

Effect of Spatial and Temporal Variability on Water Relations and Growth in Pinyon Pine: III. Whole Tree Response

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Abstract—This paper is the final report in a larger study of water relations in pinyon pine ecosystems. This last study looks at whole-tree response to climatic variability; water use efficiency was studied using ^{13}C measurements of tree-rings.

The purpose of this study is to explore the physiological response of pinyon pine to spatial and temporal variability on a whole tree level using information on physiology and growth recorded in tree-rings. The rationale of this approach is that water relations of pinyon pine and any long-lived species can only be truly understood in the context of the spatiotemporal heterogeneity inherent to natural environments. In addition to providing a more complete characterization, exploring a wide range of spatial and temporal scales can lead to deeper ecological insights (Betancourt 1993, Ehleringer & Field 1993, Gosz, J.R. 1993, Gosz and Sharpe 1989, O'Neill 1986). In semiarid regions, annual precipitation provides a dominant limitation of the ecosystem biomass, but is insufficient for predicting community structure and composition. Rather, temporal variability in precipitation has been hypothesized to more directly constrain community structure (Noy-Meir 1993, Crawford & Gosz 1982, Neilson and others 1992, Sala and others 1992). In addition to temporal variability, the high degree of spatial variability inherent in natural environments also plays an important role in community and ecosystem dynamics (Bazzaz 1993).

This study is the final part of a larger study that explores the water relations in pinyon pine on a variety of spatial and temporal scales. The first stage of the study examined physiological responses at a stomatal level measuring instantaneous and seasonal responses to changes in soil and atmospheric moisture. The second stage of this study measured physiological response at a needle level integrating stomatal responses at annual and interannual time scales. This study measures whole-tree response to climatic variability using tree-rings and represents an integrated response of both stomata and different-aged needle cohorts over a period of five years. These layers of complexity in water relations of pinyon pine have been examined in order to answer such questions as: Which climatic variables are

most important in affecting stomatal behavior and water use efficiency and at what scale are they important: diurnal, seasonal or annual? What is the diversity in physiological response between individuals? Is there a physiological difference between ecotonal, xeric sites and mesic sites?

Since maximizing carbon gain and minimizing water loss can be crucial in arid ecosystems where water is limiting, the ability to adjust water use efficiency in response to changing availability of water is an ecologically important characteristic. In this study, water use efficiency is studied using ^{13}C measurements of tree-rings. The development of isotopic models relating ^{13}C to water use efficiency (Farquhar and others 1982) has shown great promise in providing physiologists with a powerful tool to investigate physiological response at scales of growing seasons (Farquhar and others 1988, Leavitt & Long, 1989, Leavitt 1994). Net instantaneous water use efficiency (WUE), the ratio of carbon assimilation to evapotranspiration, has been found to correspond to high ^{13}C —high ^{13}C values corresponding to high water use efficiency and vice versa (Farquhar and others 1988). For long-lived species such as trees, combining this technique with tree-ring analysis provides a long-term record of physiological response to changing climatic regimes.

Specifically, this part of the study will address the following questions:

1. Does water use efficiency change from year to year in response to climatic patterns?
2. Does the whole tree response differ from the response of different-aged needle cohorts?
3. Is winter or summer precipitation more important in determining water use efficiency and growth in pinyon pine?
4. Is the physiological response different at an ecotonal/xeric site than at a more mesic site?
5. Is there a relationship between the plasticity of water use efficiency and growth?

Methods

Site Description

The field sites are located in the Los Pinos Mountains on the Sevilleta LTER in central New Mexico. There are two field sites within about 3 to 4 kms of each other—one at 1700 m and the other at 2000 m elevation. Although the two sites are in close proximity with only a small elevation change, the site characteristics differ quite markedly. Goat

In: Finch, Deborah M.; Whitney, Jeffrey C.; Kelly, Jeffrey F.; Loftin, Samuel R. 1999. Rio Grande ecosystems: linking land, water, and people. Toward a sustainable future for the Middle Rio Grande Basin. 1998 June 2-5; Albuquerque, NM. Proc. RMRS-P-7. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Draw, is an open woodland located at the pinyon-juniper woodland/juniper-grassland ecotone. The higher site, Cerro Montoso, is a densely vegetated pinyon-juniper stand. The lowest elevation site is representative of pinyon-juniper to juniper-grassland ecotone. The density of pinyon pine is much lower relative to the density of juniper. The higher elevation site is representative of pinyon in the middle of its range. Both sites are located on slopes of 10 to 20 degrees with N-NW facing aspects. The soils of both sites are derived from a granitic substrate and are coarse-grained in texture. The physiological characteristics of both sites have been studied extensively in previous studies. The Goat Draw site is also an LTER site where population, growth and physiological characteristics have been studied.

Sample Collection

Cores were collected from four individual trees from each site. The trees selected were those from which extensive physiological measurements had been made in the previous portion of this project. Two cores were collected from each tree: one in the north cardinal direction and one in the south cardinal direction. The cores were surfaced and dendrochronologically dated. The rings from individual years 1990 to 1986-1984 were separated under a binocular microscope using a razor blade combining the material from the north and south cores and analyzed for ^{13}C . The samples chosen for wood analysis were the same years on which leaf ^{13}C analysis had been conducted. Leaf ^{13}C analysis was dependent on the retention time of the needles.

Isotope Analysis

Isotope analysis was conducted on the cellulose isolated in a procedure after Green (1963) as modified by Leavitt and Danzer (1994) for small samples. The samples were combusted to carbon dioxide in an oxygenated atmosphere at 800°C in a recirculating microcombustion line. The carbon dioxide was analyzed mass-spectrometrically and ^{13}C was computed relative to the PDB standard (Craig 1957). All analysis was conducted at University of Arizona Laboratory of Tree-ring Research.

Climate Data

Monthly PDSI and precipitation values were obtained from Socorro Weather Station. Annual Palmer Drought Severity Index (PDSI) and precipitation was represented by taking the mean value from October of the previous year until October of the current year. Winter PDSI and precipitation was presumed to be represented by the mean values from the months of November of the previous year until March of the current year. Summer PDSI and precipitation was estimated by taking the mean of the monthly values from the period July to October.

Results

Variation in ^{13}C Over Time

The results of ^{13}C analysis of wood shows the year to year variation in water use efficiency in pinyon pine (fig. 1). These

results show that although patterns for individuals through time are very similar, the absolute values vary between individuals. This would suggest that while individual trees have different water use efficiencies, their response to year to year climate variability is similar. These results are very similar to those of Leavitt (1994) which showed that the absolute values varied among individuals of same species at a site while the patterns through time were similar in both coniferous and deciduous trees. The most marked feature of these patterns is the dramatic increase in ^{13}C for all trees at both sites in 1989. For the most part the weather patterns during the years measured were close to normal years of precipitation, 1989, however, was an extremely dry year. There does not appear to be much difference in the range and patterns of ^{13}C between sites. The mean value and standard deviation of ^{13}C values at Goat Draw is $-20.66 \pm .66$ and at Cerro Montoso it is $-20.71 \pm .75$.

The carbon isotope values of annual rings in pinyon pine represent the integrated measure of water use efficiency of

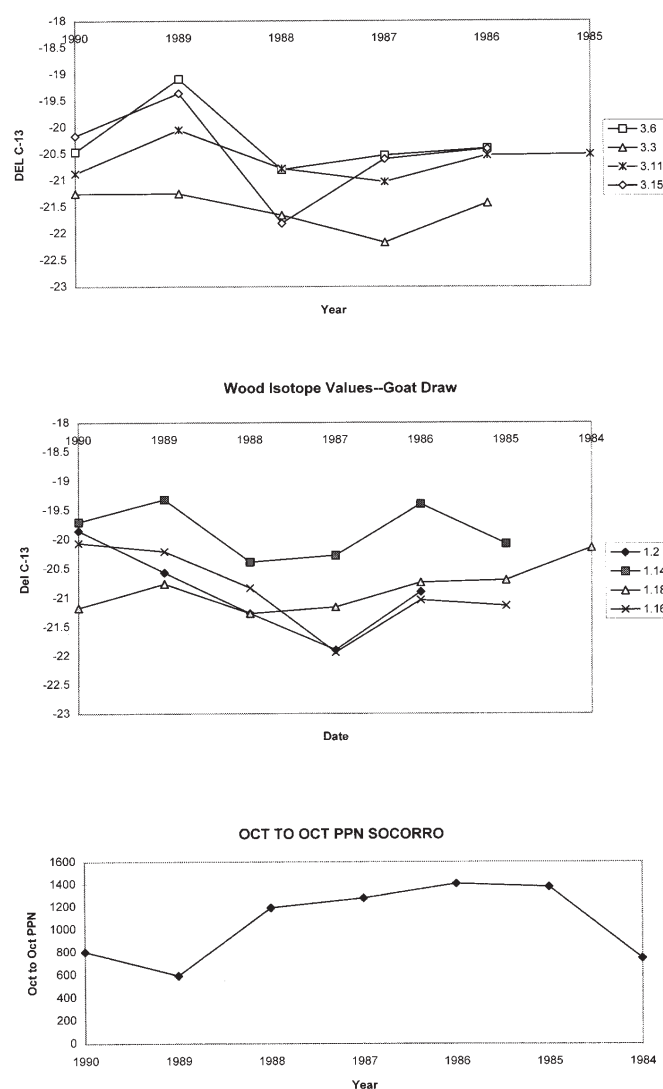


Figure 1—Results of isotope analysis on wood at Goat Draw and Cerro Montoso.

all leaf cohorts over whole tree over the course of a year with some lag factors due to carbon translocation and storage. Typically, needle retention in pinyon pines at these sites is between five to seven years. A comparison of same year needle and annual ^{13}C values show that while the wood values tend to be isotopically lighter the patterns of changes from year to year are very similar (fig. 2, 3). The fact that the patterns of ^{13}C are similar to ^{13}C in needles suggests that

the overall water use efficiency of the tree is most likely under physiological control (i.e., the instantaneous response of stomata to changes in water status) rather than anatomical control (i.e., wax layers, number of stomata, sunkness of stomata, photosynthetic efficiency, etc.). It also suggests that decreased water use efficiency due to aging of needles is not an important factor determining the overall water use efficiency of the whole tree.

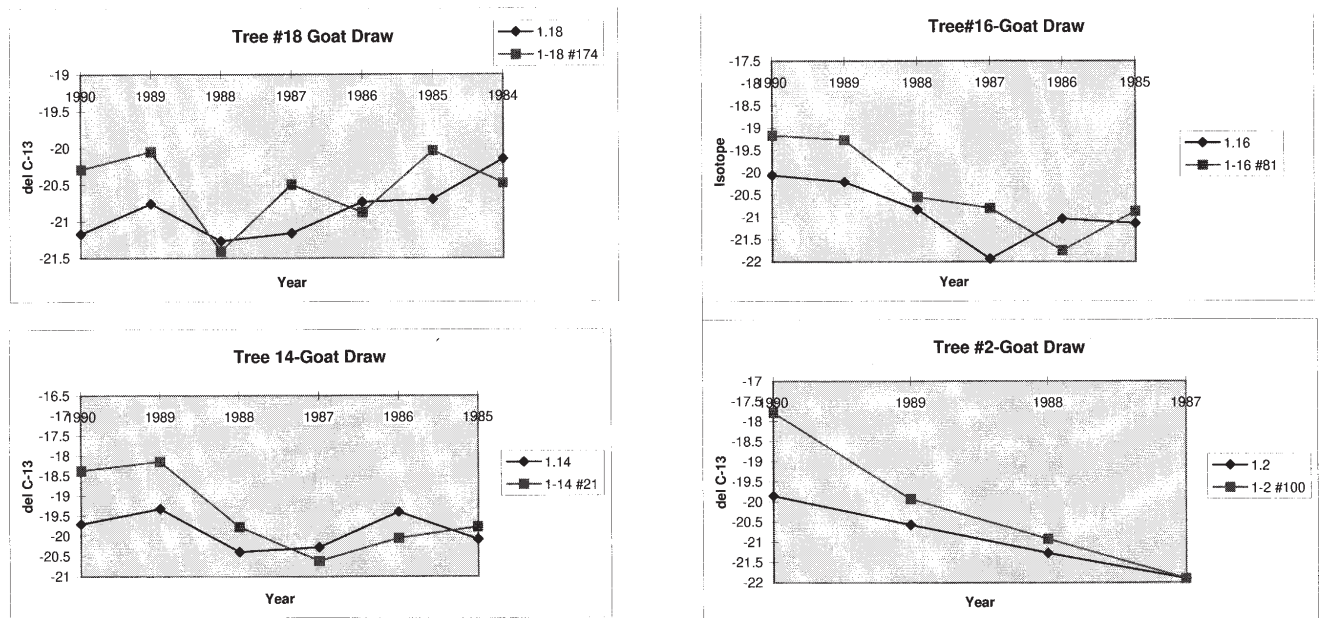


Figure 2—A comparison of leaf and wood isotope values for Goat Draw.

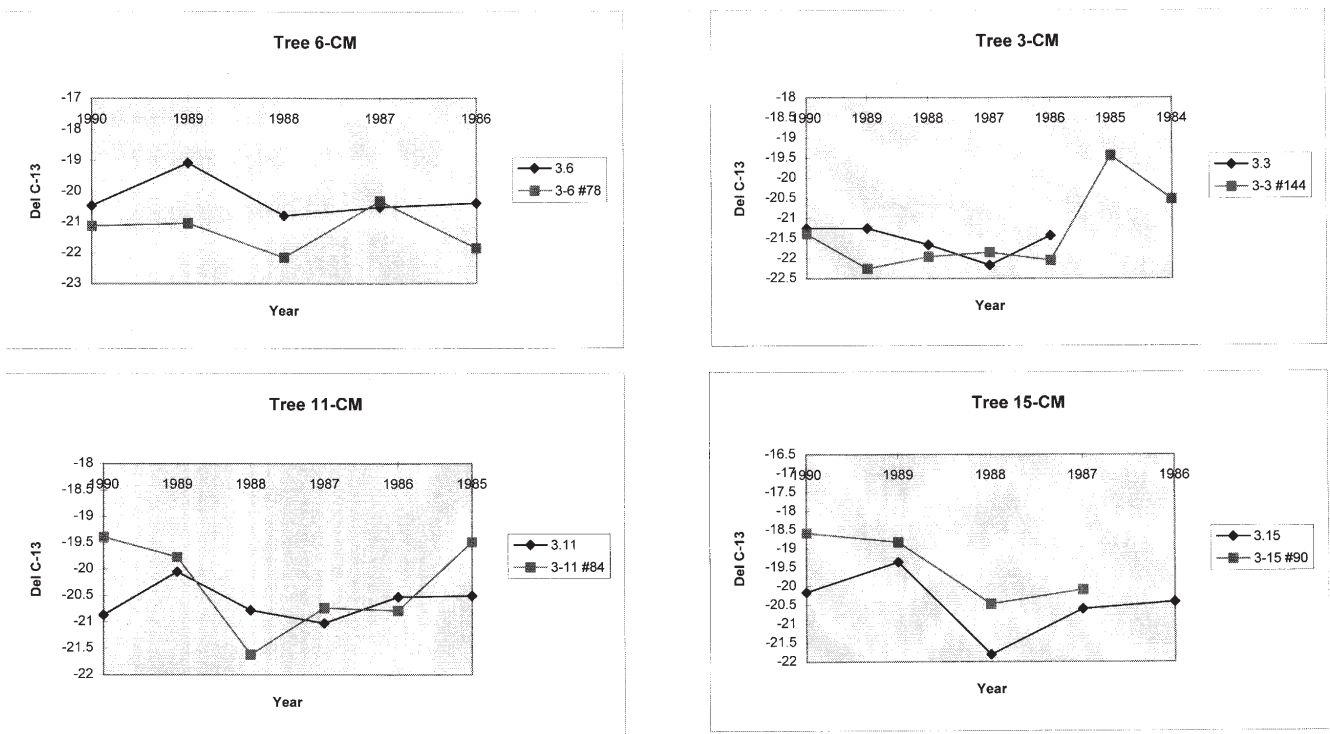


Figure 3—A comparison of leaf and wood isotope values for Cerro Montoso.

Table 1—Results of regression analyses of climate vs. C¹³ values for Goat Draw—r² values.

Tree #	October to October		July to October		November to March	
	PDSI	PPN	PDSI	PPN	PDSI	PPN
Tree#2	.87	.43	.76	.05	.92	.88
Tree#14	.39	.23	.31	.03	.38	.45
Tree#16	.93	.61	.83	.04	.92	.51
Tree#18	.09	.08	.04	.01	.07	.00
Site average	.57	.34	.49	.03	.57	.46

Relationship of Climate with ¹³C

This next section explores the relationship between ¹³C and climate. Since the absolute values of ¹³C varied from tree to tree separate regressions were done for each individual tree and ¹³C for the site was obtained by taking the average of the correlation coefficients for individual trees. Based on the typical rainfall cycles in New Mexico, three periods were considered with respect to ¹³C values: annual (October to October), winter (November to March) and summer (July to October).

Goat Draw—Results of regression analyses show that October to October PDSI has a strong influence on the isotopic composition of the wood in pinyon pine ($r^2 = .57$) while October to October precipitation has only a moderate influence ($r^2 = .34$) (see table 1 and fig. 4). There is a large spread of responsiveness to PDSI from individual to

individual. In the summer the difference in response to PDSI vs. precipitation is most pronounced ($r^2 = .49$ v. $r^2 = .03$). This reflects the importance of evaporative demand as well as water availability. These results are consistent with studies on stomatal response to vapor pressure deficit which showed that stomatal conductance is sensitive to changes in vapor pressure deficit and relative humidity as well as leaf water potential (Newberry, in prep.). In the winter PDSI and precipitation have roughly equal influence on carbon isotope values ($r^2 = .57$ v. $r^2 = .46$) and, therefore, one may conclude that evaporative demand does not play an important role in winter due to cool temperatures. Both winter PDSI and summer PDSI are equally important in determining ¹³C values in pinyon pine ($r^2 = .57$ v. $r^2 = .49$) while winter precipitation is much more important than summer precipitation ($r^2 = .46$ v. $r^2 = .03$). One interpretation of this is that winter precipitation plays a greater role than summer

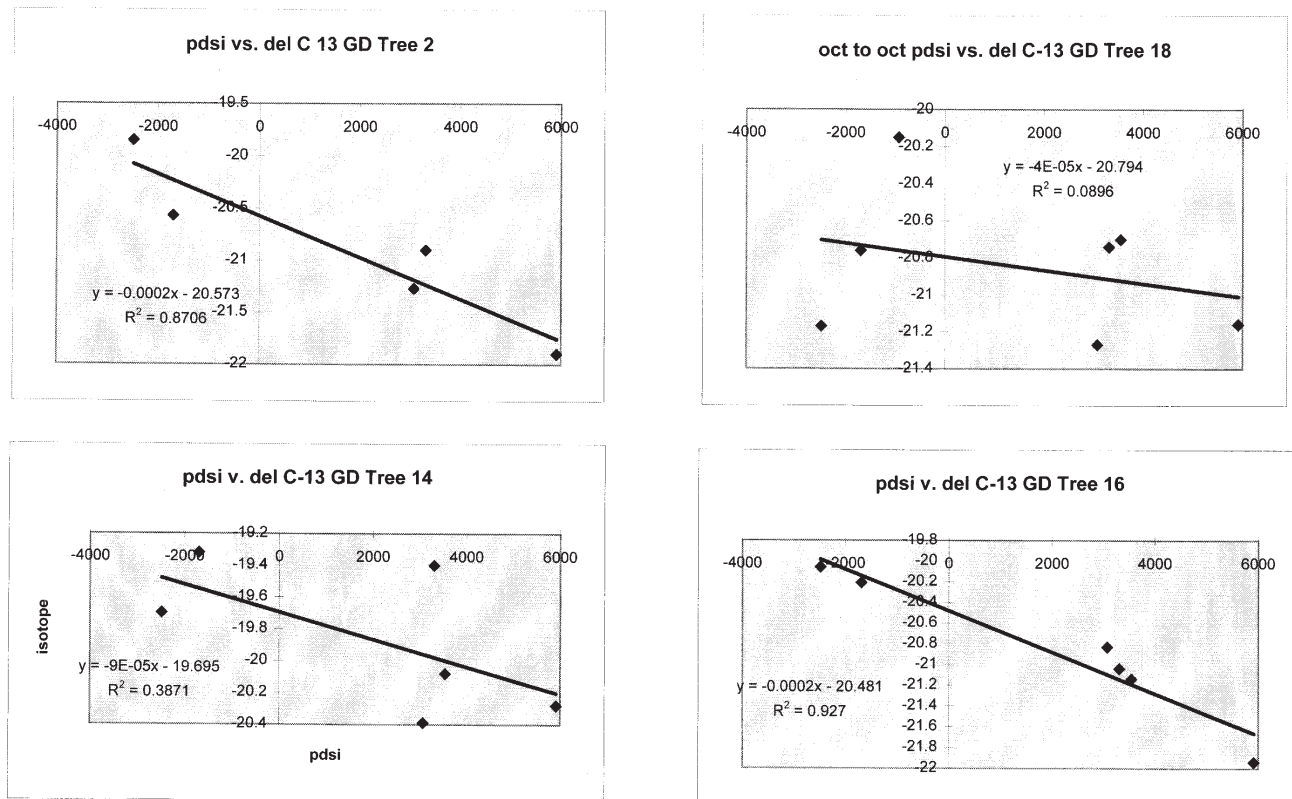


Figure 4—October to October PDSI and carbon isotope values at Goat Draw.

Table 2—Results of regression analyses of climate vs. C¹³ values for Cerro Montoso—
r² values.

Tree #	October to October		July to October		November to March	
	PDSI	PPN	PDSI	PPN	PDSI	PPN
Tree#3	.30	.38	.33	0	.24	.98
Tree#6	.78	.54	.62	.07	.78	.14
Tree#11	.19	.18	.13	.05	.16	.06
Tree#15	.34	.41	.36	.37	.32	.19
Site average	.40	.38	.36	.12	.38	.34

rainfall in determining water use efficiency in pinyon pine for the subsequent growing season due to recharge of soil water by snowfall while overall weather conditions (reflected in PDSI) of both seasons play the strongest role.

Cerro Montoso—Overall the response of PDSI and precipitation was lower at Cerro Montoso than at Goat Draw (table 2 and fig. 5). For example at Goat Draw r² was .57 for October to October PDSI while at Cerro Montoso it was .40. This is consistent with previous results which showed that the stomata of the trees at Goat Draw were more sensitive to changes in environmental conditions than at Cerro Montoso (Newberry, in prep.). Like Goat Draw, summer PDSI had a greater effect on carbon isotope values and thus water use efficiency than summer precipitation (r² = .36 v. r² = .12). Like Goat Draw, ¹³C values were equally dependent on

winter PDSI and winter precipitation. Also winter and summer PDSI were equally important in determining the annual water use efficiency of pinyon pine.

Growth and Climate

At Goat Draw growth is most strongly dependent on October to October PDSI (r² = .70) (table 3). This relationship is curvilinear. October to October precipitation also plays an important role in determining the annual growth rate in pinyon pine (r² = .55). Summer and winter PDSI and precipitation appear to have equal importance in determining growth rates. There is some variability in growth response of individuals, but not as great as the range of water use efficiency response (r² = .57 to .85 for Oct to Oct.

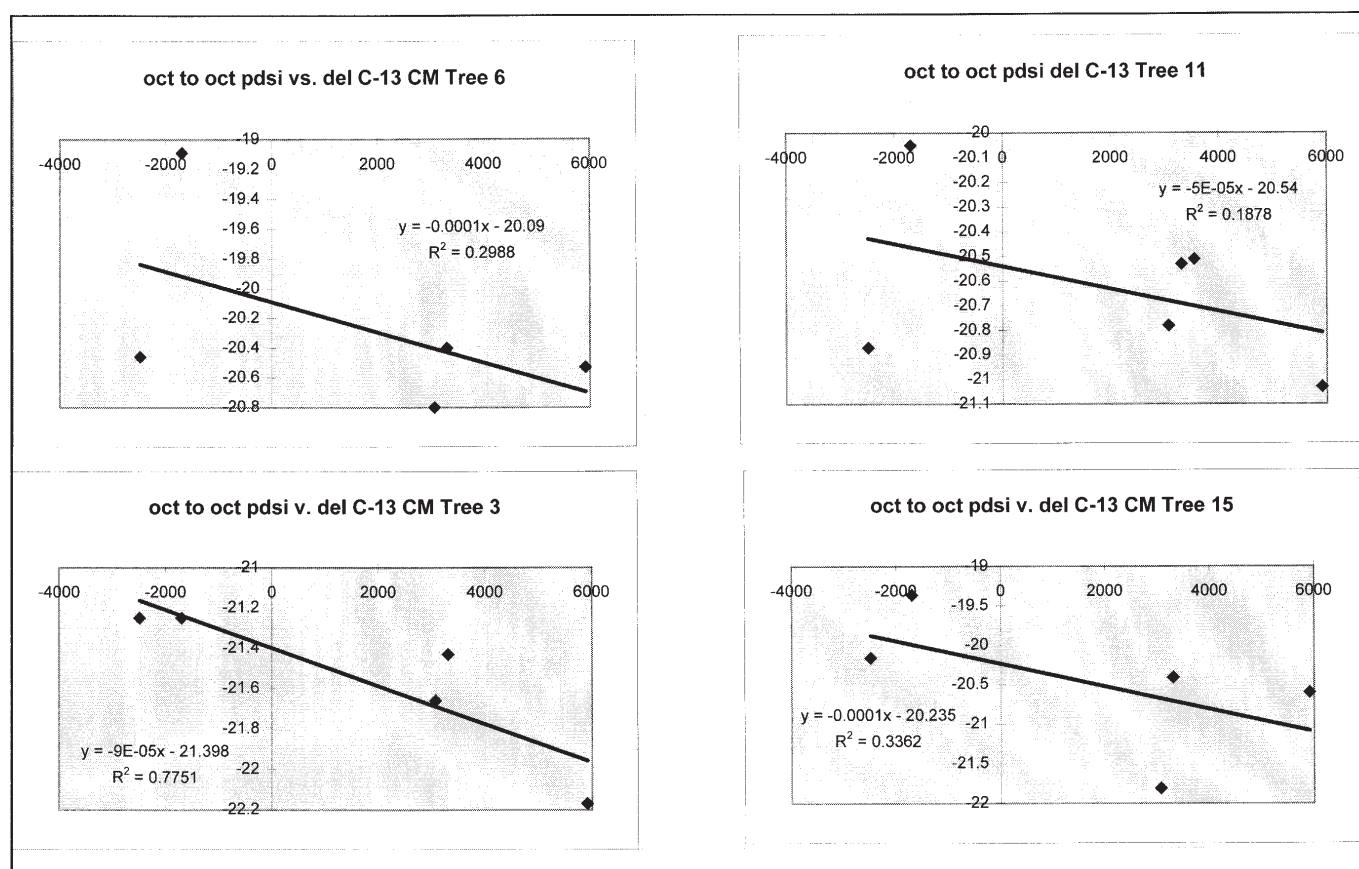


Figure 5—October to October PDSI and carbon isotope values at Cerro Montoso.

Table 3—Results of regression analyses of climate vs. growth for goat draw and Cerro Montoso- r^2 values.

Tree #	October to October		July to October		November to March	
	PDSI	PPN	PDSI	PPN	PDSI	PPN
Goat Draw	.70*	.55	.54	.31	.62*	.30
Cerro Montoso	.54*	.49	.62*	.22	.48*	.33

*curvilinear relationship

PDSI & growth). Some trees had a curvilinear growth response while in others the relationship was linear.

At Cerro Montoso growth is most strongly dependent on July to October PDSI ($r^2 = .62$) although this is only just slightly greater than the correlations with October to October PDSI ($r^2 = .54$) and November to March PDSI ($r^2 = .48$). These relationships are curvilinear. October to October precipitation has an r^2 of .49. Similar to Goat Draw some trees have a linear growth response while others have a curvilinear growth response. There is also a range of growth responses ranging from $r^2 = .49$ to .87 for July to October PDSI & growth.

Growth and Water Use Efficiency

A question of great ecological significance is do the trees with the ability to increase their water use efficiency during periods of drought have higher growth rates. Unfortunately, it is impossible to answer this question directly because in years of drought, growth rate is reduced. The relationship between growth and physiological response to climate can be examined indirectly however using several different approaches. The following questions could be asked: Does the ability of individual trees to respond to drought by maximizing water use efficiency increase the total growth over the time period studied? And, does a strong correlation of ^{13}C with climate mean a higher year to year variability in growth? Regarding the correlation coefficients of ^{13}C and annual PDSI, total growth over the period studied, and the standard deviation of annual growth over the period studied, there does not appear to be any relationship between any of these variables. This does not mean that water use efficiency does not maximize growth in pinyon pine, but instead that other factors influencing growth such as photosynthetic rates, duration of photosynthesis and total leaf area are very important in determining growth rates in pinyon pine.

Conclusions

Water use efficiency in pinyon is variable from year to year in response to PDSI. Precipitation plays a secondary role relative to PDSI in determining water use efficiency especially in the summer months when evaporative demand is high. These results are consistent with previous studies which have shown the stomata to be sensitive to both soil moisture and vapor pressure deficits (Newberry, in prep.). Both winter and summer PDSI are equally important in determining water use efficiencies in pinyon pine. Winter

PDSI is most likely very important because of the winter precipitation recharges soil water by snowfall prior to the next year's growing season.

At Goat Draw growth is most highly dependent on October to October PDSI while at Cerro Montoso, Cerro Montoso is most highly dependent on July to October PDSI although this is just slightly greater than the dependence on October to October PDSI. A comparison of the summer and winter PDSI and precipitation shows that both seasons are important in determining growth rates for both Goat Draw and Cerro Montoso.

The patterns of wood isotope values through time are very similar to the leaf patterns although the wood tends to be isotopically lighter than the leaf material. This result suggests that the overall water use efficiency of the whole tree is a function of physiological factors such as the instantaneous response of stomata to changes in water status rather than anatomical factors such as wax layers, number of stomata, sunkenness of stomata, photosynthetic efficiency, etc. It also suggests that decreased water use efficiency due to aging of needles is not an important factor in determining the overall water use efficiency of the whole tree and the ^{13}C composition of the tree.

Although patterns of ^{13}C through time are very similar among individuals at both sites, there is a high range in absolute ^{13}C values and thus one would conclude that there are differences in water use efficiencies between individuals. The results of the regression analyses of ^{13}C with climatic factors show that there is also a range in the responsiveness of water use efficiency to year to year changes in weather conditions—although as mentioned above the trees almost always move directionally in the same way. My attempt to show that trees that were able to increase water use efficiency would have higher growth rates was unsuccessful. This is most likely because other factors contributing to growth such as total leaf area, time spent photosynthesizing and photosynthetic rates also play an important role in determining growth rates. In fact, results of a previous study show that pinyon is a drought avoider and will completely shut its stomata in response to drought as opposed to keeping stomata open while increasing water use efficiency (Newberry, in prep.).

Although, the mean and standard deviation of ^{13}C values the two sites were identical, there were differences in the correlations of ^{13}C to year to year changes in climate. Goat Draw trees more strongly tracked changes in annual precipitation and PDSI than Cerro Montoso trees and their growth was more dependent on climate. This result is consistent with previous results which showed that stomata of the trees are much more sensitive to changes in

environmental conditions than at Cerro Montoso (Newberry, in prep.) Since the standard deviation at both sites is nearly identical while the correlation with climate is different, one may conclude that Cerro Montoso is responding other sources of variation. These sources of variations could be biotic in origin such as shading, herbivory and competition for water since the higher elevation site is more densely vegetated.

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