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Experimental manipulations of precipitation seasonality: effects on oak (Quercus) seedling demography and physiology

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Increasing atmospheric carbon dioxide concentration is expected to increase global temperatures and thereby alter the amount, seasonality, and intensity of precipitation on global to regional scales (Houghton et al. 1996, Mahlman 1997, Giorgi et al. 1998). Although considerable research has described the effects of increasing atmospheric carbon dioxide concentration (e.g., Koch and Mooney 1996, Körner and Bazzaz 1996) and expected increase in temperature (e.g., Chapin et al. 1995, Harte and Shaw 1995, Beerling and Woodward 1996) on ecosystems, little research has focused on potential changes in precipitation regimes, which embodied 50% changes to quantities of summer and winter precipitation, and encompassed a continuum of precipitation from 359 mm · year⁻¹ to 946 mm · year⁻¹. However, survival and physiological performance of seedlings were negatively impacted by seasonal environmental conditions common to all treatments, especially during the annual pre-‘monsoon’ drought. Seedling predawn leaf water potentials, net CO₂ assimilation, and stomatal conductance indicate that growing conditions for *Q. emoryi* seedlings at this site are generally restricted to periods with adequate soil moisture (i.e., April and August). Results contrast with an assumption implicit to the “two-layer” soil water resource partitioning hypothesis that woody plants in all life history stages are more dependent upon winter than summer precipitation. In fact, summer precipitation appears more important than winter precipitation for *Q. emoryi* seedling recruitment and growth.

Key words: Quercus emoryi, precipitation seasonality, seedling recruitment, population demographics, carbon isotope discrimination, leaf gas exchange.

We investigated how amount and seasonality of precipitation affect the physiologic and demographic performance of oak (Quercus L.) seedlings in oak savannas of the southwestern United States (Brown 1982, McClaran and McPherson 1999). This region is characterized by a bimodal precipitation regime, with peaks in amount of precipitation in both summer (52% of annual precipitation) and winter (29% of annual precipitation). This regional precipitation regime is likely to change within the next century as atmospheric CO₂ concentration increases (Houghton et al. 1996, Giorgi et al. 1998), although the extent and direction of these changes are difficult to predict (Mahlman 1997).

We used a manipulative field experiment to simulate potential scenarios of precipitation redistribution that southwestern oak savannas may experience by the mid- to late 21st century. Recruitment and production of seedlings of the dominant savanna tree, Quercus emoryi Torr. (Emory oak), are described in Weltzin and McPherson (2000). The objectives of this study were to (1) assess physiological performance of these seedlings and (2) compare measures of seedling physiology with seedling demographic responses.

**Materials and Methods**

**Study Site**

We conducted research between 1994 and 1996 at the lower (and drier) margin of temperate, evergreen oak woodland at the base of the Huachuca Mountains in southeastern Arizona, USA. The ecotone between oak woodland and adjacent semidesert grassland is characterized by Q. emoryi–dominated savannas bordered by semidesert grassland dominated by C₄ perennial bunchgrasses (Brown 1982, McClaran and McPherson 1999).

The study site is located in lower Garden Canyon (31°29′N, 110°20′W) on Fort Huachuca Military Reservation (FHMR) near Sierra Vista, Arizona. During the study period overstory tree cover within the savanna was 11%, as estimated from aerial photographs (Haworth and McPherson 1994). Herbaceous vegetation was dominated by the perennial bunchgrass Trachypogon montufari (H.B.K.) Nees. The site is 1550 m in elevation with a 5% slope on a northeastern aspect. Soils developed from gravelly alluvium. Climate is semiarid, with an average annual temperature of 20°C. Average annual precipitation of 602 mm is bimodally distributed, with peaks during the summer ‘monsoon’ (July–September) and during winter (December–February; NOAA 1996). Weltzin and McPherson (2000) provide further details on climate, vegetation, and soils at this site.

**Experimental Design**

In June 1994 we initiated a field experiment consisting of 5 simulated precipitation treatments applied to plots isolated from ambient precipitation and soil moisture. The 1st treatment received simulated precipitation equivalent to the long-term (30-year) mean annual precipitation for the site (602 mm year⁻¹; Table 1). The other 4 treatments received all possible combinations of 50% additions and reductions of summer (July–September) and winter (December–February) precipitation relative to the long-term seasonal mean. Treatments received equal amounts of precipitation in spring (defined herein as March–June) and autumn (October–November).

This experimental design incorporated changes to both seasonal and total precipitation because changes in atmospheric circulation that will accompany climate change will produce regional changes in both the amount and seasonality of precipitation (Houghton et al. 1996, Mahlman 1997, Giorgi et al. 1998). Because effects of interannual variation in total precipitation on plant communities have been well studied (e.g., Weaver and Clements 1929, Stephenson 1990), we focused on the little-studied component of precipitation seasonality (see Neilson 1986, Neilson et al. 1992).

Treatments were arranged within a randomized complete block design (n = 4). Blocks
were established within homogeneous stands of perennial bunchgrasses. Within each block, we linearly arranged five 1.2 m × 1.5 m-plots at 1.5-m spacing. The perimeter of each plot was trenched to 1-m depth and lined with polyethylene film to prevent lateral movement of soil water. The edge of each plot was bordered to prevent lateral movement of surface water. Vegetation in each plot was left intact. A permanent precipitation shelter (16 m × 4 m) constructed of steel tubing, clear polyethylene film, and fence posts was erected over each block to exclude ambient precipitation (Fig. 1). The pitched roof of each shelter was 2.2 m aboveground at its apex and 1.5 m high along the sides and ends. Poultry netting (2.5-cm mesh) was wired to fence posts and rebar stakes around each block to form a 60-cm-tall vertebrate exclosure.

We kept the shelters open-sided to minimize microclimatic impact. Shelters reduced photosynthetically active photon flux density by 29% ± 10% (mean ± 1sx) at solar noon on a clear, midsummer day. Although shelters likely altered other, unquantified microenvironmental variables (e.g., ambient temperature, relative humidity), experimental units were affected equally.

Precipitation collected and stored on-site was applied to plots according to a randomly generated precipitation regime that simulated natural precipitation patterns (Nicks and Lane 1989; CLIGEN, USDA-ARS Southwestern Watershed Research Center, J. Stone, personal communication). Simulated precipitation events, ranging from 1 mm to 120 mm, were applied by hand-watering 57 times annually (Table 1). Additional details of the experimental design are in Weltzin and McPherson (2000).

On 17 July 1995 we collected Q. emoryi acorns from trees on-site, sorted them by visual examination and flotation (Nyandiga and McPherson 1992), and planted 49 acorns at 10-cm spacing into each plot. Survival of emerged seedlings was monitored throughout the experiment. When seedlings were about 8 months old, we started our assessments of leaf water potential and leaf gas exchange. Quercus emoryi are evergreen and accumulate little aboveground biomass during the first several years after germination (Weltzin and McPherson 2000). Because seedlings in this experiment developed few, if any, new leaves in 1996, we sampled leaves initiated in 1995.

We determined Q. emoryi predawn leaf water potential (Ψ) with a Scholander-type pressure chamber (PMS Instrument Company, Corvallis, OR) on 20 April, 30 June, 22 August, and 17 October 1996. In particular, on each date we selected one seedling at random from each plot. During a period of 1–3 hours before the beginning of the daily photoperiod, we collected one leaf at random from near the top of the seedling canopy for determination of Ψ (n = 4). On each date we also used a portable open-loop photosynthesis system (CIRAS-1 CO2/H2O Infrared Gas Analysis System, PP Systems, Haverhill, MA) to determine midday net CO2 assimilation (A), the ratio of leaf intercellular to ambient CO2 concentration (ci/ca), and stomatal conductance (gs) (n = 4) of randomly selected seedlings other than those used for assessment of Ψ.

Quercus emoryi leaves used for Ψ were retained for carbon isotope (δ13C) analysis (Brugnoli and Farquhar 2000). We measured δ13C on finely ground, oven-dried (70°C for 48 hours) samples using an isotope ratio mass spectrometer (delta S, Finnigan MAT, San Jose, CA) at the University of Utah Stable Isotope Ratio Facility for Environmental Research.

<table>
<thead>
<tr>
<th>Season</th>
<th>Months</th>
<th>Frequency</th>
<th>Long-term mean</th>
<th>Summer dry/</th>
<th>Summer dry/</th>
<th>Summer wet/</th>
<th>Summer wet/</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>winter wet</td>
<td>winter dry</td>
<td>winter wet</td>
<td>winter dry</td>
</tr>
<tr>
<td>Spring</td>
<td>MAMJ</td>
<td>7</td>
<td>62</td>
<td>62</td>
<td>62</td>
<td>62</td>
<td>62</td>
</tr>
<tr>
<td>Summer</td>
<td>JAS</td>
<td>29</td>
<td>315</td>
<td>158</td>
<td>158</td>
<td>473</td>
<td>473</td>
</tr>
<tr>
<td>Autumn</td>
<td>ON</td>
<td>7</td>
<td>53</td>
<td>53</td>
<td>53</td>
<td>53</td>
<td>53</td>
</tr>
<tr>
<td>Winter</td>
<td>DJF</td>
<td>14</td>
<td>172</td>
<td>258</td>
<td>86</td>
<td>258</td>
<td>86</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>57</td>
<td>602</td>
<td>531</td>
<td>359</td>
<td>846</td>
<td>674</td>
</tr>
</tbody>
</table>

Table 1. Season, frequency of application, and amount (mm) of 5 precipitation treatments (n = 4) applied to plots isolated from ambient precipitation and soil moisture at an oak savanna site in southeastern Arizona, USA. Long-term mean represents the 30-year average seasonal precipitation for the site, and seasonal wet and dry treatments represent 50% additions and reductions, respectively, of the long-term seasonal mean.
δ13C values of leaves were used to calculate discrimination as
\[ \Delta = \frac{(\delta_a - \delta_p)}{(1 + \delta_p)} \] (1)
where \(\delta_p\) is δ13C of leaves and \(\delta_a\) is that of the air (–8‰) according to Farquhar et al. (1989).

\(\Delta\) during photosynthesis is directly related to \(c_i/c_a\) as
\[ \Delta = a + (b - a)c_i/c_a \] (2)
where \(a\) and \(b\) represent fractionations associated with CO2 diffusion into the leaf (4.4‰) and carboxylation (27‰), respectively. The \(\Delta\) value forms the basis of a flux integrated estimate of \(c_i/c_a\) in C3 plants (Farquhar et al. 1989) and reflects the balance between biochemical demand for CO2 by the chloroplasts and CO2 supply through stomata. \(\Delta\) integrates \(c_i/c_a\) over the active periods of photosynthesis and leaf formation and is frequently correlated to stomatal conductance and drought stress (Ehleringer 1990, Meinzer et al. 1992).

To assess relationships between seedling physiology and demography by assessing correlations between \(\Delta\) and seedling survival rates. Seedling survival rates were calculated as the change in percentage survival divided by the number of days within a given time period, and are expressed as % day\(^{-1}\). Seedling survival rates were determined for 4 time periods: 60 and 30 days before determination of \(\Delta\) (PRE60 and PRE30, respectively), and 30 and 60 days after determination of \(\Delta\) (POST30 and POST60, respectively). These 30- and 60-day time periods do not correspond exactly with monthly and bimonthly assessment of seedling survival and \(\Delta\), respectively, because survival and \(\Delta\) were not necessarily determined on the same date of the month. POST30 and POST60 were not determined for the October sample date because the experiment was terminated shortly thereafter.

Statistical Analyses
For each sample date we used analysis of variance (ANOVA; SAS procedure GLM, SAS Institute 1989) to evaluate random and fixed effects of block and treatment, respectively, on seedling survival, \(A\), \(c_i/c_a\), \(g_s\), \(\Psi\), and \(\Delta\). We used Fisher’s protected LSD (Fisher 1960) \textit{a posteriori} mean separation tests for significant treatment effects \((P < 0.05\) unless otherwise indicated). In addition, we compared summer-
NET CO2 assimilation (A) and \( \frac{c_i}{c_a} \) at midday did not differ between treatments on any date (Table 2). Stomatal conductance \( (g_s) \) differed between treatments only in April, when \( g_s \) was about 2.5 times higher in winter-wet than winter-dry treatments (Table 2). On all sample dates carbon isotope discrimination (\( \Delta \)) was greater (contrast \( P < 0.06 \)) for seedlings in wet summer treatments than seedlings in dry summer treatments (Table 2).

Percent seedling survival was positively correlated with \( \Delta \) when all dates were considered collectively (\( r = 0.28, P = 0.01, n = 79 \)) and in August (\( r = 0.50, P = 0.02, n = 20 \)). Percent survival and \( \frac{c_i}{c_a} \) were negatively correlated only when all dates were considered (\( r = -0.29, P = 0.01, n = 77 \)). Percent survival was not correlated with \( A, g_s, \) or \( \Psi \) for any given sample date or when all dates were considered (\( P > 0.16, \) data not shown).

Carbon isotope discrimination (\( \Delta \)) was not correlated with rates of seedling survival either 30 or 60 days before or after assessment of \( \Delta \) when sample dates were considered collectively (Table 3). In contrast, PRE60 and POST60 were positively correlated with \( \Delta \) determined in August and June, respectively. Although variations in \( \Delta \) explained only about 38% of the variation in survival rates, survival rates between June and August were greater in summer-wet plots, where seedlings had higher \( \Delta \) values, than in summer-dry plots, where seedlings had lower \( \Delta \) values (Fig. 2).

The ratio of intercellular to ambient CO2 concentration (\( \frac{c_i}{c_a} \)) was a poor predictor of \( \Delta \) across the growing season, and for most dates within the growing season. In particular, \( \frac{c_i}{c_a} \) and \( \Delta \) were correlated only in August (\( r = 0.51, P = 0.03 \)) and, to a lesser extent, in April (\( r = 0.45, P = 0.06 \)) and October (\( r = 0.40, P = 0.09 \)). \( \frac{c_i}{c_a} \) and \( \Delta \) were uncorrelated in June (\( r = 0.02, P = 0.94 \)) and when all dates were considered (\( r = 0.05, P = 0.67 \)).

DISCUSSION

Q. emoryi Demography and Physiology

Surprisingly, seedling survival differed little between treatments, which embodied 50% changes in quantities of summer and winter precipitation and represented a continuum of precipitation from 359 mm \( \cdot \) year\(^{-1} \) to 846 mm \( \cdot \) year\(^{-1} \) (Table 1). There were also few treat-
ment effects on point measures of leaf gas exchange (A, gs, ci/ca, Ψ) and leaf water potential (Ψ). Further, there were few correlations between percent survival and point measures of seedling physiology (A, gs, ci/ca, Ψ) at any given date or across the growing season. In all, these results suggest that once established, Q. emoryi seedlings were relatively insensitive to environmental conditions imposed in this study (see also Weltzin and McPherson 2000).

However, seedling survival and physiological performance were negatively impacted by environmental conditions common to all treatments. Seedling survival across all treatments declined on average from 83% to 50% during the course of the growing season. The seasonal drought that occurs during May and June prior to the onset of the summer rains in July appeared to be most detrimental to seedling demography. First, rates of seedling survival were lowest during this period, with apparent lag effects on survival lasting until August (Weltzin and McPherson 2000). Second, at the height of the pre-monsoon drought in June, seedlings exhibited low rates of stomatal conductance, negative rates of CO2 assimilation, ci/ca ratios near one, and predawn leaf water potentials lower than our instrument could measure. Other studies have similarly suggested that the pre-monsoon drought is a critical bottleneck to Q. emoryi seedling demography (Pase 1969, Neilson and Wullstein 1983, McPherson 1992, Germaine and McPherson 1998, 1999, Weltzin and McPherson 2000).

Although data presented herein represent only a single growing season, survival rates for a separate Q. emoryi seedling cohort in this same experiment differed little between treatments after 3 growing seasons (Weltzin and McPherson 2000). In contrast, Q. emoryi seedling recruitment rates (i.e., the number of individuals added to the population) for both cohorts were as much as 300% greater in summer-wet than summer-dry treatments. Recruitment was more directly attributable to treatment effects on emergence of seedlings from acorns planted during the summer monsoon.

In contrast to point measures of leaf gas exchange, seedling survival rates could roughly be predicted from ∆, which is an integrated

### Table 2. Mean (±sx) survival (%), predawn leaf water potential (Ψ; MPa), net CO2 assimilation (A; µmol m⁻² s⁻¹), ci/ca, stomatal conductance (gs; mol m⁻² s⁻¹), and carbon isotope discrimination (Δ) of Q. emoryi seedlings (n = 4).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Variable</th>
<th>Date</th>
<th>Long-term mean</th>
<th>Summer dry/ winter wet</th>
<th>Summer dry/ winter dry</th>
<th>Summer wet/ winter wet</th>
<th>Summer wet/ winter dry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival (%)</td>
<td>April</td>
<td>79 (2)</td>
<td>76 (6)</td>
<td>90 (4)</td>
<td>85 (4)</td>
<td>85 (6)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>52 (11) a</td>
<td>70 (7) ab</td>
<td>87 (5) b</td>
<td>66 (17) a</td>
<td>69 (13) ab</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>39 (9)</td>
<td>38 (7)</td>
<td>41 (19)</td>
<td>58 (18)</td>
<td>57 (14)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>38 (6)</td>
<td>58 (7)</td>
<td>40 (20)</td>
<td>58 (18)</td>
<td>57 (14)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ψ (MPa)</td>
<td>April</td>
<td>-1.5 (0.2)</td>
<td>-1.1 (0.1)</td>
<td>-2.0 (0.2)</td>
<td>-1.4 (0.5)</td>
<td>-2.0 (0.7)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>-0.9 (0.4)</td>
<td>-1.4 (0.6)</td>
<td>-0.6 (0.1)</td>
<td>-0.6 (0.1)</td>
<td>-0.6 (0.2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>-3.5 (0.2) a</td>
<td>-4.2 (1.2) ab</td>
<td>-5.4 (0.7) b</td>
<td>-1.6 (0.2) c</td>
<td>-2.1 (0.2) c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>8.8 (2.4)</td>
<td>7.8 (0.9)</td>
<td>7.2 (1.6)</td>
<td>7.0 (2.0)</td>
<td>5.8 (2.2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A (µmol m⁻² s⁻¹)</td>
<td>April</td>
<td>8.8 (2.4)</td>
<td>7.8 (0.9)</td>
<td>7.2 (1.6)</td>
<td>7.0 (2.0)</td>
<td>5.8 (2.2)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>-1.9 (1.4)</td>
<td>-0.9 (0.8)</td>
<td>-0.5 (0.6)</td>
<td>-0.2 (1.6)</td>
<td>-0.1 (0.8)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>6.2 (0.2)</td>
<td>4.6 (1.7)</td>
<td>4.4 (1.2)</td>
<td>8.9 (3.3)</td>
<td>3.5 (1.4)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>0.1 (0.9)</td>
<td>-0.7 (0.3)</td>
<td>-0.8 (0.6)</td>
<td>1.0 (1.3)</td>
<td>0.9 (0.3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ci/ca</td>
<td>April</td>
<td>0.13 (0.08)</td>
<td>0.40 (0.15)</td>
<td>0.15 (0.15)</td>
<td>0.44 (0.09)</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>1.18 (0.14)</td>
<td>1.02 (0.09)</td>
<td>0.97 (0.04)</td>
<td>1.00 (0.21)</td>
<td>0.96 (0.17)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>0.79 (0.03)</td>
<td>0.73 (0.01)</td>
<td>0.74 (0.04)</td>
<td>0.74 (0.04)</td>
<td>0.81 (0.04)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>0.91 (0.14)</td>
<td>1.01 (0.03)</td>
<td>1.09 (0.09)</td>
<td>0.79 (0.15)</td>
<td>0.84 (0.03)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>gs (mol m⁻² s⁻¹)</td>
<td>April</td>
<td>0.041 (0.009) a</td>
<td>0.079 (0.023) a</td>
<td>0.036 (0.006) a</td>
<td>0.063 (0.014) a</td>
<td>0.016 (0.007) b</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>0.059 (0.024)</td>
<td>0.025 (0.003)</td>
<td>0.061 (0.021)</td>
<td>0.040 (0.014)</td>
<td>0.014 (0.003)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>0.164 (0.008)</td>
<td>0.084 (0.026)</td>
<td>0.093 (0.011)</td>
<td>0.191 (0.067)</td>
<td>0.090 (0.026)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>0.026 (0.002)</td>
<td>0.026 (0.005)</td>
<td>0.029 (0.013)</td>
<td>0.034 (0.008)</td>
<td>0.036 (0.007)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δ</td>
<td>April</td>
<td>18.1 (0.8)</td>
<td>18.5 (0.5)</td>
<td>17.3 (1.0)</td>
<td>19.4 (0.4)</td>
<td>19.3 (0.4)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>19.0 (0.2) ac</td>
<td>18.2 (0.4) ab</td>
<td>17.7 (0.06) b</td>
<td>19.2 (0.3) c</td>
<td>19.3 (0.4) c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>17.3 (0.4)</td>
<td>17.5 (1.0)</td>
<td>17.2 (0.9)</td>
<td>19.7 (0.6)</td>
<td>18.7 (0.4)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>18.3 (0.1) a</td>
<td>18.1 (0.4) a</td>
<td>16.7 (0.8) b</td>
<td>19.0 (0.4) a</td>
<td>19.4 (0.3) a1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Means in rows with different lowercase letters differed (ANOVA, P < 0.05).
measure of leaf gas exchange. Generally, seedling survival was positively correlated with $\Delta$, which is consistent with the expectation that metabolic activity is coupled with population demographics. Correlations between $\Delta$ and seedling survival were greatest during the annual summer monsoon, which suggests that the demographics of these stress-tolerant seedlings can best be predicted from $\Delta$ when environmental conditions are suitable for extended periods of carbon assimilation.

However, observed differences in $\Delta$ between summer-wet and summer-dry treatments in April and June 1996 (i.e., prior to experimental application of summer precipitation in 1996) suggest that carbon fixed during summer 1995 was retained in the evergreen leaves of these seedlings into the next year. This could reduce the sensitivity of $\Delta$ to environmental conditions in other seasons when resource gradients are less intense, and constrains the usefulness of whole evergreen leaves as measures of plant response on relatively short (i.e., a single season) temporal scales.

### Seasonal Precipitation and Q. emoryi Demographics

Seedling predawn leaf water potentials, net CO$_2$ assimilation, and stomatal conductance indicate that growing conditions for Q. emoryi seedlings at this site are generally restricted to periods with adequate soil moisture (i.e., April and August). This conclusion supports observations that 1- and 2-year-old Q. emoryi seedlings at this same research site use soil water derived from both winter and summer precipitation (Weltzin and McPherson 1997).

#### Table 3. Pearson correlation coefficients (top) and associated $P$-values (bottom) for $\Delta$ vs. integrated seedling survival (PRE60, PRE30, POST30, POST60).

<table>
<thead>
<tr>
<th>Sample date</th>
<th>PRE60</th>
<th>PRE30</th>
<th>POST30</th>
<th>POST60</th>
</tr>
</thead>
<tbody>
<tr>
<td>All dates</td>
<td>0.08</td>
<td>-0.06</td>
<td>-0.03</td>
<td>-0.002</td>
</tr>
<tr>
<td>20 April</td>
<td>0.46</td>
<td>0.61</td>
<td>0.83</td>
<td>0.99</td>
</tr>
<tr>
<td>30 June</td>
<td>-0.26</td>
<td>-0.32</td>
<td>-0.36</td>
<td>-0.34</td>
</tr>
<tr>
<td></td>
<td>0.28</td>
<td>0.19</td>
<td>0.13</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>-0.34</td>
<td>-0.45</td>
<td>0.36</td>
<td>0.60</td>
</tr>
<tr>
<td>22 August</td>
<td>0.14</td>
<td>0.05</td>
<td>0.11</td>
<td>0.005</td>
</tr>
<tr>
<td>0.62</td>
<td>0.34</td>
<td>0.25</td>
<td>0.23</td>
<td></td>
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<tr>
<td>0.004</td>
<td>0.14</td>
<td>0.30</td>
<td>0.34</td>
<td></td>
</tr>
<tr>
<td>17 October</td>
<td>0.25</td>
<td>-0.04</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>0.29</td>
<td>0.87</td>
<td>—</td>
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</tr>
</tbody>
</table>

*PRE60 and PRE30 = slope of seedling survival over 60- and 30-day period (% day$^{-1}$) before determination of $\Delta$, respectively, and POST30 and POST60 = slope of seedling survival over 30- and 60-day period (% day$^{-1}$) after determination of $\Delta$, respectively. Significant coefficients after sequential Bonferroni correction (Rice 1989) are in boldface.

Fig. 2. Relationship between $\Delta$ for Q. emoryi leaves sampled 22 August and seedling survival rate (% day$^{-1}$) for 60-day period before (PRE60) determination of $\Delta$ ($r^2 = 0.38$, $P = 0.004$).

However, carbon isotope discrimination values ($\Delta$) and $c_i/c_a$-$\Delta$ relationships suggest that summer precipitation is more important than winter precipitation for Q. emoryi carbon accumulation in leaves. This conclusion is supported by recent research which indicates that recruitment of Q. emoryi seedlings was positively correlated with the quantity of summer precipitation but was independent of quantity of winter precipitation (Weltzin and McPherson 2000). Other empirical studies further indicate the importance of summer precipitation to Q. emoryi seedling recruitment (Pase 1969, Neilson and Wullstein 1983, McPherson 1992, Germaine and McPherson 1999, Weltzin and McPherson 1999, 2000).

Although changes in regional precipitation regimes are not well predicted by general circulation models, particularly for topographically complex regions such as the southwestern United States, predicted changes in atmospheric circulation and surface temperatures are likely to affect the amount and seasonality of precipitation and soil moisture in this region (e.g., Kattenberg et al. 1996, Giorgi et al. 1998). Results from this study and Weltzin and McPherson (2000) indicate that changes in summer precipitation regimes would likely constrain Q. emoryi population dynamics through changes in seedling recruitment rates. Further, although adult and sapling (ca 1 m tall) Q. emoryi and coexisting grasses at this savanna site access water from relatively deep and shallow in the soil profile, respectively, Q. emoryi seedlings are unable to access deep sources of soil water for at least the first 3 growing seasons after germination (Weltzin and McPherson 1997, 2000). These results contrast with an assumption implicit to the "two-layer" hypothesis (Walter 1954, 1979) that woody plants in all life history stages are more dependent upon winter precipitation than summer precipitation. Thus, models developed to predict the effect of changing climates on the abundance and distribution of woody plants (e.g., Emanuel et al. 1985, VEMAP Members 1995, Iverson and Prasad 1998) should consider spatial and temporal processes that constrain the establishment of individuals (Grubb 1977, Harper 1977, McPherson 1997, Scholes and Archer 1997). This should be facilitated by the development of dynamic global vegetation models (e.g., Foley et al. 1998, Neilson and Drapek 1998) that incorporate such transient processes as emergence and recruitment.

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