

Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: A modeling analysis

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Abstract

We used the patch arid land simulator (PALS-FT) – a simple, mechanistic ecosystem model – to explore long-term variation in evapotranspiration (ET) as a function of variability in rainfall and plant functional type (FT) at a warm desert site in southern New Mexico. PALS-FT predicts soil evaporation and plant transpiration of a canopy composed of five principal plant FTs: annuals, perennial forbs, C_4 grasses, sub-shrubs, and evergreen shrubs. For each FT, the fractional contribution to transpiration depends upon phenological activity and cover as well as daily leaf stomatal conductance, which is a function of plant water potential, calculated from root-weighted soil water potential in six soil layers. Simulations of water loss from two plant community types (grass- vs. shrub-dominated) were carried out for the Jornada Basin, New Mexico, using 100 years of daily precipitation data (1891–1990). In order to emphasize variability associated with rainfall and fundamental differences in FT composition between communities, the seasonal patterns cover of perennials were held constant from year to year. Because the relative amount of year to year cover of winter and summer annual species is highly variable in this ecosystem, we examined their influence on model predictions of ET by allowing their cover to be variable, fixed, or absent.

Over the entire 100-yr period, total annual ET is highly correlated with total annual rainfall in both community types, although T and E alone are less strongly correlated with rainfall, and variation in transpiration is nearly 3 times greater than evaporation and 2 times greater than variation in rainfall (CV of rainfall = 35%). Water use shows a relatively high similarity between the grass- and shrub-dominated communities, with a 100-yr average T/ET of 34% for both communities. However, based on a year-by-year comparison between communities, T/ET was significantly greater in the grass-dominated community, reflecting the fact that over the long term more than half of the rain occurs in the summer and is used slightly more efficiently (T>E) by the C₄-grass community in a given year. Percent of water lost as transpiration (T/ET) suggests that while there is a general trend toward increased T/ET with rainfall in both community types, T/ET is extremely variable over the 100-yr simulation, especially for normal and below normal amounts of rainfall (T/ET values range from 1 to 58% for the grass-dominated site and 6 to 60% for the shrub-dominated site).

These predictions suggest that because of the relatively shallow distribution of soil water, there is little opportunity for vertical partitioning of the soil water resource by differential rooting depths of the plant FTs, in contrast to the two-layer hypothesis of Walter (1971). However, functional types may avoid competition by keying on particular 'windows' of moisture availability via differences in phenologies. We found very little differences in average, long-term model predictions of T, E, and ET when annual plant cover was variable, fixed, or absent. The results of our simulations help reconcile some of the disparate conclusions drawn from experimental studies about the relative contribution of transpiration vs. evaporation to total evapotranspiration, primarily by revealing the great year-to-year variability that is possible.

Introduction

Arid and semi-arid ecosystems of the southwestern United States are particularly vulnerable to climate variability, of which precipitation is the most important component (McClaran and Van Devender 1995). Since water is a major determinant of many processes in these desert ecosystems, a slight shift in seasonal precipitation and/or the frequency of extreme rain events could potentially lead to major ecological and biogeochemical impacts (Reynolds et al. 1999a; Schlesinger et al. 1990). Thus, in order for us to predict how these systems may respond to future climate change and other disturbances, we must have a quantitative understanding of how atmospheric, plant, and soil factors interact to control water fluxes. We must also understand how variation in vegetation cover and soil types may bring about changes in soil water distribution.

However, our current knowledge of atmospheric, plant, and soil interactions in aridlands is limited. For example, investigations of evapotranspiration have produced equivocal results, leading to very different conclusions regarding the importance of transpiration vs. evaporation in water loss. The percentage of total evapotranspiration attributable to transpiration is estimated to vary from as little as 7%, to as much as 80% in various arid and semi-arid ecosystems in North America (see Table 1). While some of these experimental differences are likely due to differences in methodologies, there are undoubtedly a number of significant underlying factors that could be important in controlling the timing and amounts of water lost as transpiration vs. evaporation. Because of the complexity of the many cause-effect relationships that exist within and between soils (e.g., infiltration, storage, surface evaporation, transpiration), plants (physiological mechanisms, phenology, plant-plant competition, etc.), and the atmosphere (radiation balance, variability in rainfall, etc.), it is extremely difficult for experimental studies to quantify the magnitude and importance of many of these interactions, particularly for longer time periods. Furthermore, these field studies were carried out in different locations and over relatively short time periods. As a result, these data provide an incomplete representation of the variability of evapotranspiration, especially as a function of annual variability in rainfall.

In this paper, we conduct a modeling analysis that focuses on several key components of the integrated system in order to examine – within the framework of a strict set of assumptions – how certain soil and plant factors may potentially interact to affect the loss of soil water (evapotranspiration) and the potential impact of long-term variation in rainfall upon evapotranspiration in an arid ecosystem. We use a physiologically-based ecosystem model to explore several specific aspects of soil water distribution and usage by various plant functional groups characteristic of plant communities of the northern Chihuahuan Desert, New Mexico. We address the following questions: (1) How do the relative amounts of transpiration and evaporation vary from year to year as a function of long term variation (100 years) in rainfall?; (2) Given the major vegetation changes that have occurred during the past century in many ecosystems of the southwestern U.S., how does the relative amount of grass vs. shrub cover affect the ratios of transpiration and evaporation?; (3) How does the relative amount of year to year cover of the most variable functional type in the northern Chihuahuan Desert – winter and summer annual species – affect model predictions of evapotranspiration?; and (4) What are the relative contributions of soil water from different soil layers to the transpirational water components from grass and shrub communities?

Methods

Site description

Our modeling research is based on data gathered at the Jornada Basin Long Term Ecological Research (LTER) site, which is located in a semi-arid rangeland of south-central New Mexico about 40 km NNE of Las Cruces, Doña Ana County. The Jornada Basin is part of the Mexican Highlands Section of the Basin and Range Physiographic Province and is at the extreme northern end of the Chihuahuan Desert.

Conley et al. (1992) characterized the climate of the Jornada as having three distinct seasons: hot, dry springs (April–June); hot, moist summers (July–October); and cold, moderately dry winters (November–March). Total annual precipitation is ca. 230 mm. Of this, nearly 65% falls during the summer period as localized showers associated with thunderstorms; about 25% falls in winter as rain and snow associated with frontal storms over the region; and about 10% occurs in the spring. Following Reynolds et al. (1999b), we simplify this by considering just two seasonal components: *summer* (June 1–September 30) and *winter/spring* (October 1–May 31).

The Jornada Basin was formerly dominated by warm-season perennial grasses (e.g. *Bouteloua eriopoda*), but much of the area is now dominated by shrubs (e.g., *Larrea tridentata* and *Prosopis glandulosa*) (Figure 1). This transition was initiated in the late 1800s and early 1900s as a result overgrazing, climate change, or other factors (Buffington and Herbel 1965). The Jornada Basin now contains remnant grassland communities, but most areas are dominated by shrubs

Table 1. Experimental estimation of water loss in various arid and semi-arid ecosystems in North America. Key: T=transpiration; ET=evapotranspiration.

Desert – Location	Community type	% Plant cover	% T/ET	Experimental method	Reference
Sonoran – Arizona, USA	Larrea	22	7	Large lysimeter (compared bare soil vs. vegetated)	Sammis & Gay (1979)
Sonoran – Arizona, USA	Mixed	10–30	5–25	Soil water budget or lysimeter (bare soil vs. vegetated)	Evans et al. (1981)
Mojave – Nevada, USA	Mixed shrub	-	35	Integrated leaf transpiration (plant and whole canopy) & measured evaporation from bare soil)	Smith et al. (1995)
Death Valley - California, USA	Mixed shrub	-	53	Separate measurements of plant transpi- ration and soil evaporation (bare areas)	Stark (1970)
Great Basin – Utah, USA	Ceratoides- Atriplex	_	54	Integrated leaf transpiration (plant and whole canopy) & soil water budget (with assumptions about evaporation from bare soil)	Caldwell et al. (1977)
Chihuahuan – New Mexico, USA	Larrea	30	72	Thermocouple hygrometers in vegetated vs. bare soil plots.	Schlesinger et al. (1987)
Sonoran – Arizona, USA	Larrea	-	80	Distribution of isotopes in soil to estimate long-term soil water budget (^{36}Cl) and seasonal evaporation $(^{2}H, ^{18}O)$	Liu et al. (1995)



Figure 1. Changes in the percent of land area dominated by shrubs and grass on the Jornada Experimental Range from 1858 through 1962. Areas with greater than 55% mesquite (*Prosopis*) increased from 2500 to 27,000 ha, creosotebush (*Larrea*) from 0 to 5000 ha, and tarbush (*Flourensia*) from 0 to 1800 ha. At the same time 'brush free' grassland dropped from 34,000 to 0 ha. Adapted from Buffington & Herbel (1965).

or co-dominated by shrubs, sub-shrubs, forbs, succulents, and grasses. Further details of the Jornada LTER site and data collection are provided in Wierenga et al. (1987), Cornelius et al. (1991) and Kemp et al. (1997); the geomorphology and soils of the study site have been described by Gile et al. (1981).

Vegetation, weather, and soils data used for the model development and validation reported in this paper were collected from a 2700-m transect established in 1982 as part of the Jornada LTER (Figure 2). The vegetation along this transect encompasses a variety of plant assemblages and soil types (Cornelius et al. 1991; Wierenga et al. 1987), which may represent various stages in the grass-shrub transition or, at least, are composed of different combinations of plant functional types (FT) representative of this transition. For our simulation study of soil water distribution and predicted evapotranspiration, we selected two plant communities from along the transect as surrogates of two distinct stages in the grass - shrub transition shown in Figure 1: Station 35, which is dominated by grasses and annual species (representative of ca. 1930) and Station 65, which is dominated by the evergreen shrub L. tridentata and various species of sub-shrubs (representative of since ca. 1970).

Model description

The Patch Arid Land Simulator (PALS) is a physiologically-based ecosystem model that contains principal components of ecosystem carbon, water, and nitrogen cycling (Chen and Reynolds 1997; Reynolds et al. 1997, 1999a). PALS-FT consists of three modules: soil water, energy-budget/atmospheric environ-



Figure 2. Elevation and distribution of sand and clay along transect at Jornada Basin LTER site in New Mexico. Small squares show location of two stations used to develop and test PALS-FT. Vegetation varies along the transect with generally high cover of grass (*Panicum obtusum*), annuals, and forbs in the playa (stations 1–7), honey mesquite (*Prosopis glandulosa*) and grass (*Muhlenbergia porteri* and *Hilaria mutica*) in the playa fringe (stations 8–10), a broad zone of relatively open mixed vegetation dominated by grasses (e.g., *Aristida longiseta* and *Erioneuron pulchellum*) and annuals and with sub-shrubs (*Xanthocephalum sarothrae*) and forbs (stations 11–57), a zone dominated by creosotebush (*Larrea tridentata*; stations 58–72) in the middle bajada, and a grassland (e.g., *Bouteloua eriopoda, Muhlenbergia porteri*, and *Erioneuron pulchellum*) on piedmont slopes at the base of Mt. Summerford (stations 73–90).

ment, and the physiology and phenology of the principal plant functional types (life forms) found in the Jornada Basin. The modules interact with one another in a one-dimensional fashion, although the model represents patches of vegetation of approximately 1-10 m² (a size that includes all of the functional types listed above; see Reynolds et al. 1997). The results presented here are from our phenology-based version (PALS-FT), which includes the following key plant functional types (FT) of the northern Chihuahuan Desert (following Kemp et al. 1997):

FT: *annuals* (winter or summer active species); FT: *perennial forbs* (species active from spring through autumn);

FT: *grasses* (all are C₄, summer-active species); FT: *sub-shrubs* (primarily winter deciduous; *Xan-thocephalum* and *Zinnia* spp.);

FT: evergreen shrub (primarily Larrea tridentata).

Soil water in PALS-FT is modeled using a modified version of the SWB model (Baier and Robertson 1966). We recently performed an extensive parameterization and validation study using data from the Jornada LTER transect to compare three soil water models (Kemp et al. 1997). As a result of this study, we opted to use SWB in PALS-FT since we found its performance was as good, or better, than more detailed models at depths above 90 cm (which includes virtually all of the water transpired or evaporated at our site; Reynolds et al. 1999b). Complete details of SWB are provided in Kemp et al. (1997); a brief overview is given below.

Soil water is represented in 6 layers (the thickness of the upper two layers are 10 cm; all others are 20 cm). Infiltration adds water to soil layers in a cascading fashion according to water holding capacities of the layers, with no redistribution of water among the layers. Water holding capacity of each layer is based on soil moisture retention between water potential values of -0.025 and -10 MPa; soil water potential is determined using the equation of Campbell et al. (1993) with parameters determined from soil texture (see Table 4 in Kemp et al. 1997). Water is removed from the top two layers by evaporation and from all layers by transpiration. Removal of soil water via evaporation follows the Linacre (1973) approach, which is a function of the evaporative energy input to the soil surface (Equations 22-23 in Kemp et al. 1997). Energy to the surface is partitioned between soil (evaporation) and vegetation (transpiration) by assuming that the total leaf area of the vegetation uniformly intercepts solar radiation according to Beer's law (Equation 14 in Kemp et al. 1997, Nichols 1992, Ritchie 1972). Removal of water from the soil via transpiration is related to the transpirational capacity of the plant canopy, which is determined by a simple energy budget model and a canopy stomatal resistance function that is a composite of the resistances of the individual FTs (Equations 12-13, 15, 17 in Kemp et al. 1997). The water transpired from the soil is partitioned among the soil layers according the fraction of total roots of all FTs in each layer (Equation 4, Kemp et al. 1997).

Calculation of both transpiration of the plant canopy and water uptake from soil layers depends upon the contributions to the processes from each of the plant FTs. The composite canopy stomatal resistance (1/canopy conductance) is calculated as the reciprocal of the sum of the stomatal conductances times the leaf area index of each FT (Equation 16,

Table 2. Prescribed fractional root distributions (RF_{ij} , Equation 3) based on optimizing SWB to soil water data for the year 1986. RF_{ij} was determined using least squares fitting of predicted soil water contents to observed soil water contents at five stations along the LTER transect. Further details given in Kemp et al. (1997).

Soil depth	Plant functional type						
	Annual	Forb	Grass	Subshrub	Larrea		
0–10 cm	0.2	0.1	0.1	0.05	0.05		
10–20 cm	0.3	0.2	0.15	0.20	0.1		
20–40 cm	0.5	0.3	0.35	0.25	0.45		
40–60 cm	0	0.2	0.2	0.25	0.3		
60–80 cm	0	0.2	0.2	0.25	0.1		
80–100 cm	0	0	0	0	0		

Kemp et al. 1997). Stomatal conductances (g_j ; moles m⁻² s⁻¹) of individual plant FTs (j) are calculated as a function of plant water potentials ($\Psi_{\text{plant},j}$; MPa) and atmospheric vapor pressure deficit (VPD; kPa), where g_j is an exponential function of $\Psi_{\text{plant},j}$, with a linear reduction due to VPD:

$$g_j = a_j e^{\lfloor b_j \cdot \Psi_{\text{plant},j} \rfloor} \{1 - 0.1 \text{VPD}\}.$$
(1)

For the shrub *L. tridentata*, we use the following modified form of Equation (1):

$$g_{\text{Larrea}} = 0.52 + 0.081 \Psi_{\text{plant, Larrea}}$$
$$- 0.064 \text{VPD.}$$
(2)

Values used for parameters *a* and *b* are given in Table 1 of Kemp et al. (1997). We assume that Ψ_{plant} is at equilibrium with the average of the soil water potential (Ψ_{soil}) of all soil layers weighted by the fraction of roots in each layer, *i*:

$$\Psi_{\text{plant},j} = \sum_{i} \left[RF_{i,j} \cdot \Psi_{\text{soil},i} \right], \tag{3}$$

where RF_{ij} is the fraction of roots in soil layer *i* of functional group *j*. RF_{ij} was determined using least squares fitting of predicted soil water contents to observed soil water contents at five stations along the LTER transect (Table 2).

Model validation and simulations

First, we conducted an analysis/assessment of the behavior of PALS-FT at stations 35 and 65 based on plant cover and soil water data collected during 1986 (a year in which complementary soil and plant cover data are available). The vegetative cover of each species was measured along a 30-m line transect (perpendicular to the main transect) at each station during



Figure 3. (Top panels) Fraction of the ground covered by each functional type at stations 35 and 65 during 1986. These values are approximations based on actual measurements at 2 times during the year (ca. day 120 and 270), and on general patterns at this site recorded at biweekly intervals for the previous three years. (Bottom panel) Cover of annual functional type used to mimic values characteristic of low-to-moderate cover of winter and summer annuals during the course of a year. Used in simulation scenario (2).

spring 1986 (mid-April) and autumn (mid-October), which provides estimates of peak above-ground standing crop for the winter/spring and summer periods, respectively; a more intensive estimate of cover and plant phenology obtained biweekly on 1-m² plots at each station during a three-years period (1982–1984) prior to 1986 was used as an aid to estimate changes in cover during the growing periods leading up to the development of maximum cover (Figure 3). We estimated leaf area (required for calculations of transpiration) from plant cover data based on literature values for dominant species in each plant FT (Table 1 in Kemp et al. 1997). Volumetric soil water content at stations 35 and 65 were measured biweekly in 1986 at 30, 60, 90, 120 and 150 cm depths using a neutron scattering probe (calibrated at the middle of the transect) and soil water potential was measured biweekly at 5, 15 and 30 cm depths using thermocouple psychrometers. Further details of the soil water data collection and protocols used are given in Wierenga et al. (1987). Rainfall in 1986 was 321 mm, which was 35% above the long-term mean for the Jornada Basin (normal = 233 mm). The seasonal distribution was approximately that of an average year with about 60% falling in summer (June through September).

Second, to examine the effect of rainfall variability on evapotranspiration, we conducted 100-yr simulations where daily rainfall values from 1891-1990 were input from long-term weather data obtained from a nearby weather station in Las Cruces, NM (ca. 30 km SW of the site). Since our objective was to isolate the effects of variability in annual rainfall upon variability on soil water and evapotranspiration, we sought to minimize other sources of variability. Thus, we modeled daily temperatures, humidity, and solar radiation with the same annual progression from year to year. We did this by simply repeating these weather data for 1986, a year with essentially 'average' weather. This obviously results in errors on rainy days; however, the mean number of rainy days at this site is only 22 (the mean number of cloudy days is only 40), and we deemed these errors to have only a small impact. Furthermore, the fixed annual progression of weather is reproducible and emphasizes variation in rainfall alone.

The seasonal dynamics of vegetative cover of the perennial functional types at each station was also fixed at 1986 values (as in Figure 3). However, because the cover of annual plants is highly variable from year to year in the northern Chihuahuan Desert (Guo and Brown 1997, Kemp 1983), we explored the impact of cover of annual species on our model predictions of evapotranspiration by carrying out three scenarios (Table 3): scenario (1) *variable* seasonal cover of annuals from year to year as predicted by the phenology and growth functions in PALS-FT (described in Reynolds and Kemp [upublished manuscript], including extensive validation using LTER field data); (2) *fixed* seasonal cover of annuals in each year (Figure 3); and scenario (3) *no* annual species present.

Results

Model behavior: 1986 data

Simulated soil moisture in 1986 for station 35 (grassdominated) closely approximated the pattern of observations at 30 cm (with a slight over-estimation), whereas simulated soil moisture at 60 cm was substantially overestimated in spring (Figure 4). The error at 60 cm was probably due to soil moisture redistribution, which was not accounted for in our water budget model. Other soil water models fitted to these data - which incorporate soil water redistribution predict some redistribution from this layer, with redistribution toward the surface resulting in either greater evaporation or greater transpiration, depending upon the model (Kemp et al. 1997). Normally, soil moisture redistribution in these desert soils appears to be relatively unimportant (Kemp et al. 1997; Wierenga et al. 1987), but 1986 followed two years of much above-normal rainfall, which likely resulted in relatively high soil moisture deeper in the profile, favoring water redistribution both upward into the root zone and downward out of the root zone. However, the impact of this winter-spring redistribution upon predicted annual evapotranspiration appears minor, since even in this unusual situation, the vast majority of evaporation and transpiration occurs during the summer, when predicted patterns of soil water content more closely matched observed values.

Simulated soil moisture for station 65 (shrubdominated) deviated from observations primarily in summer and primarily at the 30-cm depth (Figure 4). We suspect that these discrepancies occur because this version of PALS-FT does not account for runoff (all precipitation enters the soil). Given the coarse-texture of this soil and its water holding capacity, PALS-FT predicted soil water recharge to 30 cm (or below) for several rainfall events in 1986 (27 mm on day 176 and 19 mm on day 190) (Figure 4). In fact, our field data shows that neither of these precipitation events resulted in recharge at 30 cm at this station. Hence, we conclude that runoff may explain these discrepancies. Runoff along this transect during some large summer rainfall events can be substantial (Schlesinger et al. 1999), but is also highly variable, depending upon rainfall intensity (primarily), antecedent soil moisture, the nature of the surface soil, and plant community type and cover. In this version of PALS-FT, we do not account for runoff along the transect since we do not have data for rainfall intensity, and attempts to incorporate runoff as a function of total daily rainfall resulted in greater error than not accounting for it all. Thus, for sites where runoff may be greater than average (such as the L. tridentata site at station 65), the model will overestimate the amount of transpiration. Similarly, transpiration will be underestimated

Table 3. Cover of functional types (FTs) used in model simulations.

	1 year	100 years (1891–1990)				
	1986 validation	Scenario (1)	Scenario (2)	Scenario (3)		
Station 35 (grass-dominated)						
Cover (all FTs, except annuals)	Figure 3 (station 35)	Figure 3 (station 35)	Figure 3 (station 35)	Figure 3 (station 35)		
Cover, annual FT	Figure 3 (station 35)	Variable, predicted by	Figure 3 (annuals fixed)	None		
		PALS-FT				
Station 65 (shrub-dominated)						
Cover (all FTs, except annuals)	Figure 3 (station 65)	Figure 3 (station 65)	Figure 3 (station 65)	Figure 3 (station 65)		
Cover, annual FT	Figure 3 (station 65)	Variable, predicted by	Figure 3 (annuals fixed)	None		
		PALS-FT				



Figure 4. PALS-FT predictions vs. measurements of soil water at 30 cm and 60 cm depths during 1986 at stations 35 and 65 of LTER transect. Based on scenario (2). See Kemp et al. (1997) for a more detailed description of an intensive validation study that we conducted for five stations along the LTER transect over a 2-y period.

	Scenario (1)		Scenario (2)		Scenario (3)	
	Mean	% CV	Mean	% CV	Mean	% CV
Precipitation (1891–1990)	22.8 cm	35	22.8 cm	35	22.8 cm	35
Station 35 (grass-dominated)						
Transpiration (T)	8.2 cm	62	8.2 cm	60	8.0 cm	58
Evaporation (E)	14.2 cm	24	14 cm	24	14.4 cm	24
T/ET ^a	34%	41	32%	40	31%	40
% of total transpiration from 0-40cm	86%		84%		82%	
Station 65 (shrub-dominated)						
Transpiration (T)	8.4 cm	63	8.3 cm	62	8.2 cm	60
Evaporation (E)	14.0 cm	26	14.1 cm	26	14.4 cm	26
T/ET ^a	34%	37	34%	36	33%	34
% of total transpiration from 0-40cm	78%		78%		76%	

Table 4. Predicted 100-year (1891–1990) means and coefficients of variation for precipitation, transpiration, and evaporation. Scenarios described in Table 3.

^aDaily values of E and T predicted by PALS-FT summed for each year to produce annual values; from this, annual T/ET calculated.

for sites that accumulate water via run-on (see example in Schlesinger and Jones 1984).

These results are based on scenario (2): a *fixed* seasonal cover of annuals each year. Patterns of soil water dynamics for scenarios (1) and (3) were generally the same and, hence, not presented (see Discussion)

1891–1990 simulation

Predicted 100-year (1891-1990) means and coefficients of variation for transpiration (T), evaporation (E), and evapotranspiration (ET) based on the three scenarios are summarized in Table 4. In Figures 5b and 5c, the predicted patterns of cover for summer and winter annual species (scenario (1)) over this 100year period are shown, along with actual rainfall. These patterns of cover for summer and winter annuals - which show great year to year variability are consistent with long term (18 years) observations reported by Guo and Brown (1997) in the Chihuahuan Desert. When compared to scenario (1), we found few differences in model predictions and essentially no differences in the 100-year means of T, E, and ET when annual plant cover was fixed (scenario (2)) or absent (scenario (3)) (Table 4). Hence, below we describe results from scenario (1) only.

Total annual ET was highly correlated with total annual rainfall in both community types (Figure 6). However, T and E alone are less strongly correlated with rainfall, and variation in transpiration is nearly 3 times greater than evaporation (coefficient of variation [CV] = 62% - 63% vs. 24% - 26%) and 2 times greater than variation in rainfall (CV of rainfall = 35%) (Table 4). A calculation of the percent of water lost as transpiration (T/ET) shows that while there is a general trend toward increased T/ET with rainfall in both community types, T/ET is extremely variable over the 100-yr simulation, especially for normal and below normal amounts of rainfall (Figure 6). T/ET values range from 1 to 58% for the grass-dominated site (station 35) and 6 to 60% for the shrub-dominated site. A comparison of the water loss over the entire 100-yr period indicates a relatively high similarity between the grass- and shrub-dominated communities (Figure 5a). T/ET averaged ca. 34% for both communities (CV = 34 to 41%). However, based on a year-byyear comparison between communities (paired *t*-test), T/ET was significantly greater (p < 0.001) in the grass-dominated community.

Sources of evapotranspiration: soil layers and FT

Water extraction via evaporation occurs primarily from the top 10 cm of soil (top soil layer) (Table 4). Although there is provision in PALS-FT for evaporation from the second 10-cm layer if the top one dries below -10 MPa, this happens only rarely, and the amount of water removed is small. Transpiration can occur from all layers in the profile, depending to some extent upon plant FTs and their root distributions. Annual plants are constrained to remove water only from the top 40 cm of the soil, whereas the other functional types



Figure 5. (A) Ratio of annual transpiration (T) to evapotranspiration (ET) expressed as a ratio comparing a grass- (station 35) to a shrub (station 65)-dominated community at the Jornada LTER site in New Mexico as predicted by PALS-FT (scenario (1)). (B-C) Predicted summer and winter annual cover; converted from model predictions of biomass (g m⁻²) using relationship in Table 1 of Kemp et al. (1997). (D) Annual and summer season rainfall from 1891–1990 from Las Cruces, N.M (40 km SW of the Jornada LTER site).

can remove water from throughout the top 80 cm (see Table 2). The source of water transpired by various FTs from different depths in the soil are shown for the average of the 100-year simulation in Figure 7. The most important source of water for all functional types is from 10 to 40 cm (Table 4). These layers are wetted by many of the rains but are not subjected to the high level of evaporation that quickly drains the top 10 cm.

In order to evaluate the contribution of shallow versus deep soil water to transpiration, we calculated the volume of water transpired from the top 40 cm and the bottom 40 cm (40-80 cm). With variable annual cover (scenario (1), Figures 5b and 5c), 90% of transpiration was from the top 40 cm of the soil in the grass community, and 86% of transpiration was from the top 40 cm of soil in the shrub community (Table 4). This small difference was significant over the 100-yr period (t = 2.52, p < 0.01). With fixed seasonal cover values for annual plants (scenario (2)), the predicted fraction of transpirational water loss from the top 40 cm was slightly lower in both communities. With no cover of annuals, the predicted percentage of transpiration from the top 40 cm was 86% for the grass community and 78% for the shrub community (t = 4.83, p < 0.001). As a further check on soil moisture distribution in shallow versus deep soil, we kept track of all water moving into the lowest soil layers (80-100 cm and below 100 cm). In only one year (1935) was there any water recharge below 100 cm, and in only two other years was water recharged below the 80-cm depth.

Discussion

Variability in annual evapotranspiration

Results from this modeling study help reconcile some of the divergent conclusions that have been reached in the literature (Table 1) regarding evapotranspiration (ET) in arid/semi-arid ecosystems, especially regarding the contribution of transpiration (T) to the total water loss. Our model predictions for a warm semiarid site in New Mexico suggest that while long-term total evapotranspiration is highly correlated with total annual rainfall, the proportion of transpiration (T/ET) is extremely variable, constituting from 1-60% of the total ET. Some of this variability is explained by variability in total annual rainfall, with T contributing proportionally more to the total water loss in wet years (Figure 6). However, for a specific annual precipitation amount, there may be quite different T/ET responses, as a result of differences in inter- and intraseasonal distribution of rainfall and its utilization by different plant functional types (FTs). For example, in 1965 and 1966, two successive years with nearly normal rainfall, predicted T/ET values for the grass-dominated community were 22% and 32%, respectively, compared to 33% and 43% for the shrub-dominated community. The variation in T among the different FTs at



Figure 6. Annual evapotranspiration (ET), transpiration (T), evaporation (E), and T/ET for grass- (station 35) and shrub (station 65)-dominated communities as predicted by PALS-FT (scenario (1)) using daily rainfall from 1891–1990. Simple linear regressions are all highly significant (p < 0.001).

these two communities for these two years is shown in Figure 8.

Even greater variation in T/ET can be found as annual precipitation declines below average. For example, in 1953 and 1970, there was similar summer and total annual precipitation but total precipitation about 40% of normal in both years. PALS-FT predicted T/ET values for the grass- and shrub-dominated communities were 1% and 13% (in 1953) vs. 24% and 32% (in 1970), respectively. In both of the examples cited above the shrub-dominated community had greater T/ET than the grass-dominated community, even though over the 100-year period the average T/ET was identical (34%, Table 4). It should also be emphasized that this variation attributable to plant functional type (FT) responses to differences in seasonal rainfall distribution, and not to changes in perennial vegetation cover per se, which was held constant between years.

Our finding that the annual plant cover, which we varied, held fixed, or omitted (i.e, scenarios (1)–(3), Table 3), had little impact (Table 4) was unexpected.



Figure 7. Model predictions of the source of soil water transpired by various plant functional types. Shown are averages of 100-y simulations grouped by three major soil depths.

We attribute this to two factors. One, the annual (winter and summer) FTs usually represent a small percent of the total community biomass and LAI compared to the perennial vegetation. Second, in the absence of annuals, the other plant FTs were able to utilize the available water and thus the overall effect on total transpiration, evaporation, and T/ET was small. However, high year to year variation in annuals may be most important in terms of their effects on biogeochemical cycling (Guo & Brown 1997), which we are not considering in this version of PALS-FT. Another somewhat unexpected result was that water loss over the entire 100-yr period suggests a relatively high similarity between the grass- and shrub-dominated communities (Figure 5a), with T/ET averaging 34% for both communities. However, based on a yearby-year comparison between communities, T/ET was significantly greater in the grass-dominated community (paired t-test). This appears to reflect the fact that over the long term more than half of the rain occurs in the summer and is used slightly more efficiently (T>E) by the C₄-grass community than the shrub community, although there were obviously some rainfall patterns that resulted in much greater T/ET in the shrub community in a given year (Figure 5a). Thus,

the T/ET response of the plant community depends heavily upon the overall amount of precipitation as well as its inter- and intra-seasonal patterns of distribution. Short-term field studies of evapotranspiration in a warm desert community will be unlikely to capture the variation that is possible at a particular site or within a particular community. Furthermore, we suggest that the variability predicted by the PALS-FT may be a relatively conservative estimate, since we do not incorporate year-to-year variation in cover of perennial plants, effects of run-on and runoff, and numerous potential feedbacks associated with nutrient availability.

In a modeling study in the northern Mojave desert, Lane et al. (1984) found that over a nine-year period T/ET varied from 15 to 37%. Although this variation is considerably less than what we found, it was over a much shorter period of time. The seasonal distribution of rainfall at this site is also different from the northern Chihuahuan desert, with about 60% of the rainfall occurring during the winter (compared to about 25% at the Jornada Basin). Nevertheless, they reached conclusions similar to ours: namely, that variability in annual rainfall produces even greater variation in transpiration, which can only be predicted by evaluating the responses of various plants to the daily (seasonal) moisture inputs and soil moisture availability.

A study by Campbell and Harris (1977) in the northwestern part of the Great Basin cold desert (sagebrush/grass community of southeastern Washington state) provides an interesting contrast with our results. Their site receives nearly the same annual rainfall $(\approx 250 \text{ mm})$ as the Jornada Basin, but a large majority falls in late autumn/winter (75% in October-March). Although they report data only for a dry year ($\approx 40\%$ below normal rainfall) and wet year (\approx 40% above normal rainfall), they concluded that the T/ET would vary directly as a function of rainfall because total soil evaporation was roughly constant annually (almost all occurring in winter/spring during periods of low PET). Variability of T/ET is probably relatively lower in this system (compared to warm deserts) also because the variability of annual rainfall is somewhat lower than at the Jornada (Heerman et al. 1971).

Sources of soil water: partitioning by functional types?

Walter (1971) hypothesized that coexistence between different life forms in semi-arid ecosystems is fostered by having a separation of soil moisture into two



Figure 8. Predicted transpiration by plant functional types during 1965 and 1966, two years with nearly identical (and average) rainfall. Note major differences between years.

reservoirs–a surface one available to grasses, forbs, and other shallow-rooted plants, and a subsurface one available only to deep-rooted shrubs and trees. While there is support for this hypothesis in semi-arid systems with annual rainfall greater than about 30 cm (e.g., Archer et al. 1988, Cable 1969, Walker and Noy-Meir 1982), studies in arid ecosystems with less rainfall have either been supportive (e.g., Caldwell 1985, Ehleringer et al. 1991, Noy-Meir 1973, Paruelo and Sala 1995, Sala et al. 1989) or not (e.g., Hunter

1989, Montaña et al. 1995, Peláez et al. 1994, Smith et al. 1995).

In our 100-year simulation, we found that most of the rainfall remained in the upper part of the soil (top 40 cm) and was quickly lost either to surface evaporation or transpiration. On average, we found only about 10–20% of the annual rainfall penetrated below 40 cm, and there was almost no deep (>80 cm) soil water recharge (three occasions in 100 years). These predictions are consistent with numerous field studies in the northern Chihuahuan desert region indicating that most rainfall remains in the surface soils with little or no deep soil water recharge: e.g., direct studies of soil water recharge during periods of average or above average rainfall (Reynolds et al. 1999b; Scanlon 1994; Wierenga et al. 1987); the development of petrocalcic layers at depths of 40–80 cm (indicating average maximum depth of soil wetting over very long periods; Gile et al. 1981; Marion et al. 1985); and penetration of 36Cl nuclear fallout to depths of less than 100 cm (indicating percolation of liquid water over a 35-y period, Phillips 1994; Scanlon 1992)

Our conclusion - that there is a general lack of deep soil water recharge in the northern Chihuahuan desert – is probably applicable to other warm desert sites in southwestern North America with similar or less annual rainfall. For example, Phillips (1994) reviewed studies of the distribution of various meteoric tracers in soils of the southwestern U.S. (Chihuahuan, Sonoran, and Mojave deserts) and concluded that the soil water distributions were remarkably similar across sites of varying climate, soils, and vegetation. The pattern of soil distribution reflects a 'dry climate regime' in which there is little deep soil water recharge because of the efficiency of extraction by vegetation and the atmosphere. Smith et al. (1995) studied soil moisture and plant water use on three different geomorphic surfaces (ephemeral wash, dissected alluvial fan, and montane slope) in the central Mojave desert and found that although the plant communities on these surfaces differed in dominant species and water-use patterns, there was no deep percolation during a year with normal rainfall.

We suggest that there is a lower threshold of rainfall (well above extreme aridity) below which there will be insufficient deep moisture percolation to maintain a subsurface reservoir. This limit will depend to some extent upon local site factors that could modify the extent of subsurface soil water recharge (e.g., soil texture, vegetation structure) (Cable 1980; Stephens 1994), but will be mostly a function of the regional climatic regime: primarily seasonal rainfall and potential evaporation. At the wetter end of semi-arid climates, there are probably several climatic regimes that could result in a two-tiered soil moisture resource. Perhaps the most common is a bimodal rainfall pattern, with winter rainfall (low potential evaporation) resulting in a single recharge of the lower soil layer and summer rainfall providing a continuous recharge of the surface layer (e.g., Ehleringer et al. 1991). A unimodal rainfall pattern, with a late spring peak also results in recharge

of the subsurface soil water (during the early part of the season) followed by a continued recharge of the surface during summer (e.g., Archer et al. 1988). As annual rainfall decreases (below ca. 25-30 cm in a subtropical climate), the climatic regimes capable of producing relatively deep soil moisture recharge will become more restricted, requiring a greater concentration of moisture during the period of lowest potential evaporation (e.g., Sala et al. 1989) and ultimately ending up with a surface resource insufficient to support substantial grass cover. In temperate climates the minimum precipitation threshold for deep soil recharge may be less than in subtropical climates, especially in regions with predominately winter rainfall, since during winter, potential evaporation is low and plants are mostly dormant during this period. For example, in much of the Great Basin cold desert region of westcentral U.S., the majority of precipitation occurs in winter and spring resulting soil moisture recharge to 1 meter or more (Caldwell 1985; Campbell & Harris 1977).

Jornada Basin: drinking from the same cup

The relatively shallow distribution of soil water in the Jornada Basin suggests that there is limited opportunity for vertical partitioning of the soil moisture resource by different functional-types in this warm desert. Certainly, the roots of desert plants differ to some extent in their distributions, and in some cases this may result in water resource partitioning (e.g., Briones et al. 1996; Sala et al. 1997). Perhaps the best examples are of relatively shallow vertical partitioning with use of only near-surface moisture by succulents and annuals (Cannon 1911; Nobel 1976; Rundel & Nobel 1991; Yeaton et al. 1977). However, most plants (including some annuals) of these warm deserts have their roots distributed throughout the top 0.5 m of soil, corresponding to where the vast majority of the soil water is distributed (e.g., Briones et al. 1996; Brisson and Reynolds 1994).

The proportions of soil water available to the various functional types depends upon the inter- and intra-seasonal distributions of the annual precipitation, in conjunction with the phenological patterns of the plants. There is phenological progression (part genetic and part plastic) among the various plant functional types that fosters a capacity for utilizing a particular 'window of moisture opportunity' (Kemp 1983). Thus, the plant functional-type makeup of the plant community can result in relatively different patterns of soil moisture use, depending upon the temporal distribution of the moisture. For example, a year with a large amount of precipitation in mid summer would favor growth (transpiration) of C₄ grasses and summer annuals; a year with a large amount of precipitation in winter and early spring would favor evergreen shrubs and winter annuals (Kemp 1983; Neilson 1986). In this sense, we are inclined to favor Hunter's (1989) analogy for warm desert systems: that most of the plants are 'drinking from the same cup with different straws.' However, we might add, '... but not always at the same time'.

While models are not a substitute for observations and experimental measurements, we believe that they can contribute to our understanding of complex and highly interacting process, such as evapotranspiration in arid and semi-arid regions. Models help overcome some of the limitations of experimentation, e.g., permitting examination of long-term variation, allowing greater controls or manipulations (e.g., fixed plant cover) than possible under field settings. At the same time, we recognize that PALS-FT represents a highly simplified view of this complex ecosystem. Nevertheless, we suggest that the results of the present study provide insight into (i) the variability that can be expected in evapotranspiration in warm desert ecosystems, and (ii) some of the key processes that control this variability. We are currently incorporating additional elements into PALS-FT, including growth dynamics, changes in perennial vegetation, and the role of decomposition and soil nutrients. These additions, plus further advances in our understanding of desert hydrology - particularly run-on and run-off processes - will help improve our ability to model the effects and interactions of various ecosystem processes and feedbacks upon soil water distribution and evapotranspiration in arid systems. This is especially interesting in the context of historical vegetation dynamics such as those that have occurred in the Jornada Basin (Figure 1).

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