

The ecohydrological role of soil texture in water-limited ecosystems.

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## The ecohydrological role of soil texture in a water-limited ecosystem

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**Abstract.** Soil texture is a key variable in the coupled relationship between climate, soil, and vegetation. This coupling and its dependence on soil texture are studied in this paper using analytical descriptions for soil moisture dynamics and the corresponding vegetation water stress. Results confirm the importance of soil texture in partitioning rainfall into the mean values of the water balance loss components, namely, evapotranspiration, leakage, and runoff, and in determining vegetation water stress for the vegetation and climatic regimes of the La Copita Research Area in Texas. Two separate mechanisms by which this sensitivity to soil texture can impact the ecological structure at La Copita are illustrated. First, dynamics similar to the inverse texture effect, whereby the optimal soil texture for a given vegetation type changes with rainfall amount, are demonstrated for the two most common species at this site. Second, it is shown that soil texture plays a major role in the modulation of the impact that interannual rainfall fluctuations have on the fitness and coexistence of trees and grasses.

### 1. Introduction

In water-limited ecosystems, soil moisture and vegetation have a coupled relationship that is basic to ecosystem dynamics. Figure 1 illustrates how soil moisture has a central role in the dynamic interaction between climate, soil, and vegetation and makes explicit the coupled dependence of the water balance and water stress processes on soil moisture. Through transpiration, plants have an active role in soil water use that heavily conditions the water balance. The water balance, in turn, impacts plant growth, reproduction, and germination through the onset of water stress.

Past studies have recognized the importance of soil texture on the above coupled interactions and have demonstrated how it influences vegetation patterns through its impact on soil water availability [e.g., Knoop and Walker, 1985]. Soil characteristics affect the distribution and duration of water stored in the soil, and these, in turn, affect plant distribution and vegetation structure. Some soil characteristics can impose drought on plants even under favorable climatic conditions, as described, for example, by Newman [1967]. Moreover, the same type of vegetation may occur preferentially on coarse soils under low-rainfall conditions and on fine soils under higher-rainfall conditions; a situation referred to as the inverse texture effect [Noy-Meir, 1973].

Recently developed analytical schemes of the probabilistic structure of the soil water balance and the related plant water stress [Laio *et al.*, 2001a; Porporato *et al.*, 2001] provide a framework for a comprehensive description of these processes. The approach allows for an analytical treatment of the links

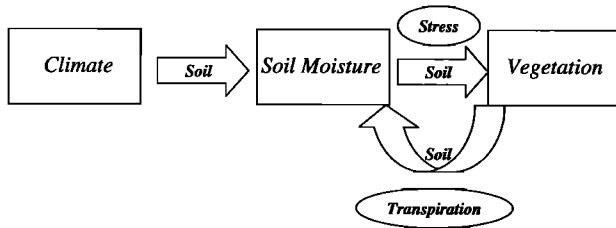
between climate, soil, and vegetation with explicit consideration of the stochastic nature of the rainfall input. The duration, frequency, and intensity of water stress periods as functions of climate, soil, and vegetation type are probabilistically characterized and constitute the basic tools to assess the relative suitability of environmental conditions for functionally different types of vegetation in water-controlled ecosystems. Using this framework, preliminary work by Laio *et al.* [2001b] hints toward the crucial role of soil texture in the coupled relationship between vegetation and soil moisture and in determining favorable conditions to the vegetation according to the previously described inverse texture effect.

This study will expand upon the results of Laio *et al.* [2001b] by considering a wider range of climatic and vegetative scenarios and all of the textural classes within the U.S. Department of Agriculture (USDA) [1951] soil textural triangle at the La Copita Research Area in the Rio Grande Plains of southern Texas. In addition, the ability of soil texture to encourage grass/tree coexistence at this savanna site is examined under different rainfall amounts. The analysis will focus on the two most common vegetation types coexisting in La Copita, namely, the herbaceous *C<sub>4</sub> Paspaleum setaceum* and the woody *Prosopis glandulosa* (honey mesquite). Throughout well-documented interannual climatic fluctuations these two species have experienced both dry and relatively wet climatic conditions. Thus the importance of soil texture on the soil water dynamics, water stress, and coexistence patterns will be assessed for two physiologically different species with different rooting depths under quite different rainfall conditions.

### 2. Soil Texture

Soil texture is a physical indicator of the size ranges of particles within a soil. All soil particle sizes can be sorted into three convenient size ranges called separates or textural fractions, namely, sand, silt, and clay. Conventionally, the overall textural classification of a soil is determined as a function of

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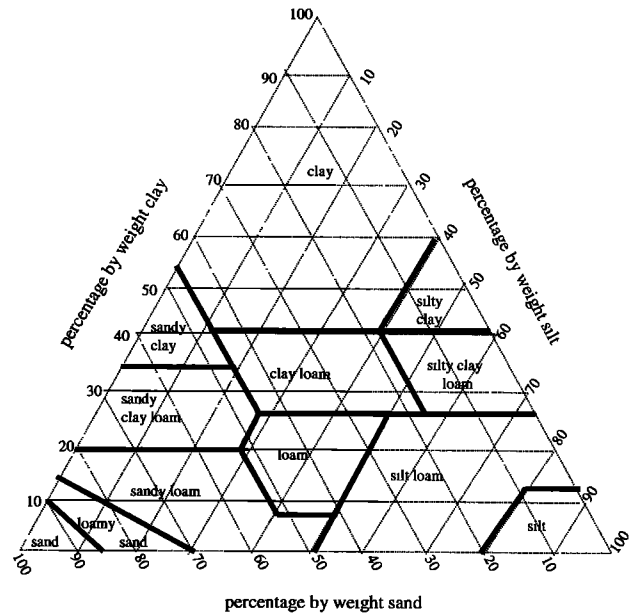


**Figure 1.** Schematic representation of the vegetation–soil moisture relationship in water-limited ecosystems.

the mass ratios of these three textural separates. Within the USDA [1951] soil textural classification, soils with different percentages of sand, silt, and clay are assigned to 12 different classes (Figure 2).

Soil texture is also used as a descriptor of soil physical properties such as porosity,  $n$ ; saturated hydraulic conductivity,  $K_s$ ; soil matric potential at saturation,  $\Psi_s$ ; and pore size distribution index,  $b$  [Cosby *et al.*, 1984]. Although other descriptors such as horizon and structural size certainly influence the hydraulic parameters of soils, Cosby *et al.* [1984] perform a two-way analysis of variance of nine descriptors to conclude that soil texture alone can account for most of the discernible patterns in  $K_s$ ,  $\Psi_s$ ,  $b$ , and  $n$ . Under given climatic and vegetation conditions the above soil-texture-dependent physical properties, through their influence on soil water movement and the energy state of the water in the soil column, determine the soil wetness values which in turn establish the water condition of the plant.

The study of the probabilistic behavior of the water balance and the water deficit for the vegetation and climate typical of La Copita was focused on the 12 textural classes within the USDA soil texture classification. The soil physical parameters controlling such dynamics, i.e.,  $n$ ,  $K_s$ ,  $\Psi_s$ , and  $b$ , were obtained using the univariate regression equations defined by Table 5 of Cosby *et al.* [1984], which relate these quantities to soil texture. These univariate regressions are sufficient to describe most of the variability in hydraulic parameters over textural classes [Cosby *et al.*, 1984]. The regressions were extrapolated in our study to include silty soils. Typical values of the above parameters for the middle point of each of the 12 textural classes within the USDA soil textural classification are given in Table 1. The values of the soil hydraulic properties



**Figure 2.** The U.S. Department of Agriculture (USDA) soil textural triangle.

obtained using the regressions by Cosby *et al.* [1984] for sandy loam (the observed soil texture at the La Copita site) are comparable to those reported at this site [USDA, 1979].

### 3. Site Description

The La Copita Research Area (27°40'N, 98°12'W) in southern Texas offers valuable data on two functional, coexisting vegetation types, namely,  $C_4$  grasses (mainly *Paspaleum setaceum*) and woody plants, primarily *Prosopis glandulosa* (honey mesquite). Table 2 contains the site vegetation parameters required for the modeling of the soil water dynamics of the two species following the analytical representation of the water balance presented by Laio *et al.* [2001a]. These parameters include the active soil depth or root depth,  $Z_r$ ; the maximum evapotranspiration rate,  $E_{max}$ ; the soil matric potential at wilting,  $\Psi_{s,w}$ ; the soil matric potential at the level of incipient stomatal closure,  $\Psi_{s,s^*}$ ; the interception depth,  $\Delta$ ; and the evaporation rate at wilting,  $E_w$  [Laio *et al.*, 2001b]. The impact

**Table 1.** Parameters Characterizing the 12 Soil Textural Classes Within the USDA Soil Textural Triangle<sup>a</sup>

Class	Silt, %	Sand, %	Clay, %	$n$ , %	$\log K_s$ , inches $h^{-1}$	$\log \Psi_s$ , cm	$b$
Sand	5	92	3	37.3	0.524	0.675	3.387
Loamy sand	12	82	6	38.6	0.371	0.806	3.864
Sandy loam	32	58	10	41.6	0.003	1.12	4.5
Loam	39	43	18	43.5	-0.226	1.317	5.772
Silty loam	70	17	13	46.8	-0.624	1.657	4.977
Sandy clay loam	15	58	27	41.6	0.003	1.12	7.203
Clay loam	34	32	34	44.9	-0.394	1.461	8.316
Silty clay loam	56	10	34	47.6	-0.731	1.749	8.316
Sandy clay	6	52	42	42.3	-0.088	1.199	9.588
Silty clay	47	6	47	48.1	-0.792	1.801	10.383
Clay	20	22	58	46.1	-0.547	1.592	12.132
Silt	88	7	5	48	-0.777	1.788	3.705

<sup>a</sup> $n$ , porosity;  $b$ , pore size distribution index;  $K_s$ , saturated hydraulic conductivity; and  $\Psi_s$ , soil matric potential at saturation. Values are obtained through the univariate regression equations of Cosby *et al.* [1984]. Note that 1 inch  $h^{-1}$  = 0.30 cm  $h^{-1}$ .

**Table 2.** Parameters Characterizing Vegetation at La Copita Research Area, Texas<sup>a</sup>

Species	$Z_r$ , cm	$E_{max}$ , cm/d <sup>-1</sup>	$\Psi_{s,s_w}$ , MPa	$\Psi_{s,s^*}$ , MPa	$\Delta$ , cm	$E_w$ , cm/d <sup>-1</sup>
<i>Paspalum setaceum</i>	40	0.476	-4.5	-0.09	0.1	0.013
<i>Prosopis glandulosa</i>	100	0.442	-3.2	-0.12	0.2	0.02

<sup>a</sup> $Z_r$ , active soil or root depth;  $E_{max}$ , maximum evapotranspiration rate;  $\Psi_{s,s_w}$ , soil matric potential at wilting;  $\Psi_{s,s^*}$ , soil matric potential at incipient stomatal closure;  $\Delta$ , interception depth;  $E_w$ , evaporation rate at wilting.

of different plant physiology and rooting depths on the water balance under variable soil texture thus may be undertaken.

Climate at the site is subtropical with an average annual temperature of 22.4°C and a mean annual rainfall of 70 cm. However, significant deviations from the long-term (1930–1986) mean rainfall over this region were observed during the 1941–1960 drought and the 1961–1983 wetter-than-average period. Statistically homogeneous growing season (i.e., May–September) rainfall statistics, namely, the mean depth of rainfall events,  $\alpha$ , and the rate of storm arrivals,  $\lambda$ , were obtained from the daily rainfall data recorded at Alice rain station, Texas (Rainfall data are available at <http://www.ncdc.noaa.gov>.) For the 1950–1960 dry period,  $\lambda_{dry}$  is estimated as 0.166 d<sup>-1</sup>, and  $\alpha_{dry}$  is estimated as 1.342 cm, with a total growing season rainfall of 34.1 cm. For the 1973–1983 relatively wet period,  $\lambda_{wet}$  is estimated as 0.202 d<sup>-1</sup>, and  $\alpha_{wet}$  is estimated as 1.417 cm, with a total growing season rainfall of 43.8 cm. In this manner, the role of soil texture in the water balance may also be assessed for different climatic scenarios.

**4. Sensitivity of Soil Water Dynamics to Soil Texture**

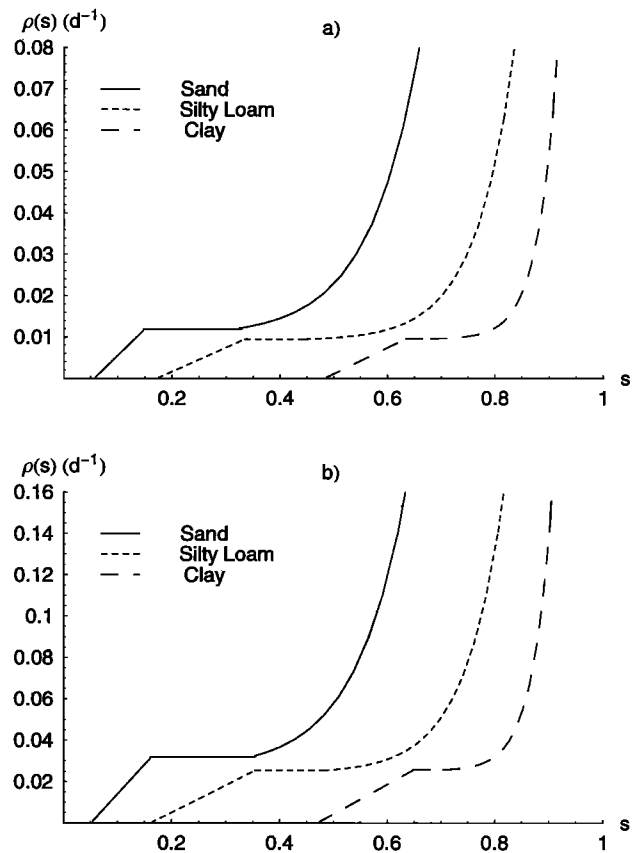
In this section, the analytical tools developed by Laio *et al.* [2001a] to characterize the probabilistic soil moisture dynamics are applied to the vegetation and climatic regimes of La Copita to investigate the role of soil texture on the water balance at this site and the manner in which this role varies with climate and vegetation type. The reader is referred to Laio *et al.* [2001a] for a detailed description of these tools. Analysis will focus on the sensitivity of the loss function (e.g., evapotranspiration plus leakage),  $\chi(s)$ ; the probability density function (pdf) of soil moisture,  $\rho(s)$ ; and the mean components of the water balance to variations in soil texture at a point.

**4.1. Soil Moisture Probability Density Function**

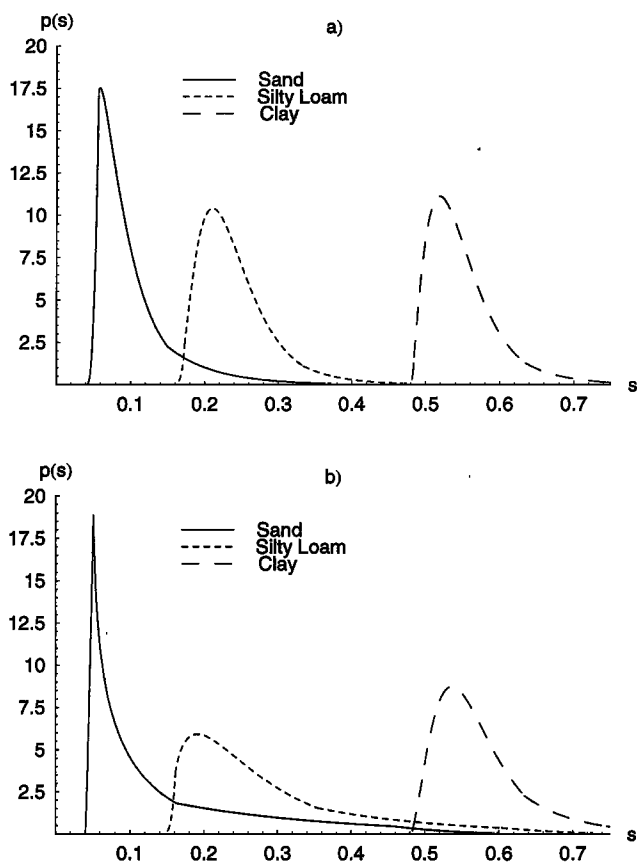
The daily average dependence during the growing season of the normalized evapotranspiration and leakage losses on relative soil moisture,  $\rho(s) = \chi(s)/nZ_r$ , is shown in Figures 3a and 3b for *Prosopis glandulosa* and *Paspaleum setaceum* and for three different soil textural classes, namely, sand, silty loam, and clay. Figure 4a shows the behavior of the growing season steady state pdf of soil moisture for *Prosopis glandulosa* on these three soil textural classes under the dry climatic conditions observed in the region during the 1950–1960 period, while Figure 4b shows the same for *Paspaleum setaceum* under the wet climatic conditions observed during the 1973–1983 period. Figure 5 shows the steady state mean soil moisture,  $\langle s \rangle$ , corresponding to the different categories of the USDA soil textural triangle for *Prosopis glandulosa* under the dry climatic conditions. Figures 3, 4, and 5 indicate that as the percentage of clay increases, the pdf and the loss function shift to higher soil moisture values (i.e., the values of the hygroscopic point,

$s_h$ ; the wilting point,  $s_w$ ; the level of incipient stomatal closure,  $s^*$ ; and field capacity,  $s_{fc}$ , in the loss function; and the mean soil moisture,  $\langle s \rangle$ , in the pdf increase). These shifts occur because as the percentage of clay increases, so do the adsorptive forces which permit higher water retention at any given suction. It is also clear from Figures 3 and 4 that these soil-texture-related patterns are robust to vegetation and climatic characteristics.

While the pdf's of soil moisture shown in Figure 4 are quite different, all of them have their mode between the corresponding  $s_w$  and  $s^*$ , indicating the high likelihood that the two species at this site are water-stressed. The mode, however, is more pronounced for sand than for silty loam or clay because of the higher probability of soil moisture being at or near  $s_w$  for sandy soils resulting from the larger slope of the loss function,  $\rho(s)$ , in the  $\{s_w, s^*\}$  range. As observed in Figure 4, shallow-

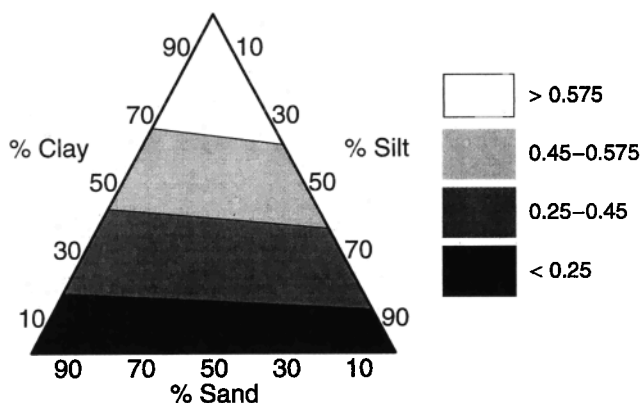


**Figure 3.** Normalized loss function  $\rho(s)$  for (a) *Prosopis glandulosa* and (b) *Paspaleum setaceum* on sand, silty loam, and clay at La Copita Research Area.  $K_s$ ,  $\psi_s$ ,  $n$ , and  $b$  were determined from soil texture using the univariate regression equations of Cosby *et al.* [1984]. The parameters characterizing *Prosopis glandulosa* and *Paspaleum setaceum* are given in Table 2.



**Figure 4.** Soil moisture probability density function for (a) *Prosopis glandulosa* under dry climatic conditions (i.e., mean depth of rainfall events  $\alpha = 1.342$  cm and rate of arrival  $\lambda = 0.166$   $\text{d}^{-1}$ ) and (b) *Paspaleum setaceum* under wet climatic conditions (i.e., mean rainfall depth  $\alpha = 1.417$  cm and frequency of the rainfall events  $\lambda = 0.202$   $\text{d}^{-1}$ ) on sand, silty loam, and clay at La Copita Research Area. See Table 2 for other parameters.

rooted species such as *Paspaleum setaceum*, with their faster temporal fluctuations in soil moisture resulting from their smaller active soil depth  $Z_r$ , tend to show larger standard deviations in the soil moisture values than deeper-rooted spe-



**Figure 5.** Impact of soil texture on mean relative soil moisture during the growing season for *Prosopis glandulosa* under dry climatic conditions (i.e., mean depth of rainfall events  $\alpha = 1.342$  cm and rate of arrival  $\lambda = 0.166$   $\text{d}^{-1}$ ) at La Copita Research Area. See Table 2 for other parameters.

cies like honey mesquite. As expected, a wetter climate results in higher  $\langle s \rangle$  values for both species (not shown).

#### 4.2. Water Balance Components

Figure 6 shows the mean levels of the components of the water balance, namely stressed evapotranspiration, unstressed evapotranspiration, runoff, and leakage, expressed as percentage of growing season rainfall for *Prosopis glandulosa* under dry climatic conditions on the 12 textural classes within the USDA soil textural classification. Their analytical expressions are given by Laio *et al.* [2001a]. Interception is independent of soil texture and is therefore not shown. Each component shows considerable variability within the soil texture triangle.

From Figures 6a and 6b one observes that sandy soils have the lowest mean levels of stressed evapotranspiration, while unstressed evapotranspiration is highest for the silty loam region of the triangle. The manner in which average percentages of stressed and unstressed evapotranspiration depend on soil texture is a consequence of the soil-texture-dependent patterns in the probability of soil moisture being below  $s^*$ ,  $P(s^*)$  (Figure 7a) and the probability of soil moisture being above  $s^*$  (the complement of Figure 7a), respectively.

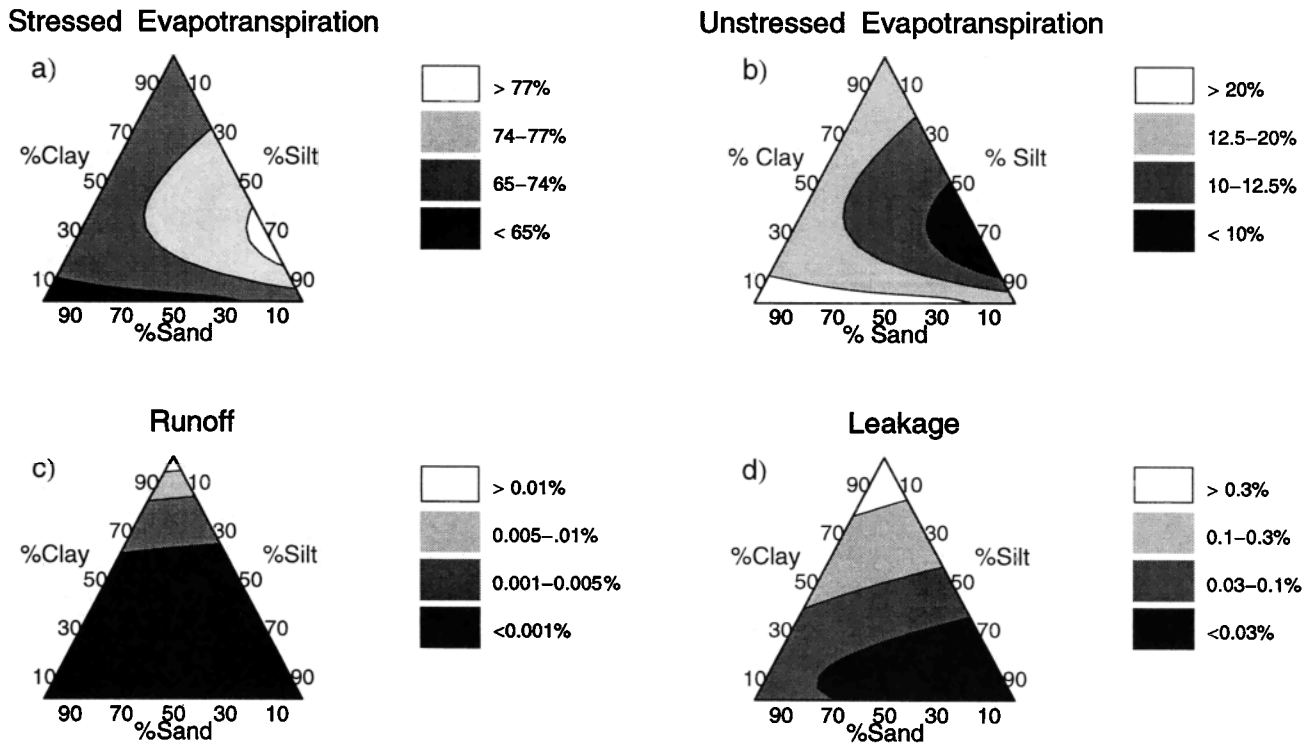
Figure 6c indicates that runoff constitutes a negligible portion of the water balance at this site and its variability within the soil triangle appears to follow gradients in mean soil moisture,  $\langle s \rangle$  (Figure 5). Clay soils, with higher mean values of soil moisture, are associated with larger amounts of runoff. Mean leakage levels are also quite small and, as shown in Figure 6d, increase as the probability of  $s$  being between  $s_{fc}$  and 1 (see Figure 7b) increases. As a consequence, for *Prosopis glandulosa* under dry climatic conditions, clay soils tend to exhibit a greater volume of leakage than sandy soils despite having a much lower  $K_s$  value, although in both cases the amounts are minimal.

Changing the climatic and vegetative characteristics at La Copita results in quantitative but not qualitative changes in the relationship between mean values of the water balance components and soil texture (not shown). For dry climatic conditions, stressed evapotranspiration is the most important loss component of the water balance in terms of its magnitude for both *Prosopis glandulosa* and *Paspaleum setaceum*. This suggests that under such climatic conditions and for any soil texture conditions both species will suffer water deficit most of the time. Leakage and runoff are negligible for *Prosopis glandulosa* and are only slightly larger for *Paspaleum setaceum*. As the climate becomes wetter, the magnitude of the unstressed evapotranspiration increases significantly for both species, and the occurrence of leakage becomes greater for the shallow-rooted plant.

The sensitivity of the soil water dynamics to soil texture is evident from the large range of values for mean soil moisture and mean levels of the components of the water balance within the USDA soil textural classification. This sensitivity is robust to vegetation and climate. Differences in soil water dynamics due to soil texture are large enough to suggest a pronounced influence on vegetation water stress regimes, which are the focus of section 5.

#### 5. Sensitivity of Soil Moisture Crossing Properties and Water Stress to Soil Texture

Porporato *et al.* [2001] derive analytical expressions for the expected frequency and duration of soil moisture excursions



**Figure 6.** Mean components of the water balance for *Prosopis glandulosa* under dry climatic conditions at La Copita Research Area for the USDA soil textural triangle. The partition of incoming rainfall among (a) stressed evapotranspiration,  $\langle E_s \rangle$ , (b) unstressed evapotranspiration,  $\langle E_{ns} \rangle$ , (c) runoff,  $\langle Q \rangle$ , and (d) leakage,  $\langle L \rangle$ , is reported here. Canopy interception ( $I$ ), not shown, is assumed constant with respect to soil texture at 0.2 cm. See Table 2 and Figure 5 for relevant parameters.

below the level of soil moisture associated with the onset of water stress, i.e.,  $s^*$ . These statistics, referred to as the crossing properties of the soil moisture process, are combined with the expected level of water stress experienced during each excursion, i.e., the static water stress, to provide a new indicator of the overall condition of a plant under given edaphic and climatic characteristics (see Porporato et al. [2001] for a detailed derivation). This new quantity is called the “dynamic water stress” of vegetation. This section uses the concepts of soil moisture crossing properties and water stress (both static and dynamic) to better understand the role of soil texture on the water deficit process for the two vegetation types and climatic conditions at La Copita.

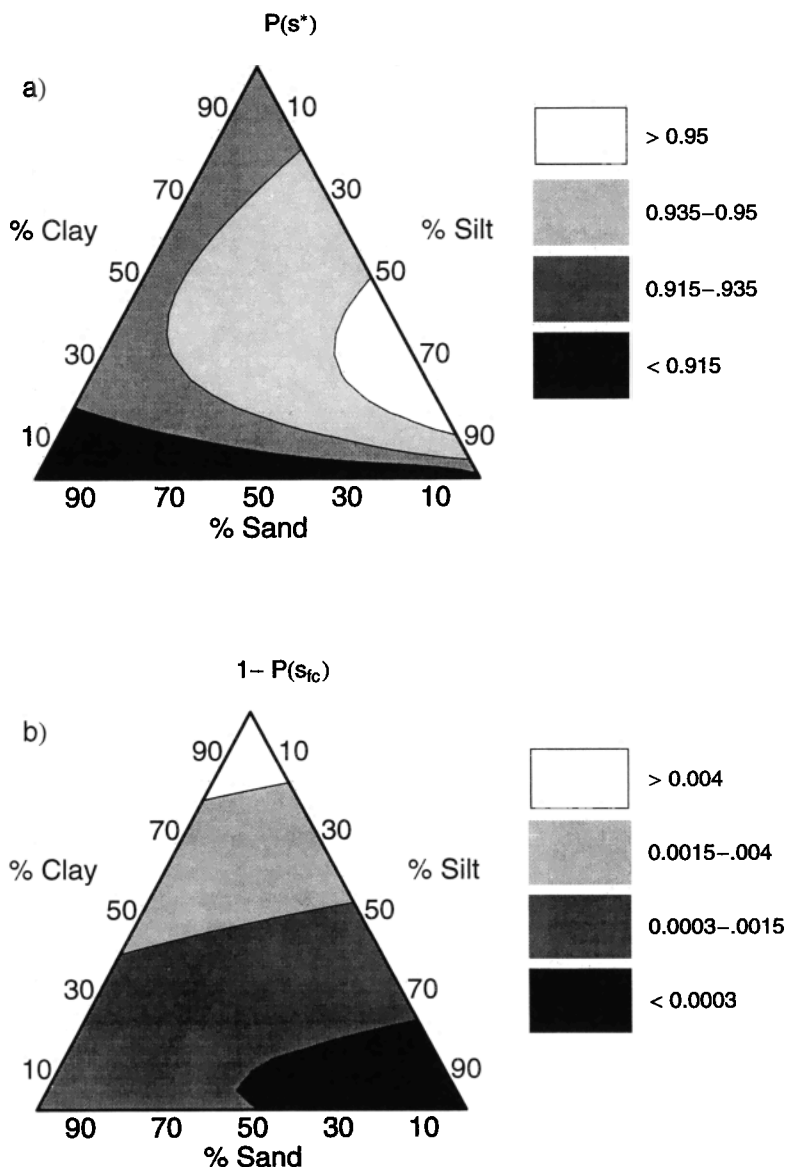
Figure 8 shows the mean duration of an excursion below  $s^*$ ,  $\bar{T}_{s^*}$ ; the mean number of crossing of  $s^*$ ,  $\bar{n}_{s^*}$ ; and the mean static water stress,  $\bar{\zeta}'$ , for *Prosopis glandulosa* under dry climatic conditions for all the soil textural classes in the USDA triangle. The maximum value of  $\zeta$  is normalized to 1, corresponding to the case when the stress event takes place at or below the wilting point of the plant [Porporato et al., 2001]. Its calculation includes the parameter  $q$ , which is a measure of the nonlinear impacts of the soil moisture on plant conditions.

According to Figure 8a the  $\bar{T}_{s^*}$  values within the soil textural triangle show a minimum for sandy soils while they show a maximum for the silty loam soils. In contrast, Figures 8b and 8c indicate that both the  $\bar{n}_{s^*}$  and  $\bar{\zeta}'$  values show the opposite pattern, i.e., a minimum for the silty loam soils and a maximum for the sandiest soils. These patterns appear to mimic the variability of the quantity  $n(s^* - s_w)$  among soil textures (Figure 9). This quantity represents the layer of water per unit

depth needed to rise the relative soil moisture content of a soil column from  $s_w$  to  $s^*$ . For soil textures with small  $n(s^* - s_w)$ , wilting and therefore water conservation occur at soil moisture levels close to the onset of stress  $s^*$ . As a result, any amount of rainfall is likely to bring the plant out of stress, diminishing the mean duration of the stress period,  $\bar{T}_{s^*}$ , but increasing the mean number of crossings of the stress level,  $\bar{n}_{s^*}$ . Small  $n(s^* - s_w)$  values also result in a higher probability of excursions of the soil moisture trace to soil moisture values near  $s_w$ , which are associated with higher values of static stress, i.e., higher  $\bar{\zeta}'$  values. Conversely, soil textures with high  $n(s^* - s_w)$  result in large  $\bar{T}_{s^*}$  and small  $\bar{n}_{s^*}$  and  $\bar{\zeta}'$ .

The above patterns of  $\bar{T}_{s^*}$ ,  $\bar{n}_{s^*}$ , and  $\bar{\zeta}'$  with respect to soil texture do not qualitatively change with vegetation type and/or climate in the case of La Copita. Nevertheless, there are important quantitative changes in those measures as the climate and the vegetation type change. For both the dry and the wet climate, shallow-rooted species such as *Paspaleum setaceum* (not shown) spend on average less time under stress and cross the stress level more often than do deep-rooted species such as *Prosopis glandulosa*. Also, the grasses tend to experience higher  $\bar{\zeta}'$  values than trees independently of the wetness of the climate. A wetter climate results, as expected, in lower  $\bar{\zeta}'$  values and lower  $\bar{T}_{s^*}$  values. Values of  $\bar{n}_{s^*}$  increase with the wetness of the climate for both species.

Values of the dynamical water stress,  $\bar{\theta}$ , are shown in Figure 10a and 10b for *Prosopis glandulosa* under dry and wet climatic conditions at La Copita, respectively. They are normalized to a maximum of 1, and their calculation includes the parameter  $k$ , representing the index of plant resistance to water stress [Por-



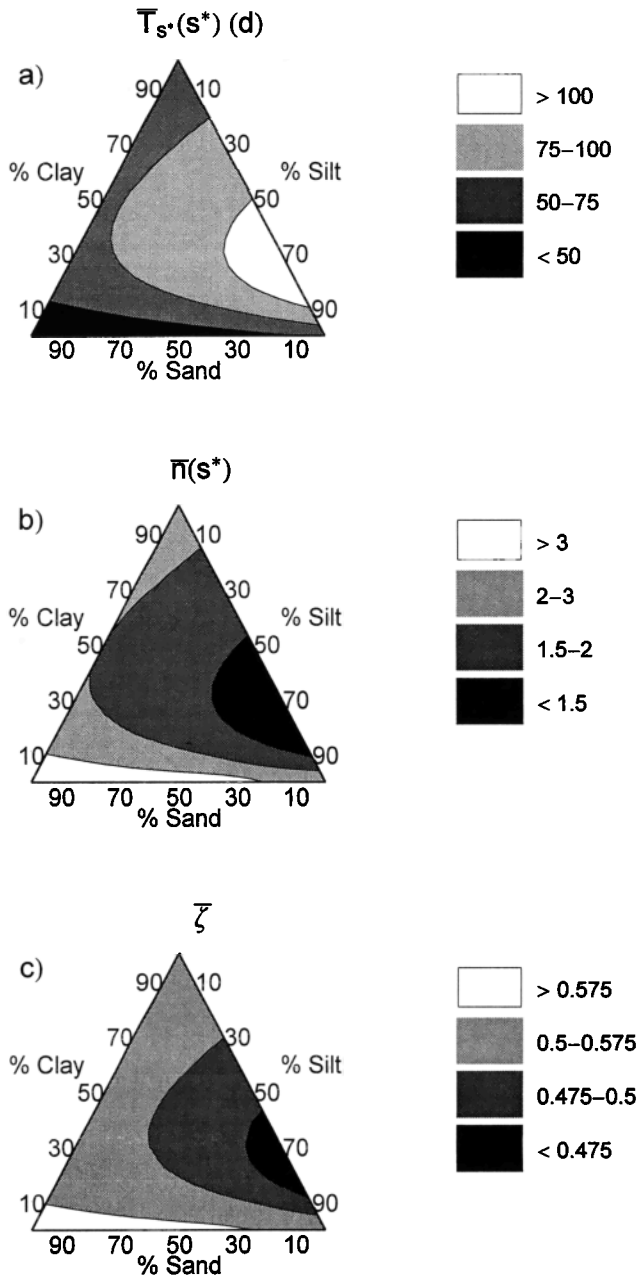
**Figure 7.** *Prosopis glandulosa* under dry climatic conditions at La Copita Research Area. (a) Probability of soil moisture to be below  $s^*$ , the onset of water stress, and (b) probability of soil moisture to be above  $s_{fc}$  field capacity. See Table 2 and Figure 5 for relevant parameters.

porato *et al.*, 2001]. Under the dry climatic scenario this vegetation type has a better overall condition (i.e., lower  $\theta$  values) on a sandier soil than on a finer texture soil such as a silty loam (Figure 10a). *Paspaleum setaceum* also prefers a coarser soil to a finer-textured soil when the climate is dry (not shown). An increase in the wetness of the climate results in a shift of the low  $\theta$  region to the finer texture soil types for both vegetation types (as can be observed in Figure 10b for *Prosopis glandulosa*), corroborating the inverse texture effect as described by Noy-Meir [1973, p. 37]: “The same vegetation type can occur at lower rainfall on coarse soils than it does on fine ones.”

Previous studies [Noy-Meir, 1973] have attributed the occurrence of the inverse texture effect to the impact of climate and soil texture on plant water availability and the manner in which this impact changes with the degree of climate aridity. Water loss in humid climates is greatly influenced by leakage losses, favoring plant growth in soils with high water-holding capacities such as silty loams. In contrast, surface evaporation is a

significant loss mechanism in more arid climates, favoring sandy soils that are capable of quickly draining water away from the surface and avoiding high levels of water loss due to direct soil evaporation.

Our vertically integrated model of soil moisture does not differentiate near-surface water available for direct soil evaporation from water available for transpiration within  $Z_r$ . Therefore it does not resolve all of the vertical processes usually associated with the inverse texture effect. Instead, the previously observed effect is, within our modeling framework, driven by the sensitivity of the overall condition of the plant to the total amount of water that it needs to make the transition from being at wilting to being above stress and the manner in which this sensitivity changes with climate. Dry climates favor soil textural types where a minimum amount of water is required to raise soil moisture levels above  $s^*$ , and thus even weak storm events are capable of taking vegetation out of water stress. Consequently, vegetation will experience lower



**Figure 8.** Crossing properties and static water stress for *Prosopis glandulosa* under dry climatic conditions at La Copita Research Area for the USDA soil textural triangle. (a) Mean duration of an excursion below  $s^*$ . (b) Mean number of down-crossings of  $s^*$ . (c) Mean static water stress using  $q = 3$ . The duration of the growing season is  $T_{\text{seas}} = 153$  days. See Table 2 and Figure 5 for other parameters.

levels of dynamic water stress for coarse-textured soils with small  $n(s^* - s_w)$ . In contrast, wetter climates favor fine-textured soils with large  $n(s^* - s_w)$  so that if  $s^*$  is reached during a drying period, the soil moisture trace does not fall to levels associated with large static stress values. Thus the finer-textured soils have the lowest dynamic water stress values under wet climatic conditions.

In terms of the inverse texture effect, soil texture and climate

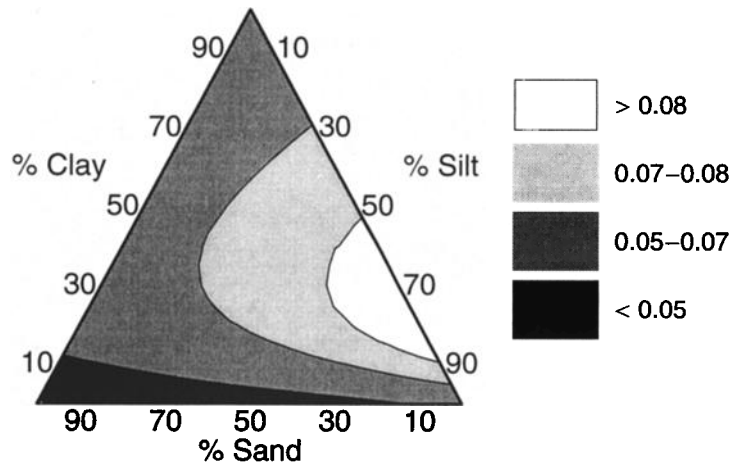
determine the importance of the mean duration, intensity, and frequency of water stress to the overall condition of a plant as expressed by the dynamic water stress  $\bar{\theta}$ .

**6. Interaction of Climate and Soil to Determine Coexistence Patterns**

This section studies the role of soil texture in the coexistence patterns of the two principal vegetation types present in La Copita, under the rainfall variability characteristic of the area. Figure 11 shows the relationship between the total growing season rainfall,  $\Theta$ , and the difference in dynamical water stress between *Paspaleum setaceum* and *Prosopis glandulosa*,  $\Delta \bar{\theta}_{Ps-Pg}$ , for six soil textural classes. As before, the corresponding  $K_s$ ,  $\Psi_s$ ,  $b$ , and  $n$  have been estimated through application of the univariate regressions by *Cosby et al.* [1984] to the midpoint of the appropriate soil textural region within the USDA textural triangle. To more accurately describe conditions at this site, the soil hydraulic properties reported by *USDA* [1979] were used to characterize the predominant soil type at La Copita (sandy loam). The six textural classes were chosen because their calculated  $\Delta \bar{\theta}_{Ps-Pg}$  values span those observed for all 12 soil textural classes in the USDA triangle. The total growing season rainfall is computed by linearly increasing, in a joint manner, the mean depth of rainfall events,  $\alpha$ , and the mean frequency of arrival of storms,  $\lambda$ , from their dry to their wet period values.

Figure 11 shows a decreasing sensitivity of the difference in the overall condition of the two species,  $\Delta \bar{\theta}_{Ps-Pg}$ , to total rainfall as the climate gets wetter. Figure 11 also shows a transition in the sign of  $\Delta \bar{\theta}_{Ps-Pg}$  with increasing growing season rainfall for all six soil textures. For dry periods, grasses tend to dominate (values of  $\Delta \bar{\theta}_{Ps-Pg} < 0$ ), while the opposite is true for wet periods (values of  $\Delta \bar{\theta}_{Ps-Pg} > 0$ ). Thus the interannual rainfall variability present at the site drives the system toward different states where soil texture plays a key role in determining the dominant vegetation type. Notice that a sandy soil in this site leads to much smaller differences in the overall condition of the two species under strong interannual rainfall variability than those occurring, for example, within a silty clay loam. Moreover, it is clear from Figure 11 that most of the impact of the interannual rainfall fluctuations tends to favor the  $C_4$  *Paspaleum setaceum*. Wet periods are more conducive to *Prosopis glandulosa*, but the differences in fitness between the two species are significantly smaller than those occurring in dry periods in favor of the grasses. This suggests that the long-term relative increase of woody plants in this area cannot be solely attributed to pronounced interannual rainfall variability existing in the region. As important as these fluctuations are in driving the system toward different vegetation states, a sizable long-term increase in woody species will also depend on the impact of grazing and fire control.

To further study the coexistence patterns at La Copita, a growing season rainfall equal to the 1950–1985 mean value of 40 cm was selected. The mean depth per rainfall event,  $\alpha$ , and the mean frequency of arrival of storms,  $\lambda$ , were then assigned from the previously described linearly varying values to match the mean rainfall (i.e.,  $\alpha = 1.387$  cm and  $\lambda = 0.188$  d<sup>-1</sup>, respectively). The corresponding  $\Delta \bar{\theta}_{Ps-Pg}$  values for the USDA soil texture triangle are shown in Figure 12, which shows that the transition between grass and tree domination

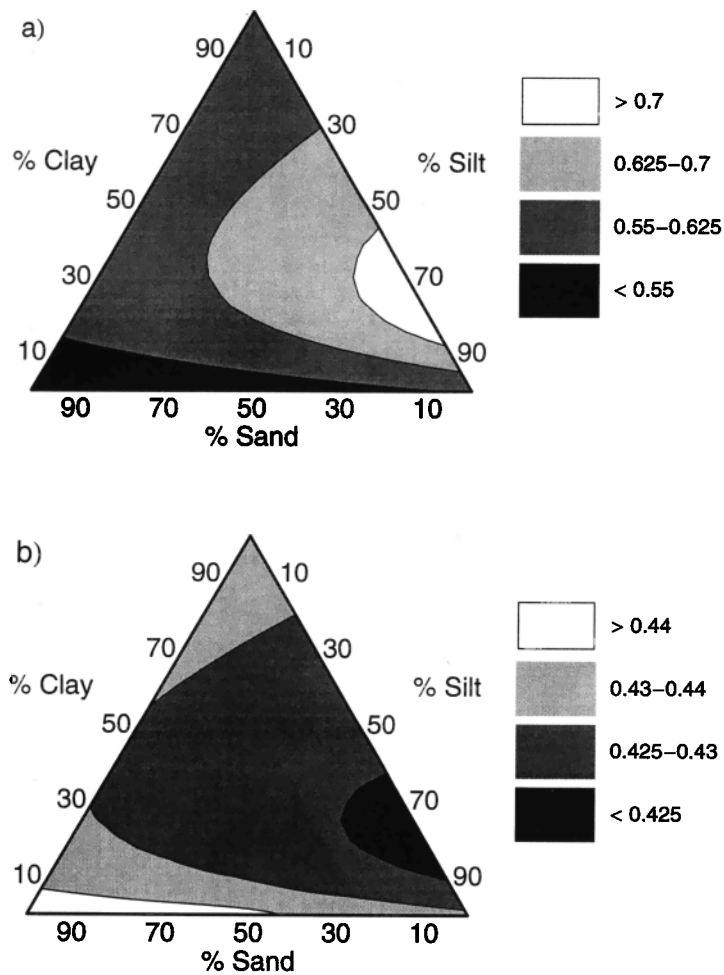


**Figure 9.** Layer of water per unit depth needed to rise the relative soil moisture content of a soil column from  $s_w$  to  $s^*$  in the case of *Prosopis glandulosa*. See Table 2 and Figure 5 for other relevant parameters.

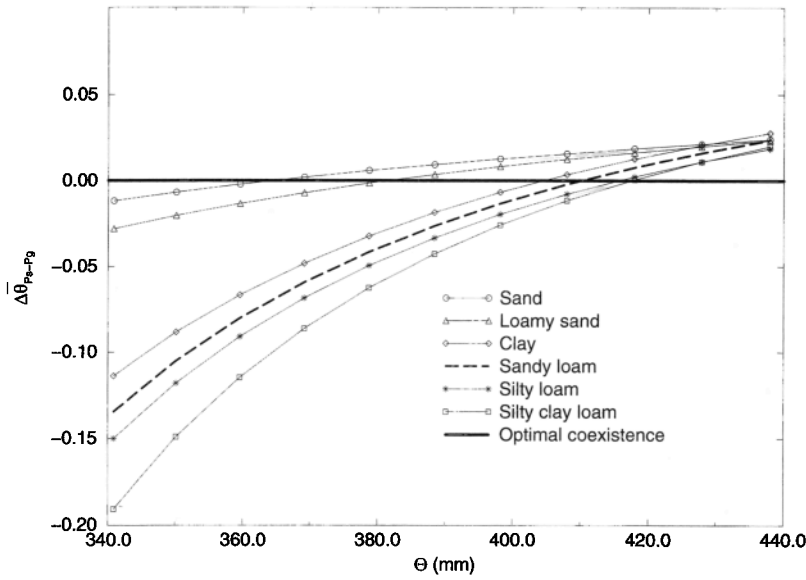
can occur at this site at almost any soil texture and even more so within the sandy loam region, which is the predominant soil in the area.

The climatic variability in this region and its impact on soil

moisture have been studied in detail by *D’Odorico et al.* [2000]. The persistence of prolonged periods of abnormally wet and dry periods combined with the impact of grazing and fire control drives the system toward states of tree or grass domination.



**Figure 10.** Dynamic water stress  $\bar{\theta}$  for *Prosopis glandulosa* on the USDA soil textural triangle under (a) dry climatic conditions and (b) wet climatic conditions.  $T_{scas} = 153$  days,  $q = 3$ , and  $k = 0.5$ . See Table 2 and Figure 5 for other parameters.



**Figure 11.** Difference in the dynamic water stress between *Paspaleum setaceum* and *Prosopis glandulosa*,  $\Delta\theta_{Ps-Pg}$ , as a function of the total incoming rainfall during the growing season,  $\Theta$ . The parameters  $\alpha$  and  $\lambda$  vary linearly with  $\Theta$  increasing from their dry to wet values.  $T_{seas} = 153$  days,  $q = 3$ , and  $k = 0.5$ . See Table 2 and Figure 5 for other parameters.

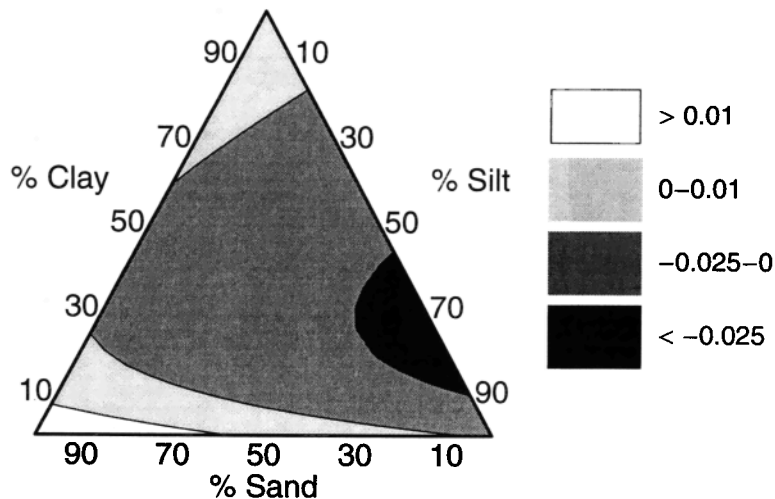
These changes in vegetation in the region are well documented by Archer *et al.* [1988] and Van Auken [2000].

**7. Conclusions**

Previous studies have hinted toward the crucial role of soil texture in the soil water balance and water stress processes [Laio *et al.*, 2001b]. Our results further corroborate these findings by extending their analysis to a broader range of vegetation, climate, and soil textures. For the two vegetation and climatic conditions at the La Copita site the coupled relationship between soil moisture and vegetation is found to be strongly dependent on soil texture. The probability density function of soil moisture and the mean levels of the compo-

nents of the water balance show high sensitivity to soil texture. Soil texture also has a controlling effect on the mean duration, frequency, and intensity of water deficit periods of the herbaceous and woody species at this site under dry and wet conditions.

A relationship between soil texture and rainfall in accordance with the inverse texture effect [Noy-Meir, 1973] was identified by Laio *et al.* [2001b] for a single species and here proves to hold for the two coexisting species at La Copita, namely, the woody *Prosopis glandulosa* and the herbaceous *Paspaleum setaceum*. Results suggest that the inverse texture effect is driven by the sensitivity of the overall condition of the plant to the total amount of water it needs to make the transition from being at wilting to being above stress and the



**Figure 12.** Difference in the dynamic water stress between *Paspaleum setaceum* and *Prosopis glandulosa*,  $\Delta\theta_{Ps-Pg}$ , for an average climate,  $\alpha = 1.387$  cm and  $\lambda = 0.188$  d<sup>-1</sup>, for the USDA soil textural triangle.  $T_{seas} = 153$  days,  $q = 3$  and  $k = 0.5$ . See Table 2 and Figure 5 for other parameters.

manner in which this sensitivity changes with climate. The inverse texture effect is observed without needing to explicitly resolve all of the vertical processes typically invoked to describe it.

It has also been shown that soil texture plays a major role in the impact that interannual rainfall fluctuations have on the relative fitness of woody and herbaceous species in southern Texas, with the difference in fitness being larger in favor of grasses during dry periods than it is in favor of trees during wet years. For typical values of rainfall occurrence and storm depths, *Prosopis glandulosa* and *Paspaleum setaceum* may co-exist in a range of soil textures at La Copita.

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