

Structure and Function of Chihuahuan Desert Ecosystem  
The Jornada Basin Long-Term Ecological Research Site  
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## 8

### **Water and Energy Balances within the Jornada Basin**

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This chapter describes general characteristics and components of the energy and water balances in arid regions, with specific examples from the Jornada Basin. Various research efforts to characterize the energy and water balances and resultant carbon dioxide fluxes in the Jornada Basin are detailed. We provide a brief overview of how plant physiology interacts with energy and water balances in this region, and characterize general abiotic conditions and some physiological traits of plants in this semiarid region.

#### **Energy Balance Characteristics of the Jornada Basin**

The surface of a landscape may be considered as a layer with some amount of vegetation. More general descriptions divide the vegetation, like the soil, into layers, but the concern here is energy balance at the interface with the atmosphere. The net energy balance of the land surface is determined by (1) inputs (radiant energy), (2) outputs (reflection [i.e., albedo], emission of longwave radiation, convective heat transfer to the atmosphere [i.e., sensible heat flux], evapotranspiration of water [i.e., latent heat flux], and conduction of heat into soil, and (3) changes in heat storage. The balance of these terms is adjusted as the surface temperature comes into steady state or nearly so. Increased solar input will drive surface temperatures higher until longwave emission and other losses come into a new balance. The net energy input, as inputs minus outputs, may be stated formally as an energy-balance equation

$$(8-1) \quad \text{Rate of heat storage} = S = Q_{SW}^+ + Q_{TIR}^+ - Q_{TIR}^- - Q_E^- - Q_H^- - Q_S^-,$$

where the superscript + indicates an input, and - indicates an output or loss, and all terms are expressed as flux density in units of  $W/m^2$ .  $Q_{SW}^+$  is the energy added to the surface layer by solar radiation from above.  $Q_{TIR}^+$  is the thermal infrared radiation emitted by gases in the atmosphere, principally water vapor and  $CO_2$ , whereas  $Q_{TIR}^-$  is the thermal infrared radiation emitted from components of the Earth's surface and lost back to the atmosphere.  $Q_E^-$  is the latent heat flux from the heat of vaporization of water vapors resulting from soil evaporation (E) and plant transpiration, generally measured as the composite evapotranspiration flux (ET).  $Q_H^-$  is the sensible heat transfer from surface to atmosphere by convection.  $Q_S^-$  is conduction of heat into soil. Heat storage (S) in the vegetation is only significant in thick, voluminous vegetation such as closed stands of trees (absent on the Jornada) or at the single-plant level for cactus phyllodes (Nobel 1978). An alternative formulation of the energy budget is

$$(8-2) \quad \text{Rate of heat storage} = S = R_n - LE - SH - G,$$

where the first three terms of equation 8-1 are represented as total net radiation,  $R_n$ , and the other terms are analogous to equation 8-1.  $LE$  is latent heat flux,  $SH$  is the sensible heat flux, and  $G$  is soil heat conduction.

The Jornada Basin is characterized by low mean cloud cover, moderately high elevation (about 1,350 m), moderately low aerosol burden, and low latitude ( $32.5^\circ N$ ), such that solar energy input is large. Details of the climate are described in chapter 3. Surface temperatures are high on summer days, despite rather reflective soils (about 35% of shortwave energy is reflected). Cooling by evapotranspiration is often low, as water is frequently depleted from soil surfaces and from vegetation. Mean annual

precipitation is 245 mm with more than 54% of total rainfall falling between July and September. Mean annual temperatures range from 3.8°C in January to 26.0°C in July. The clear skies and low water vapor content, which produce low absorptivity for thermal infrared radiation leaving the surface, allow strong radiative cooling. Thus daily fluctuations in surface and air temperatures are very large, commonly exceeding 20°C even without passage of weather fronts. The large diurnal and seasonal ranges of temperature strongly condition the performance and survival of plants.

On large spatial scales, the Jornada and adjoining arid regions are usually a net source of sensible heat flux to the atmosphere, a weak source of latent heat flux or ET, and a modest sink (above the atmosphere) for net radiation (total radiant energy flux density in minus total radiant energy flux density out; Hartmann 1994). The net heat flux out is the net result of an input of heat from compressive heating of the air subsiding here from the tropics minus the output from hot surface to the cooler air transported over hundreds of km. On the scale of tens of km, the sensible heat flux helps drive convective storm activity in summer. On larger scales, the heat flux contributes to setting regional atmospheric circulations that determine climatic patterns.

Energy leaves this surface in several ways. One is by reflection of solar radiation, commonly accounted in the solar input as net absorption. Vegetation absorbs strongly in the photosynthetically active radiation (PAR) band from 400 to 700 nm wavelength, which reduces the landscape's reflectivity (i.e., albedo) of solar radiation. Changes in the composition of vegetation and the amount of vegetation change the albedo of landscape. For example, shrub encroachment into former grasslands generally resulting in higher albedo, because bare soil usually increases, and it is generally lighter in color and thus

more reflective (Kurc and Small 2004). However, individual shrub canopies are often darker in color than some grass species or subshrub species depending on the time of year, and this can also alter reflectance (Franklin et al. 1993).

Thermal infrared radiation (TIR or  $Q_{TIR}$ ) is emitted by the surface in close proportion to the fourth power of the absolute (Kelvin) temperature and emitted by gases in the atmosphere. The TIR gain from the sky and loss from the surface actually make up the major part of the annual energy budget of the surface (about 290 and 390 W/m<sup>2</sup>, respectively). TIR fluxes are less variable than other energy exchanges. TIR emission from the surface changes by only 5 W/m<sup>2</sup> per 1°C shift in surface temperature when surface temperatures are near 15°C. In contrast, sensible and latent heat fluxes vary by hundreds of W/m<sup>2</sup> diurnally, weekly, or seasonally. As mentioned, the low water vapor content of the skies leads to low  $Q_{TIR}^+$  in dry regions, and the effective radiative temperature of the sky is many tens of degrees below air temperature. Commonly on a summer day with an air temperature of 35°C, the sky radiative temperature is below 0°C. This leads to radiative deficits at night that cause “radiation frosts” in winter (Leuning 1988; Jones 1992): Horizontal surfaces (such as leaves) may stabilize at temperatures up to 5°C lower than air temperature.

Sensible heat flux ( $Q_H$  or  $H$ ) constitutes a net loss when surface temperatures exceed air temperature, and the rate is proportional to that temperature difference multiplied by the surface boundary-layer conductance. The conductance rises with wind speed and also with surface roughness, which is in part determined by vegetation structure. During sunlight hours, soils are commonly sources of sensible heat transfer to the air, whereas plant leaves vary. Fast-transpiring leaves are sinks for sensible heat flux,

and water-stressed, slow-transpiring leaves are sources of sensible heat flux. In the Jornada Basin because vegetation cover is low, soil heat transfer commonly dominates sensible heat flux.

Another energy loss is conduction of heat into soil ( $Q_s$  or  $G$ ). Hot soil surfaces send heat into soil. There is a characteristic lag in the diurnal cycle of four hours, so that peak heat flux outward occurs about four hours before dawn. Soil heat flux is very modest in thicker vegetation, such as crops, because soil is shielded from much radiant exchange by high canopy cover of vegetation. In deserts, soil heat transfer can be much larger, on the order of  $50 \text{ W/m}^2$ , and is also quite variable spatially depending on whether soil heat flux is being measured in open interspaces, partial canopy cover, or full canopy cover (Kustas et al. 2000).

With physical models of heat propagation (e.g., Campbell and Norman 1998), it can be predicted how peak soil temperature decreases with depth in the soil. This peak decreases by a factor of  $1/e = 0.37$  times the daily amplitude over a characteristic damping depth of  $D = \sqrt{2K/\omega}$ , where  $K$  is the thermal diffusivity and  $\omega$  is the angular frequency of the cycle ( $2\pi$  per day or  $7.27 \times 10^{-5}/\text{s}$  for the daily cycle). The depth at which peak soil temperature begin to dampen in dry Jornada soils is commonly around 10 cm, when volumetric water content is below 10%, as is typical on the Jornada (see chapter 5). The surface soil temperature in the summer may range between  $20^\circ\text{C}$  at night and  $62^\circ\text{C}$  in the day. Thus the mean temperature in the top 10 cm is close to  $41^\circ\text{C}$ , and below 10 cm in depth soil temperature begins to damp with depth to eventually reach the long-term mean of  $15^\circ\text{C}$ . The amplitude is one-half the total swing, or  $21^\circ\text{C}$  at the surface, damping

with depth  $z$  as  $\exp(-z/D)$ . Roots may tolerate  $50^{\circ}\text{C}$  repeatedly, though shallow-rooted cacti may go higher, to  $56^{\circ}\text{C}$  in one study (Jordan and Nobel 1984). To damp to a peak temperature of only  $50^{\circ}\text{C}$ , soil must be found where the amplitude is only  $9^{\circ}\text{C}$ . This occurs at about 8.5 cm in dry Jornada soils. The decline of temperature with depth from the annual cycle is superimposed on the diurnal cycle. This falloff is about  $1^{\circ}\text{C}$  per 10 cm. It shifts the depth at which  $50^{\circ}\text{C}$  is expected upward by about 1 cm. High soil temperatures result in high evaporation from bare soil, and both increased root respiration costs and some soil temperatures may be lethal to plants. However, water in root tissues, shading by plant canopies and heterogeneity of soil water complicates the soil temperature profile.

Another energy loss is latent heat flux resulting from the heat of vaporization from ET ( $Q_E$  or LE). Tall vegetation with access to the groundwater and much exposure to wind may give fluxes up to  $500 \text{ W/m}^2$ , even in arid regions in riparian zones (Schaeffer et al. 2000). An average value of  $Q_E^-$  can be calculated from the average annual precipitation of 245 mm on the Jornada Basin. Evaporating  $245 \text{ kg H}_2\text{O/m}^2$  requires 610 MJ. Spread out over  $3.1 \times 10^7$  seconds in a year, this is an average flux density of  $19 \text{ W/m}^2$ , assuming all evaporation occurred equally throughout the year. The amount of energy leaving through the latent heat flux term is low compared to global standards and in comparison to other components of the energy budget. For example, average incoming  $Q_{sw}$  is approximately  $209 \text{ W/m}^2$ . Plants affect the partitioning of latent heat flux into its component fluxes of evaporation and transpiration, by their (partial) control of ET via their regulation of both stomatal conductance and leaf area

development which determine the transpiration component of ET. If ET is curtailed, due to soil water deficits, while solar inputs are not changed, the other losses must increase, with surface temperatures rising to strike the new balance. Indeed, the temperature difference from surface to air is a useful measure of water stress, as well as of sensible heat flux (in crops, Jackson et al. 1981; over arid lands and other sparse vegetation, Humes et al. 1994; Shuttleworth and Gurney 1990; Kustas et al. 1994).

### **Water Balance Characteristics of the Jornada Basin**

The Jornada Basin is a region with low precipitation and high potential evapotranspiration (PET) due to the characteristics of the energy budget and consequently low hydrologic yield (chapter 3). A simplified version of the water budget for the region is

$$(8-3) \quad \text{Precipitation} + \text{Run-in} = \text{Evapotranspiration} + \text{Runoff} - \text{Recharge} .$$

The basin, by virtue of its geomorphology, is closed hydrologically (see chapter 2). There is little runoff other than locally, and there are no perennial stream flows. Lateral subsurface flows in aquifers or in the vadose (unsaturated) soil zone are essentially absent on all but small spatial scales, such as in the playas and then only episodically. Soil hydraulic conductivity is generally low given the predominantly low water content, and terrain relief is slight except for some localized hill slopes. Hydrologic recharge of deep soil is minimal in most years (Phillips 1994), but may occur under certain rainfall conditions (Small 2005; see also chapter 5), and there is great spatial variation in recharge rates due to local geomorphology (Scanlon et al. 1999). Playas, fissures, gullies, and burrow pits have recharge rates up to 120 mm/yr (Scanlon and Goldsmith 1997) but cover a very minimal portion of surface area. Thus, essentially all precipitation is lost

through soil evaporation ( $E$ ) and plant transpiration. Despite the lack of water inputs, salinity is rare in soils of the Jornada Basin. However, calcium concentrations can exceed limits tolerated by calcifuge vegetation.

Evapotranspiration is approximately 95% of total precipitation inputs. In fact, Dugas et al. (1996) report that ET is  $100\% \pm 12\%$  for the Jornada Basin. However, even though almost all water is lost through ET, whether water is lost through soil evaporation or plant transpiration pathways is important to ecosystem processes because evaporation and transpiration drive different processes. Evaporation ( $E$ ) largely determines soil processes (soil respiration, soil water recharge), whereas transpiration drives plant productivity (Huxman et al. 2005).

Conversion of grassland to shrubland has resulted in changes in both the horizontal distribution of plant cover and the horizontal and vertical distribution of plant roots. In the horizontal dimension, grass cover is rather uniform, whereas shrub cover is patchy. For example, on the mesquite (*Prosopis glandulosa*) dunes of the Jornada, crown cover (defined as to the edge of the crown, ignoring the partial nature of light interception within the crown boundaries) is 15–30% (Rango et al. 2000). Roots systems of 11 shrub species were mapped in the Jornada Basin (Gibbens and Lenz 2001). Maximum root spread was found above petrocalcic and calcic horizons at depths above 1 m and ranged from 1 to 3 m from the center of the plant for tarbush (*Flourensia cernua*) and creosotebush (*Larrea tridentata*) and was greater than 6 m for some mesquite shrubs. Ten of the 11 shrub species had roots that penetrated the petrocalcic and calcic horizons and grew to depths of 5 m (roots were not mapped below this depth). Roots of 11 grass species were found to extend radially between 0.5 m and 1.4 m in sandy soils but did not

penetrate petrocalcic and calcic horizons and did not extend to depths greater than 1.6 m. The conversion from grassland to shrubland may affect the water balance of the Jornada Basin because deep-rooted shrub species may transpire deep water to the atmosphere that was previously below the root zone of grass and forb species. Additionally, many shrub species, particularly the evergreen creosotebush, have longer periods of phenological activity than grasses, which extend the period of time that water is transpired to the atmosphere (Reynolds et al. 1999b). The total amount of water lost will also depend on the rates of transpiration by various plant species. However, greater transpiration by individual shrub species may be offset by evaporative water losses in larger open interspaces. The partitioning of ET depends on rainfall characteristics, plant species composition, plant phenology, and photosynthetic pathway of vegetation cover, soil and air temperatures, and nutrient availability. Empirical estimates on the relative contribution of E and transpiration in semiarid regions have found disparate results with the ratio transpiration/ET ranging from 7–80% (see review in Reynolds et al. 2000; Dugas et al. 1996). Modeled estimates of plant transpiration showed high variability (1–60% of ET) that was largely in response to rainfall patterns (Reynolds et al. 2000).

Additionally, shrubs can redistribute water horizontally through their effects on overland flow (see chapter 7) and can also affect the ET component by altering interception losses and stem flow. Whitford et al. (1997) found that stem flow in creosotebush was  $16.8\% \pm 1.9\%$  of bulk precipitation. Stem flow effectively concentrated rainfall amounts around the bases of shrubs and may allow for deeper infiltration in the plant rooting zone than would be predicted based on soil texture and storm size. However, this effect varies by storm size and events smaller than 6 mm were not found to

cause measurable stem flow. Canopy interception is another mechanism whereby plants may interact with the hydrologic cycle. Tromble (1983) found that 20% of artificially applied rainfall was intercepted by creosotebush leaves. When scaled to the average crown cover of native creosotebush stands (approximately 30.5% crown cover) 22% of bulk precipitation could be lost through interception. In terms of small storm sizes, there may be disproportionate effects on the amount of intercepted precipitation. In the Jornada Basin the majority of storms are less than 6 mm. If an average storm size of 3 mm is used, nearly 12% of 3 mm rainfall may be lost through this pathway in creosotebush communities (Tromble 1983).

Changes in the surface energy balance or in vegetation cover and composition may produce interactions that can potential modify regional or local climates (Anthes 1984; Lyons et al. 1993; Sud et al. 1993; Pielke et al. 1998). For example, clearance of vegetation, all else being equal, increases the albedo in arid zones with light-colored soils, thus decreasing the average sensible heat flux to the atmosphere. Charney (1975), Charney et al. (1976), and Otterman (1974, 1975) proposed that the lower sensible heat flux leads to lower convection and cloud formation in the troposphere, producing a feedback that would stabilize desertification by reducing precipitation. Empirical proof has not been found (Le Houerou 1996), even though general circulation models show albedo effects acting at least on the scale of continents (Garratt 1993). More sophisticated climate modeling with global change models has revealed more complex interactions. For example, in the African Sahel coupling of ocean surface conditions to land surface conditions is critical for understanding precipitation characteristics. (review by Lau 1992; Myneni et al. 1996). On the spatial scale of the Jornada Basin (2,500 km<sup>2</sup>) and with its

absence of excess upwind surface water, there may be little effect of vegetation change on precipitation. ET is the ultimate source of virtually all precipitation globally. However, vegetation change on the Jornada may have little effect on regional precipitation because total accumulated ET is generally low and the recycling ratio (fraction of precipitation derived from local evapotranspiration; Eltahir and Bras 1996) is low. The recycling ratio clearly increases with spatial scale (becoming 1.0 over the globe) and is highest for any choice of spatial scale in Amazonia. Although coupled regional atmospheric models may find subtle differences in latent and sensible heat flux from vegetation change (Beltrán-Przekurat et al. 2005), it is unclear if these small changes can produce changes in weather patterns. On larger scales, the feedback of depleted water supply to depleted atmospheric humidity to depleted rainfall is expected (Bravar and Kavvas 1991). Consequently a drought cycle must be broken by a large-scale disturbance in atmospheric circulation.

### **Measurement of Energy Balance and CO<sub>2</sub> and H<sub>2</sub>O fluxes in the Jornada Basin**

The interactions of the energy and water balance with the composition of vegetation and soil processes determine the amount of carbon dioxide that is either taken up by vegetation or released by the terrestrial ecosystem to the atmosphere. Consequently some efforts to measure these balances have also included measurements of CO<sub>2</sub> flux. Surface energy balances and CO<sub>2</sub> and H<sub>2</sub>O fluxes are commonly measured using one of two micrometeorological methods: the eddy covariance method, a direct measurement of flux (Baldocchi et al. 1996) and the Bowen ratio method, an indirect or calculated flux measurement (Dugas 1993; Dugas et al. 1999). The Bowen ratio technique has commonly been used in studies of the Jornada Basin. This technique measures gradients

in both air temperature and air humidity over a vertical span above the canopy. The ratio of sensible heat flux to latent heat flux ( $H/LE$ ) is in proportion to the ratio of these gradients. If measures of the net radiation flux density,  $R_n$  (the sum of the first three terms in equation 8-1), and soil heat flux density are taken, then  $LE$  can be computed, for example, as  $(R_n - G)/(1 + H/LE)$ . The method is commonly estimated as having an error band of 50–100  $W/m^2$  (Bertela 1989; Dunin et al. 1989). Errors in measuring net radiation are dominant (Kustas et al. 1998), latent heat flux is used to determine  $ET$  flux, and if additional  $CO_2$  sensors are used, then  $CO_2$  fluxes can be determined.

The first effort to determine how energy balance components varied over five distinct vegetation types during a two-year period used the Bowen ratio energy balance (BREB) technique (Dugas et al. 1996). Mini-soil lysimeters were employed to partition  $ET$  into soil  $E$  and plant transpiration. The communities measured included tobosa (*Plueraphis mutica*), black grama (*Bouteloua eriopoda*), tarbush, creosotebush, and mesquite (see chapters 10 and 11 for community descriptions). For all communities there were high percentages of bare soil, and and high percentages of solar radiation incident on the soil surfaces resulting in high soil heat flux. Net radiation was similar in all communities with the exception of mesquite where midday  $R_n$  was 20% lower likely due to a highly reflective soil surface. Total accumulated  $ET$  was  $\pm 35$  mm of accumulated precipitation, indicating that nearly all precipitation was lost as  $ET$ .  $ET$  rates were comparable among all community types, with the exception of the tarbush community, where it was 50% higher. This was attributed to both increased herbaceous cover in this shrub community and its typical downslope position, which makes it the recipient of runoff water. The proportion of soil  $E$  to total  $ET$  ranged from 0.3 to 0.6, increasing in

creosotebush and mesquite communities probably because of large open interspaces between shrubs. The ratios are biased toward high soil E rates because the minilysimeters were measured following precipitation events. In general, differences in energy balance components were minimal, reflecting changes in the size of interspaces and water availability. These minimal differences did not appear to be directly attributable to differences in plant community types.

Results of Dugas et al. (1996) were supported by research at the Sevilleta LTER site in New Mexico, approximately 340 km north of the Jornada Basin (Kurc and Small 2004). The Sevilleta study used BREB methodology to quantify difference in energy balance components over three summer monsoon seasons in a nearly monospecific black grama grassland site and a monospecific creosotebush site. Midday ET rates were similar between these two sites, indicating that shallow soil water is the primary source of water for ET losses and direct evaporation is likely a large component of ET. Midday ET rates were similar because other components of the energy balance varied between the two sites. The similarity in ET rates was attributed to differences in midday available energy. Midday available energy was higher at the grassland than the shrubland by 20% due to differences in net radiation and soil heat flux. Net radiation was greater at the grassland because emitted longwave radiation was decreased in the grassland, due to a 3% lower albedo of the grassland site. Differences in soil heat flux also contributed to greater midday available energy. Soil heat fluxes at the shrubland site at midday were 30% greater than the grassland, probably due to the 30% greater amount of bare ground in the shrub community.

Shorter intensive campaigns in the Jornada Basin have used the more direct method of eddy covariance (Hipps et al. 1999) in which vertical fluxes caused by atmospheric turbulent eddies are directly detected. These studies have been limited to upland grassland and mesquite-dominated communities. Precipitation events were not coincident with the studies, so that only the rapid decline of transpiration (or ET) during the two weeks following rainfall events was characterized. This study also compared BREB methodology with eddy covariance (EC) methodology and found that BREB measurements were in agreement with EC measurements for the grassland site, but that in mesquite coppice dunes BREB measurements were unable to resolve small gradients in LE fluxes during dry conditions.

Concerns over global climate change have led to regional networks to measure net ecosystem exchange of carbon (NEE). Though much research has been done in forested systems, far less data exists in semiarid and arid rangelands. The next major effort to provide long-term measurement of NEE and ET in the Jornada Basin was part of a USDA ARS network of Bowen ratio towers in 11 rangelands sites. The Bowen ratio tower was installed on the Jornada in 1996. A compilation of the first six years of data (Mielnick et al. 2004) summarized NEE fluxes over this period (figure 8-1).

These data indicate that for the majority of days in a year, the Jornada Basin hovers around zero, or there is a slight source of carbon efflux to the atmosphere. When rainfall events occur, there is an initial burst of carbon efflux, which is likely due to increased heterotrophic activity of soil microbes. However, if the rainfall is of large magnitude, the system may shift to net carbon uptake due to increased photosynthetic assimilation of plants and perhaps assimilation by biological soil crusts

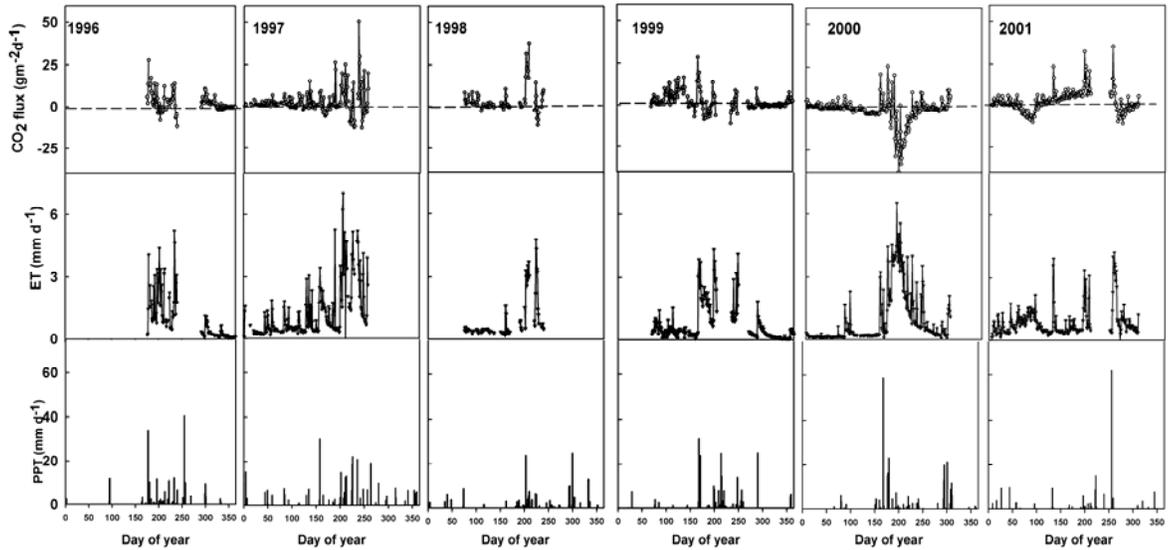


Fig. 8-1. Daily total CO<sub>2</sub> flux, evapotranspiration (ET), and precipitation (PPT) for 1996 through 2001. (Negative CO<sub>2</sub> flux indicates uptake). Redrawn from Mielnick et al. 2004

(Cable and Huxman 2004). The analysis by Mielnick et al. (2004) found that when averaged through time the Jornada Basin was a fairly significant source of carbon efflux through this time period (+145.3 g C/m<sup>2</sup>/yr). Daily ET rates were at a maximum in July through September, and maximum ET rates ranged from 5 mm/day in dry or average precipitation years, but increased to 7 mm/day in the two wet years. Average ET rates ranged from 0.15 mm/day in December to 2.15 mm/day in August. Average yearly ET was 299 mm, indicating that as expected all precipitation was lost to the atmosphere via this pathway.

Although the interpretation by Mielnick et al. (2004) indicates that on average the Jornada Basin was a net carbon source during this time period, there are several potential limitations to applying this estimate to the heterogeneous Jornada Basin as whole. The instrumented site was a grassland site. This type of vegetation occupies only a small

percentage (7%) of total vegetation cover in the Jornada Basin (Gibbens et al. 2005; see also chapter 10). Additionally, because of the nature of continuous data, periods of missing data existed. During a 6-year period, 1,243 days of actual data existed of the 2,190 total days possible (~ 57% of the total days in a 6-year period), and the data averaging techniques provide no indication of the daily variance in CO<sub>2</sub> flux. So a small daily positive efflux number was multiplied by a large time period, which produced a large efflux estimate. Estimates of variance may indicate that small positive effluxes are not significantly different from zero. Last, even though this is a long period of record for CO<sub>2</sub> data, in terms of semiarid and arid ecosystem dynamics the period of record may not adequately reflect the rainfall variability. For example, during this period of measurement, if the Jornada Basin had high rainfall distributed throughout the growing season, the source/sink outcome may have been different. The Jornada Basin is characterized by pulses of rainfall and intervening dry periods, consequently data gaps or data-filling techniques based on previous periods of measurement may miss important pulse events that quickly change the CO<sub>2</sub> fluxes of these systems. Although These flux data support the conclusion that these grasslands are a potential carbon source. However, they also illustrate potential limitations of these methods in a highly pulse-driven environment, such as that of the Jornada Basin.

A simple reanalysis of these data illustrates the effect of variance on these estimates and the effect of eliminating one dry year and adding another wet year. We used daily data from 1996, 1997, 1999, 2000, and 2001 (1998 was excluded because the BREB tower was only working for 70 days). No attempt was made to fill missing data values. The idea was only to estimate the variance associated with daily CO<sub>2</sub> flux when

the tower was functioning properly. Mean daily C flux ( $\pm 1$  SD) was  $0.36 \pm 1.7$  (g C/m<sup>2</sup>/d) and was significantly different than zero ( $p < 0.0001$ ). On a daily basis this site exhibited high variability and could be either a source or sink, though on average this site was a small source of CO<sub>2</sub> for the period of record. To examine how another wet year would affect these results, 2001 data values from a dry year were eliminated and data from the wet year of 2000 were used twice in the same analysis. This produced a mean daily carbon flux of  $0.07 \pm 1.8$  (g C/m<sup>2</sup>/d) and this mean value was not significantly different from zero ( $p > 0.16$ ). These simple analyses demonstrate the importance of temporal variability and the need for longer term records of CO<sub>2</sub> flux that encompass the decadal variation in rainfall patterns (Snyder and Tartowski 2005). The difference in variability in CO<sub>2</sub> flux between the Jornada and a site in Niwot Ridge, Colorado, characterized by a coniferous forest with relatively steady-state declines in soil water availability through time, was addressed using composite flux duration curves (see Huxman et al. 2004). Composite flux duration curves were constructed from the probability distribution of CO<sub>2</sub> fluxes for multiple years and are analogous to stream flow duration curves (Potts and Williams 2004). The comparison between the two sites showed that in terms of CO<sub>2</sub> fluxes, the Jornada fluxes were more frequently near zero and were punctuated by infrequent positive and negative values of NEE. Niwot Ridge had a gentler slope, indicative of less variable NEE responses. CO<sub>2</sub> fluxes of the Jornada Basin site are strongly driven by large rainfalls that occurred infrequently during the period of record for the Mielnick et al. (2004) study. Although these large rainfalls are inherently infrequent, the period of CO<sub>2</sub> record may need to be longer to capture desert rangeland dynamics that are largely event driven.

### **Interactions of Plants with the Energy and Water Balance**

The characteristics of the energy and water budgets in the Jornada Basin produce high incoming solar radiation, high variability in surface and soil temperature, and frequently low water availability, which also limits nitrogen availability. Consequently, plants of the Jornada Basin reflect a diverse array of adaptive strategies. Obviously, the major water-related challenge for plants is drought. Drought stress originates from both low soil water content and from high evaporative demand (i.e., atmospheric drought; Schulze 1986). Both types of drought stress are prominent in the Jornada Basin. Drought stress on the Jornada covers multiple time scales, from weeks between shallow wetting rain events in the monsoon to years of reduced precipitation (chapter 3). Specific plant strategies in controlling their physiological behavior, allocation, and phenologies are diverse and discussed elsewhere (see Gutschick 1987). In general, there are four basic strategies: drought escape, drought avoidance, drought tolerance, and drought endurance (Gutschick 1987). Most annual plants on the Jornada complete their life cycles outside the times of drought, therefore achieving drought escape. In drought avoidance, some plants, largely perennials, retain access to water supplies, by being phreatophytic (Neilson 1986) or by accessing deep water, and partially decoupling physiologic function from highly variable summer precipitation. Drought tolerance is the ability to tolerate low tissue water status and maintain continued physiological function. Common drought tolerance mechanisms are osmotic adjustment to maintain cell volume (and turgor in plants) and accumulation of solutes that protect membranes, (Jones 1992 discusses these mechanisms in plants). Other organisms show drought endurance, ceasing function to help maintain viability in

drought. Cryptogamic cyanobacteria in soil crusts are an extreme example in that they tolerate drying to perhaps  $-100$  MPa in water potential and temperatures up to  $70^{\circ}\text{C}$ .

Important correlates of summer drought are high temperatures and high radiation loads, which may have independent effects that must be understood to resolve plant tolerance to drought. Several direct interactions with drought are important. At the time of lowest water availability, relief of high leaf temperatures by transpirational cooling is least affordable. Jornada plants reduce the temperature load by having small leaves that have effective leaf–air heat transfer, so that even leaves in full sun with minimal transpiration do not rise far above air temperature. Among perennials, tarbush has the largest leaves with a minor axis of about 2 cm, and these leaves are mostly drought-deciduous and show the high temporal variation in response to rainfall patterns.

Dominant grass and shrub species are characterized by two different photosynthetic pathways— $\text{C}_4$  and  $\text{C}_3$ , respectively.  $\text{C}_4$  plants possess an effective biochemical pump for concentrating  $\text{CO}_2$ . Consequently they can maintain higher intracellular concentrations of  $\text{CO}_2$  ( $c_i$ ) at lower leaf conductances and smaller stomatal apertures. Reduced stomatal aperture reduces the amount of water lost to atmosphere in exchange for gaining  $\text{CO}_2$ . Therefore the efficiency of water use, the ratio of carbon gain per unit water loss, is generally higher for  $\text{C}_4$  species relative to  $\text{C}_3$  species. The temperature optimum and light saturation point is also higher for the  $\text{C}_4$  plants than for  $\text{C}_3$  plants. These characteristics of  $\text{C}_3$  plants may make them more adapted to dry environments, but as  $\text{CO}_2$  levels increase, the relative advantage may become less important. Also, conservative use of water may not be the best strategy if competing species extract water at high rates.

Survival of long and severe droughts is only one aspect of drought fitness. Drought recovery is equally important in ensuring that plants respond rapidly enough and fully enough to use evanescent water resources. Assimilation and transpiration in creosotebush continue at low levels in severe drought. Net CO<sub>2</sub> assimilation remains in the range 1–3 μmol/m<sup>2</sup>/s in creosotebush as late as 4–6 h after sunrise, dropping to near zero later. However, dark respiration is significant, typically 1.5–3 μmol/m<sup>2</sup>/s. This respiration may be derived from continuous repair of photodamage; chlorophyll fluorescence shows strong down-regulation of photosystem II, but recovery is strong after 2 h in the dark and overnight. It is plausible that protective complexes form, as they appear to do in other species prone to photodamage (Ball et al. 1991; Gilmore and Ball 2000). Such complexes may explain protection in creosotebush, although the elaborate spectroscopic measurements have yet to be done. In any event, recovery of all function on relief of drought is rapid and complete. Photosynthetic capacity, stomatal conductance, leaf water potential, leaf relative water content, and even subjective greenness and leaf area index all recover within 10–14 days of sufficient cumulative rainfall.

Some of the dominant shrubs of the Jornada Basin, particularly creosotebush and mesquite, may be adapted to severe water stress by their hydraulic architecture. In particular, their xylem vessels resist catastrophic cavitation to very low water potentials. We have measured water potentials to our instrumentation limit of –6 MPa in creosotebush during summer months over multiple years. Narrow xylem vessels are correlated with this resistance, particularly for freezing-induced cavitation (Davis et al.

1999); so, too, are narrow interconduit pits in tension-induced cavitation (Pockman et al. 1995). However, these vessels bear the cost of low hydraulic conductance. This feature does not appear to limit ability to grow and use water resources when they are available. Leaf photosynthetic rates reach high levels on an aerial basis (15–20  $\mu\text{mol}/\text{m}^2/\text{s}$ ) after recovery from drought in creosotebush and, readily, 30  $\mu\text{mol}/\text{m}^2/\text{s}$  in mesquite.

Empirical evidence exists, in a variety of systems, that drought fitness (DF) and water-use efficiency (WUE) are negatively correlated (Thomas 1986; Grieu et al. 1988). A more mechanistic relation may be afforded by the observations for creosotebush. Continued respiration for photodamage control or repair requires continued assimilation and transpiration. This reduces season total WUE by requiring water expenditure at times of inherently low WUE (high vapor pressure deficit). Continuous recovery processes in drought-active plants may enable plants to quickly use evanescent water resources when they become available.

## **Conclusions**

High solar radiation, high air and soil temperature, and low and variable precipitation strongly condition the water relations of plants in the Jornada Basin. Trade-offs between drought fitness and water use efficiency may be necessary to ensure rapid use of pulses of rainfall after intervening dry periods. In addition, characteristics of rainfall such as the size and frequency of rainfall events may elicit different responses from plant species that employ different drought strategies and fitness. The  $\text{C}_4$  grasses are primarily active during the warmest months and, being shallow-rooted, rely principally on summer rains for their survival. Because summer rainfall is even more variable

interannually than is total precipitation, the productivity of C<sub>4</sub> grasses is highly variable.

The C<sub>3</sub> shrubs are remarkably resistant to a paucity of summer rainfall. These physiological differences between grasses and shrubs in this basin illustrate the importance of plant community composition on energy and water balances.