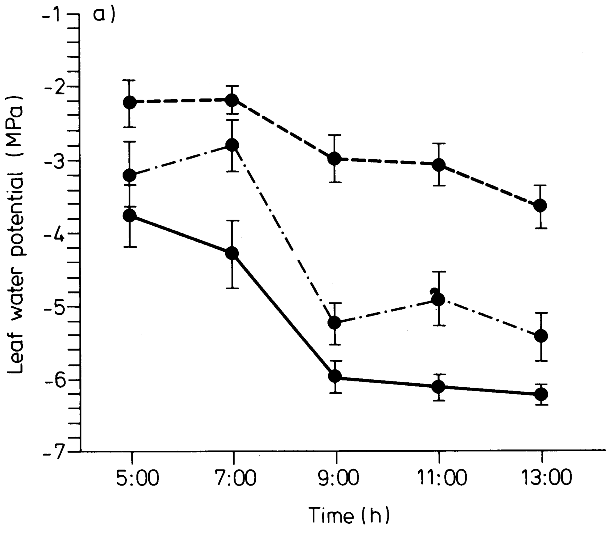

Fig. 3. Daily pattern of leaf water potential (±standard error; $N=10$) for *Bouteloua gracilis* before (——), the first day after (– – – –), and the second day after (–·–·–·–) addition of 5 mm of water

Water inputs to the experimental area were controlled by excluding natural rainfall and artificially watering. We excluded natural rainfall by covering the area with a canvas tarp supported by a portable structure 50 cm above the ground. Environmental conditions beneath the tarp were minimally modified because the area was covered and immediately uncovered after the rainfall occurred. Moreover, precipitation events were mostly thunderstorms of short duration which occurred in the late afternoon or early evening when the effect of covering the grassland was minimal.

Results

During the 20-day period previous to the experiment we applied 40 mm of artificial rainfall, 10 mm of which was applied during the week prior to the start of the experiment. Potential evapotranspiration during this period averaged 4 mm per day (Penman 1948). The simulated conditions represented a typical rainfall regime for this region. Soil water availability (Fig. 2) was very low, similar to that found for the same site at the end of a drying cycle (Sala et al. 1981). The 5-mm simulated rainfall applied on August 19 wetted approximately 5 cm of the soil profile, and its effect on soil water potential was still significant ($P < 0.05$) at a 5-cm depth in the early morning of the second day.

Leaf water potential before watering was −3.8 MPa pre-dawn and −6.2 MPa during the middle of the day, indicating severe water stress (Fig. 3). These values were even lower than those reported by Sala et al. (1981) for the same species and the same site at the end of a 56-day drying cycle (−1.8 MPa pre-dawn and −5.0 MPa after noon). Addition of 5 mm of water the previous afternoon significantly ($P < 0.05$) increased leaf water potential, which at noon achieved values typical of non-stress conditions. This effect continued through the second day after watering. Rapid response of leaf water potential to watering following drought has been reported but never before as a result of such a small addition of water (Boyer 1971; Fereres et al. 1979). Parton et al. (1981), working at the same site, reported that a small rainfall event modified the ratio of actual:potential evapotranspiration also for two days.

Leaf conductance to water vapor was less responsive to watering than leaf water potential (Fig. 4). Differential sensitivity of leaf water potential and conductance has been attributed to the negative feedback of drought on stomatal behavior via growth

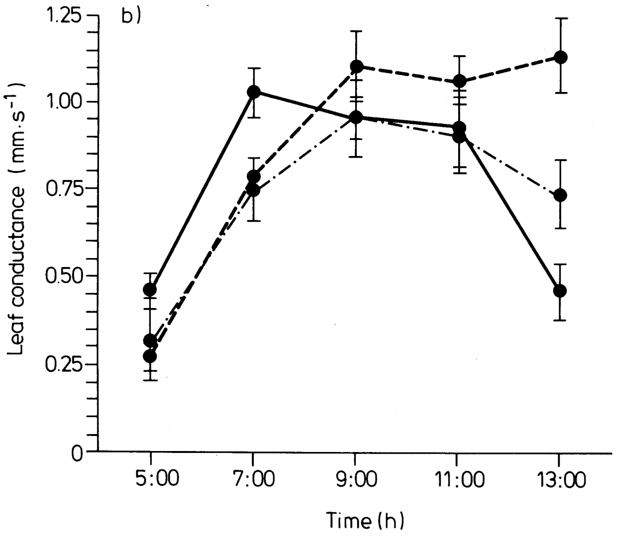

Fig. 4. Daily pattern of leaf conductance (±standard error; $N = 10$) for *Bouteloua gracilis* before (——), the first day after (– – – –), and the second day after (–·–·–·–) addition of 5 mm of water

regulators (Mizrahi et al. 1970; McMichael and Hanny 1977). The immediate response of leaf conductance to watering was the absence of a midday depression in conductance on the following day. This response can be accounted for by the direct influence of leaf water potential on stomatal behavior (Ludlow and Ibaraki 1979; Sala et al. 1981). The midday leaf conductance before watering was $0.46\ \mathrm{mm \cdot s^{-1}}$, which is quite similar to the minimum values previously observed for this species, and lies in the range where stomatal control does not depend on leaf water potential (Sala et al. 1981). The simulated rainfall event significantly ($P < 0.05$) increased the leaf conductance, which attained a value of $1.14\ \mathrm{mm \cdot s^{-1}}$. This value is characteristic of a non-stress condition and although it may seem low for those used to working with plants adapted to mesic conditions, such as crops, it represents one of the highest values reported for this species. Szarek and Woodhouse (1976) reported similar values of leaf conductance for their desert plants. Under those conditions they reported gross photosynthesis rates between 2 and 8 mg $\mathrm{CO_2 \cdot dm^{-2} \cdot h}$.

Discussion

The variables chosen to assess the response of blue grama to a small rainfall event had broad ecological implications and are physiologically simple enough to be expected to show measurable responses to a small stimulus. Leaf water potential is related to many important plant processes such as photosynthesis, respiration, translocation and transpiration. Leaf conductance to water vapor regulates transpiration and is closely related to CO_2 uptake. Stomatal behavior is the major control vascular plants have upon the compromise between water loss and carbon gain. Therefore, the ecological significance of changes in leaf water potential and leaf conductance as a result of a small rainfall event is related to their influence upon the water and carbon cycles.

The inability of currently held ideas of "effective" precipitation to account for significant and rapid responses of semiarid systems (or components) to small rainfall events resides largely with the most often assessed response criterion, plant biomass production. The "effectiveness" of a precipitation event has been assessed by its ability to initiate measurable increments in biomass. Because of the difficulty of measuring small changes in the biomass of a plant community, the importance of small events has been previously underrated. While our response variables do not represent measurements of biomass, they are indicators of the potential for biomass production (Ludlow et al. 1980).

An important question is whether these physiological responses of *B. gracilis* to a 5-mm rainfall event might be expected to influence its persistence as a dominant species in the steppe region. Additional analyses of the growing season precipitation regime will help clarify this issue. An average of 32 precipitation events occur during each growing season (May through August). Five events are greater than 10 mm. Most events are ≤5 mm; the exact distribution by size is: two are 5 mm, two are 4 mm, four are 3 mm, five are 2 mm, and nine are 1 mm. The remaining five events are >5 and ≤10 mm. If we assume that the seven rainfall events between 5 and 10 mm will produce physiological responses equal to or greater than those reported here (two days), then small rainfall events could be expected to modify the physiological activity of *B. gracilis* for 14 days. It is quite possible that the larger events will result in responses lasting longer than two days. What now can be said about the importance of events smaller than 5 mm? A potential role may be suggested based upon a first order Markov chain analysis of daily growing season precipitation which clearly indicated that rainfall events are not evenly distributed but tend to occur in groups (Bertolin and Rasmussen 1969). It is probable that a 1- to 4-mm event following a larger event may be important in sustaining the burst in physiological activity. In addition, two 5-mm events on successive days should have a greater physiological impact than the same two events 10 days apart.

We can think of different plant processes as having specific response times to increases or decreases in the water status of the environment. This characteristic response time or time constant is a measure of the inertia of each process (Orians 1975; Westman 1978), which controls the response to a stimulus. The inertia of each process varies among species and depends upon the current level of physiological activity. Applying the concepts of inertia and time constant one can make qualitative and quantitative predictions about the responses of a plant to a rainfall event. Therefore, an ecologically significant rainfall event is one which alters the water status of the environment of a plant for a period equal to or longer than the smallest time constant of those processes which influence its survival. The inertia of each species will determine which rainfall resources it will utilize. Species with low inertia and therefore small time constants will be able to utilize small precipitation events which alter water status for short periods. Inertia will be one of the major characteristics defining the ecological niche of semiarid species since it is intimately related to the capacity to utilize different portions of the water resource. The concept of an ecologically significant rainfall event can be developed also for an ecosystem. It can be defined as an event which alters the water status of the environment for a period equal to or longer than the smallest time constant of the system.

The remarkable potential of *B. gracilis* for a rapid response to a 5-mm rainfall event led us to conclude that small precipitation events were ecologically significant and that they represent an important resource for ecosystems in semiarid regions. We visualize small precipitation events as having a qualitatively distinct effect upon ecosystem dynamics. Small events frequently activate those processes related to the nutrient cycles which are concentrated near the soil surface and are tightly controlled by water availability. On the other hand, water received in large events is stored in deeper soil layers and is available for plant use, but only a small portion for the microorganisms responsible for the nutrient cycle processes. In summary, we hypothesize that small events have a relatively larger effect (activity/mm) on ecosystem dynamics than large events and that the dominance of *B. gracilis* is related to its ability to utilize small events.

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