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Water Status of Soil and Vegetation in a Shortgrass Steppe

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Summary. In an attempt to describe some major relationships between soil and plant compartments in a shortgrass steppe, the process of water loss from the system and plant water relations throughout a drying cycle were studied. The water supply was manipulated and some soil and plant variables monitored throughout a drying cycle. Leaf conductance and leaf water potential of blue grama *(Bouteloua gracilis)* were measured periodically at predawn and noon. Soil water content and water potential of different layers were also monitored.

Three different periods were distinguished in the water loss process throughout a drying cycle. These distinctions were made taking into account the relative contribution of different soil layers. Leaf conductance and water potential at noon slowly declined throughout the first 50 days of plant growth. After that, they rapidly decreased, reaching values of 0.29 mm s^{-1} and -5.0 MPa, respectively. The predawn leaf water potential remained unchanged around -0.5 MPa during the first 45 days, then rapidly decreased. This occurred when soil water of the wettest soil layer was near depletion.

Predawn leaf water potentials were highly correlated with water potentials of the wettest layer. Leaf conductance and water potential at noon were correlated with effective soil water potential (soil water potential weighted by the root distribution in the profile). We concluded that root surface area limited the water flow through an important part of the day in this semiarid ecosystem. Axial root resistance did not appear important in determining the equilibrium status between leaves and the wettest soil layer.

Introduction

Variability in productivity among years in the semiarid shortgrass steppe region of North America is largely accounted for by patterns of water availability. These patterns affect not only ecosystem functions such as production, consumption, and decomposition (Lauenroth and Sims 1976) but also the structure of the system represented by composition, biomass, cover, and density (Hyder et al. 1975; Lauenroth et al. 1978).

Successful management of semiarid ecosystems must be based upon knowledge of their functioning. Techniques based upon empiricism are becoming less efficient and are rapidly nearing their upper limit of usefulness. With an awareness of the key role that water plays in semiarid ecosystems and of the limited possibilities for manipulating this resource with economic benefit, we began this work to provide new information about the water relations of a semiarid system. Our specific objectives were to describe (1) the status and transfers of water among the soil-plant-atmosphere compartments during a drying cycle, (2) the pattern of water losses from a completely wet soil profile, and (3) how some physiological plant variables were affected throughout a drying cycle.

Site Description

The Pawnee Site is on the piedmont of northcentral Colorado approximately 61 km northeast of Fort Collins and 40 km south of Cheyenne, Wyoming (40°49′ N latitude, 104°47′ W longitude). This site is on the Central Plains Experimental Range, which is administered by the USDA Science and Education Administration, Federal Research. The topography of the area consists of gently rolling hills with broad tops separated by wide ephemeral stream courses. The average elevation is 1,650 m.

Native vegetation of the area has been described by Klipple and Costello (1960). The principal perennial species on the study site are blue grama (*Bouteloua gracilis* (H.B.K.) Lag.), fringed sagewort (*Artemisia frigida* Willd.), plains pricklypear (*Opuntia polyacantha* Haw.), and needleleaf sedge (*Carex eleocharis* Bailey). Data were collected from a weighing lysimeter of 3 m diameter where instruments to measure soil water variables had previously been installed. This small area was mainly occupied by blue grama because it was periodically weeded to simplify the system under study.

Climate of the Pawnee Site is typical of mid-continental areas, except for the strong influence of the Rocky Mountains approximately 60 km to the west. Mean annual precipitation is 311 mm, with a range of 110 to 580 mm recorded over the past 31 years at the Central Plains Experimental Range. Approximately 70% of the mean annual precipitation occurs during the April to September growing season. Mean monthly temperatures range from below 0° C in December and January to 22° C in July.

Materials and Methods

Measurements of plant and soil water status were made on 15 dates during a 56-day drying cycle. The cycle began in June 1979 with the soil profile completely and homogeneously wet. During rainy periods

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thereafter the experimental area was covered with a canvas before each rainfall event.

Plant water status was assessed by measuring leaf water potential and leaf conductance to water vapor. Both measurements were done exclusively on blue grama, always utilizing the most recent fully expanded leaves. These leaves were considered the most physiologically important. This criterion was previously used by Redmann (1976) for thickspike wheatgrass (*Agropyron dasystachyum* (Hook.) Scribn.). Leaf water potential was measured using the pressure chamber technique (Scholander et al. 1965). Leaf water potentials were measured at predawn and after noon between 1,300 and 1,400 h. Those times of the day were selected because leaf water potentials were at near maximum at predawn and largely independent of atmospheric conditions. Plants were at or near maximum daily water stress after noon and leaf water potential was highly dependent upon atmospheric water demand. Ten replications for leaf water potential measurements were used on each sample date. This number was adequate to maintain the standard error below 7% of the mean.

Leaf conductance was measured by means of a diffusion porometer following the technique described by Kanemasu et al. (1969). The data were collected on those dates when leaf water potential was measured, but only once during a day. Leaf conductance was measured only in the afternoon between 1,300 and 1,400 h because at predawn, as well as during the night, leaf conductance of blue grama was extremely low and independent of plant water status. Variability for measurements of conductance was larger than for leaf water potential, therefore the number of replications was increased to 15 to maintain the standard error below 7% of the mean.

The status of soil water was assessed by measurements of soil water potential and soil water content. The 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. Soil water content was assessed by means of a neutron probe (Gardner and Kirkham 1952). Measurements were taken at depths of 15, 30, 45, 60, 75, and 90 cm in two different access tubes. Water loss from each layer was calculated as the difference between consecutive measurements of water content.

Soil water potential, which is a measure of the energetic status of water, provided information about the availability of water to the plants. Soil water content data provided complementary information that allowed us to assess the pattern of water flow through the soil profile and to evaluate environmental influences that drive this process.

The information about root distribution was supplied by J.L. Dodd (unpublished). The relative root biomass within a soil layer was obtained by dividing the root biomass of a given layer by the total root biomass.

Significant differences in water content, soil and leaf water potential, and stomatal conductance were assessed using 95% confidence intervals. Multiple linear regression was used to assess relationships between plant and soil water variables.

Results

Water loss at the beginning of the cycle occurred exclusively from the top layer (Fig. 1a). After that the next deeper layer also began contributing water to total loss. This process continued downward with a corresponding delay. Sixteen days expired before water potential values significantly different ($p < 0.05$) from zero were recorded in the 15 cm layer (Fig. 1b). In the deepest layer (60 cm), values different from zero occurred 39 days after the beginning of the experiment. Measurements of water content were more sensitive to small changes than water potential measurements when the soil was wet and were less sensitive under dryer conditions (Fig. 1a and b). Large differences in the water content of the top layer were recorded during the first few days of the experiment, and differences in water potential were proportionately smaller. No significant differences in the water content of the top layer occurred after the 4th day, whereas significant changes in water potential still occurred until day 28. The top layer reached a minimum water potential value of −6.0 MPa. Other layers exhibited higher water potentials at the end of the experiment. Homogeneous water potential values were not expected at the end of the experiment, since soil characteristics and processes driving water flow, such as absorption and evaporation, changed throughout the profile. Also there was no reason to consider water in all soil layers to be depleted, since the experiment was terminated based upon a plant water status criterion.

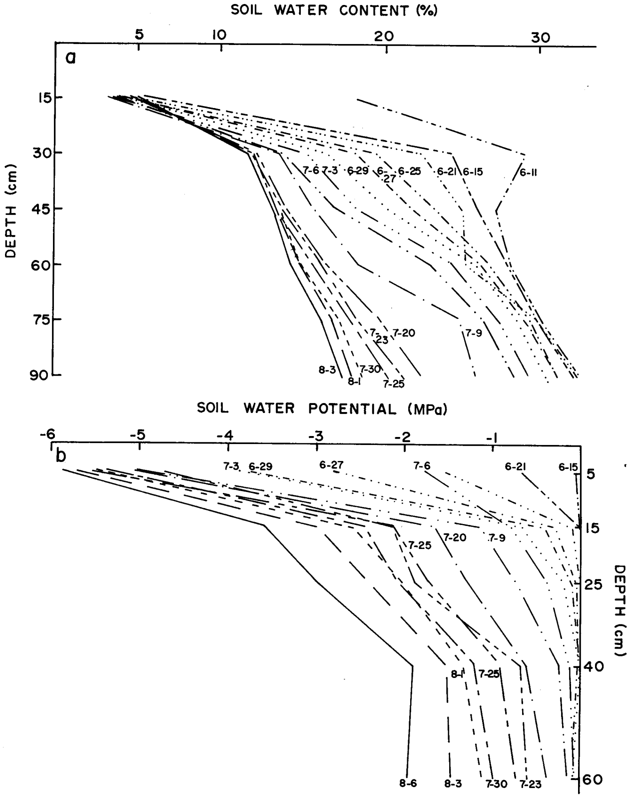

Fig. 1. (**a**) Soil water content as a function of depth throughout a drying cycle; (**b**) Soil water potential as a function of depth throughout a drying cycle

Water status of the soil changed uniformly throughout the drying cycle, but trends of water status in blue grama were quite different. Values for leaf water potential at predawn remained unchanged around −0.5 MPa during the first 44 days of the experiment until 25 July (Fig. 2). Leaf water potential did not reflect changes in soil water status during this time. However, after 25 July predawn leaf water potentials decreased steadily until the end of the experiment, when they reached −1.8 MPa. The change in the slope of the predawn leaf water potential curve occurred when the wettest soil layer, in this case the lowest layer, showed that the first water potentials were significantly different ($p < 0.05$) from zero (Fig. 1b). The values for leaf water potentials at noon steadily decreased from the beginning of the experiment until 1 August (−2.3 to −3.6 MPa). It is probable that those leaf water potentials neither resulted in severe water stress nor impaired photosynthesis or respiration (Dye 1972). After 1 August, a large change in the slope of the curve occurred so that leaf water potentials below −4.0 MPa and −5.0 MPa were experienced by the end of the experiment. Variability in atmospheric water demand throughout the soil drying cycle was responsible in part for the variability in leaf water potentials at noon. Variability in leaf

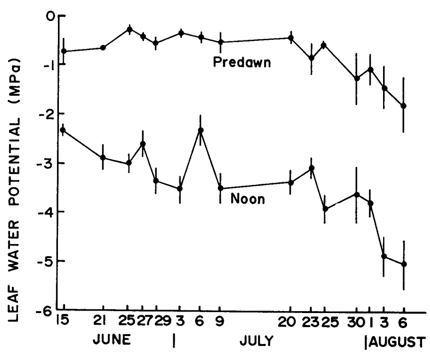

Fig. 2. Leaf water potential of blue grama on 15 dates. The lower and upper lines represent values at predawn and noon, respectively. Each point represents the mean of ten leaves and vertical bars represent the 95% confidence interval

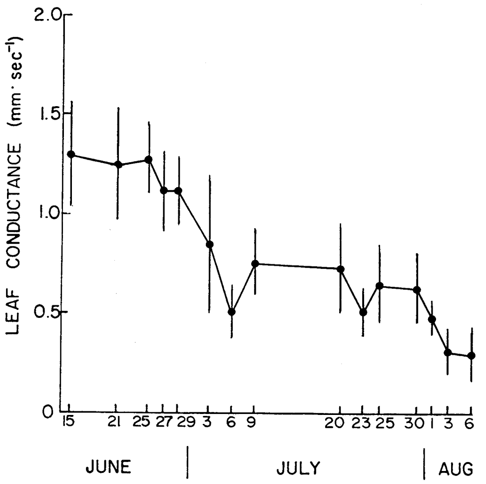

Fig. 3. Leaf conductance of blue grama on 15 dates. Each point represents the mean of 15 leaves and vertical bars represent 95% confidence interval

water potential increased as the mean decreased throughout the drying cycle. Individual leaf differences, which were not noticeable at the beginning of the cycle, became obvious under severe water deficit.

The trend for mid-day leaf conductance to water vapor throughout the drying cycle was similar to that of leaf water potential at noon (Fig. 3). The values of leaf conductance steadily decreased from 1.29 mm s^{-1} to 0.62 mm s^{-1} during the first 49 days of the experiment. Then the slope of the curve changed and leaf conductance decreased rapidly until a plateau was reached around 0.30 mm s^{-1}, close to the end of the experiment. The increase in the slope of the leaf conductance curve coincided with the change in slope of the curve for leaf water potential at noon. Both inflection points occurred when the wettest soil layer had supplied 73% of its total content of water. Soil water potential in this deep layer had rapidly declined and plants were unable to attain a minimum water potential of −0.5 MPa at predawn. From that time on, plants started each day with a water deficit.

Discussion

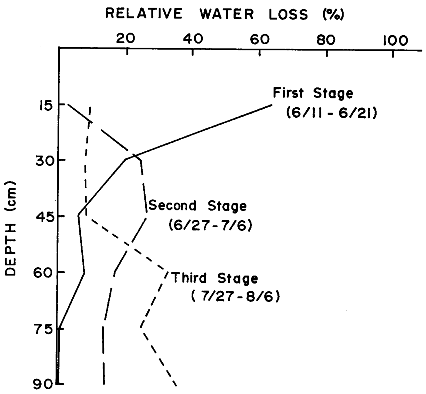

Fig. 4. Relative water loss from different soil layers for three characteristic periods at the beginning, middle, and end of a drying cycle

Water was lost from different soil layers throughout the drying cycle. We distinguished among three stages in the water loss process throughout the drying cycle. Similarly, Belmans et al. (1979) reported a gradual shift of the zone from which the root system obtains the plant's water supply. The first was characterized by the unevenness of the water loss from different soil layers (Fig. 4). The upper layer supplied 64% of the total water evapotranspired from the system. The second stage was characterized by an even distribution of water loss among all the soil layers explored by roots. No layer supplied more than 26% of the total water loss. All layers except the upper one provided more than 15% of the total water loss. This phenomenon was related to the distribution of water potentials within the soil and the pattern of daily dynamics in leaf water potential. Water uptake from a specific layer is driven by the water potential gradient between the leaf and soil. Leaf water potential has a daily pattern with a maximum near predawn and a minimum after noon. The leaf to soil water gradient has an opposite pattern. In the early morning the gradient is small so plants extract water only from the wetter, lower layers. Water begins flowing from dryer layers by mid-day following an order of decreasing water potential. The dryest layer is the last to supply water, and the period of time water flows from a specific layer is proportional to its water potential. In dryer soil layers, water flow is limited by the lack of a sufficient gradient. In the wetter, lower layers, the flow is limited not by the gradient but by the small root surface area and the axial root resistance. The third stage was characterized by unevenness of water loss. All the upper soil layers were depleted and only the lower layers were able to supply water at the end of the study period.

A model of the relative contribution of different soil layers to total water loss from the system is useful to recognize more important layers for determining the water status of vegetation. Our data agreed in general with models developed by Waring and Running (1976) and Van Bavel and Ahmed (1976) for different systems but under similar environmental conditions. A soil profile that is completely wet and loses water until it is depleted is not the most common situation in nature but is certainly the easiest for assessing the problem of water loss. In contrast to our conditions, Gregory et al. (1978) monitored the water status of different soil layers throughout a growing cycle of winter wheat *(Triticum aestivum)* under natural conditions. In their case, a large set of processes were acting together (evaporation, transpiration, deep seepage, and upward and downward water movement in the effective rooting area) in an environment in which natural rainfall events of different frequencies and intensities made understanding of the water loss process even more difficult.

Some relationships between the plant and soil compartment remained constant throughout the drying cycle. The predawn leaf water potential of blue grama was related to the soil water potential of the wettest layer ($r^2 = 0.92$, Fig. 5a). Each night blue grama

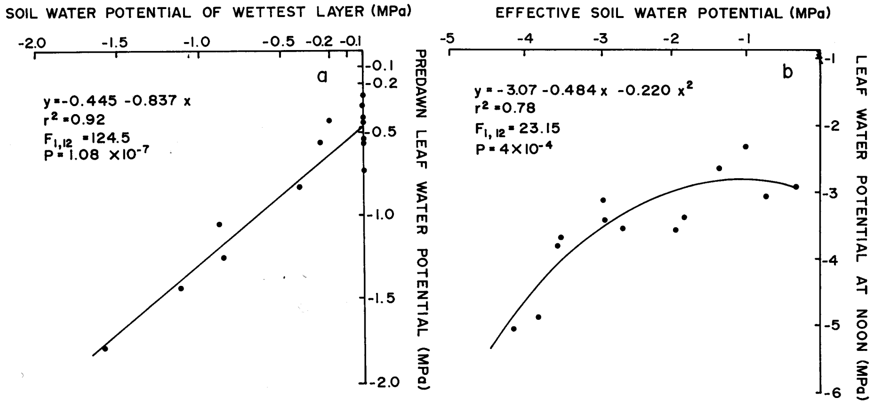

Fig. 5. (**a**) Predawn leaf water potential of blue grama as a function of water potential of the wettest layer of soil; (**b**) Leaf water potential of blue grama at noon as a function of effective soil water potential

leaves reached an equilibrium status with the water potential of the wettest soil layer. The occurrence of this equilibrium was independent of the atmospheric water demand. This happened regardless of the depth of the wettest soil layer and the distance from the water source to the leaves. This indicated that axial root resistance did not play an important role in controlling predawn leaf water potential.

Leaf water potential at noon was also related to a calculated effective soil water potential (Fig. 5b). The effective soil water potential was obtained as the summation of the water potential of each soil layer multiplied by the relative biomass of roots within that layer (Van Bavel and Ahmed 1976). Root biomass declined exponentially with depth; therefore, the effective soil water potential was greater in upper soil layers if the same amount of water was concentrated there as at lower depths. Effective soil water potential stressed the importance of the root absorption area. The total water uptake by roots may be considered as the product of the water flow per unit root surface times the total root surface actually absorbing water. Root surface may be replaced by a highly correlated variable such as length or biomass. The observed relationship between effective soil water potential and leaf water potential ($r^2=0.78$) suggested that root surface was limiting water absorption by blue grama when water was not available in soil layers with abundant roots. When the upper layers of soil were depleted, water was absorbed from layers with less root biomass and the absorbing surface area became the limiting factor in water uptake during the day. The function that related leaf water potential at noon and effective soil water potential was

$$y = -3.07 - 0.484\,X - 0.220\,X^2$$

(X, $F_{1,12}=23.15$, $p<0.001$; X^2, $F_{1,11}=5.97$, $p=0.03$). A decrease in the effective soil water potential from 0 to -2.0 MPa did not affect the status of leaf water potential. Beyond the threshold of -2.0 MPa, changes in the availability and location of water in the soil profile were reflected in leaf water potential. Redmann (1976), working with thickspike wheatgrass in a growth chamber experiment, found a similar relationship between leaf water potential and soil water content of pots. On the other hand, Sivakumar and Shaw (1978) working with soybeans *(Glycine max)* in a field experiment found a different trend. They related leaf water potential to the average soil water potential at 30 and 60 cm depths and a straight line function was fitted with an $r^2=0.79$. However, their experiment occurred under conditions of lower water stress, the minimum soil water potential reached was only -1.4 MPa.

Leaf conductance in blue grama was related with leaf water potential when both were measured at noon (Fig. 6). The model that represented the relationship between these two variables was characterized by three different areas. The first was a small plateau where leaf conductance remained constant and was not affected by changes in leaf water potential. In the next area, between -3.0 and -4.0 MPa, leaf conductance was highly dependent on leaf water potential. Beyond -4.0 MPa further decreases in leaf water potential were not reflected in conductance. This relationship is similar to one reported by Ludlow and Ibaraki (1979) for the legume Siratro *(Macroptilium atropurpureum)* in a semiarid pasture. Szarek and Woodhouse (1976) measured leaf conductance and leaf water potential in two Sonoran desert plants. Their data followed a similar pattern, and conductance values for the same leaf water potential were quite comparable. The blue grama system, however, was subjected to more severe water stress. In the Sonoran desert they reported leaf water potentials between 0 and -3.5 MPa, whereas our data ranged between -2.3 and -5.0 MPa. Sivakumar and Shaw (1978) reported a straight line function that related leaf conductance with water potential for a soybean crop under more mesic conditions. Their data fluctuated over a range higher than those observed for plants on the Sonoran desert or shortgrass steppe.

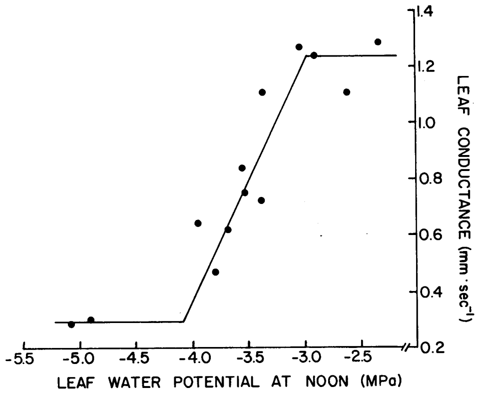

Fig. 6. Leaf conductance of blue grama as a function of leaf water potential. Data points and suggested model

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