

IMPLICATIONS OF PRECIPITATION REDISTRIBUTION FOR SHIFTS IN TEMPERATE SAVANNA ECOTONES

JAKE F. WELTZIN¹ AND GUY R. MCPHERSON

School of Renewable Natural Resources, University of Arizona, Tucson, Arizona 85721 USA

Abstract. In contrast to documented increases in woody plant dominance of former savannas and grasslands of North America, ecotones between oak (*Quercus* L.) woodlands and semi-desert grasslands of the southwestern United States and northwestern Mexico have been relatively stable over the past several centuries. Soil resource partitioning, wherein shallow-rooted grasses use summer precipitation and deep-rooted woody plants use winter precipitation, may have contributed to the stable coexistence of grasses and trees that form savannas at this ecotone. Thus, predicted changes in regional precipitation patterns and soil moisture caused by anthropogenic trace gas emissions have the potential to alter interactions between woody plants and grasses with potential ramifications for their relative abundance and distribution.

We used a field experiment to investigate the response of the dominant woodland and savanna tree *Quercus emoryi* to simulated potential scenarios of precipitation redistribution within the context of shifts in the woodland–grassland ecotone. Experimental soil volumes isolated from ambient precipitation and soil moisture were hand-watered between July 1994 and October 1996. Control plots received mean annual precipitation (602 mm), whereas treated plots received all possible combinations of 50% additions and reductions to mean summer and winter precipitation ($n = 4$). Increases in summer precipitation increased seedling emergence and recruitment rates as much as threefold, whereas emergence and recruitment were independent of altered winter precipitation regimes. Seedling survival, size, growth, and biomass allocation were largely independent of shifts in seasonal precipitation regimes.

We conclude that *Q. emoryi* recruitment and subsequent abundance and distribution would more likely be affected by changes in summer precipitation than changes in winter precipitation. For example, increases in summer precipitation that increase rates of seedling emergence and establishment may facilitate downslope shifts in the woodland–grassland ecotone. Similarly, this mechanism may explain downslope shifts in this ecotone that occurred coincident with particularly high summer precipitation during the “Medieval Warm” period, 645–1295 yr BP. Further, whereas soil moisture resource partitioning between adult *Q. emoryi* and coexisting grasses may contribute to savanna maintenance, soil resource partitioning does not occur within the first three growing seasons after *Q. emoryi* germination. Results illustrate the importance of consideration of the regeneration niche, which is often overlooked when predicting the response of woody plants to impending climate change.

Key words: climate change; ecotone; Emory oak; precipitation seasonality; *Quercus emoryi*; savanna; seedling establishment; soil moisture resource partitioning; treeline; woodland.

INTRODUCTION

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). In arid and semi-arid regions where vegetation is highly dependent upon precipitation, changes in seasonal precipitation and soil moisture regimes may cause major shifts in plant composition, distribution, and abundance (Ste-

phenson 1990). For example, predicted increases in winter soil water content (Manabe and Wetherald 1986, Mitchell and Warrilow 1987) may favor plants with the C_3 photosynthetic pathway over C_4 grasses (Neilson 1986, 1993, Melillo et al. 1993). Alternatively, increases in summer precipitation (Schlesinger and Mitchell 1987) should favor shallow-rooted species and C_4 grasses (e.g., Walter 1954, 1979, Knoop and Walker 1985, Ehleringer et al. 1991, Lauenroth et al. 1993, Burgess 1995).

Historic increases in woody plant stature and abundance in savannas and grasslands have been documented worldwide (Archer 1995). The proximate factors that influence rates, dynamics, and patterns of vegetation change are not well understood, although several mechanisms for changes in woody plant abundance

Manuscript received 20 April 1998; revised 14 February 1999; accepted 5 May 1999; final version received 9 July 1999.

¹ Present address: Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1610 USA.

and distribution have been proposed (e.g., fire suppression, alteration of herbivory by native or introduced herbivores, directional climate change; Archer 1994, Polley et al. 1996, McPherson 1997, Weltzin et al. 1997). Factors that contribute to stability of savannas include periodic disturbance such as fire or drought (e.g., Whittaker 1975), topographic constraints (Bartolome et al. 1994), positive feedbacks (e.g., Skarpe 1991, Wilson and Agnew 1992), or niche differentiation (e.g., Walter 1979).

Soil moisture partitioning is one example of niche differentiation that is widely invoked to explain coexistence of grasses and trees in savannas and woodlands throughout the world (Knoop and Walker 1985, Sala et al. 1989, Brown and Archer 1990, Peláez et al. 1994, Schulze et al. 1996). According to this two-layer model (Walter 1954, 1979), grasses use shallow sources of soil moisture derived from summer precipitation, whereas deep-rooted woody plants use precipitation that percolates deep into the soil profile during the nongrowing season. As such, shifts in the proportional seasonality of precipitation would alter the relative abundance and distribution of these two life forms. However, the two-layer model does not explicitly consider the woody plant regeneration niche (*sensu* Grubb 1977); environmental conditions sufficient for survival of adult plants may be insufficient for recruitment of seedlings.

The ecotone between temperate oak woodland and adjacent semi-desert grassland in the southwestern United States and northwestern Mexico ranges from discrete lower treelines to more diffuse savannas (Brown 1982, McClaran and McPherson 1999). This ecotone is characterized by a bimodal precipitation regime, with summer and winter peaks in precipitation. However, 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 change is difficult to predict (Mahlman 1997).

We examined how changes in the amount and seasonality of precipitation may affect oak (*Quercus* L.) seedling recruitment and its implications for shifts in the woodland–grassland ecotone. We used manipulative experiments to simulate potential scenarios of precipitation redistribution that both trees and grasses may experience by the mid- to late 21st century (Houghton et al. 1996, Giorgi et al. 1998). This research enabled us to test the importance of soil moisture resource partitioning as a constraint on savanna structure within the context of the woody plant regeneration niche (*sensu* Grubb 1977). We predicted that winter precipitation would be correlated with recruitment and growth of tree seedlings at the ecotone, whereas summer precipitation would not affect seedling recruitment and growth.

METHODS

Study site

Research was conducted between 1994 and 1996 at the lower, xeric margin of temperate, evergreen–oak woodland at the base of the Huachuca Mountains in southeastern Arizona, USA. In particular, the study site was located in lower Garden Canyon (31°29' N, 110°20' W) on Fort Huachuca Military Reservation (FHMR) near Sierra Vista, Arizona (site GW in Weltzin and McPherson 1999). The site is 1550 m in elevation with a 5% slope on a northeastern aspect. Soils vary from Aridic Haplustalfs to Pachic Haplustolls (USDA 1994; E. Pendall, *unpublished manuscript*). Climate is semi-arid, with an average annual temperature of 20°C. Average annual precipitation is 602 mm, and is bimodally distributed, with peaks during the summer “monsoon” (July–September; 50%) and during winter (December–March; 30%) (National Oceanic and Atmospheric Administration 1996).

The site is characterized by *Quercus emoryi* Torr. (Emory oak)-dominated savannas bordered by semi-desert grassland dominated by C₄ perennial bunchgrasses (Brown 1982, McClaran and McPherson 1999). Tree cover within the savanna is 11% (Haworth and McPherson 1994) and includes *Quercus emoryi* with scattered *Juniperus deppeana* Steud. (alligator juniper) and *Quercus arizonica* Sarg. (Arizona white oak). Herbaceous vegetation within the savanna and adjacent grasslands is dominated by *Trachypogon montufarii* (H.B.K.) Nees. (crinkleawn), *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama), *Andropogon cirratus* Hack. (Texas bluestem), and *Eragrostis intermedia* Hitchc. (plains lovegrass). Dominant C₃ herbaceous dicots include *Heterotheca subaxillaris* (Lam.) Britton & Rusby (camphorweed) and *Evolvulus arizonicus* Gray. The site burned most recently in 1982, and has not been grazed by livestock since the early 1950s (J. Miller, *personal communication*). Detailed information about the site is provided by Weltzin and McPherson (1999).

Experimental design

In June 1994, we initiated a field experiment consisting of five simulated precipitation treatments applied to plots isolated from ambient precipitation and soil moisture (see Appendix). The first treatment received simulated precipitation equivalent to the long-term (i.e., 30-yr) mean annual precipitation for the site (602 mm/yr; Table 1). The other four 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 (March–June) and autumn (October–November). This experimental design necessarily confounds seasonal treatments with total precipitation; equivalent proportional reductions or additions to both

TABLE 1. Season, frequency of application, and amount (mm) of five precipitation treatments ($n = 4$) applied to plots isolated from ambient precipitation and soil moisture at an oak savanna site in southeastern Arizona, USA.

Season	Months	Frequency	Treatments				
			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	85
Total	...	57	602	531	359	846	674

Note: Long-term mean represents the 30-yr average seasonal precipitation for the site, and seasonal wet and dry treatments represent 50% additions and reductions, respectively, of the long-term seasonal mean.

summer and winter mean precipitation, which currently differ by a factor of almost two, result in a broad range of total annual precipitation (Table 1). 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 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, five 1.2×1.5 m plots were arranged linearly 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 (16×4 m) constructed of steel tubing, clear polyethylene film, and fence posts was erected over each block to exclude ambient precipitation. The pitched roof of each shelter was 2.2 m above ground level 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.

Shelters were open sided to minimize microclimatic impact. Shelters reduced photosynthetically active photon flux density by $29 \pm 10\%$ (mean ± 1 SE) 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 onsite was applied to plots according to a randomly generated precipitation regime that simulated natural precipitation patterns (Nicks and Lane 1989; J. Stone, *personal communication*). Simulated precipitation events ranged from 1 mm to 120 mm, and were applied by hand-watering 57 times annually (Table 1).

On 19 July 1994 and 17 July 1995, coincident with the onset of the summer rains (i.e., the Arizona monsoon), we planted 49 *Q. emoryi* acorns at 10-cm spacing into each plot. Acorns were collected on the day of planting from at least 20 trees onsite and were sorted

by visual examination and flotation (Nyandiga and McPherson 1992).

In each year, seedling emergence and survival were monitored at two-week intervals until the end of October. Thereafter, seedling survival for each cohort was monitored monthly until experiment termination on 26 October 1996. Insecticide (Carbaryl 4L; Platte Chemical, Fremont, Nebraska, USA) was applied to all seedlings monthly during the growing season to minimize invertebrate herbivory.

Gravimetric soil moisture content at 10 cm and 50 cm in each plot was determined by extracting a ~ 20 g soil sample using a 2 cm diameter coring tool. Core holes were backfilled with tamped soil. At the end of each growing season, standing herbaceous biomass within each plot was estimated by double-sampling (Pechanec and Pickford 1937) five randomly located 0.0625 m² subplots per plot.

At experiment termination, we recorded height of live seedlings in each cohort, and clipped seedlings at ground level for determination of aboveground biomass. We sampled herbaceous root biomass by extracting soil with a bucket auger from two randomly-located 10 cm diameter cores in successive 20-cm increments to 1 m depth. Plots were then excavated to 1 m depth to determine root biomass (in 20-cm increments) and taproot length for two seedlings selected at random (and treated as subsamples) from each cohort. Seedling roots were extracted by hand, and herbaceous roots were later extracted by hand separation, flotation in brine, and subsequent sieving through 2.0-mm mesh. All plant tissue samples were oven-dried at 60°C for 72 hr before weighing.

Statistical analyses

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 prior to analysis of variance (ANOVA; SAS procedure GLM; SAS Institute 1989). Proportional seedling emergence (emerged seedlings/acorns planted) was transformed using an arcsine-square-root function (Zar 1996) prior to ANOVA. For all ANOVA models, precipitation treatment and block were treated as fixed and random

TABLE 2. Emergence, survival at experiment termination, and recruitment of *Q. emoryi* seedlings planted in 1994 (Cohort 1) and 1995 (Cohort 2) in plots watered to simulate mean seasonal precipitation (mean) and all combinations of 50% additions (wet) and reductions (dry) to summer (JAS) and winter (DJF) precipitation relative to the seasonal mean ($n = 4$) at lower treeline in southeastern Arizona, USA.

Treatment		Cohort 1			Cohort 2		
		Emergence (%)	Survival (%)	Recruitment (%)	Emergence (%)	Survival (%)	Recruitment (%)
Summer	Winter						
Mean	Mean	50.8 ^a	47.7 ^a	24.2 ^a	47.1 ^a	35.0 ^a	16.5 ^a
Dry	Wet	19.9 ^b	54.2 ^{ab}	10.8 ^b	32.4 ^a	57.8 ^b	18.7 ^a
	Dry	21.1 ^b	54.3 ^{ab}	11.5 ^b	38.7 ^a	43.7 ^{ab}	16.9 ^a
Wet	Wet	59.7 ^a	61.1 ^{ab}	36.5 ^c	52.1 ^a	63.9 ^b	33.3 ^b
	Dry	62.2 ^a	61.8 ^b	38.4 ^c	48.2 ^a	58.8 ^b	28.3 ^b

Note: Means with the same letter did not differ significantly ($P > 0.05$) within cohort for emergence (Fisher's protected LSD test), survival (Wald χ^2), and recruitment (Z tests).

effects, respectively. We used Fisher's protected LSD (Fisher 1960) a posteriori mean separation tests to compare levels within factors for all significant effects ($P < 0.05$ unless otherwise indicated). Mean seedling height and root length, and seedling and herbaceous shoot and root biomass within each plot were used in all analyses.

Proportional hazards regression analysis (PHREG; SAS procedure PHREG; Allison 1995, SAS Institute 1996) was used to test for differences between survivorship curves of emerged seedlings for each cohort. For each cohort, we used PHREG to compare subsets of survivorship curves equivalent to all possible pairwise treatment combinations. To determine whether cohorts responded similarly to the different treatments, we compared survivorship curves within treatment that encompassed the duration of the experiment for cohort two (i.e., 460 days), and the first 460 days of cohort one.

Seedling recruitment was defined as the product of seedling emergence and survival of emerged seedlings at experiment termination as determined by proportional hazards regression analysis. We used Z tests of proportions (Zar 1996) to compare recruitment between all pairwise treatment combinations.

Data for shoot height and root length, shoot, total root, and total (shoot + total root) biomass, and total root:shoot biomass ratios of surviving *Q. emoryi* seedlings at experiment termination were analyzed with ANOVA. Total aboveground and belowground herbaceous biomass were analyzed by year and at experiment termination, respectively, using ANOVA. We used multivariate analysis of variance (MANOVA; Pillai's Trace in SAS procedure GLM; SAS Institute 1989) models to analyze data for seedling root biomass and grass root biomass in successive 20 cm soil depth increments to 1 m (von Ende 1993).

We used ANOVA to evaluate treatment effects on soil moisture content at 10 cm and 50 cm soil depths for each sample date ($N = 31$ dates). In addition, we used single degree of freedom contrasts (Scheffé 1953) to test specific hypotheses regarding effect of treatment on soil moisture content; for each date, we used con-

trasts to compare wet and dry treatments (i.e., summer wet vs. summer dry, winter wet vs. winter dry).

RESULTS

Seedling emergence.—Seedling emergence was affected by treatment, but the intensity of treatment effects was cohort dependent (Table 2). Seedling emergence in summer wet treatments was three times that of summer dry treatments for cohort one (contrast $P < 0.0001$). Treatment effects on seedling emergence were similar for cohort two (contrast $P = 0.08$), but differences were attenuated relative to cohort one by both increased emergence in summer dry treatments and decreased emergence in summer wet treatments.

Seedling survivorship.—Seedling survivorship curves were characterized by (1) low mortality during the first two months after emergence, (2) higher rates of mortality between two and four months, (3) periods of low mortality during the November–March nongrowing season, and (4) periods of higher seedling mortality during the annual seasonal drought between April and June, particularly in 1996 (Figs. 1 and 2).

Seedling survivorship was dependent upon both treatment and cohort (Table 2). Survivorship curves for cohort one did not differ ($P > 0.21$) with one exception: seedling survival in the mean precipitation treatment was lower than in the summer wet–winter dry treatment ($P = 0.04$). Although seedling survivorship was somewhat extended in winter dry treatments, relatively high rates of mortality in all treatments during the 1996 premonsoon drought attenuated treatment-induced differences in survivorship (Fig. 1).

Survivorship curves for cohort two did not differ ($P > 0.27$) with the exception of the mean precipitation treatment: seedling survival was lower with mean precipitation than all other treatments ($P < 0.04$ except summer dry–winter dry where $P = 0.06$). In contrast to cohort one, seedling mortality during the 1996 premonsoon drought exacerbated treatment-induced differences in survivorship (Fig. 2).

Temporal patterns of seedling survivorship differed between cohort one and cohort two, regardless of treatment ($P < 0.04$). Seedling survival during the first

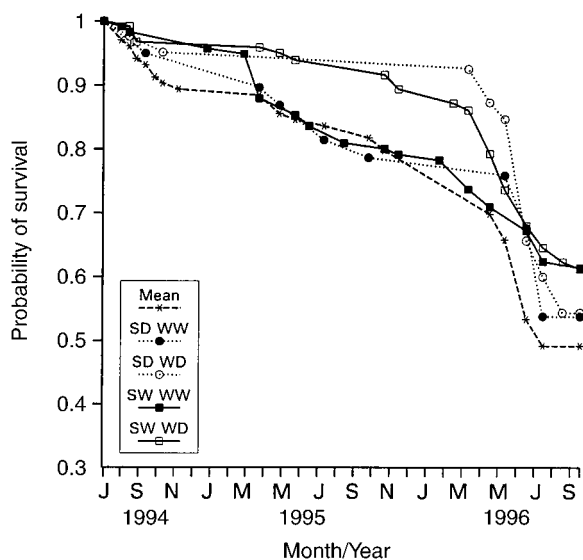


FIG. 1. Survivorship curves of *Q. emoryi* seedlings planted on 19 July 1994 at lower treeline in southeastern Arizona, USA. Acorns were planted into plots ($n = 4$) watered to simulate mean seasonal precipitation (mean) and combinations of 50% additions (W = wet) and reductions (D = dry) to summer (S = July–September) and winter (W = December–February) precipitation relative to the seasonal mean (e.g., SD WW = summer dry, winter wet).

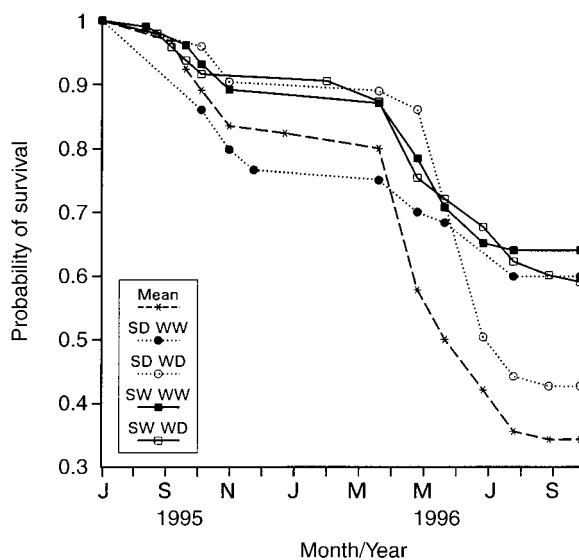


FIG. 2. Survivorship curves of *Q. emoryi* seedlings planted on 17 July 1995 at lower treeline in southeastern Arizona, USA. See Fig. 1 for legend explanation.

growing and nongrowing seasons (i.e., July–March) was comparable for the two cohorts. However, during the second growing season (in 1995 and 1996 for cohorts one and two, respectively), survival rates of seedlings in cohort one remained relatively high, but declined dramatically for cohort two. Seedlings from cohort one that were in their third growing season in 1996 also experienced high rates of mortality.

Seedling recruitment.—Seedling recruitment (i.e., the number of individuals added to the population) reflected the combined effects of emergence and subsequent survivorship within the different treatments and cohorts (Table 2). Recruitment ranged from 1.5 to 3 times greater in summer wet than summer dry treatments for both cohorts. Recruitment for cohort one was least in summer dry treatments, intermediate in the mean treatment, and greatest in summer wet treatments ($P < 0.004$). Recruitment for cohort two did not differ between the mean and summer dry treatments ($P > 0.65$), and was greatest in summer wet treatments ($P < 0.04$).

Seedling size and production.—Within each cohort, seedling size and production parameters at experiment termination were unrelated to the different treatments (Table 3). For both cohorts, treatment did not affect shoot height ($P > 0.66$), root length ($P > 0.63$), shoot biomass ($P > 0.60$), total root biomass ($P > 0.13$), total (shoot + total root) seedling biomass ($P > 0.22$), or root:shoot biomass ratios ($P > 0.79$). MANOVA indicated that the effect of treatment, and its interaction

with soil depth, did not affect seedling root biomass distribution within the soil profile for either cohort ($P > 0.10$). In all treatments, seedling root biomass was concentrated in the top 20 cm of the soil profile, particularly for cohort two (Fig. 3). Mean seedling size and production are comparable to those observed for *Q. emoryi* in other studies at this site (McPherson 1993, McClaran and McPherson 1999) and at other locations within the region (Pase 1969, Germaine and McPherson 1999). Mean root extension rates of 18 cm/yr for both cohorts are similar to rates of 17 cm/yr reported by Pase (1969).

Herbaceous production.—Total aboveground herbaceous biomass did not differ ($P > 0.49$) between treatments for the first growing season (i.e., 1994). However, differences in the second (1995) and third (1996) growing season reflected longer term effects of the treatments on herbaceous production (Table 4). In both 1995 and 1996, herbaceous biomass, which consisted largely of C_4 perennial grasses, was about two times greater in summer wet than summer dry treatments, and was intermediate in the mean precipitation treatment. Results are consistent with other observations that total herbaceous production in similar systems dominated by C_4 grasses is correlated with warm-season precipitation (Nelson 1934, Cable 1975, Kemp 1983, Burgess 1995).

Total belowground biomass of herbaceous plants at experiment termination was not affected by treatment ($P = 0.20$). MANOVA indicated that effect of treatment, and its interaction with soil depth, did not affect herbaceous root biomass distribution within the soil profile ($P > 0.18$). Regardless of treatment, herbaceous root biomass was concentrated within the top 20 cm

TABLE 3. *Q. emoryi* seedling shoot height and root length (cm), shoot, root, and total biomass (g), and root : shoot ratios.

Co-hort	Summer	Winter	Response variable					
			Shoot height (cm)	Root length (cm)	Shoot biomass (g)	Root biomass (g)	Total biomass (g)	Root : shoot ratio
1	Mean	Mean	14	74	0.92	1.72	2.64	3.1
	Dry	Wet	7	39	0.09	0.26	0.35	3.0
		Dry	6	43	0.19	0.39	0.58	3.5
	Wet	Wet	10	59	0.43	0.96	1.39	3.8
		Dry	7	49	0.23	0.47	0.70	2.8
2	Mean	Mean	8	42	0.25	0.37	0.62	1.8
	Dry	Wet	7	37	0.17	0.38	0.56	2.3
		Dry	7	31	0.18	0.39	0.57	2.7
	Wet	Wet	8	43	0.20	0.38	0.58	1.9
		Dry	8	29	0.14	0.22	0.36	1.6

Notes: Seedlings were grown from acorns planted in 1994 (Cohort 1) and 1995 (Cohort 2) in plots watered to simulate mean seasonal precipitation (mean) and all combinations of 50% additions (wet) and reductions (dry) to summer (JAS) and winter (DJF) precipitation relative to the seasonal mean ($n = 4$) at lower treeline in southeastern Arizona, USA. Within each cohort, means within each column did not differ ($P > 0.13$).

of the soil profile, but extended to depths of at least 1 m (Fig. 3).

Soil moisture.—Soil moisture was affected by treatment, depth, and sample date (Fig. 4). Statistical contrasts (i.e., summer wet vs. summer dry, and winter wet vs. winter dry treatments) confirmed that soil moisture reflected the different watering treatments established and applied within the context of the experimental design. Within both summer (July–September) and winter (December–February), soil moisture at 10 cm and 50 cm in wet treatments exceeded that of dry treatments ($P < 0.05$ except July 1994 at 50 cm where $P = 0.09$). Differences between wet and dry treatments exhibited a one-month lag into the following season

(i.e., spring or autumn, with one exception) when all treatments were receiving the same volume of water. Soil moisture was more variable in the mean precipitation treatment than other treatments (*data not shown*), depending on sample date and soil depth. However, within the summer and winter seasons, soil moisture contents in mean plots either did not differ from, or were between, soil moisture contents in wet or dry treatments ($\alpha = 0.05$; *data not shown*).

Regardless of treatment, soil moisture generally was two times greater in winter than in summer, and was lowest in June (Fig. 4). Seasonal soil moisture exhibited the greatest absolute range at 10 cm depth. In summer, soil moisture at 50 cm tended to lag that at 10 cm by about two months.

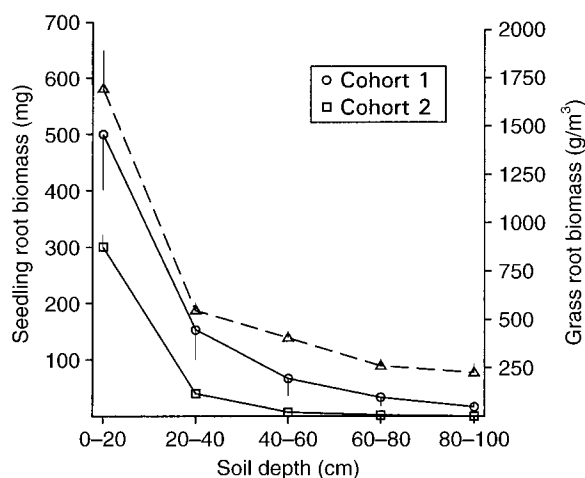


FIG. 3. Mean root biomass (mg) for *Q. emoryi* seedlings (solid line) planted on 19 July 1994 (Cohort 1; open circles) and 17 July 1995 (Cohort 2; open squares), and mean grass root biomass (g/m^3 ; broken line, open triangles), in 20-cm soil depth increments ($n = 20$) at experiment termination (26 October 1996) in experimental plots at lower treeline in southeastern Arizona, USA. Vertical lines represent 1 SE.

DISCUSSION

Q. emoryi seedling demography

Simulated shifts in the amount and seasonality of precipitation within this oak savanna produced differences in *Q. emoryi* recruitment rates. Results failed to support the prediction that winter precipitation would be directly correlated with recruitment (i.e., addition of individuals to the population) and growth of tree seedlings. In contrast, summer precipitation was most important for *Q. emoryi* seedling emergence and early establishment (Table 2), although seedling growth was unaffected (Table 3). Differences in recruitment, which ranged from 1.5- to 3-fold greater in summer wet than summer dry treatments, were shaped by the impacts of summer precipitation regime on both seedling emergence and survival.

These results are consistent with observations that *Q. emoryi* seedling recruitment is constrained by interannual and seasonal variation in precipitation regimes (Pase 1969, Neilson and Wullstein 1983, McPherson 1992, Germaine and McPherson 1999). Sim-

TABLE 4. Aboveground herbaceous biomass (g/m^2) at the end of the 1994, 1995, and 1996 summer growing seasons, and belowground herbaceous biomass (g/m^3) to 1 m depth at experiment termination in 1996, in plots watered to simulate mean seasonal precipitation (mean) and all combinations of 50% additions (wet) and reductions (dry) to summer months (JAS) and winter months (DJF) precipitation relative to the seasonal mean ($n = 4$) at lower treeline in southeastern Arizona, USA.

Treatment		Aboveground biomass (g/m^2)			Belowground biomass (g/m^3)
Sum- mer	Winter	1994	1995	1996	1996
Mean	Mean	161 ^a	262 ^{ac}	298 ^a	2095 ^a
Dry	Wet	89 ^a	159 ^{ab}	147 ^b	2663 ^a
	Dry	109 ^a	133 ^b	149 ^b	2872 ^a
Wet	Wet	122 ^a	299 ^c	391 ^c	4272 ^a
	Dry	174 ^a	329 ^c	252 ^a	2837 ^a

Note: Within year, means with the same letter did not differ significantly ($P > 0.05$).

ilarly, establishment of other woody plants (e.g., *Acacia*, *Juniperus*, *Pinus*, *Prosopis*, *Quercus*) within arid and semi-arid grasslands has been attributed to intra- to interannual periods of above average precipitation or soil moisture (Johnsen 1962, Griffin 1971, McPherson and Wright 1990, Archer 1990, Richardson and Bond 1991, O'Connor 1995, McPherson 1997).

Climate change and *Q. emoryi* population dynamics

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., Manabe and Wetherald 1986, Schlesinger and Mitchell 1987, Mitchell et al. 1990, Schneider 1993, Kattenberg et al. 1996, Giorgi et al. 1998). Results from this study indicate that changes in summer precipitation regimes would likely constrain *Q. emoryi* population dynamics through changes in seedling recruitment rates.

In contrast, shifts in winter precipitation should be less important to *Q. emoryi* population dynamics. First, *Q. emoryi* acorns ripen, are dispersed, and emerge coincident with the summer monsoon (McPherson 1992), the importance of which has been demonstrated herein. Second, although seedling, sapling, and adult *Q. emoryi* utilize winter precipitation during the early growing season, they are also capable of utilizing summer-derived precipitation even in relatively dry summers (Weltzin and McPherson 1997). However, the importance of winter precipitation to flowering and seed set for this species have not been determined.

Once established, *Q. emoryi* populations will likely persist in the face of all but extreme environmental change (sensu Grime 1979, Warner and Chesson 1985). *Q. emoryi* seedlings were relatively insensitive to en-

vironmental conditions imposed in this study (e.g., soil moisture, herbaceous interference). Mature *Q. emoryi* are tolerant of environmental perturbation because they are long lived (Sanchini 1981), and are capable of vegetative reproduction following top removal by fire or drought (Bahre 1991, Caprio and Zwolinski 1995). This tolerance of unfavorable conditions, coupled with relatively rapid recruitment during summers with favorable precipitation, suggests that *Q. emoryi* should persist on landscapes where seedling emergence occurs (cf. Chesson and Huntley 1989, Archer 1990, McPherson 1997). Further, although historic fire regimes may have constrained *Quercus* seedling recruitment, increases in livestock grazing, habitat fragmentation, and fire suppression activities have reduced the contemporary and future importance of fire as a factor controlling the spatial distribution of this ecotone (Weltzin and McPherson 1995).

The observation that early seedling establishment is a critical stage to woody plant population dynamics is not new (e.g., Darwin 1859, Grubb 1977, Harper 1977, McPherson 1997, Scholes and Archer 1997). However, predictions of climate change effects on woody plant abundance and distribution have not always considered this bottleneck to recruitment (e.g., Idso and Quinn 1983, Emanuel et al. 1985, Solomon 1986, Peters 1990, Neilson et al. 1992, Woodward 1992, Neilson 1993, Vegetation/Ecosystem Modeling and Analysis Project Members 1995, Woodward and Lee 1995, Fuller and Prince 1996, Martin 1996, Iverson and Prasad 1998; but see Neilson and Wullstein 1983, Neilson 1986, Pastor and Post 1988, Harte and Shaw 1995, Polley et al. 1996). However, the development of dynamic global vegetation models (e.g., Foley et al. 1998, Hurtt et al. 1998, Neilson and Drapek 1998) should facilitate the incorporation of transient processes such as recruitment. Experiments such as this one can (1) provide empirical data on soil-plant-water relationships, the basis for a mechanistic determination of rates of recruitment, migration, and dieback of different plant functional types under changing climates (Walker 1996), and (2) demonstrate unexpected responses of population processes to changing environmental conditions (see also Harte and Shaw 1995).

Soil moisture resource partitioning and savanna maintenance

Soil resource partitioning is widely considered a mechanism for stable coexistence of grasses and trees in savannas and woodlands throughout the world (Knoop and Walker 1985, Sala et al. 1989, Brown and Archer 1990, Peláez et al. 1994, Schulze et al. 1996). Similarly, recent research indicates that soil moisture resource partitioning facilitates the coexistence of mature *Q. emoryi* and grasses at this savanna site (Weltzin and McPherson 1997). However, Weltzin and McPherson (1997) found that 1- and 2-yr-old *Q. emoryi* seedlings and grasses obtained water from similar

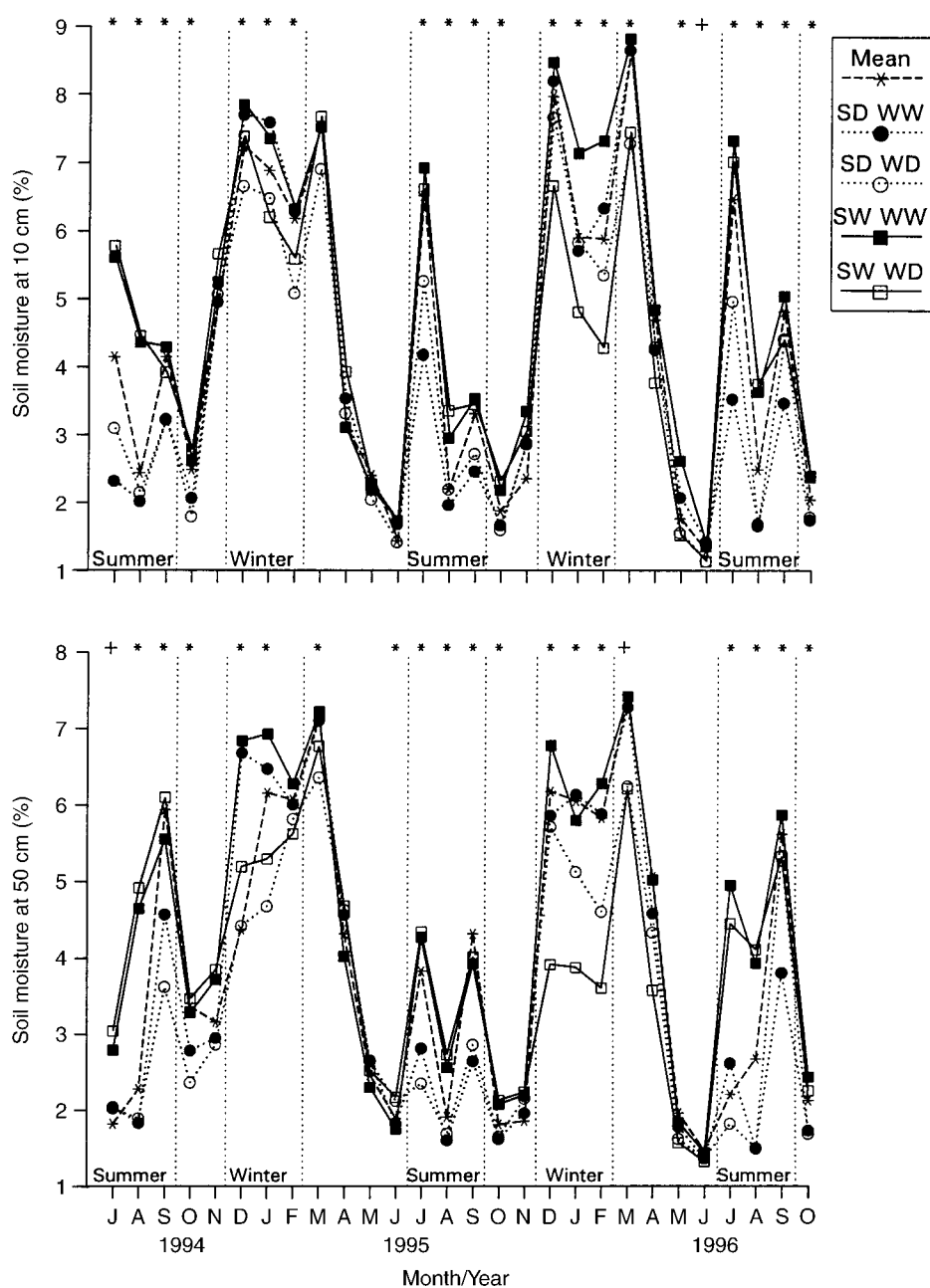


FIG. 4. Gravimetric soil moisture (%) at 10 cm (top) and 50 cm (bottom) depth determined monthly between July 1994 and October 1996 in experimental plots at lower treeline in southeastern Arizona, USA. Differences between seasonal wet and dry treatments were tested with multiple contrasts for each date: +, $P < 0.10$, *, $P < 0.05$. See Fig. 1 for legend explanation.

depths in the soil profile, which suggested that soil moisture partitioning between *Q. emoryi* and coexisting grasses does not occur for at least two years after seedling germination.

Results from this study support Weltzin and McPherson's (1997) conclusion that spatial and temporal soil moisture resource partitioning does not occur between *Q. emoryi* seedlings and grasses for at least two

years after germination. First, *Q. emoryi* germination, emergence, and early establishment occurred in the summer, when most herbaceous plants were actively growing. This suggests seedling roots can tolerate belowground interference from grass roots long enough to penetrate beyond their influence (Brown and Archer 1990). Second, experimental manipulations of winter precipitation did not affect recruitment or growth of *Q.*

emoryi during their first three growing seasons. This suggests that these seedlings are incapable of using winter-derived moisture from deep in the soil profile. Third, relatively short root lengths observed for both *Q. emoryi* seedling cohorts, regardless of precipitation treatment, indicate a physical limitation to acquisition of deeper water sources (see also Pase 1969, McPherson 1993).

Results from this study and Weltzin and McPherson (1997) illustrate an important limitation to the application of the soil resource partitioning model to explain interactions between woody plants and grasses in this savanna. In particular, the response of woody plants to environmental conditions is dependent on life-history stages that dictate their belowground morphology. Consequently, environmental conditions that are sufficient for survival of adult plants (e.g., adequate winter precipitation) may be insufficient for recruitment of seedlings (cf. Harper 1977, Schupp 1995, Weltzin and McPherson 1999), and the response of seedling and mature plants to environmental variation may be decoupled. Accordingly, we propose that the woody plant regeneration niche (Grubb 1977) should be explicitly considered when applying Walter's two-layer hypothesis (1954, 1979) to explain coexistence of woody plants and grasses.

Spatial and temporal dynamics of the woodland-grassland ecotone

Recent research suggests that oak woodland-semidesert grassland ecotones are stabilized by self-enhancing feedback mechanisms of overstory shade, seed dispersal, and seedling establishment, coupled with strong abiotic constraints beyond the current ecotone (Germaine and McPherson 1999, Hubbard and McPherson 1999, Weltzin and McPherson 1999). These processes stabilize the woodland-grassland ecotone both spatially and temporally (cf. Wilson and Agnew 1992). Further, observed (McPherson et al. 1993) and potential future downslope shifts in the ecotone occur when periodic climatic conditions simulate, or negate the importance of, conspecific biogenic safe sites. Results of this research demonstrate that increases in summer precipitation are one mechanism that would facilitate downslope shifts in the woodland-grassland ecotone. This interpretation is consistent with that of McClaran and McPherson (1995), who concluded that the last downslope shift in this ecotone, which occurred 700–1700 yr BP, coincided with a period of particularly high summer precipitation in the region (i.e., the Medieval Warm period, 645–1295 yr BP; Davis 1994).

ACKNOWLEDGMENTS

L. Abbott, D. Angell, J. Atchley, R. Brooks, P. Ford, A. Hubbard, G. Lawson, S. Lowe, R. Matson, P. R. Meixner, S. Merrigan, A. Nicholas, M. O'Dea, K. Rojahn, P. Roller, K. Snyder, J. Stone, K. Suedkamp, J. Villanueva-Diaz, K. Weltzin, and P. Weltzin assisted with experiment establishment, maintenance, monitoring, and disassembly. In addition, H.

Germaine and M. Meixner were particularly instrumental in their assistance from start to finish. This research could not have been conducted without the facilitation of Sheridan Stone, Fort Huachuca Office of Game Management, and the help of J. Miller and J. Murray, FHMR. B. Steidl provided statistical advice. Suggestions from J. Clark, L. Graumlich, M. McClaran, R. Neilson, K. Owens, T. Thompson, D. Williams, and two anonymous reviewers helped us improve this manuscript. Research was supported by USDA-CSRS National Research Initiative Grant #92-37101-7435 and McIntire-Stennis project ARZT-139017-M-12-118. Weltzin was supported in part by a UA/NASA Space Grant Graduate Student Fellowship, a Flinn Foundation Biology 21 Graduate Fellowship, a William G. McGinnies Scholarship in Arid Lands Studies, and a Graduate College Fellowship.

LITERATURE CITED

- Allison, P. D. 1995. Survival analysis using the SAS system: a practical guide. SAS Institute, Cary, North Carolina, USA.
- Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, USA. *Journal of Biogeography* 17:453–462.
- Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. Pages 13–68 in M. Vavra, W. Laycock, and R. Pieper, editors. Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, Colorado, USA.
- Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Écoscience* 2:83–99.
- Bahre, C. J. 1991. A legacy of change. University of Arizona Press, Tucson, Arizona, USA.
- Bartolome, J. W., B. H. Allen-Diaz, and W. D. Tietje. 1994. The effect of *Quercus douglasii* removal on understory yield and composition. *Journal of Range Management* 47:151–154.
- Brown, D. E., editor. 1982. Biotic communities of the American southwest—United States and Mexico. *Desert Plants* 4:1–342.
- Brown J. R., and S. R. Archer. 1990. Water relations of a perennial grass and seedling vs. adult woody plants in a subtropical savanna, Texas. *Oikos* 57:366–374.
- Burgess, T. L. 1995. Desert grassland, mixed shrub savanna, shrub steppe, or semidesert scrub? The dilemma of coexisting growth forms. Pages 31–67 in M. P. McClaran and T. R. Van Devender, editors. The desert grassland. University of Arizona Press, Tucson, Arizona, USA.
- Cable, D. R. 1975. Influence of precipitation on perennial grass production in the semidesert southwest. *Ecology* 56:981–986.
- Caprio, A. C., and M. J. Zwolinski. 1995. Fire and vegetation in a madrean oak woodland, Santa Catalina Mountains, southeastern Arizona. Pages 389–399 in L. F. DeBano, G. J. Gottfried, R. H. Hamre, C. B. Edminster, P. F. Ffolliott, and A. Ortega-Rubio, technical coordinators. Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and Northwestern Mexico. U.S. Forest Service General Technical Report RM-264.
- Chesson, P., and N. Huntley. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology and Evolution* 4:293–298.
- Darwin, C. 1964. The origin of species. First edition, 1859. Harvard Facsimile, Cambridge, Massachusetts, USA.
- Davis, O. K. 1994. The correlation of summer precipitation in the southwestern USA with isotopic records of solar activity during the Medieval Warm Period. *Climatic Change* 26:271–287.

- Ehleringer, J. R., S. L. Phillips, W. S. F. Schuster, and D. R. Sandquist. 1991. Differential utilization of summer rains by desert plants. *Oecologia* **88**:430–434.
- Emanuel, W. R., H. H. Shugart, and M. Stevenson. 1985. Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. *Climatic Change* **7**:29–43.
- Fisher, R. A. 1960. The design of experiments. Seventh edition. Hafner, New York, New York, USA.
- Foley, J. A., S. Levis, I. C. Prentice, D. Pollard, and S. L. Thompson. 1998. Coupling dynamic models of climate and vegetation. *Global Change Biology* **4**:561–579.
- Fuller, D. O., and S. D. Prince. 1996. Rainfall and foliar dynamics in tropical southern Africa: potential impacts of global climatic change on savanna vegetation. *Climatic Change* **33**:69–96.
- Germaine, H. L., and G. R. McPherson. 1999. Effects of biotic factors on emergence and survival of *Quercus emoryi* at lower treeline, Arizona, USA. *Écoscience* **6**:92–99.
- Giorgi, F., L. O. Mearns, C. Shields, and L. McDaniel. 1998. Regional nested model simulations of present day and 2 × CO₂ climate over the central plains of the United States. *Climatic Change* **40**:457–493.
- Griffin, J. R. 1971. Oak regeneration in the upper Carmel Valley, California. *Ecology* **52**:862–868.
- Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, UK.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review* **52**:107–145.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.
- Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science* **267**:876–880.
- Haworth, K., and G. R. McPherson. 1994. Effects of *Quercus emoryi* on herbaceous vegetation in a semi-arid savanna. *Vegetatio* **112**:153–159.
- Houghton, J. T., G. Miera, B. Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Maskell, editors. 1996. Climate change 1995: the science of climate change. Cambridge University Press, Cambridge, UK.
- Hubbard, J. A., and G. R. McPherson. 1999. Do seed predation and dispersal limit downslope movement of a semi-desert grassland/oak woodland transition? *Journal of Vegetation Science* **10**:739–744.
- Hurt, G. C., P. R. Moorcroft, S. W. Pacala, and S. A. Levin. 1998. Terrestrial models and global change: challenges for the future. *Global Change Biology* **4**:581–590.
- Idso, S. B., and J. A. Quinn. 1983. Vegetational redistribution in Arizona and New Mexico in response to a doubling of the atmospheric CO₂ concentration. Climatological Publications; Scientific Paper No. 17, Laboratory of Climatology, Arizona State University, Tempe, Arizona, USA.
- Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs* **68**:465–485.
- Johnsen, T. N., Jr. 1962. One-seed juniper invasion of northern Arizona grassland. *Ecological Monographs* **32**:187–207.
- Kattenberg, A., F. Giorgi, H. Grassl, G. A. Meehl, J. F. B. Mitchell, R. J. Stouffer, T. Tokioka, A. J. Weaver, and T. M. L. Wigley. 1996. Climate models—projections of future climate. Pages 285–357 in J. T. Houghton, G. Miera, B. Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Maskell, editors. Climate change 1995: the science of climate change. Cambridge University Press, Cambridge, UK.
- Kemp, P. R. 1983. Phenological patterns of Chihuahuan desert plants in relation to the timing of water availability. *Journal of Ecology* **71**:427–436.
- Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* **73**:235–253.
- Lauenroth W. K., D. L. Urban, D. P. Coffin, W. J. Parton, H. H. Shugart, T. B. Kirchner, and T. M. Smith. 1993. Modeling vegetation structure—ecosystem process interactions across sites and ecosystems. *Ecological Modelling* **67**:49–80.
- Mahlman, J. D. 1997. Uncertainties in projections of human-caused climate warming. *Science* **278**:1416–1417.
- Manabe, S., and R. T. Wetherald. 1986. Reduction in summer soil wetness induced by an increase in atmospheric carbon dioxide. *Science* **232**:626–628.
- Martin, P. H. 1996. Climate change, water stress, and fast forest response: a sensitivity study. *Climatic Change* **34**:223–230.
- McClaran, M. P., and G. R. McPherson. 1995. Can soil organic carbon isotopes be used to describe grass—tree dynamics at a savanna—grassland ecotone and within the savanna? *Journal of Vegetation Science* **6**:857–862.
- McClaran, M. P., and G. R. McPherson. 1999. Oak savanna in the American Southwest. Pages 275–287 in R. C. Anderson, J. S. Fralish, and J. M. Baskin, editors. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, UK.
- McPherson, G. R. 1992. Ecology of oak woodlands in Arizona. Pages 24–33 in P. F. Ffoliott, G. J. Gottfried, D. A. Bennett, V. M. Hernandez C., A. Ortega-Rubio, and R. H. Hamre, technical coordinators. Ecology and management of oak and associated woodlands: perspectives in the southwestern United States and northern Mexico. U.S. Forest Service General Technical Report **RM-218**.
- McPherson, G. R. 1993. Effects of herbivory and herbs on oak establishment in a semi-arid temperate savanna. *Journal of Vegetation Science* **4**:687–692.
- McPherson, G. R. 1997. Ecology and management of North American savannas. University of Arizona Press, Tucson, Arizona, USA.
- McPherson, G. R., T. W. Boutton, and A. J. Midwood. 1993. Stable carbon isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in southeastern Arizona, USA. *Oecologia* **93**:95–101.
- McPherson, G. R., and H. A. Wright. 1990. Establishment of *Juniperus pinchotii* in western Texas: environmental effects. *Journal of Arid Environments* **19**:283–287.
- Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore III, C. J. Vorosmarty, and A. L. Schloss. 1993. Global climate change and terrestrial net primary production. *Nature* **363**:234–240.
- Mitchell, J. F. B., S. Manabe, V. Meleshko, and T. Tokioka. 1990. Equilibrium climate change and its implications for the future. Pages 131–172 in J. T. Houghton, G. J. Jenkins, and J. J. Ephraums, editors. Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge, UK.
- Mitchell, J. F. B., and D. A. Warrilow. 1987. Summer dryness in northern latitudes due to increased CO₂. *Nature* **330**:238–240.
- National Oceanic and Atmospheric Administration. 1996. Climatological data annual summary: Arizona. Department of Commerce, Asheville, North Carolina, USA.
- Neilson, R. P. 1986. High-resolution climatic analysis and southwest biogeography. *Science* **232**:27–34.
- Neilson, R. P. 1993. Transient ecotone response to climatic change: some conceptual and modeling approaches. *Ecological Applications* **3**:385–395.
- Neilson, R. P., and R. J. Drapek. 1998. Potentially complex biosphere responses to transient global warming. *Global Change Biology* **4**:505–521.
- Neilson, R. P., G. A. King, and G. Koerper. 1992. Toward a rule-based biome model. *Landscape Ecology* **7**:27–43.
- Neilson, R. P., and L. H. Wullstein. 1983. Biogeography of

- two southwest American oaks in relation to atmospheric dynamics. *Journal of Biogeography* **10**:275–297.
- Nelson, E. W. 1934. The influence of grazing and precipitation upon black grama grass range. USDA Technical Bulletin 409.
- Nicks, A. D., and L. J. Lane. 1989. Weather generator. Pages 2.1–2.19 in L. J. Lane and M. A. Nearing, editors. USDA—Water erosion prediction project: hillslope profile model documentation. NSERL Report No. 2, USDA-ARS National Soil Erosion Research Laboratory, West Lafayette, Indiana, USA.
- Nyandiga, C. O., and G. R. McPherson. 1992. Germination of two warm-temperate oaks, *Quercus emoryi* and *Quercus arizonica*. *Canadian Journal of Forest Research* **22**:1395–1401.
- O'Connor, T. G. 1995. *Acacia karoo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* **103**:214–223.
- Pase, C. P. 1969. Survival of *Quercus turbinella* and *Quercus emoryi* in an Arizona chaparral community. *Southwestern Naturalist* **14**:149–156.
- Pastor, J., and W. M. Post. 1988. Response of northern forests to CO₂-induced climate change. *Nature* **334**:55–58.
- Pechanec, J. F., and G. D. Pickford. 1937. A weight estimate method for determination of range or pasture production. *Journal of the American Society of Agronomy* **29**:894–904.
- Peláez, D. V., R. A. Distel, R. M. Bóo, O. R. Elia, and M. D. Mayor. 1994. Water relations between shrubs and grasses in semi-arid Argentina. *Journal of Arid Environments* **27**:71–78.
- Peters, R. L. 1990. Effects of global warming on forests. *Forest Ecology and Management* **35**:13–33.
- Polley, H. W., H. B. Johnson, H. S. Mayeux, and C. R. Tischler. 1996. Are some of the recent changes in grassland communities a response to rising CO₂ concentrations? Pages 177–195 in C. Körner and F. A. Bazzaz, editors. Carbon dioxide, populations, and communities. Academic, San Diego, California, USA.
- Richardson, D. M., and W. J. Bond. 1991. Determinants of plant distribution: evidence from pine invasions. *American Naturalist* **137**:639–668.
- Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* **49**:101–110.
- Sanchini, P. J. 1981. Population structure and fecundity patterns in *Quercus emoryi* and *Quercus arizonica* in south-eastern Arizona. Dissertation. University of Colorado, Boulder, Colorado, USA.
- SAS Institute. 1989. SAS/STAT user's guide, version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.
- SAS Institute. 1996. SAS/STAT software: changes and enhancements through release 6. 11. SAS Institute, Cary, North Carolina, USA.
- Scheffé, H. 1953. A method of judging all contrasts in the analysis of variance. *Biometrika* **40**:87–104.
- Schlesinger, M. E., and J. F. B. Mitchell. 1987. Climate model simulations of the equilibrium climatic response to increased carbon dioxide. *Review of Geophysics* **25**:760–798.
- Schneider, S. H. 1993. Scenarios of global warming. Pages 9–23 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, Massachusetts, USA.
- Scholes, R. J., and S. R. Archer. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**:517–544.
- Schulze, E.-D., H. A. Mooney, O. E. Sala, E. Jobbagy, N. Buchmann, G. Bauer, J. Canadell, R. B. Jackson, J. Loreti, M. Oesterheld, and J. R. Ehleringer. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* **108**:503–511.
- Schupp, E. W. 1995. Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany* **82**:399–409.
- Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). *Biometrika* **52**:591–611.
- Skarpe, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science* **2**:565–572.
- Solomon, A. M. 1986. Transient response of forests to CO₂-induced climate change: simulation modeling experiments in eastern North America. *Oecologia* **68**:567–579.
- Stephenson, N. L. 1990. Climatic control of vegetation distribution: the role of the water balance. *American Naturalist* **135**:649–670.
- USDA. 1994. Soil survey of Fort Huachuca 1, Cochise County, Arizona. Prepared for the U.S. Department of the Army. USDA Soil Conservation Service, Washington, D.C., USA.
- Vegetation/Ecosystem Modeling and Analysis Project Members. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochemical Cycles* **9**:407–437.
- von Ende, C. N. 1993. Pages 113–137 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- Walker, B. H. 1996. Predicting a future terrestrial biosphere: challenges to GCTE science. Pages 595–607 in B. Walker and W. Steffen. Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, UK.
- Walter, H. 1954. Die verbuschung, eine erscheinung der subtropischen savannengebiete, und ihre ökologischen ursachen. *Vegetatio* **5**/ **6**:6–10.
- Walter, H. 1979. Vegetation of the earth and ecological systems of the geo-biosphere. Springer-Verlag, New York, New York, USA.
- Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *American Naturalist* **125**:769–787.
- Weaver, J. E., and F. E. Clements. 1929. Plant ecology. McGraw-Hill, New York, New York, USA.
- Weltzin, J. F., S. Archer, and R. K. Heitschmidt. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* **78**:751–763.
- Weltzin, J. F., and G. R. McPherson. 1995. Potential effects of climate change on lower treelines in the southwestern United States. Pages 180–193 in L. F. DeBano, G. J. Gottfried, R. H. Hamre, C. B. Edminster, P. F. Ffolliott, and A. Ortega-Rubio, technical coordinators. Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and Northwestern Mexico. USDA Forest Service General Technical Report **RM-264**.
- Weltzin, J. F., and G. R. McPherson. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* **112**:156–164.
- Weltzin, J. F., and G. R. McPherson. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecological Monographs* **69**:513–534.
- Whittaker, R. H. 1975. Communities and ecosystems. Second edition. Macmillan, New York, New York, USA.

- Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* **23**:263–336.
- Woodward, F. I. 1992. A review of the effects of climate on vegetation: ranges, competition, and composition. Pages 105–123 in R. L. Peters and T. E. Lovejoy, editors. *Global warming and biological diversity*. Yale University Press, New Haven, Connecticut, USA.
- Woodward, F. I., and S. E. Lee. 1995. Global scale forest function and distribution. *Forestry* **68**:317–325.
- Zar, J. H. 1996. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, New Jersey, USA.

APPENDIX

The experimental system for capturing and redistributing precipitation at the woodland–grassland ecotone in southeastern Arizona is shown in the photograph below (Fig. A1). A color version is also available in digital form from ESA's Electronic Data Archive: *Ecological Archives* E081-020.



FIG. A1. Experimental system for capturing and redistributing precipitation at the woodland/grassland ecotone in southeastern Arizona. Precipitation shelters (16×4 m; $n = 4$) were covered with clear polyethylene film to exclude ambient precipitation from experimental plots. Gutters routed ambient precipitation to storage tanks. Collected precipitation was applied to plots according to a protocol designed to simulate natural precipitation patterns. Each shelter contained five 1.2×1.5 m plots arranged linearly 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 and soil in each plot were left intact.