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LONG-TERM SOIL WATER DYNAMICS IN THE SHORTGRASS STEPPE[1]

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Abstract. To assess the temporal and spatial dynamics of soil water at a shortgrass steppe site in northcentral Colorado, we evaluated the precipitation regime for a 33-yr period and ran a simulation model for this period. Small precipitation events accounted for a large fraction of the total number of events and represented a source of water with small interannual variability. The difference between wet and dry years was related to the occurrence of a few large events.

Average daily precipitation was concentrated during the warmest months of the year with a maximum in late spring. Water in the surface soil layers had a short residence time and no seasonal pattern. Intermediate layers reflected the seasonal pattern of precipitation. Maximum soil water availability occurred in the late spring, but this was also the period with the highest interannual variability.

The wettest layer was at 4–15 cm of depth. The frequency of wet conditions decreased above this layer because of the strong influence of evaporation and below because recharge was infrequent. No deep percolation events were recorded. During dry years distribution of soil water was very shallow and during wet years wet conditions reached to depths of 120–135 cm.

This shallow distribution of soil water matches the distribution of processes and structural elements in the steppe suggesting that there is a cause-effect relationship between them. We speculate that the pattern of water availability interacts with biotic constraints and determines the rate of ecosystem processes. The depth distribution of water in dry and wet years is compared to the root distribution of grasses, shrubs, herbs, and succulents to suggest the response of each group to modal and extreme conditions. Comparison of long-term soil water patterns and traits of the major species allows us to suggest why *Bouteloua gracilis* is the dominant species in the shortgrass steppe.

Key words: deep percolation; droughts; North American grassland; potential evapotranspiration; shortgrass steppe; small precipitation events; soil water; spatial pattern; temporal variability; transpiration.

INTRODUCTION

The availability of water in time and space is the single most important factor determining the structure and dynamics of ecosystems in semiarid regions (Noy-Meir 1973). Identification of the significant scales of temporal and spatial variability of soil water and evaluation of the processes accounting for this variability can provide critical insight into ecosystem behavior. The most frequent state of soils in semiarid regions is dry. This nearly continuous dry state is interrupted by brief wet periods. The temporal distribution of the wet periods, their duration, and the depth distribution of the resulting water availability is critical explanatory information for both the structure of ecosystems and the rates of processes. Because of the tight linkages between water and mineral nutrient availability, accounting for the dynamics of water often also accounts for some of the important effects of nutrients. Nitrogen availability is closely coupled to water availability through its effects on mineralization and movement in the soil profile (Schimel and Parton 1986).

Our objectives were: (1) to characterize the temporal and vertical spatial distribution of water for the most common soil, a sandy loam, at the Central Plains Experimental Range (CPER) in northcentral Colorado; (2) to assess the relative importance of water loss pathways and their temporal distribution; (3) to compare these patterns with structural characteristics such as the distribution of life-forms in time or the distribution of roots in the soil profile; and (4) to relate the water and structural patterns with the temporal and spatial pattern of ecosystem processes ranging from nitrogen mineralization to primary production.

First, we evaluated the precipitation pattern in terms of the contribution of different size classes and the

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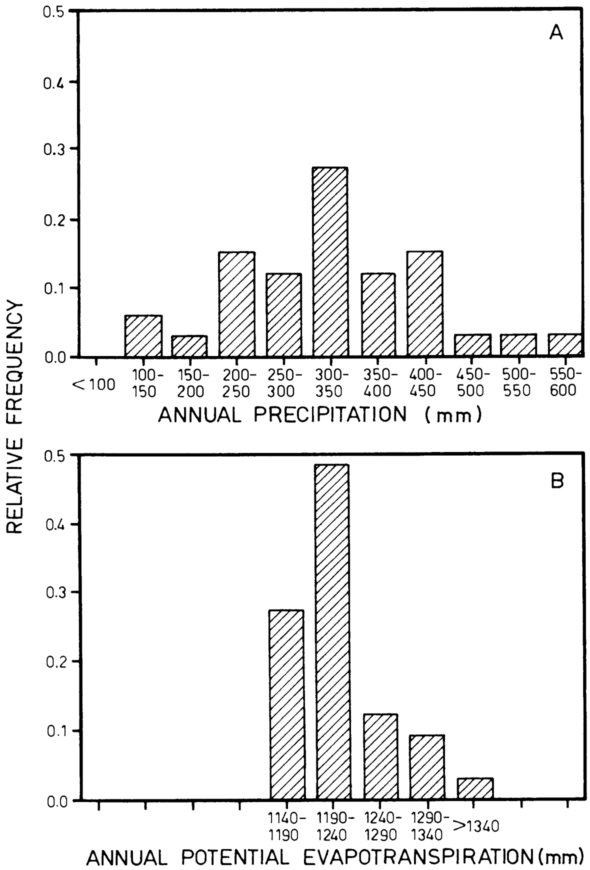

FIG. 1. (A) Relative frequency distribution of annual precipitation recorded from 1950 to 1983 at the Central Plains Experimental Range in northcentral Colorado. Average annual precipitation was 327 ± 101 mm ($\bar{X}$ ± 1 SD). (B) Relative frequency distribution of annual potential evapotranspiration for the same period and site as above. Average PET was 1254 ± 225 mm.

seasonal and interannual variability. Second, we used a simulation model of soil water dynamics that required few input variables and ran it for a long period of time (Parton 1978). The model required daily precipitation and temperature for which we had a 33-yr data set from the CPER.

MATERIALS AND METHODS

We evaluated the pattern of precipitation and potential evapotranspiration using a data set of daily temperature and precipitation for the Central Plains Experimental Range (CPER; 40°49′ latitude, 104°47′ longitude) collected from 1950 to 1983. We compared the interannual and seasonal variability of precipitation and potential evapotranspiration calculated using Penman's (1948) equation. We analyzed the contribution of different precipitation size classes and how it changed along a gradient of annual precipitation.

We used a model developed for the shortgrass steppe and validated against a data set collected during 1972 at the CPER (Parton 1978). The structure of the model is similar to that of other soil water models (Kohler and Richards 1962, Nimah and Hanks 1973) and operates with a daily time step. The model simulates the movement of water through the plant canopy and 11 soil layers (0–2.5, 2.5–4, 4–15, 15–30, 30–45, 45–60, 60–75, 75–90, 90–105, 105–120, 120–135 cm). Rainfall interception, infiltration into the soil, rapid and slow soil drainage, transpiration, and evaporation from the canopy and the soil are included.

Inputs to the model were daily values of temperature and precipitation. We used the same data set that we used to characterize the patterns of precipitation and potential evapotranspiration for the CPER. Soil parameters represented an Ascalon soil with sandy loam texture, which is a common rangeland soil in northcentral Colorado. The natural vegetation of the area is representative of a large portion of the shortgrass steppe and is dominated by the C_4 perennial bunchgrass *Bouteloua gracilis* H.B.K. Lag. Common associated species include *Buchloe dactyloides* (Nutt.) Engelm., *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, *Artemisia frigida* Willd., *Sphaeralcea coccinea* (Pursh) Rydb., and *Opuntia polyacantha* Haw.

Output variables from the model were soil water potential for each of the 11 layers, transpiration, bare soil evaporation, litter interception, standing dead interception, deep drainage and potential evapotranspiration. We tabulated daily values for these variables for the 33-yr period simulated. To summarize this large data set we calculated the frequency of wet days as a function of soil depth or of seasonality. A wet day was one in which soil water potential was > -1.0 MPa, based upon the characteristics of the soil and of the major plant species (Sala et al. 1981). We present the results of the 8 yr with the lowest precipitation and the 8 yr with highest precipitation separately from the rest of the years. We also report seasonal trends of losses, and their variability.

RESULTS

An important distinguishing characteristic among climate types is the relationship between the supply and the atmospheric demand for water. Mean annual precipitation for the CPER was 327 mm from 1950 to 1983, while potential evapotranspiration (PET) was 1254 mm. The lowest values of PET still exceeded precipitation during the wettest years by a factor of 2 (Fig. 1). Maximum annual PET exceeded minimum precipitation by a factor of 10. This overwhelming dominance of dry air leads to the conclusion that water should be a frequent limiting variable for ecological processes, which is supported by evidence from field experiments (Lauenroth et al. 1978). In addition to large differences in the magnitudes of water supply and atmospheric demand, the interannual variability of these two characteristics is also considerable. Precipitation was almost twice as variable (CV = 31%) as PET (CV = 18%). The relative constancy of PET compared

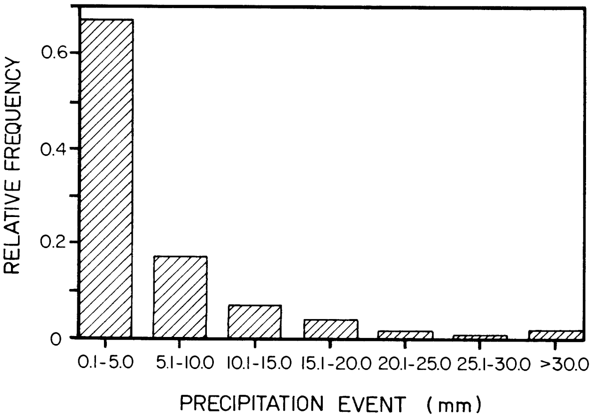

FIG. 2. Distribution of precipitation events by size class from 1950 to 1983 at the Central Plains Experimental Range, Colorado.

to precipitation provides an explanation for why precipitation is such a powerful explanatory variable for processes in semiarid regions (Noy-Meir 1973).

An important characteristic of the precipitation regime in semiarid regions is that most events are small (Smith and Schreiber 1974, Sala and Lauenroth 1982). Small precipitation events (≤5 mm) account for 67% of the total number of events recorded at the CPER between 1950 and 1983 (Fig. 2).

The structure of the precipitation regime was different for dry and wet years, indicating that the difference between wet and dry years is related to the presence or absence of a few storms that deposit large amounts of precipitation (Fig. 3). The amount of water received in large precipitation events (≥10 mm) increased as annual precipitation increased. By contrast, water received in small events (≤5 mm) changed very little from dry to wet years. During the driest year in the record (1964), small precipitation events accounted for 42 mm and during the wettest year (1967) they contributed 69 mm, which represented 39 and 12% of annual precipitation. Large events account for most of the interannual variability in precipitation.

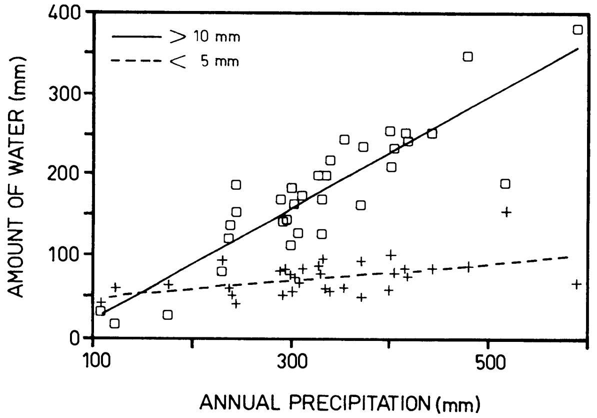

FIG. 3. Amount of water per year received in rainfall events ≥10 mm (□) and ≤5 mm (+) calculated for 33 yr from 1950 to 1983. Least squares regression shows that the amount of water received in large rainfall events (≥10 mm, ——, *L*) sharply increased as annual precipitation (PPT) increased ($L = -4.7 + 0.69 \cdot \text{PPT}$, $r = 0.88$, $P \leq .05$). In contrast, the amount of water received in small rainfall events (*S*, - - -) increased very slowly ($S = 3.7 + 0.11 \cdot \text{PPT}$, $r = 0.51$, $P \leq .05$).

Precipitation is clearly concentrated during the warmest months of the year, which provides an important definition for the growing season. The fact that average daily precipitation is always exceeded by PET by at least a factor of 2 suggests that a complete recharge of the soil profile is not likely to be a common event in this system. Parton et al. (1981) reached a similar conclusion when analyzing 3 yr of data from a weighing lysimeter. Average precipitation reached a maximum of 3 ± 0.62 mm/d ($\bar{X} \pm 1$ SE) in late spring during the 1st wk in June (Fig. 4) and rapidly decreased reaching a value of 1 ± 0.3 mm/d by the beginning of July. Variability among years did not mask the occurrence of these maximum and minimum values. During the last week in July precipitation increased reaching another maximum at 1.8 mm/d.

Each soil layer has a distinct pattern of water availability depending upon its connection with input and output processes (Fig. 5). The surface layer (0–2.5 cm) showed no seasonal pattern because of the large effect of evaporation, which results in the residence time of water being very short. Intermediate-depth layers (15–45 cm) clearly reflected the seasonal pattern of precipitation, with the maximum frequency of wet days occurring in early June and late July. Deep layers (45–60 cm) remained wet only during the early growing season. In contrast, there is a high probability of finding water in upper layers during the entire year. However, this resource is available for plants only for short periods of time since water is absorbed or evaporated very rapidly from these layers.

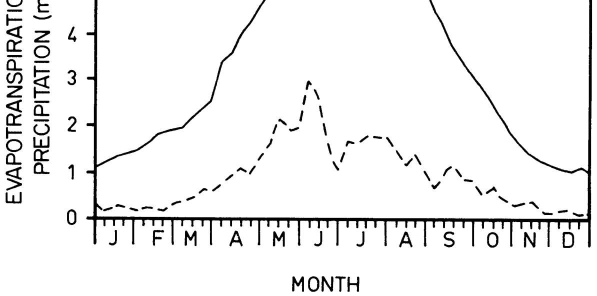

FIG. 4. Potential evapotranspiration (PET) calculated using the method of Penman (1948) and precipitation (PPT) for the Central Plains Experimental Range, Colorado. Each data point (shown as inflection in curve) represents the weekly average for 33 yr from 1950 to 1983.

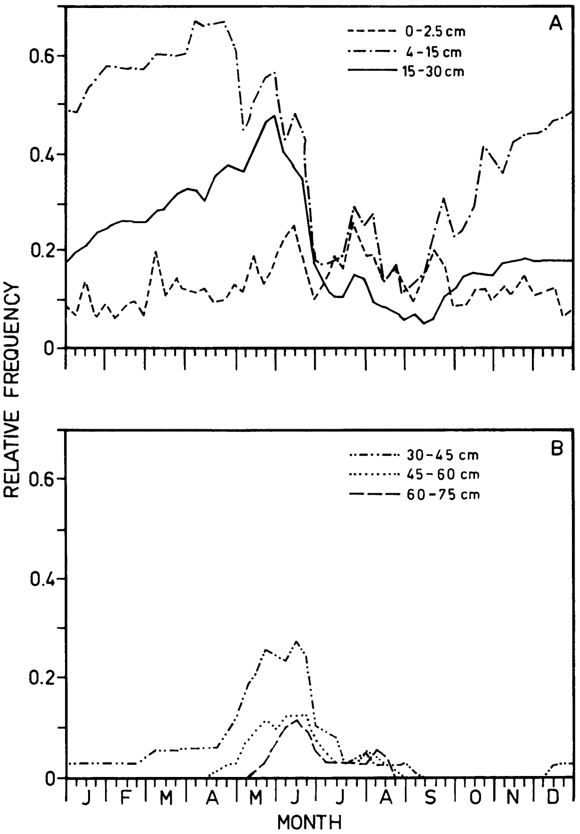

FIG. 5. Frequency of occurrence of soil water potential >-1.0 MPa through time for different soil depth layers in the shortgrass steppe of northcentral Colorado. The frequency was calculated as the number of days in each calendar week that had soil water potential >-1.0 MPa, out of 231 d (33 yr·7 d/wk). Soil water potential between 0 and -1.0 MPa indicates that water is available for plants. (A) for upper soil layers and (B) for lower soil layers.

Average transpiration is concentrated during the growing season when water availability and temperature adequate to growth coincide (Fig. 6). The pattern of transpiration through time also is coincident with the pattern of leaf area, photosynthetic rate, and aboveground green biomass (Knight 1973, Monson et al. 1986). Leaf area index of the shortgrass steppe is null during the nongrowing season and reaches a maximum of ≈0.5 (Knight 1973). The lack of transpiration during the winter explains the occurrence of weeks of wet soil during this time of the year even though precipitation is very low.

Intermediate and deep layers show a seasonal pattern in the interannual variability of soil water potential (Fig. 7). In contrast, no such pattern is observed in the upper layer. Variability is maximum during spring and early summer. This period of the year has the highest frequency of wet weeks and the highest variability. Water availability is less reliable during the early growing season than during midsummer that is a drier but less variable period. The dominant species, *Bouteloua gracilis*, is adapted to use water during the less variable and drier period, whereas *Agropyron smithii* Rydb., a C_3 species with an earlier phenological response, is better adapted to use resources available during spring (Sala et al. 1982*b*).

Over the 33 simulated years, the 4–15 cm soil depth had the highest frequency of soil water potential >-1.0 MPa (Fig. 8). The frequency of wet conditions decreased both above and below this depth. Above the 4–15 cm layer evaporation is such an important influence on the duration of wet condition that the soil is rarely wet. Below this layer, recharge is infrequent. No deep percolation beyond 135 cm was recorded during the 33-yr period. This remarkably shallow distribution of soil water is the result of (1) a distribution of event sizes bias towards small events (Fig. 2), (2) a rainy season in synchrony with the warm season which constrains the possibilities of recharge of the soil profile (Fig. 4), and (3) a rate of potential evapotranspiration higher than precipitation.

Although the location of the wettest layer did not change between dry and wet years the distribution of water in the soil profile did change (Fig. 8). During wet years the distribution of soil water was relatively even throughout the soil profile, and wet conditions reached the 120–135 cm layer. In contrast, during dry years water was concentrated in the upper soil layers and the deepest layer that reached a soil water potential higher than -1.0 MPa was located at 30–45 cm.

DISCUSSION

Classification of sites with dry climates based upon amounts of annual precipitation is a convenient method for climatologists and geographers. From the point of view of the ecologist or agronomist, it is the adequacy of precipitation that is the key variable for classifying ecological or agricultural sites (Bailey 1979). Evaluation of the adequacy of precipitation involves assessment of the amount received and its subsequent

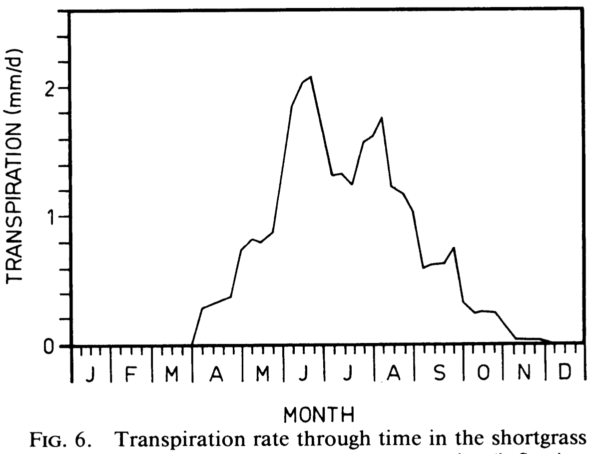

FIG. 6. Transpiration rate through time in the shortgrass steppe in northcentral Colorado. Each data point (inflection in curve) represents the weekly average for 33 yr from 1950 to 1983.

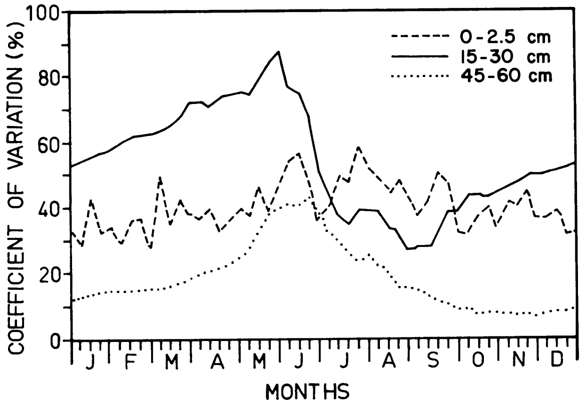

FIG. 7. Coefficient of variation of average soil water potential (n = 33 yr) through time for three different soil depth layers in the shortgrass steppe of northcentral Colorado.

storage and loss. The conclusion reached about adequacy will be dependent upon the temporal scale chosen for the assessment. At the annual scale, the CPER has the appearance of continuously dry conditions (Figs. 1 and 4). The atmospheric demand for water (PET) always exceeds the supply rate (PPT).

The depth distribution of wet soil appears to contradict the conclusion from the analysis of the ratio of PPT/PET that the soil should always be dry (Fig. 4). The fact that the relative frequency of wet soil in several of the layers is >0 indicates that averaging water supply and atmospheric demand and then calculating their ratios results in a dry soil bias. The magnitude of the bias depends upon the temporal scale of the data used in the calculation. We calculated the number of times, during the growing season, when the PPT/PET ratio was >1 for different time scales (Fig. 9). At a daily time scale, the PPT/PET ratio was >1 for ≈10% of the days. The frequency of PPT/PET >1 declined to 8% at a weekly time scale, and was ≈1% at monthly and longer time scales. This analysis explains the greater-than-zero frequencies of wet soil found in field data (Sala et al. 1981) and model results (Fig. 5).

In addition to the effect of averaging time on the results, the differences in the natural time scale of precipitation and potential evapotranspiration also explain the presence of wet soil in this apparently very dry climate. Precipitation events, defined as days with measurable precipitation, tend to be concentrated in time and can be described by a first-order Markov process (Noy-Meir 1973). The higher probability of a wet day following a wet day increases the likelihood that some of the water received will infiltrate into the soil and remain for a number of days. Further, the intensity of precipitation events (in millimetres per hour) exceeds the intensity of potential evapotranspiration and ensures that water supply will exceed demand during the event. Small events may only deposit enough water to keep the surface soil wet for a short time (Figs. 2 and 3; Sala and Lauenroth 1982). Large events will wet the soil to depths beyond the influence of evaporation resulting in stored water that will be lost mostly via transpiration.

The size distribution of precipitation events in the shortgrass steppe is biased toward the smallest sizes with events <10 mm accounting for >80% of all of the events. Small and large events have different effects on ecosystem processes and plant populations (Westoby 1980, Knoop and Walker 1985, Sala et al. 1989). Small precipitation events occur in similar numbers from year to year and provide approximately the same amount of water; they represent a small but less vari-

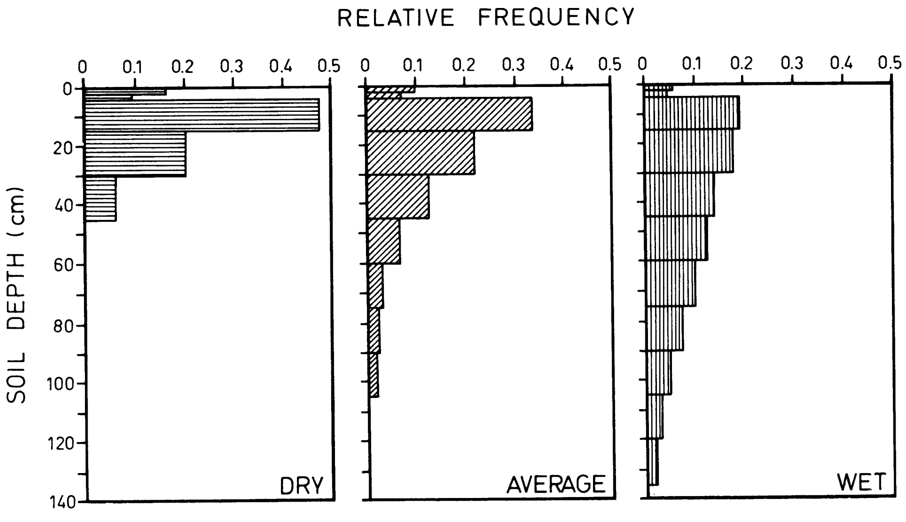

FIG. 8. Relative frequency of available water, as a function of depth in soils of the shortgrass steppe of northcentral Colorado, calculated as the proportion of the total number of wet days (all layers) that occurred in each layer. Wet days were defined as those that had a soil water potential > −1.0 MPa. Results from the eight driest and eight wettest years are graphed separately from the remaining 17 yr.

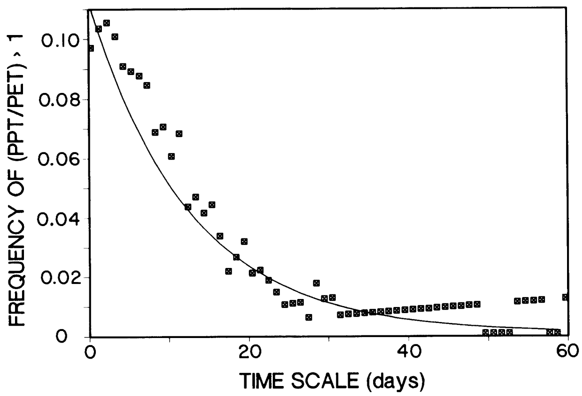

FIG. 9. Relative frequency of PPT/PET > 1 as a function of time scale. We calculated the relative number of times that PPT/PET > 1 when the time interval ranged from 1 to 60 d throughout the growing seasons of 33 yr. At a daily time scale, the relative frequency was defined as the number of 1-d periods when PPT/PET > 1, out of 5214 d (33 yr·158 d per growing season). At a 60-d time scale, it was the number of opportunities when PPT/PET > 1 out of 86 periods 60 d long. We fit a negative exponential model to represent the relationship between frequency of PPT/PET > 1 and time scale $y = 0.127 \cdot e^{-0.08x}$ ($r = 0.77$, $P < .01$).

able and more reliable resource than large events. However, water from such events wets only the surface soil layers and can be utilized only by plants with a very short response time (Sala et al. 1982*a*).

The interplay between the atmospheric demand for water and the size and frequency of precipitation events results in certain soil layers being wet more frequently and staying wet longer than others (Fig. 8). The atmospheric environment of the CPER is such that the demand for water is always high (Fig. 4). The size distribution of precipitation events is highly biased toward the smallest sizes. Sala and Lauenroth (1985) evaluated the potential of small events (5 mm) to wet soils differing in texture and antecedent soil water conditions and found that the depth of wetting was never greater than 8 cm. This suggests that sites with precipitation regimes dominated by small events will have soil water regimes characterized by the highest frequency of wet soil in the shallowest layers. The CPER is a good example of such a location. The layer with the highest frequency of wet conditions occurs between 4 and 15 cm. The layers above this are wet by precipitation more frequently, but the duration of wet conditions is less because of the large effect of evaporation.

The shallow depth distribution of available soil water matches the distribution of roots in the soil profile at the CPER. Of the total fine-root biomass, 56% is located in the 0–15 cm layer, and 75% is accounted for in the first 30 cm of the profile (Leetham and Milchunas 1985, Liang et al. 1989). The distribution of soil processes also has a pattern that matches that of soil water availability, suggesting a cause-effect relationship. Net nitrification and net nitrogen mineralization were maximal in the 5–10 cm layer (Schimel and Parton 1986). Phosphorus mineralization was maximal at the 2.5–7.5 cm layer (Cole et al. 1977).

The pattern of water availability in the soil profile as represented in the model changed from dry to wet years (Fig. 8). Dry years received fewer events and disproportionately fewer large events, which resulted in a decrease of the maximum depth of wet soil. During wet years deep layers became wet and soil water was more evenly distributed throughout the soil profile than during dry years.

Shortgrass steppe vegetation comprises four life-forms, grasses, shrubs, herbs and succulents, each possessing different patterns of root distribution (Dougherty 1986, Lee 1990). Succulents have the shallowest root systems followed by grasses that concentrate their biomass in the upper 15 cm of the profile (Dougherty 1986). In contrast, shrubs and herbs have deeper root systems. These characteristics of the different groups constrain the use of water from different soil layers. Grasses concentrate their roots where most of the available water is located, which may explain why this life-form dominates at the CPER and the shortgrass steppe. Grasses and *Bouteloua gracilis,* in particular, because of its rapid response to precipitation events, are able to use the least variable water resource (Sala and Lauenroth 1982). Herbs and shrubs have deep roots, suggesting that they use a more variable resource than the grasses. Succulents because of their shallow root systems are constrained to use a resource with a very short residence time but also with little variability among years. Therefore succulents should not be very sensitive to interannual variability in precipitation. From an analysis of the effects of wet and dry years upon the pattern of available water, and the rooting characteristics of different life-forms, we deduced that herbs and shrubs should have an advantage during the wettest years. In contrast, succulents may have an advantage during the driest periods. Grasses appeared to be best suited to utilize modal resources.

Analysis of the pattern of phenology and of seasonal availability of water suggests that species with an early phenological response, most of them C_3 species, should be using a deeper and more variable water resource than C_4 species. First visible growth occurs in the C_4 *Bouteloua gracilis* in mid-May, 1.5 mo later than in the C_3 *Agropyron smithii* (Dickinson and Dodd 1976). Since the former dominates the shortgrass steppe, we can speculate that in semiarid regions reliability may be an important characteristic of the resource exploited. We expect C_3 species in the shortgrass steppe to have deeper root systems than C_4 species. The northern mixed prairie that adjoins the shortgrass steppe on the north has the same grass species, but in a different proportion. Coupland and Johnson (1965) found for the northern mixed prairie that roots of the dominant C_3 species *Agropyron smithii* were deeper than *Bouteloua gracilis* where they grew in association.

The temporal and vertical spatial dynamics of soil water in the shortgrass steppe are dominated by infrequent wet conditions and a shallow depth distribution. Losses via evaporation occur throughout the year whereas transpiration is limited to the months when favorable temperature and water availability coincide. Patterns of soil water availability interact with morphological and physiological constraints of plant types (Orians and Solbrig 1977, Tilman 1988) to determine the life-form structure of vegetation and the associated root patterns. Finally, the vegetation structure along with the time–space pattern of available water defines the temporal and spatial pattern of ecosystem processes from nutrient cycling to primary production.

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Literature Cited

Bailey, H. P. 1979. Semi-arid climates: their definition and distribution. Pages 73–96 *in* A. E. Hall, G. H. Cannell, and H. W. Lawton, editors. Agriculture in semi-arid environments. Springer-Verlag, New York, New York, USA.

Cole, C. V., G. S. Innis, and J. W. B. Stewart. 1977. Simulation of phosphorus cycling in semiarid grasslands. Ecology **58**:1–15.

Coupland, R. T., and R. E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. Journal of Ecology **53**:475–507.

Dickinson, C. E., and J. L. Dodd. 1976. Phenological pattern in the shortgrass prairie. American Midland Naturalist **96**: 367–378.

Dougherty, R. D. 1986. The soil water resource of *Opuntia polyacantha* in semiarid grassland. Dissertation. Range Science Department, Colorado State University, Fort Collins, Colorado, USA.

Knight, D. H. 1973. Leaf area dynamics of a shortgrass prairie in Colorado. Ecology **54**:891–896.

Knoop, W. T., and B. H. Walker. 1985. Interaction of woody and herbaceous vegetation in southern African savanna. Journal of Ecology **73**:235–253.

Kohler, M. A., and M. M. Richards. 1962. Multi-capacity basic accounting for predicting runoff from storm precipitation. Journal of Geophysics Research **67**:5187–5197.

Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effect of water- and nitrogen-induced stresses on plant community structure in a semi-arid grassland. Oecologia (Berlin) **36**:211–222.

Lee, C. L. 1990. The spatial distribution of roots for three plant lifeforms in the shortgrass steppe. Thesis. Range Science Department, Colorado State University, Fort Collins, Colorado, USA.

Leetham, J. W., and D. G. Milchunas. 1985. The composition and distribution of soil microarthropods in the shortgrass steppe in relation to soil water, root biomass, and grazing by cattle. Pedobiologia **28**:311–325.

Liang, Y. M., D. L. Hazlett, and W. K. Lauenroth. 1989. Biomass dynamics and water use efficiencies of five plant communities in the shortgrass steppe. Oecologia (Berlin) **80**:148–153.

Monson, R. K., M. R. Sackschewsky, and G. J. Williams. 1986. Field measurements of photosynthesis, water-use efficiency, and growth in *Agropyron smithii* (C-3) and *Bouteloua gracilis* (C-4) in the Colorado shortgrass steppe. Oecologia (Berlin) **68**:400–409.

Nimah, M. N., and R. J. Hanks. 1973. Model for estimating soil water, plant, and atmospheric interrelations. II Field test of model. Proceedings of the Soil Science Society of America **37**:528–532.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics **4**: 25–52.

Orians, G. H., and O. T. Solbrig. 1977. A cost-income model of leaves and roots with special reference to arid and semiarid areas. American Naturalist **980**:677–690.

Parton, W. J. 1978. Abiotic section of ELM. Pages 31–53 *in* G. S. Innis, editor. Grassland simulation model. Ecological Studies Analysis and Synthesis **45.**

Parton, W. J., W. K. Lauenroth, and F. M. Smith. 1981. Water loss from a shortgrass steppe. Agricultural Meteorology **24**:97–109.

Penman, H. L. 1948. Natural evaporation from open water, bare soil, and grass. Proceedings of the Royal Society (London) **A 193**:120–145.

Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the patagonian steppe. Oecologia (Berlin) **81**:501–505.

Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events: an ecological role in semiarid regions. Oecologia (Berlin) **53**:301-304.

Sala, O. E., and W. K. Lauenroth. 1985. Root profiles and the ecological effect of light rainshowers in arid and semiarid regions. American Midland Naturalist **114**:406–408.

Sala, O. E., W. K. Lauenroth, and W. J. Parton. 1982*a*. Plant recovery following prolonged drought in a shortgrass steppe. Agricultural Meteorology **27**:49–58.

Sala, O. E., W. K. Lauenroth, W. J. Parton, and M. J. Trlica. 1981. Water status of soil and vegetation in a shortgrass steppe. Oecologia (Berlin) **48**:327–331.

Sala, O. E., W. K. Lauenroth, and C. P. P. Reid. 1982*b*. Water relations: a new dimension for niche separation between *Bouteloua gracilis* and *Agropyron smithii* in North American semiarid grasslands. Journal of Applied Ecology **19**:647–657.

Schimel, D. S., and W. J. Parton. 1986. Microclimatic controls of nitrogen mineralization and nitrification in shortgrass steppe soils. Plant and Soil **93**:347–357.

Smith, R. E., and H. A. Schreiber. 1974. Point processes of seasonal thunderstorm rainfall. 2. Rainfall depth probabilities. Water Resource Research **10**:418–426.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

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