

# Ecosystem Water Use Efficiency in a Semiarid Shrubland and Grassland Community

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## Abstract

Ecosystem water use efficiency (EWUE) is defined as the net carbon uptake per amount of water lost from the ecosystem and is a useful measure of the functionality in semiarid shrub and grassland communities.  $C_4$  grasses have higher water use efficiency (WUE) than do  $C_3$  shrubs, although it has been postulated that  $C_4$  plants have lost much of their advantage due to the rising atmospheric  $CO_2$  concentrations. The hypothesis was that  $C_4$ -grass-dominated ecosystems have a higher EWUE than  $C_3$ -shrub-dominated ecosystems under the present  $CO_2$  concentration and climatic variability. Evapotranspiration (ET) and  $CO_2$  fluxes were measured with Bowen ratio systems at a shrub and grass site for 6 years in southeastern Arizona. Two different methods were used to evaluate growing season EWUE using the ET and  $CO_2$  fluxes. The first method estimated a net daytime growing season EWUE for the grass site at  $1.74 \text{ g } CO_2 \cdot \text{mm}^{-1} \text{ ET}$  and  $1.28 \text{ g } CO_2 \cdot \text{mm}^{-1} \text{ ET}$  at the shrub site. The second method estimated maximum EWUE during part of the growing season at  $7.35 \text{ g } CO_2 \cdot \text{mm}^{-1} \text{ ET}$  for the grass site and  $4.68 \text{ g } CO_2 \cdot \text{mm}^{-1} \text{ ET}$  for the shrub site, which was considered a significant difference at  $P = 0.056$ . Data variability of the first method precluded a statistical difference determination between sites, but the results indicated that the grass-dominated ecosystem was between 1.4 and 1.6 times more water use efficient than the shrub-dominated ecosystem. Mean annual growing season precipitation and ET were similar in the two ecosystems, but the higher EWUE of the grassland system enabled it to take up more carbon during the growing season than the shrub ecosystem. Ecosystem differences in  $CO_2$  and  $H_2O$  flux have important management implications including primary productivity, C sequestration, and rangeland health.

## Resumen

La eficiencia del uso del agua del ecosistema (EWUE) es definida como la absorción neta de carbón por cantidad de agua pérdida del ecosistema, y es una medida útil de la funcionalidad de las comunidades semiáridas arbustivas y de pastizal. Los zacates  $C_4$  tienen mayor eficiencia del uso del agua (WUE) que los arbustos  $C_3$ , aunque ha sido postulado que las plantas  $C_4$  han perdido muchas de sus ventajas debido al aumento de la concentración atmosférica de  $CO_2$ . La hipótesis planteada fue que, bajo la presente concentración de  $CO_2$  y variabilidad climática los ecosistemas dominados por zacates  $C_4$  tienen una EWUE mayor que los ecosistemas dominados por arbustos  $C_3$ . En sitios de arbustos y zacates en el sudeste de Arizona se midieron por 6 años la evapotranspiración (ET) y flujos de  $CO_2$ , las mediciones se hicieron con sistemas de la relación de Bowen. Se usaron dos métodos diferentes para evaluar, con las mediciones de ET y los flujos de  $CO_2$ , la EWUE en la estación de crecimiento. El primer método estimó una EWUE neta diaria de la estación de crecimiento para el sitio de zacates en  $1.74 \text{ g } CO_2 \cdot \text{mm}^{-1} \text{ ET}$  y de  $1.28 \text{ g } CO_2 \cdot \text{mm}^{-1} \text{ ET}$  en el sitio de arbustos. El segundo método estimó la máxima EWUE durante parte de la estación de crecimiento en  $7.35 \text{ g } CO_2 \cdot \text{mm}^{-1} \text{ ET}$  para el sitio de zacates y  $4.68 \text{ g } CO_2 \cdot \text{mm}^{-1} \text{ ET}$  para el de arbustos, la cual fue considerada como una diferencia significativa a  $P = 0.056$ . La variabilidad de los datos del primer método imposibilita la determinación de una diferencia estadística entre sitios, pero los resultados indicaron que el ecosistema dominado por zacates fue entre 1.4 y 1.6 veces más eficiente en el uso del agua que el ecosistema dominado por arbustos. La precipitación promedio anual de la estación de crecimiento y la ET fueron similares entre los dos ecosistemas, pero la mayor EWUE del ecosistema de pastos le permitió absorber más carbón durante la estación de crecimiento que el ecosistema de arbustivas. Las diferencias de los ecosistemas en los flujos de  $CO_2$  y  $H_2O$  tienen importantes implicaciones de manejo, incluyendo la productividad primaria, el secuestro de carbono, y la salud del pastizal.

**Key Words:** Bowen ratio, carbon dioxide, evapotranspiration, EWUE

## INTRODUCTION

Rangeland ecosystems make up about 40% of the global land surface, and therefore have a great potential to produce biomass and help alleviate the increasing carbon dioxide concentration in

the atmosphere (Svejcar et al. 1997). In semiarid environments, water usually is considered the limiting factor in biomass production. Information on the relationships between biomass production and water use is critical to understanding how different rangeland ecosystems take up carbon, interact, and function. These functional relationships influence hydrosphere and biosphere interactions (Loik et al. 2004).

Ecosystem water use efficiency (EWUE) relates an ecosystem's exchange of carbon to its water use (i.e., evapotranspiration [ET]). Law et al. (2002) investigated EWUE for many of the world's major biomes and found they were similar, with the exception of arctic tundra, which was lower. The more

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common term, water use efficiency (WUE), compares plant uptake of carbon to plant water use in the form of transpiration. Within semiarid rangeland ecosystems there are dominant plant communities with different WUE based on the photosynthetic pathways (i.e.,  $C_3$ ,  $C_4$ , and CAM) possessed by the dominant plants. This would imply an inherently wide variation in EWUE for these plant communities. These plant communities also have different vegetation structures, plant densities, biomass, litter, and canopy cover that would influence ET and the resultant EWUE. Rangeland WUE research has been conducted by changing  $CO_2$  concentrations in order to evaluate WUE of individual plants (Ham et al. 1995; Lutze and Gifford 1995), whereas ecosystem response, EWUE, has been largely ignored. Increasing  $CO_2$  concentrations increases WUE of  $C_3$  and  $C_4$  plants, but it is more beneficial to  $C_3$  plants (i.e., shrubs) when subjected to water stress (Polley et al. 1997). This response of  $C_3$  plants has been proposed as one of the factors responsible for expansion of shrubs into grasslands (Bond and Midgley 2000; McCarron and Knapp 2001). Recent studies using controlled  $CO_2$  concentrations from subambient to superambient indicated that much of the WUE gain in  $C_3$  plants has already been reached with the current  $CO_2$  concentrations in the atmosphere (Anderson et al. 2001; Gill et al. 2002; Polley et al. 2002). Present and future increases in atmospheric  $CO_2$  concentration might not favor increased WUE in  $C_3$  plants, and much of the WUE advantage for  $C_4$  plants could be lost. Hence, an appropriate way to evaluate different plant communities would be to use EWUE.

Ecosystem water use efficiency can be defined and evaluated in at least two different ways. One method uses the ratio of net ecosystem exchange (NEE) of carbon dioxide to evapotranspiration (ET) by the ecosystem for the growing season or some other time period (Tubiello et al. 1990). A more instantaneous evaluation method of EWUE is the regression of daily daytime NEE vs. ET with the slope value of the regression line a measure of EWUE (Balocchi et al. 2001). Bowen ratio and eddy covariance systems are direct methods used to measure NEE of carbon dioxide and ET water fluxes. Daytime measurements are used because they are more accurate than nighttime; also, during daytime plants are actively taking up carbon (Ohmura 1982).

Rangelands are water-limited ecosystems where biomass production can be influenced by temperature, humidity, radiation, precipitation sequences, climatic variability, and numerous other factors besides the WUE of the individual plants themselves (Dugas et al. 1996; Polley et al. 2002). The EWUE of rangeland shrub and grass communities is not just a function of the WUE of individual plants, but also of  $CO_2$  loss from plant respiration and microbial decomposition of organic materials and evaporation of moisture from the soil surface. Precipitation pulses, in terms of timing and amounts, influence  $CO_2$  and ET fluxes (Huxman et al. 2004a, 2004b) that potentially impact the EWUE of shrub and grass plant communities in different ways. The hypothesis for this study was that the EWUE of a  $C_4$  grass-dominated community is greater than that of a  $C_3$  shrub-dominated community under the present  $CO_2$  concentration and variable climatic conditions. Six years of Bowen ratio  $CO_2$  and water vapor flux data and two distinct methods of analysis were used to quantify EWUE.

### Experimental Site Descriptions

The two sites for this study were located on the Walnut Gulch Experimental Watershed in southeastern Arizona. The climate is semiarid with cool winters and warm summers. Long-term annual average precipitation is 356 mm and temperature is  $17^\circ C$ . A present-day shrub community known as Lucky Hills (lat  $31^\circ 44' 37''$  N, long  $110^\circ 3' 5''$  W; elevation 1 372 m) was selected as a study site. The dominant shrubs at this site are whitethorn Acacia (*Acacia constricta* Benth.), tarbush (*Flourensia cernua* D.C.), creosotebush (*Larrea tridentata* [D.C.] Cov.), and desert zinnia (*Zinnia pumila* A. Gray). The only grass species remaining at the site, which was historically a black grama (*Bouteloua eriopoda* [Torr.] Torr.) community, is bush muhly (*Muhlenbergia porteri* Scribn. ex Beal). The botanical nomenclature is from the USDA-NRCS plants database (<http://plants.usda.gov>). The soil at this site is Lucky-hills series (coarse-loamy, mixed, thermic Ustochreptic Calciorthids) with 3% to 8% slopes. Surface A horizon (0–6 cm) contained  $650 \text{ g} \cdot \text{kg}^{-1}$  sand,  $290 \text{ g} \cdot \text{kg}^{-1}$  silt, and  $60 \text{ g} \cdot \text{kg}^{-1}$  clay with  $290 \text{ g} \cdot \text{kg}^{-1}$  coarse fragments ( $> 2 \text{ mm}$ ),  $8 \text{ g} \cdot \text{kg}^{-1}$  organic carbon, and  $21 \text{ g} \cdot \text{kg}^{-1}$  inorganic carbon.

The grass community site was identified as Kendall (lat  $31^\circ 44' 10''$  N, long  $109^\circ 56' 28''$  W; elevation 1 526 m). Vegetation at the site is predominantly sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), black grama, hairy grama (*Bouteloua hirsuta* Lag.), and Lehmann lovegrass (*Eragrostis lehmanniana* Nees), with a few existing shrubs of fairy duster (*Calliandra eriophylla* Benth.), and burweed (*Isocoma tenuisecta* Greene). The soils at the site are a complex of Stronghold (coarse-loamy, mixed, thermic Ustollic Calciorthids), Elgin (fine, mixed, thermic, Ustollic Paleargids), and McAllister (fine-loamy, mixed, thermic, Ustollic Haplar-gids) soils, with Stronghold the dominant soil. Slopes range from 4% to 9%. The Stronghold surface A horizon (0–3 cm) contains  $670 \text{ g} \cdot \text{kg}^{-1}$  sand,  $160 \text{ g} \cdot \text{kg}^{-1}$  silt, and  $170 \text{ g} \cdot \text{kg}^{-1}$  clay with  $790 \text{ g} \cdot \text{kg}^{-1}$  coarse fragments ( $> 2 \text{ mm}$ ),  $11 \text{ g} \cdot \text{kg}^{-1}$  organic carbon, and  $7 \text{ g} \cdot \text{kg}^{-1}$  inorganic carbon.

Biomass and soil cover at the sites were measured by the line transect method using 12 transects, 30 m in length, with 33 measurements per transect. Canopy cover was determined as percent shrub, grass, or forb. Soil cover was determined as soil, rock ( $> 1.0 \text{ cm}$ ), litter, and plant basal area for both grasses and shrubs.

### Micrometeorological Measurements

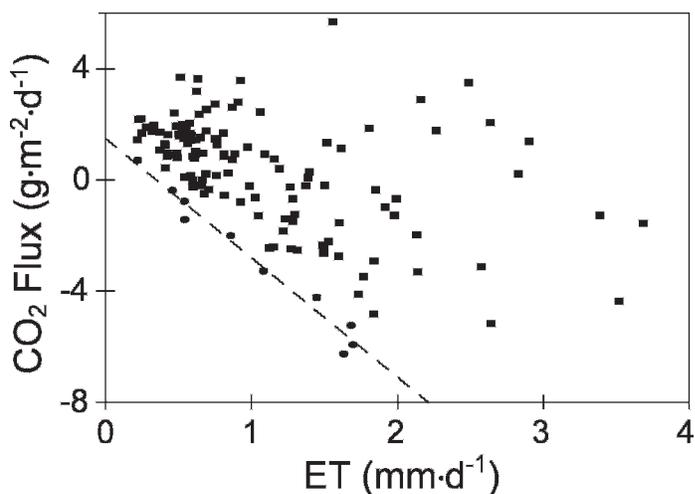
Continuous, 20-minute average carbon dioxide and water vapor flux measurements were made at both sites using Bowen ratio energy balance systems (BREB; model 023/ $CO_2$ ; Campbell Scientific Inc, Logan, UT). The systems were placed in locations with a fetch of 200+ m in all directions. The theory and procedures used to calculate the fluxes have been presented in detail by Dugas (1993) and Dugas et al. (1999). Briefly, atmospheric gradients of air temperature, moisture, and  $CO_2$  were measured every 2 seconds and averaged every 20 minutes. The 20-minute averages were stored in a datalogger (model 21X, Campbell Scientific). Kendall grass site gradients were measured at 1 and 2.5 m, and the Lucky Hills shrub site at 1.5

and 3.0 m above the soil surface. Vegetation canopy height at the grass community ranged from 0.4 to 0.7 m during the growing season and a constant 1-m height at the shrub community. Atmospheric carbon dioxide and moisture concentration gradients were measured with an infrared gas analyzer (IRGA; LI-6262; LI-COR Inc, Lincoln, NE).

Simultaneously, the following meteorological data were obtained: net radiation from a net radiometer at a height of 3 m (model Q\*7; REBS, Seattle, WA), soil heat flux from five heat flux plates at 8 cm depth (model HFT3; REBS), soil temperature above each heat flux plate from averaging thermocouples, wind speed, and direction from an anemometer/windvane (model 03001 R. M. Young Wind Sentry Set; R. M. Young Company, Traverse City, MI), and air temperature and relative humidity from a T/RH probe (model HMP35C; Vaisala Inc, Woburn, MA). Soil moisture values needed for the soil heat flux calculation were determined for the first 2 years using soil percent water samples collected immediately after precipitation events and repeated sample collection until constant soil moisture. From these data, a relationship was developed between precipitation and soil moisture content and used for rest of the study. Net radiometers were calibrated yearly over a grass canopy. Carbon dioxide, water vapor, and energy fluxes were calculated from the 20-minute average data. Temperature and water vapor gradients were used to calculate Bowen ratios. Bowen ratio, net radiation, soil heat flux, and soil temperature were used to calculate sensible heat flux. Eddy diffusivity was calculated from sensible heat fluxes and temperature gradients and assumed to be equal for heat, water vapor, and CO<sub>2</sub>.

Eddy diffusivity could not be calculated when sensible/latent heat flux was in the opposite direction of temperature/water vapor gradients, or when the Bowen ratio approached -1.0 (Ohmura 1982). Under these conditions, eddy diffusivity was calculated by using wind speed, atmospheric stability, and canopy height (Dugas et al. 1999). This alternative method for calculating eddy diffusivity was used about 12% of the time, primarily at night when gradients and fluxes were small, hence any errors from the alternative method would have minimal impact on the calculated flux values. For short periods of time, usually at sunset or sunrise and when the Bowen ratio was near -1.0, fluxes were estimated by linear interpolation with less than 5% of the data interpreted in this way. For longer time periods (i.e., days usually associated with equipment failure) when there was a clear trend in the flux data, linear interpolation was used to estimate daily fluxes; otherwise no estimate was made. Normally, fluxes were calculated as the product of the eddy diffusivity and water vapor and CO<sub>2</sub> gradients corrected for vapor density gradients at the two heights (Webb et al. 1980). Temperature corrections for the two heights were not applied because Angell et al. (2001) have shown the temperature differences to be insignificant as the air enters the IRGA for analysis. For this study negative, CO<sub>2</sub> flux values were considered uptake of CO<sub>2</sub> by the ecosystem.

The BREB systems performance at the sites in this study has been appraised for the functional relationships between ET, CO<sub>2</sub> flux, and net radiation (Emmerich, 2003; Figs. 1 and 2). The BREB systems were able to measure ET and CO<sub>2</sub> flux changes that are closely related to changes in net radiation. The influence of the incoming radiation on ET and CO<sub>2</sub> uptake was



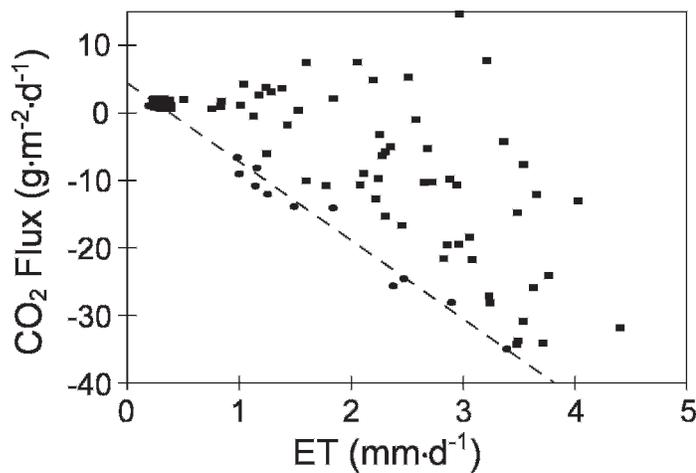
**Figure 1.** Daytime CO<sub>2</sub> flux vs. evapotranspiration (ET) for the Lucky Hills shrub community in 1998. Maximum ecosystem water use efficiency (EWUE) analysis is shown by the dashed regression line and the round circles were the data points used for the regression analysis. Negative values indicate net CO<sub>2</sub> uptake.

observed at the 20-minute time steps of the data during the growing season.

#### Ecosystem Water Use Efficiency Evaluation

Ecosystem water use efficiency for this study was quantified using two different methods with data obtained during the growing season. It was defined as the ratio of daily daytime NEE of CO<sub>2</sub> flux to a daily daytime ET flux ( $\text{g CO}_2 \cdot \text{mm}^{-1} \text{H}_2\text{O}$ ) summed for the growing season or as the regression slope value for daily daytime CO<sub>2</sub> fluxes vs. ET for the data points with maximum CO<sub>2</sub> uptake flux and minimum ET flux ( $\text{g CO}_2 \cdot \text{mm}^{-1} \text{H}_2\text{O}$ ). The slope values of the regression lines are a measure of the EWUE with greater EWUE represented by a more negative slope (Baldocchi et al. 2001). The data for the maximum regressions equations was selected by taking daily data points with maximum CO<sub>2</sub> uptake with minimum ET from all the daily data points within the growing season. The slopes for the maximum EWUE were selected to evaluate EWUE because they were the most likely to show differences between plant communities. The summer growing season starts and ends with the summer monsoon precipitation. Day of year (DOY) 150–300 was selected as the summer growing season to include all the plant growth in typical years. This also allowed for a constant time period for comparisons between years and plant communities. Daytime CO<sub>2</sub> and ET fluxes were used to evaluate EWUE because this was when the measurements are more accurate and the plants are actively taking up CO<sub>2</sub> and the ET fluxes are the greatest. Analysis with inclusion of nighttime fluxes increased the variability in the data.

A two-way analysis of variance analysis was done on the yearly ratio of CO<sub>2</sub> to ET fluxes and the maximum yearly slope values to test for differences between sites, with year as a random effect. Values were considered significant at the  $P = 0.05$  level. A Student *t* test was used to test for differences in maximum EWUE slopes for years within sites.



**Figure 2.** Daytime CO<sub>2</sub> flux vs. evapotranspiration (ET) for the Kendall grass community in 2002. Maximum ecosystem water use efficiency (EWUE) analysis is shown by the dashed regression line and the round circles were the data points used for the regression analysis. Negative values indicate net CO<sub>2</sub> uptake.

## RESULTS

### CO<sub>2</sub> to ET Flux Ratio EWUE

The yearly variability in the CO<sub>2</sub> to ET flux ratios was quite large (Table 1). Large variability in annual precipitation and timing influenced the CO<sub>2</sub> and ET flux responses and were largely responsible for the ratio variability. The variability in growing season precipitation between years was so large that in 1998 at the shrub site and 2003 at the grass site, there was a net loss of CO<sub>2</sub> as a result of low precipitation. Therefore, mean yearly flux ratios were used to reduce variability in the evaluation of EWUE. The grass site had a mean uptake of 1.74 g CO<sub>2</sub> · mm<sup>-1</sup> ET, and the shrub site had a mean uptake of 1.28 g CO<sub>2</sub> · mm<sup>-1</sup> ET. These values indicate the grass site was about 1.4 times more efficient in CO<sub>2</sub> uptake per unit of ET than the shrub site. However, this was not a significant difference ( $P = 0.61$ ) because of large data variability between years, but it does provide an indication that the sites were different.

### Maximum EWUE

Days of maximum EWUE resulted during the growing season when plant growth stages and environmental conditions were most favorable. The high coefficients of determination for the regression analysis and low yearly variability indicated a relatively distinct maximum EWUE for the shrub and grass sites (Table 2). The 6-year mean negative slope values of the regression lines indicated that the shrub site had a maximum EWUE of 4.68 g CO<sub>2</sub> · mm<sup>-1</sup> ET and the grass site 7.35 g CO<sub>2</sub> · mm<sup>-1</sup> ET. This is a factor of 1.6 times greater EWUE at grass site, which is similar to the factor of 1.4 times determined by utilizing the ratio of CO<sub>2</sub> to ET fluxes for EWUE evaluation. With less variability in the yearly data, the sites were considered significantly different at  $P = 0.056$ .

The maximum CO<sub>2</sub> vs. ET flux data analysis revealed higher individual daytime rates of CO<sub>2</sub> uptake for the grass site compared to the shrub site (Figs. 1 and 2). This difference was evident when the scales of the Figures 1 and 2 are considered

and with up to six times more CO<sub>2</sub> uptake in a day. These data points represent the absolute maximum daytime CO<sub>2</sub> uptake and minimum ET for an individual site and year. The maximum regression slope values for years within sites were relatively similar, except for one year at each site (Figs. 3 and 4). At the shrub site, the slope for 2001 was significantly different ( $P < 0.05$ ) from 1998, 1999, and 2003. At the grass site, 2002 was significantly different from the other years.

## DISCUSSION

The yearly variability in EWUE indicated that it is not a constant property of shrub and grass plant communities and that precipitation variability has a principal influence on EWUE. Data variability in the data of the methods used to evaluate the ecosystems prevented a statistical determination for both methods used. The maximum EWUE method, with less data variability, had a  $P$  value of 0.056, which was considered significant because of the data variability and indicated the grass site was more efficient than the shrub site. Under the present carbon dioxide concentration and climate variability of this study, the overall results are indicating the C<sub>4</sub> grass plant community is more water-use-efficient than the C<sub>3</sub> shrub.

In semiarid environments, precipitation timing and amounts can be an important driving force for CO<sub>2</sub> and ET fluxes, hence on the determination of EWUE (Xu and Baldocchi 2004). The annual precipitation varied from 101 mm above to 158 mm below the long-term average (Table 1). Growing season precipitation variability ranged from 97% in 1999 to a low of 66% in 2003 of the annual precipitation. The variability in precipitation between years, especially in 1999, had a big effect on CO<sub>2</sub> and ET fluxes. In 1999 and 2000, a large amount of precipitation during the growing season produced some of the highest CO<sub>2</sub> and ET fluxes at both plant community sites. Even within these high precipitation years, variability in precipitation in 1999 and 2000 produced large differences in CO<sub>2</sub> and ET fluxes between these years. Almost all the precipitation in 1999 occurred in July and August at the peak of the summer growing season whereas in 2000 about 40% occurred at the end of the growing season in October. In 2000, the vegetation had completed most of its growth for the year, and consequently the plant communities did not utilize the growing season precipitation as efficiently (Table 2). Hence, the yearly EWUE variability was not directly dependent on total annual and growing season precipitation, but more on precipitation timing and amount.

The low precipitation years of 1998 at the shrub site and 2003 at the grass site showed a daytime net loss of CO<sub>2</sub>, but were still included as part of the EWUE evaluation (Table 1). Leaving these years out would give a biased estimate of long-term EWUE. Many of the precipitation events were small, which would stimulate microbial activity at the soil surface to break down soil organic and litter material, but would have limited infiltration into the soil for use by plants (Huxman et al. 2004b). There were days of net CO<sub>2</sub> uptake and new biomass production, even during low precipitation growing seasons with a net CO<sub>2</sub> loss. This indicates that microbial activity dominates CO<sub>2</sub> flux to produce a net loss of CO<sub>2</sub> during

**Table 1.** Daytime evapotranspiration (ET) and CO<sub>2</sub> flux between day of year (DOY) 150–300, ratio of CO<sub>2</sub> to ET flux, and precipitation in a grassland and shrubland dominated community in Arizona. Negative values indicate net CO<sub>2</sub> uptake.

| Year                               | Daytime ET (mm) | Daytime CO <sub>2</sub> (g · m <sup>-2</sup> ) | Ratio CO <sub>2</sub> to ET (g CO <sub>2</sub> · mm <sup>-1</sup> ) | Precipitation DOY 150–300 (mm) | Precipitation annual (mm) |
|------------------------------------|-----------------|------------------------------------------------|---------------------------------------------------------------------|--------------------------------|---------------------------|
| ----- Lucky Hills shrub site ----- |                 |                                                |                                                                     |                                |                           |
| 1998                               | 153             | 32                                             | 0.21                                                                | 131                            | 201                       |
| 1999                               | 253             | -352                                           | -1.39                                                               | 302                            | 314                       |
| 2000                               | 288             | -198                                           | -0.69                                                               | 372                            | 457                       |
| 2001                               | 193             | -812                                           | -4.21                                                               | 187                            | 279                       |
| 2002                               | 189             | -85                                            | -0.45                                                               | 191                            | 230                       |
| 2003                               | 195             | -224                                           | -1.15                                                               | 170                            | 246                       |
| Mean                               | 212             | -273                                           | -1.28 (1.54) <sup>1</sup>                                           | 226 (92)                       | 288 (92)                  |
| ----- Kendall grass site -----     |                 |                                                |                                                                     |                                |                           |
| 1998                               | 248             | -410                                           | -1.65                                                               | 258                            | 349                       |
| 1999                               | 346             | -763                                           | -2.21                                                               | 321                            | 330                       |
| 2000                               | 249             | -339                                           | -1.36                                                               | 356                            | 436                       |
| 2001                               | 35 <sup>2</sup> | -63 <sup>2</sup>                               | -1.80                                                               | 203                            | 282                       |
| 2002                               | 172             | -656                                           | -3.81                                                               | 166                            | 219                       |
| 2003                               | 149             | 56                                             | 0.38                                                                | 130                            | 198                       |
| Mean                               | 233             | -445                                           | -1.74 (1.51)                                                        | 239 (89)                       | 302 (88)                  |

<sup>1</sup>Standard deviation.

<sup>2</sup>Low ET and CO<sub>2</sub> values due to missing data, therefore not included in means and SD.

growing seasons with low precipitation. The net loss of growing season CO<sub>2</sub> only occurred in the lowest precipitation growing season years.

The maximum EWUE method was developed from the analysis of the regression relationship between CO<sub>2</sub> vs. ET flux which showed a clear boundary-line cutoff in the data, indicating a maximum EWUE (Figs. 1 and 2). The maximum EWUE occurred when the amount of CO<sub>2</sub> uptake was greatest for the minimum amount of ET. Distinctness of the boundary-line data is also evident in the coefficients of determination for the regression equations (Table 2). Horton et al. (2001) used

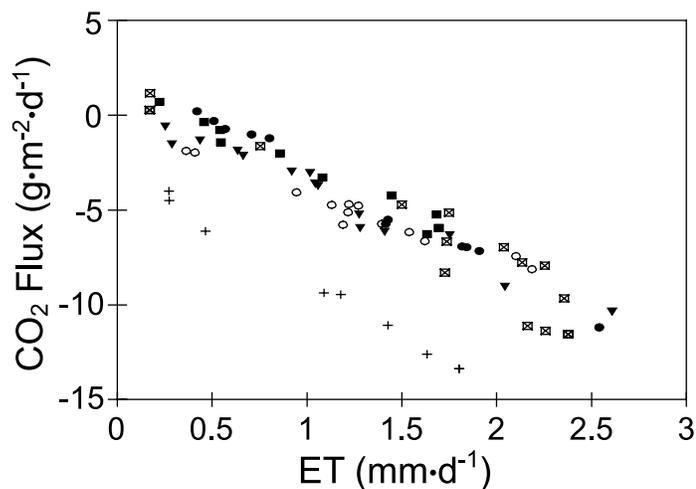
a similar boundary-line analysis to evaluate various Sonoran Desert trees for relationships between stomatal conductance and photosynthesis as a function of a leaf-to-air vapor pressure deficit (VPD). In their analysis, boundary-line cutoffs in the data indicated limits at which the trees could exchange water and conduct photosynthesis based on VPD at the leaf level. The boundary-line limits in this study indicated the maximum that the ecosystems could take up CO<sub>2</sub> with minimum ET.

The CO<sub>2</sub> uptake values along the maximum regression lines are the result of many factors including precipitation amounts

**Table 2.** Coefficients of determination, constants, and slopes for maximum ecosystem water use efficiency (EWUE) regression equations of CO<sub>2</sub> flux vs. evapotranspiration (ET) between day of year (DOY) 150–300. Negative slope values indicate CO<sub>2</sub> uptake.

| Year                               | r <sup>2</sup> | Constant | Slope                     |
|------------------------------------|----------------|----------|---------------------------|
| ----- Lucky Hills shrub site ----- |                |          |                           |
| 1998                               | 0.97           | 1.49     | -4.30                     |
| 1999                               | 0.96           | 0.52     | -4.29                     |
| 2000                               | 0.99           | 2.49     | -5.29                     |
| 2001                               | 0.99           | -2.84    | -5.86                     |
| 2002                               | 0.91           | 1.75     | -4.97                     |
| 2003                               | 0.96           | -0.87    | -3.36                     |
| Mean                               | 0.96           | 0.42     | -4.68 (0.88) <sup>1</sup> |
| ----- Kendall grass site -----     |                |          |                           |
| 1998                               | 0.99           | 3.16     | -6.28                     |
| 1999                               | 0.98           | 1.19     | -6.26                     |
| 2000                               | 0.90           | 2.83     | -6.54                     |
| 2001                               | 0.98           | 1.96     | -5.17                     |
| 2002                               | 0.98           | 4.42     | -11.64                    |
| 2003                               | 0.97           | 2.47     | -8.23                     |
| Mean                               | 0.97           | 2.67     | -7.35 (2.32)              |

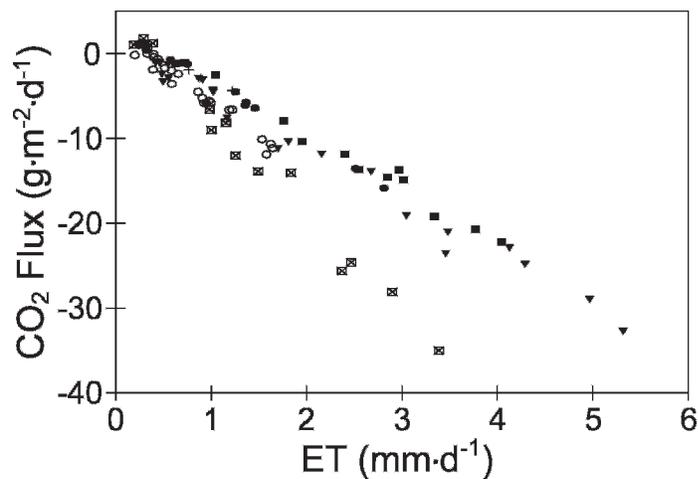
<sup>1</sup>Standard deviation.



**Figure 3.** CO<sub>2</sub> vs. evapotranspiration (ET) regressions of maximum ecosystem water use efficiency (EWUE) data points for the Lucky Hills shrub community in Arizona for 6 successive years including 1998 (■); 1999 (▼); 2000 (●); 2001 (+); 2002 (⊠); 2003 (○). Negative values indicate net CO<sub>2</sub> uptake.

and timing, plant growth stage, temperature, and net radiation. Data values of the CO<sub>2</sub> vs. ET regressions that are to the right of the maximum regression line indicate a loss of EWUE from the maximum (Figs. 1 and 2). The additional ET at this time was probably evaporation from the soil surface. The shrub site graphs showed a tendency toward having more data points farther to the right of the maximum regression lines. This added ET loss, primarily in the form of evaporation, would be part of the overall lower EWUE of the shrub plant community. The canopy and soil cover data support lower evaporation from the soil surface at the grass site. The percent soil, rock, litter, and plant basal cover at the shrub site was 39%, 47%, 10%, and 4% respectively, and 20%, 53%, 20%, and 6% at the grass site. The canopy cover at the shrub site was 54%, and 69% at the grass site. With greater canopy cover, air movement slows down over the soil surface, reducing evaporation. The feature of higher surface cover at the grass site also acts as a physical barrier and as a mulch to slow soil surface evaporation.

The regression lines for maximum CO<sub>2</sub> uptake with minimum ET were generally similar among years, with a 1 year exception at each site (Figs. 3 and 4; Table 2). Xu and Baldocchi (2004) found that precipitation timing, more than amount, can have significant influence on CO<sub>2</sub> and ET fluxes, hence can provide some explanation for the unusual years. In 2001, the shrub site maximum regression line had a more negative slope and a shift to more CO<sub>2</sub> uptake with less ET as represented by the larger negative regression constant (Fig. 3; Table 2). Precipitation in 2000 at the shrub site was much more than the long term average of 356 mm (Table 1). In the fall of 2000 by day 265, NEE of carbon was positive, indicating a loss of CO<sub>2</sub> and the ending of plant growth. Precipitation at the shrub site in 2000, from day 280 through 365, was 205 mm, with the next highest at 37 mm for this time period. Then in the spring of 2001, from day 1 through 150, there was 77 mm of precipitation received, with the next highest at 50 mm during this time period. These unusual fall 2000 through spring 2001



**Figure 4.** CO<sub>2</sub> vs. evapotranspiration (ET) regressions of maximum ecosystem water use efficiency (EWUE) data points for the Kendall grass community in Arizona for 6 successive years including 1998 (■); 1999 (▼); 2000 (●); 2001 (+); 2002 (⊠); 2003 (○). Negative values indicate net CO<sub>2</sub> uptake.

precipitation timing and amounts at the shrub site provided enough soil moisture for plant growth to produced carbon uptake from about day 95 through 150. The only other year showing early carbon uptake was 1998 at about one-third the 88 g CO<sub>2</sub> · m<sup>-2</sup> for this spring time period. This extra fall, winter, and into spring precipitation produced an unusual early plant growth stage which allowed the shrubs to put out new leaves and prime the shrubs. When the small amount of summer precipitation came, they were able to utilize it more efficiently, enabling more CO<sub>2</sub> uptake than any of the other growing season (Table 1). The grass site experienced similar 2000 and 2001 precipitation sequences, but equipment failure prevented proper evaluation of the summer growing season in 2001 (Table 1).

The unusual year for the maximum regression line slope at the grass site came in 2002 (Fig. 4). Again, precipitation timing and amount accounted for the higher EWUE with a more negative slope (Table 2). In 2002, 166 mm or 75% of the annual precipitation occurred in the growing season and 71% of that within DOY 200–220. These factors provided ample moisture at the peak time for warm-season grass growth period. The grasses were able to efficiently use the moisture and produce one of the highest amounts of CO<sub>2</sub> uptake with one of the lowest amounts of ET loss (Table 1). These two years of 2001 and 2002 at the sites illustrate that precipitation variability can produce significant yearly differences in EWUE and that EWUE was not constant from year to year. This implies that a number of years are needed to properly evaluate EWUE.

## MANAGEMENT IMPLICATIONS

Common management goals in semiarid environments are to convert shrub to grass lands and thereby increase grass biomass and to maintain and promote healthy grassland ecosystems. In semiarid ecosystems where water is limited, the grassland site in this study had a higher EWUE that was 1.4 to 1.6 times greater

than the shrub site and was able to take up more carbon during the growing season even with similar precipitation amounts. Management should take advantage of this higher EWUE of grasslands to produce more biomass. If additional carbon can be retained in the soil, added management benefits will be obtained. The biomass belowground, especially at the grass site, would increase the potential for long-term incorporation into soil organic matter (Cox et al. 1986; Kurc and Small 2004). The ecosystem differences in CO<sub>2</sub> and H<sub>2</sub>O flux also have important management implications including primary productivity, C sequestration, and rangeland health (Herrick et al. 2002).

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