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EXPERIMENTAL MANIPULATIONS OF PRECIPITATION SEASONALITY: EFFECTS ON OAK (*QUERCUS*) SEEDLING DEMOGRAPHY AND PHYSIOLOGY

Jake F. Weltzin^{1,2}, Keirith A. Snyder¹, and David G. Williams¹

ABSTRACT.—Predicted changes in regional precipitation patterns and soil moisture caused by anthropogenic trace gas emissions may affect the distribution and abundance of woody plants in arid and semiarid regions. To test the response of woody plants to potential changes in precipitation regimes, we manipulated summer and winter precipitation on plots that contained seedlings of *Quercus emoryi* Torr. (Emory oak), the dominant tree in oak savannas of the southwestern United States. Throughout the growing season, we monitored seedling survival and physiology (predawn leaf water potential, midday instantaneous gas exchange, and leaf carbon isotope discrimination). Seedling survival and physiological performance differed little between treatments, which embodied 50% changes to quantities of summer and winter precipitation, and encompassed a continuum of precipitation from 359 mm · year⁻¹ to 846 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.

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 effects of changes in the amount or seasonality of precipitation anticipated in the next few decades (Weltzin and McPherson 1995). However, changes in precipitation regimes are expected to have important ramifications for the structure, composition, and diversity of ecosystems (e.g., VEMAP Members 1995, Neilson and Drake 1998).

In arid and semiarid regions where vegetation is highly dependent upon precipitation,

changes in seasonal precipitation and soil moisture regimes may cause major shifts in plant species composition, distribution, and abundance (Stephenson 1990). For example, potential increases in winter soil moisture content may favor deeply rooted woody plants with the C₃ photosynthetic pathway and facilitate their recruitment within arid and semiarid grasslands dominated by C₄ grasses (Neilson 1986, 1993, Melillo et al. 1996). Alternatively, increases in summer precipitation may favor shallow-rooted species and C₄ grasses (e.g., Walter 1954, 1979, Knoop and Walker 1985, Ehleringer et al. 1991, Lauenroth et al. 1993, Burgess 1995, Neilson and Drake 1998).

However, recent research suggests that as the ratio of summer to winter precipitation increases, long-lived (woody) perennials will shift from preferential development of deep roots to a dimorphic root system with active roots in both deep and shallow soil layers (Ehleringer and Dawson 1992, Dawson and Pate 1996, Weltzin and McPherson 1997,

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Williams and Ehleringer 2000). Similarly, both the physiologic performance and demographic performance of woody plants in western North America are often coupled to the quantity and timing of *summer* precipitation (Neilson and Wullstein 1983, 1985, Ehleringer et al. 1991, Lin et al. 1996, Weltzin and McPherson 2000, Williams and Ehleringer 2000). Physiologic and demographic studies of adult woody plants are constrained by the fact that environmental conditions sufficient for survival of adult plants are often insufficient for recruitment of seedlings (*sensu* Grubb 1977).

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 domi-

nated 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

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.

Season	Months	Frequency	Treatment				
			Long-term mean	Summer dry/ winter wet	Summer dry/ winter dry	Summer wet/ winter wet	Summer wet/ winter dry
Spring	MAMJ	7	62	62	62	62	62
Summer	JAS	29	315	158	158	473	473
Autumn	ON	7	53	53	53	53	53
Winter	DJF	14	172	258	86	258	86
TOTAL		57	602	531	359	846	674

were established within homogeneous stands of perennial bunchgrasses. Within each block, we linearly arranged five 1.2 m \times 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 \times 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 enclosure.

We kept the shelters open-sided to minimize microclimatic impact. Shelters reduced photosynthetically active photon flux density by 29% \pm 10% (mean \pm 1 $s_{\bar{x}}$) 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 (c_i/c_a), and stomatal conductance (g_s) ($n = 4$) of randomly selected seedlings other than those used for assessment of Ψ .

Quercus emoryi leaves used for Ψ were retained for carbon isotope ($\delta^{13}\text{C}$) analysis (Brugnoli and Farquhar 2000). We measured $\delta^{13}\text{C}$ 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

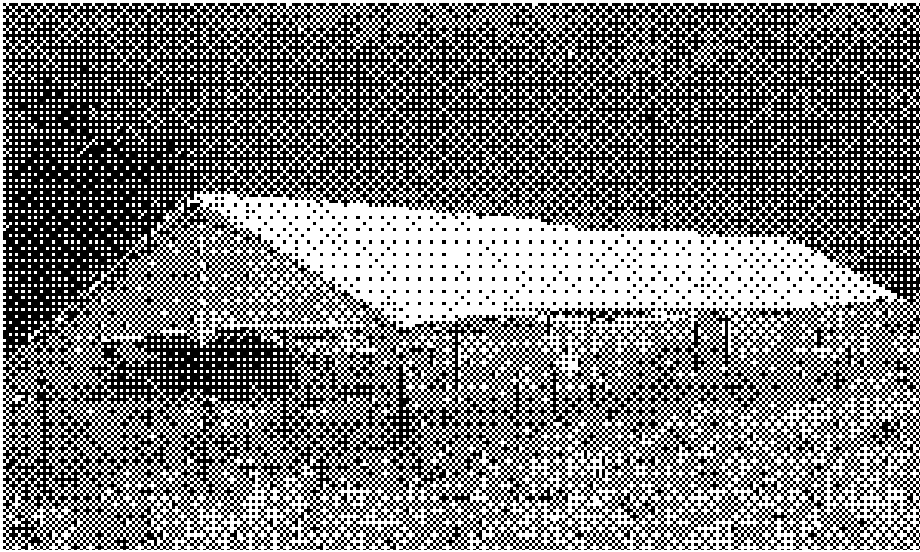


Fig. 1. Experimental system for capturing and redistributing precipitation. Each of 4 precipitation shelters (16 m \times 4 m) was covered with clear polyethylene film to exclude ambient precipitation from experimental plots. Ambient precipitation was stored in on-site tanks for later application to plots.

(SIRFER). $\delta^{13}\text{C}$ values of leaves were used to calculate discrimination as

$$\Delta = (\delta_p - \delta_a) / (1 + \delta_p) \quad (1)$$

where δ_p is $\delta^{13}\text{C}$ of leaves and δ_a is that of the air (-8‰) according to Farquhar et al. (1989). Δ during photosynthesis is directly related to c_i/c_a as

$$\Delta = a + (b - a)c_i/c_a \quad (2)$$

where a and b represent fractionations associated with CO_2 diffusion into the leaf (4.4‰) and carboxylation (27‰), respectively. The Δ value forms the basis of a flux integrated estimate of c_i/c_a in C_3 plants (Farquhar et al. 1989) and reflects the balance between biochemical demand for CO_2 by the chloroplasts and CO_2 supply through stomata. Δ 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 on each sample date, and for all dates combined, we examined correlations between seedling survival and A , c_i/c_a , g_s , Ψ , and Δ . We further investigated relationships between seedling physiology and

demography by assessing correlations between Δ 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 $\% \text{ day}^{-1}$. Seedling survival rates were determined for 4 time periods: 60 and 30 days before determination of Δ (PRE60 and PRE30, respectively), and 30 and 60 days after determination of Δ (POST30 and POST60, respectively). These 30- and 60-day time periods do not correspond exactly with monthly and bimonthly assessment of seedling survival and Δ , respectively, because survival and Δ 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 , Ψ , and Δ . We used Fisher's protected LSD (Fisher 1960) *a posteriori* mean separation tests for significant treatment effects ($P < 0.05$ unless otherwise indicated). In addition, we compared summer-

wet vs. summer-dry and winter-wet vs. winter-dry treatments using single-degree-of-freedom contrasts (Zar 1996; P -values are for ANOVAs unless otherwise indicated).

We used Pearson and Spearman rank correlation procedures (SAS procedure CORR, SAS Institute 1989) to assess correlations between percent seedling survival and A , c_i/c_a , g_s , Ψ , and Δ for each sample date ($n = 20$) and for all sample dates combined ($n = 80$). Spearman rank correlation coefficients for Δ vs. PRE60, PRE30, POST30, and POST60 were determined for all treatments at each sample date ($n = 20$ except POST30 and POST60 in October), and for all sample dates combined ($n = 80$ except POST30 and POST60 where $n = 60$). For each correlation analysis, we performed sequential Bonferroni corrections to control the group-wide type I error rate (Rice 1989). We used least-squares regression analysis (SAS procedure REG, SAS Institute 1989) to investigate the relationship between c_i/c_a and Δ for all treatments for each date ($n = 20$), and for all dates combined ($n = 80$).

Prior to analysis, all data were tested for normality with the Shapiro-Wilk W -statistic (Shapiro and Wilk 1965). Data not normally distributed ($P < 0.05$) were transformed or ranked as appropriate. Percent seedling survival data were arcsine-transformed prior to analysis (Zar 1996).

RESULTS

Seedling survival rates ranged from 76–90% in April to 38–58% in October (Table 2). Survival rates differed between treatments only in June ($P = 0.06$), when survival was greater in the summer-dry/winter-dry treatment than in the summer-wet/winter-wet and long-term mean treatments. Additional details of seedling survival are in Weltzin and McPherson (2000).

Seedling predawn leaf water potentials (Ψ) differed ($P = 0.002$) between treatments only in October, when Ψ was lower in summer-dry (–4.8 MPa) than summer-wet plots (–1.9 MPa), and long-term mean plots were intermediate (–3.5 MPa; Table 2). Ψ did not differ ($P > 0.05$) between treatments in April (–1.6 MPa) or August (–0.8 MPa). Ψ in June were less than –6 MPa (i.e., the lower limit of the pressure chamber) for all sample units.

Net CO_2 assimilation (A) and c_i/c_a at mid-day 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 (Δ) 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 Δ 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 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 Ψ for any given sample date or when all dates were considered ($P > 0.16$, data not shown).

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

The ratio of intercellular to ambient CO_2 concentration (c_i/c_a) was a poor predictor of Δ across the growing season, and for most dates within the growing season. In particular, c_i/c_a and Δ 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 ($r = 0.40$, $P = 0.09$). c_i/c_a and Δ 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 · year⁻¹ to 846 mm · year⁻¹ (Table 1). There were also few treat-

TABLE 2. Mean ($\pm s_x$) survival (%), predawn leaf water potential (Ψ ; MPa), net CO₂ assimilation (A ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), c_i/c_a , stomatal conductance (g_s ; $\text{mol m}^{-2} \text{s}^{-1}$), and carbon isotope discrimination (Δ) of *Q. emoryi* seedlings ($n = 4$).

Variable	Date	Treatment				
		Long-term mean	Summer dry/ winter wet	Summer dry/ winter dry	Summer wet/ winter wet	Summer wet/ winter dry
Survival (%)	April	79 (2) ¹	76 (6)	90 (4)	85 (4)	85 (6)
	June	52 (11) a	70 (7) ab	87 (5) b	66 (17) a	69 (13) ab
	August	39 (9)	58 (7)	41 (19)	58 (18)	59 (14)
	October	38 (6)	58 (7)	40 (20)	58 (18)	57 (14)
Ψ (MPa)	April	-1.5 (0.2)	-1.1 (0.1)	-2.0 (0.2)	-1.4 (0.5)	-2.0 (0.7)
	June	<-6	<-6	<-6	<-6	<-6
	August	-0.9 (0.4)	-1.4 (0.6)	-0.6 (0.1)	-0.6 (0.1)	-0.6 (0.2)
	October	-3.5 (0.2) a	-4.2 (1.2) ab	-5.4 (0.7) b	-1.6 (0.2) c	-2.1 (0.2) c
A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	April	8.8 (2.4)	7.8 (0.9)	7.2 (1.6)	7.0 (2.0)	5.8 (2.2)
	June	-1.9 (1.4)	-0.9 (0.8)	-0.5 (0.6)	-0.2 (1.6)	-0.1 (0.8)
	August	6.2 (2.0)	4.6 (1.7)	4.4 (1.2)	8.9 (3.3)	3.5 (1.4)
	October	0.1 (0.9)	-0.7 (0.3)	-0.8 (0.6)	1.0 (1.3)	0.9 (0.3)
c_i/c_a	April	0.13 (0.08)	0.40 (0.15)	0.15 (0.15)	0.44 (0.09)	—
	June	1.18 (0.14)	1.02 (0.09)	0.97 (0.04)	1.00 (0.21)	0.96 (0.17)
	August	0.79 (0.04)	0.73 (0.01)	0.74 (0.04)	0.74 (0.04)	0.81 (0.04)
	October	0.91 (0.14)	1.01 (0.03)	1.09 (0.09)	0.79 (0.15)	0.84 (0.03)
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	April	0.041 (0.009) a	0.079 (0.023) a	0.036 (0.006) a	0.063 (0.014) a	0.016 (0.007) b
	June	0.059 (0.024)	0.025 (0.003)	0.061 (0.021)	0.040 (0.014)	0.014 (0.003)
	August	0.164 (0.008)	0.084 (0.026)	0.093 (0.011)	0.191 (0.067)	0.090 (0.026)
	October	0.026 (0.002)	0.026 (0.005)	0.029 (0.013)	0.034 (0.008)	0.036 (0.007)
Δ	April	18.1 (0.8)	18.5 (0.5)	17.3 (1.0)	19.4 (0.4)	19.3 (0.4)
	June	19.0 (0.2) ac	18.2 (0.4) ab	17.7 (0.06) b	19.2 (0.3) c	19.3 (0.4) c
	August	17.3 (0.4)	17.5 (1.0)	17.2 (0.9)	19.7 (0.6)	18.7 (0.4)
	October	18.3 (0.1) a	18.1 (0.4) a	16.7 (0.8) b	19.0 (0.4) a	19.4 (0.3) a ¹

¹Means in rows with different lowercase letters differed (ANOVA, $P < 0.05$).

ment effects on point measures of leaf gas exchange (A , g_s , c_i/c_a) and leaf water potential (Ψ). Further, there were few correlations between percent survival and point measures of seedling physiology (A , g_s , c_i/c_a , 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 con-

ductance, negative rates of CO₂ assimilation, c_i/c_a 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 Δ , which is an integrated

TABLE 3. Pearson correlation coefficients (top) and associated *P*-values (bottom) for Δ vs. integrated seedling survival (PRE60, PRE30, POST30, POST60).

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

^aPRE60 and PRE30 = slope of seedling survival over 60- and 30-day period (% day⁻¹) before determination of Δ , respectively; and POST30 and POST60 = slope of seedling survival over 30- and 60-day period (% day⁻¹) after determination of Δ , respectively. Significant coefficients after sequential Bonferroni correction (Rice 1989) are in boldface.

measure of leaf gas exchange. Generally, seedling survival was positively correlated with Δ , which is consistent with the expectation that metabolic activity is coupled with population demographics. Correlations between Δ 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 Δ when environmental conditions are suitable for extended periods of carbon assimilation.

However, observed differences in Δ 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 Δ 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 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). 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).

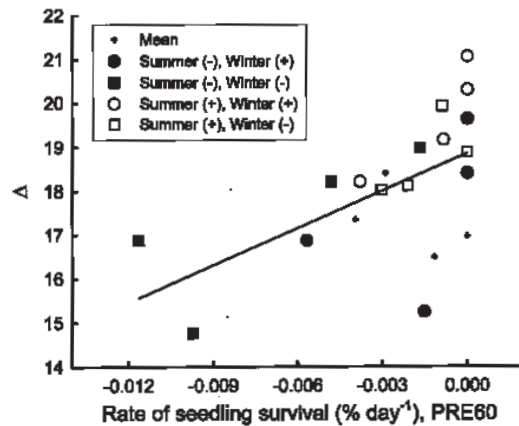


Fig. 2. Relationship between Δ for *Q. emoryi* leaves sampled 22 August and seedling survival rate (% day⁻¹) for 60-day period before (PRE60) determination of Δ ($r^2 = 0.38$, $P = 0.004$).

However, carbon isotope discrimination values (Δ) and c_i/c_a - Δ 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).

Similarly, physiologic performance and demographic performance of other woody plants in western North America are often coupled to the quantity and timing of summer precipitation (Neilson and Wullstein 1983, 1985, Ehleringer et al. 1991, Lin et al. 1996, Williams and Ehleringer 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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