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## Shrub establishment under experimental global changes in a California grassland

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### Abstract

Accelerating invasion of grasslands by woody species is a widespread global phenomenon. The native shrub *Baccharis pilularis* has recently increased in abundance in some California grasslands, with large local community and ecosystem effects. I investigated potential contributions of (1) future global climate and atmospheric changes and (2) variation in moisture and nutrient availability to increased *Baccharis* germination and early establishment rates. I examined responses of *Baccharis* seeds and seedlings to simulated warming (+1–2 °C) and elevated CO<sub>2</sub> (+300 ppm) in a 2-year field experiment. Warming and CO<sub>2</sub> treatments were applied at ambient and increased water and nitrogen levels chosen to simulate future increases in precipitation (+50%) and N deposition (+7 gN m<sup>-2</sup> y<sup>-1</sup>). Elevated CO<sub>2</sub> and water addition each increased or accelerated germination. Herbivory strongly reduced seedling populations during the winter wet season; drought further reduced seedling survival in the spring. Overall *Baccharis* survivorship was extremely low (<0.1%) across all treatments, complicating the interpretation of global change effects.

### Introduction

Changes in plant species composition have strong potential to influence ecosystem responses to climate and atmospheric changes. Multi-year experiments in a wide range of plant community types have reported shifts in plant species composition in response to future levels of elevated CO<sub>2</sub> and warming (Chapin et al. 1995; Harte and Shaw 1995; Grime et al. 2000) as well as N deposition and increased precipitation (Nie et al. 1992; Robinson et al. 1998; Reich et al. 2001). Ecosystem components such as soil carbon pools, litter chemistry, and decomposition rates show mixed responsiveness to simulated warming and elevated CO<sub>2</sub>, responding little in some cases (Norby et al.

2001; Hungate et al. 1997; Dukes and Field 2000) and significantly in others (Franck et al. 1996; Hobbie 1996; Hungate et al. 1996). However, these ecosystem responses consistently depend on plant species composition.

Global change-driven shifts from herbaceous to woody vegetation have particular potential to affect ecosystem function (Joffre and Rambal 1993; Asner et al. 1998; Paruelo et al. 1998) and have already been linked to changes in biogeochemistry (Belsky et al. 1989; Schlesinger et al. 1990; Guenther et al. 1999). Woody and herbaceous vegetation differ markedly in traits that influence ecosystem function, including lifespan, phenology, structural complexity, tissue chemistry, rooting depth and distribution, and biomass allocation

(Diaz and Cabido 1997). Invasion of grasslands by woody species is a widespread global phenomenon that has accelerated greatly in the last century (Polley et al. 1996). While vegetation shifts in some regions followed changes in fire management (Bragg and Hulbert 1976) or grazing (Archer 1994), others appear to have been influenced by changes in climate or atmospheric CO<sub>2</sub> (Nielson 1986; Williams et al. 1987; Polley et al. 1996; Brown et al. 1997). Previous findings suggest that warming, elevated CO<sub>2</sub>, and precipitation changes can drive shifts from herbaceous to woody vegetation in savanna (Polley et al. 1994), annual grassland (Williams and Hobbs 1989), alpine meadow (Harte and Shaw 1995), and tundra (Chapin et al. 1995). Woody invasions of herb-dominated systems are therefore useful model systems for experimental study of the links between vegetation shifts and ecosystem response to climate and atmospheric changes.

The native shrub *Baccharis pilularis* var. *consanguinea* has increased in abundance in some California grasslands in the last century (McBride and Heady 1968). However, its establishment is episodic and strongly dependent on resource availability (Williams and Hobbs 1989). *Baccharis* is highly sensitive at the establishment stage to inter-annual variation in moisture availability (Williams and Hobbs 1989), which is often affected by elevated CO<sub>2</sub> (Owensby et al. 1993; Field et al. 1997; Fredeen et al. 1997) and likely to be affected by climate change (IPCC 2001). *Baccharis* establishment also depends on competition from herbaceous vegetation (DaSilva and Bartolome 1984; Williams and Hobbs 1989), which is responsive to elevated CO<sub>2</sub> (Owensby et al. 1993), nitrogen deposition (Tilman 1987), and climate changes (Chapin and Shaver 1996; Shaw et al. 2002). Once established, *Baccharis* resists drought, herbivory, fire and competition from herbs (Hobbs and Mooney 1986; Martinez and Fuentes 1993). Its spread is therefore not easily reversed (McBride 1974). Global change effects on *Baccharis* demography from germination through establishment will therefore likely have lasting and significant impacts on both community composition and ecosystem function.

In this paper, I report the effects of simulated future warming, elevated CO<sub>2</sub>, nitrogen deposition, and precipitation changes on the early (first growing season) emergence and demography of a grassland-colonizing shrub, *Baccharis pilularis* var. *consan-*

*guinea* [(DC.) Kuntze]. To examine the interacting effects of these four global change factors, I made use of the Jasper Ridge Global Change Experiment (JRGCE), a long-term collaborative project in coastal California (Shaw et al. 2002). I also took advantage of nitrogen and water treatments to investigate the roles of resource limitation in mediating warming and CO<sub>2</sub> effects on *Baccharis* demography. I did this in two ways. First, I used *Baccharis* responses to water and nitrogen additions to test the hypothesis that elevated CO<sub>2</sub> and warming effects on species responses are simply mediated by changes in the availability of these key, limiting resources. Second, I examined the influences of water and nitrogen additions on the magnitude of elevated CO<sub>2</sub> and warming effects on *Baccharis* demography. This allowed me to address whether varying resource availability can alter the responses of species to global changes.

## Methods

### *Experimental design and site*

This study was conducted in annual grassland at Stanford University's Jasper Ridge Biological Preserve in the interior foothills of the central coast range south of San Francisco, California, USA. The study site has a Mediterranean-type climate with summer droughts typically extending from April to October and winter rains typically extending from November to March. Water limitation is severe in the summer and is important both in the fall, during germination, and in the spring, when peak growth rates and reproduction are occurring.

The JRGCE, a long-term study of grassland responses to climate and atmospheric changes, was initiated in fall 1997. Eight replicate blocks, each containing four circular plots 2 m in diameter, were established at an annual-dominated grassland site that has remained undisturbed for >25 years. Within each block, each of the four plots was randomly assigned to one of the following primary treatments: control, elevated CO<sub>2</sub>, warming, and elevated CO<sub>2</sub> + warming. CO<sub>2</sub> was elevated to ambient + 350 ppm using mini-FACE technology (Miglietta et al. 1996), with a three-part ring of copper emitters ~20 cm high that fumigated plots continuously throughout the growing season (October–late June). Warming of 1–2 °C in the

plant canopy was applied with infrared overhead heat lamps equipped with reflector domes to even the distribution of heat over each plot. Control and single-factor plots were equipped with dummy heaters, emitter rings, or both. All plots were surrounded with fiberglass soil partitions extending from the surface to 50 cm depth to isolate the plot rhizosphere from surrounding vegetation.

Each circular plot was additionally divided with 50 cm-deep soil partitions into four quadrants, each of which was randomly assigned one of the following soil resource treatments: ambient, water addition, nitrogen addition, and water + nitrogen addition. Partitions extended 2–3 cm above the soil surface to prevent surface flow of water across quadrants. Significant soil moisture differences between watered and unwatered quadrants, but not between unwatered and procedural control quadrants (see below), indicate that the soil partitions effectively isolated watered and unwatered quadrants from each other (Zavaleta 2001). Watered plots received 50% (1998–1999, Year 1) more than ambient rainfall delivered by drip tubes (Year 1) or overhead sprinklers (1999–2000, Year 2) within 2 days after each natural rain event in both years. Watered quadrants also received water 10 and 20 days after the last rains of the year each spring to simulate delayed onset of seasonal drought. Nitrogen addition quadrants received a total of 7 gN m<sup>-2</sup> yr<sup>-1</sup>, divided into a liquid Ca(NO<sub>3</sub>)<sub>2</sub> pulse with the first fall rains and a time-release pellet application (Osmocote) in January of each year. The level of nitrogen addition was chosen to simulate widespread anthropogenic nitrogen deposition (Townsend et al. 1996).

In four of the eight blocks, an additional procedural control plot was established that lacked the apparatus and modifications of the other 32 plots. To protect the plots from damage, the entire experiment was surrounded with a fence to exclude deer, and smaller mammals including gophers, ground squirrels, and rabbits were trapped and removed from inside the fence. CO<sub>2</sub> and warming treatments were turned on in November 1998 at the onset of the Year 1 growing season.

#### *Environmental variables*

Total live aboveground biomass (herbaceous vegetation) and surface litter biomass were measured

by harvesting a 141 cm<sup>2</sup> area of each quadrant (> 10 cm from any *Baccharis* seedling) to the soil surface, sorting litter from live material, drying for 72 h at 60 °C, and weighing. Aboveground biomass was harvested on 3–5 May, 1999 and 17–20 April, 2000, during peak annual biomass. To quantify light availability to the *Baccharis* seedlings, percent transmission of photosynthetically active radiation (PAR) at 2 cm above the soil surface was measured on 29 April, 2000, the period of peak canopy biomass (E. Levy, unpublished data). Air temperature and precipitation were continuously monitored throughout the study period at a location < 200 m from the experimental site (Jasper Ridge Biological Preserve, unpublished data). Soil moisture at 0–15, 15–30, and 30–45 cm depth intervals was measured biweekly to semiweekly throughout the 2-year study period using time domain reflectometry (TDR) (Topp et al. 1980).

#### *Baccharis demography*

Individuals of the shrub *Baccharis pilularis* var. *consanguinea* were introduced into all 136 quadrants of the Global Change Experiment in both years. In Year 1, individual, greenhouse-reared seedlings (height < 0.5 cm) were transplanted by block into five locations in each of the study quadrants from 27 January to 12 February, 1999 (totaling 680 transplants). Nearly all seedlings were consumed by slugs (Gastropoda: Pulmonata), so new transplants were placed at each transplant location between 17 February and 4 March, 1999. A small number of quadrants were replanted twice rather than once because they were entirely cleared by slugs a second time while I was still replanting the site. Each transplant was surrounded by a 2 cm section of copper tubing 2.5 cm in diameter, which was secured in the soil to reduce slug herbivory. Because treatment differences in slug herbivory bias the mean transplant dates for each treatment, data on the later demography of the shrubs in Year 1 must be viewed with caution. Data on Year 1 transplants were collected until all of the seedlings died or were consumed.

In Year 2, *Baccharis* seeds were sown directly into the study plots. During December 1–6, 1999 and proceeding by block, 23 ± 1 seeds were placed into each of the five locations in each quadrant (totaling ~15,640 seeds). In Year 2, germination percentages

were recorded for each quadrant on 29 December, and 10, 19, and 26 January, after which little additional germination occurred. Early establishment was defined as survival into the first-year drought, past the date when global change treatments were terminated for the summer in early July.

Herbivory was monitored at least once per week in both years by recording the number of *Baccharis* locations in each quadrant cleared by herbivores. In Year 1, herbivores consumed most (93%) of the *Baccharis* seedlings in the first 2 months of the study. Results for Year 1 are therefore expressed as the number of days elapsed before 50% of the seedlings in a quadrant were killed by herbivores. Herbivory in Year 2 was much lower and rarely achieved 50% mortality in a quadrant. Herbivory results for Year 2 are therefore expressed as the proportion of seedlings cleared by herbivores in each quadrant. In both years, seedlings generally were either consumed entirely or left intact. This may have reflected the extremely small size of seedlings throughout the growing season and the relatively large size of the dominant gastropod herbivores. All reported herbivory is therefore complete consumption of seedlings.

In both years, seedling survival was monitored during the seasonal drought onset, which begins with the end of the last winter rains in late March and culminates in the senescence of the dominant annual vegetation by mid-June.

To quantify treatment effects on aboveground seedling growth, I measured seedling height, leaf number, and area of largest leaf on each surviving seedling on May 20, 2000. Total leaf area was estimated as the area of the largest leaf on the plant \* (1 + 0.5(total number of leaves - 1)), based on the observation that the largest leaf on a plant was typically ca. double the length of other leaves. For analysis, mean values of each growth measure across all surviving seedlings in a given quadrant were used. Measures of seedling size taken in May 1999 are not reported because they are biased by the large variation in transplant and re-transplant dates among seedlings.

### Analysis

Where data did not meet model assumptions, data were transformed using  $X' = \log_{10}(X+1)$ . When transformation did not improve data fit to model

assumptions, untransformed data were analyzed using a General Linear Model (GLM) and the results compared to those of a nonparametric Kruskal–Wallis test with rank transformation (Zar 1996). Where nonparametric and parametric results are consistent, GLM results are reported; otherwise, nonparametric results are reported.

Precipitation and N deposition effects were analyzed from data from control (unwarmed, ambient CO<sub>2</sub>) plots using GLM in Systat 9.0 with water and N as fixed factors, an interaction term, and plot as a random factor. To test for CO<sub>2</sub> and warming effects, GLM was applied to data from the 32 ambient water and N quadrants with CO<sub>2</sub> and warming as fixed factors, an interaction term, and block as a random factor. This model was then run for each of the three remaining combinations of water and N levels (+water, +N, and +both). For germination and survival, a repeated-measures ANOVA was used with Huynh–Feldt  $\epsilon$ -corrected  $p$ -values reported (vonEnde 2001). *Post hoc* ANOVA tests for individual dates were performed when repeated-measures analysis yielded significant treatment effects.

Survival was expressed as the proportion of seedling locations occupied out of the total number occupied on the first day of drought onset, in late March. Occasional values >1 occurred when late germinants appeared after the beginning of drought onset. Establishment results were first analyzed for CO<sub>2</sub> and warming effects with whole-plot  $\chi^2$  tests for presence of survivors on 7/5/00.  $\chi^2$  tests were then used to compare additional effects of water and nitrogen within the eight plots successfully colonized by *Baccharis*.

Effects on seedling size were estimated with MANOVA including height, leaf number, and total leaf area. Where multivariate results are significant (using Wilks'  $\lambda$ ), univariate ANOVAs were performed for each size response variables and Bonferroni corrected (Scheiner 2001). Two-way Kolmogorov–Smirnov goodness of fit tests and Pearson correlation were used to examine the relationship between PAR on 29 April 2000, survival on 30 April, 2000 and establishment as of 5 July, 2000. The linear regression subroutine of Systat 9.0 was used to test the relationship between live biomass and light transmission. Nonparametric Kruskal–Wallis tests were used to test for relationships between successful establishment and soil moisture, live canopy biomass, litter biomass,

and seedling size. All values reported in text are mean  $\pm$  1 SD.

## Results

### *Environmental variables*

Fall maximum temperatures (September 15 to December 31) were lower in Year 1 than in Year 2. Precipitation in each of the two study seasons was similar, at 766 mm and 721 mm for Year 1 and Year 2, respectively. May–June soil moisture, however, was 4–5% lower in 1999 than in 2000, reflecting an end to spring rains in early April, 1999, as compared to in mid-June, 2000 (Zavaleta 2001) (Figure 1). Fall rain events were also larger and more frequent in 1998 than in 1999. Mid-winter droughts longer than 3 weeks occurred in both study years in late December–January. Soil moisture on June 30, 2000 in the quadrants still containing live seedlings did not differ significantly from that in quadrants without survivors ( $21.6 \pm 4.57\%$  vs.  $19.0 \pm 3.52\%$ ).

Neither litter biomass nor live aboveground biomass was related to *Baccharis* survival at the time of peak grassland biomass in late April or at the end of treatments in early July. Aboveground biomass was strongly negatively related to % PAR transmission (linear regression  $t = -3.02$ ,  $p = 0.003$ ,  $n = 128$ ,  $R^2_{\text{adj}} = 0.06$ ). *Baccharis* seedling survival on 4/30/00, the time of peak aboveground canopy biomass, was slightly positively related to % PAR transmission (Bartlett  $\chi^2 = 2.92$ ,  $p = 0.088$ ).

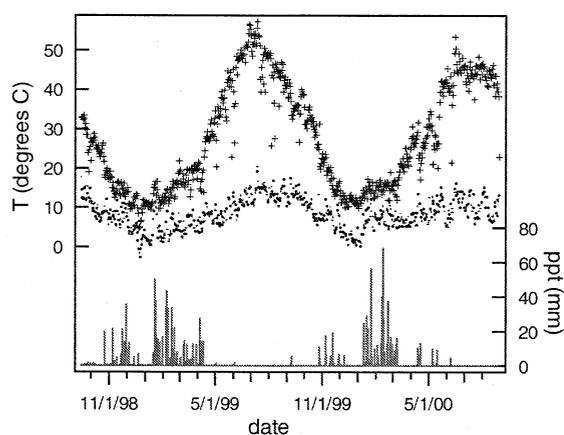


Figure 1. Precipitation events (lines to bottom axis) and maximum (+) and minimum (●) daily temperatures at the study site, 1998–2000.

### *Baccharis demography*

In Year 2, nearly all *Baccharis* germination occurred before 26 January, 2000. By that date,  $76 \pm 21\%$  of the individual sowed locations in each quadrant (5 per quadrant) contained at least one germinant (mean  $2.5 \pm 1.7$ ). All 136 quadrants in the experiment had at least one successful germinant. Added water (at ambient warming,  $\text{CO}_2$ ) increased the number of locations that contained early germinants (*post hoc* ANOVA for 28 December:  $n = 16$ ,  $F = 7.74$ ,  $p = 0.01$ ; Figure 2). Elevated  $\text{CO}_2$  increased early or overall germination under most soil resource conditions, while warming had little effect (Figure 3).

Herbivory was the dominant source of seedling mortality until late March in both years and killed 93% of transplanted seedlings in Year 1. Slugs (Gastropoda: Pulmonata) were the most frequently observed herbivores on *Baccharis* seedlings. Warming, water and N additions did not affect the rate of herbivory in either year. In Year 1, elevated  $\text{CO}_2$  reduced herbivory at ambient soil resource levels ( $n = 16$ ,  $F = 6.73$ ,  $p = 0.015$ ) and with added water ( $F = 7.41$ ,  $p = 0.011$ ) (Figure 4a). In Year 2, elevated  $\text{CO}_2$  reduced total herbivory under N addition ( $n = 16$ ,  $F = 6.69$ ,  $p = 0.015$ ) (Figure 4b). Elevated  $\text{CO}_2$  therefore reduced herbivory in both years; but it did so mainly in unfertilized quadrants in Year 1 and only in fertilized quadrants in Year 2.

Soil moisture declined rapidly from late March to June in both years, affecting survival (Zavaleta et al. 2003). While herbivory continued to be an occasional source of mortality in the spring of both years, most mortality appeared to result from water stress (wilting and desiccated, unconsumed seedlings). In Year 1, during the moisture-limited period of drought onset ( $p > 0.15$ ), 100% mortality occurred most quickly under N addition ( $p > 0.15$ ; Figure 5a). In Year 2, added N decreased survival throughout the spring ( $n = 14$ ,  $F = 7.56$ ,  $p = 0.011$ ; Figure 5b). Surprisingly, added water did not affect spring seedling survival in either year. Elevated  $\text{CO}_2$  and warming also had little overall effect on spring seedling survival, with the exception that elevated  $\text{CO}_2$  in conjunction with added water enhanced seedling survival in May–June of Year 1 ( $n = 13$ ,  $F_{\text{CO}_2} = 8.08$ ,  $p_{\text{CO}_2} = 0.009$ ;  $F_{\text{date} \times \text{CO}_2} = 4.79$ ,  $p_{\text{date} \times \text{CO}_2} = 0.001$ ).

In Year 2, by the time seedlings grew large enough to measure their size accurately, there were

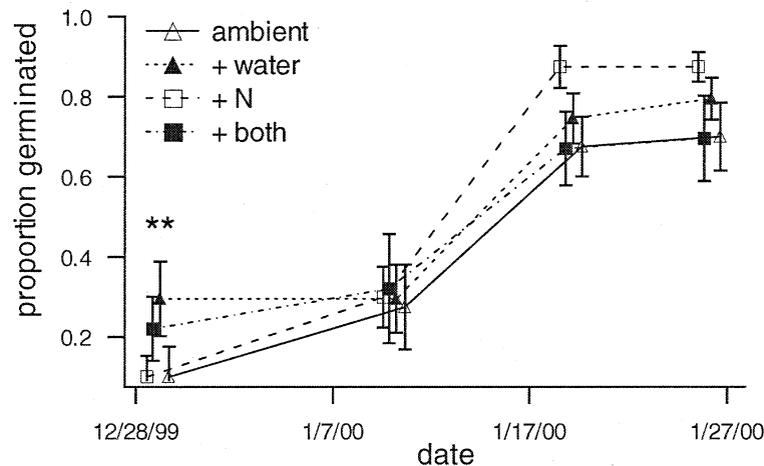


Figure 2. Effects of increased precipitation and N deposition on the proportion of locations containing one or more germinated *Baccharis*. Error bars are  $\pm 1$  SE. Measurements taken on the same date are offset for clarity. Significant differences in germination percentages between watered and unwatered quadrants are shown for  $p \leq 0.01$  as \*\* ( $n=8$ , post hoc ANOVA).

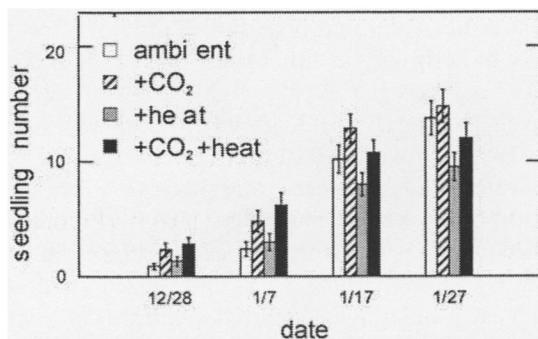


Figure 3. Effects of elevated CO<sub>2</sub> and warming on *Baccharis* germination in 2000. Significant differences in germination rate between ambient and elevated CO<sub>2</sub> occurred under certain soil resource conditions: Low N, water:  $F=5.78$ ,  $p=0.023$ ; +N:  $F=4.064$ ,  $p=0.044$ ; +water: NS; +N+water:  $F=5.950$ ,  $p=0.022$ .

no seedlings in +N quadrants. Seedlings were smaller in watered quadrants ( $n=8$ ,  $F=26.1$ ,  $p=0.012$ ) mainly through height reduced from  $1.2 \pm 0.17$  to  $0.60 \pm 0.27$  cm ( $F=10.5$ ,  $p_{\text{corr}}=0.069$ ). Across water levels, plots with elevated CO<sub>2</sub> tended to contain larger seedlings and warmed plots contained smaller seedlings (Table 1).

No early establishment occurring in Year 1, as all seedlings perished before July. When warming and CO<sub>2</sub> treatments were ended for the summer in Year 2 (on July 5), eight of 32 study plots contained at least one healthy, surviving seedling (Figure 6). All eight were warmed plots (8/8 plots,

$\chi^2=10.67$ ,  $p=0.001$ ), and seven of these eight survivors or clusters of survivors occurring in watered quadrants of the warmed plots (7/8 quadrants,  $\chi^2=4.50$ ,  $p<0.05$ ). Larger size benefited early establishment; the eight seedlings that had established as of July had higher mean total leaf area on May 20, 2000 than all other seedlings still alive on that date ( $n=39$ , Mann-Whitney  $U=67.5$ ,  $\chi^2 \sim 3.864$ ,  $p=0.049$ ) and greater total leaf area (Mann-Whitney  $U=13.5$ ,  $\chi^2 \sim 8.424$ ,  $p=0.004$ ), more leaves (Mann-Whitney  $U=16.5$ ,  $\chi^2 \sim 7.492$ ,  $p=0.006$ ), and slightly greater height (Mann-Whitney  $U=32.5$ ,  $\chi^2 \sim 2.608$ ,  $p=0.106$ ) than all other seedlings in warmed plots that did not survive to July ( $n=22$ ). The eight shrubs surviving to July also tended to germinate earlier than other seedlings did; half of the eight surviving in July had germinated by the first survey date (29 December 1999), vs. 26.6% of those that did not survive to July.

## Discussion

*Baccharis* establishment in the 2 years of my study was an extremely rare demographic event, with only eight out of nearly 20,000 planted seeds and seedlings surviving their first growing season. Previous studies indicate that *Baccharis* recruitment is episodic, occurring only in unusually warm, wet years (Williams et al. 1987; Williams

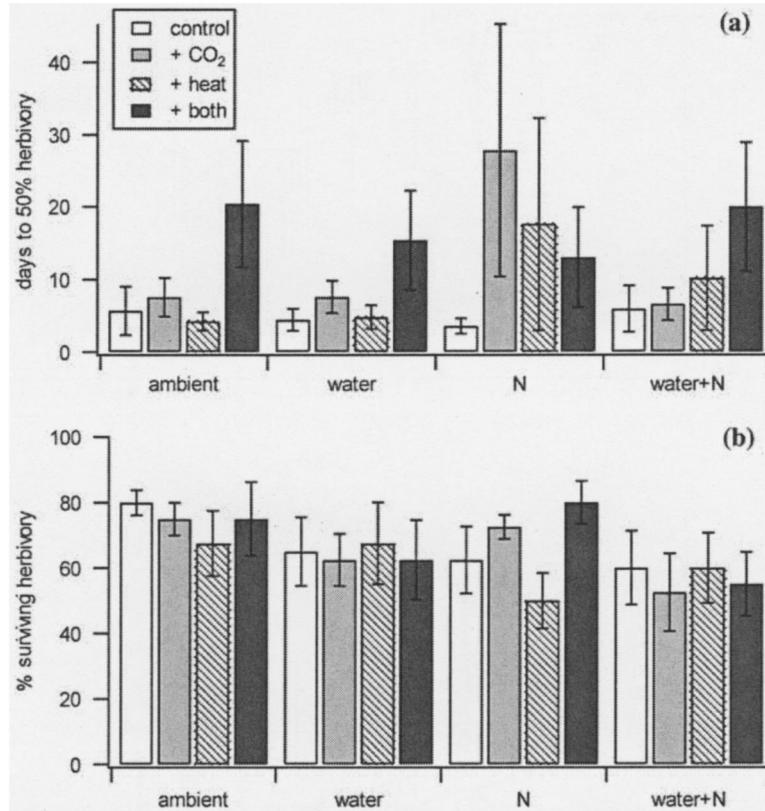


Figure 4. Treatment effects on herbivory rates in (a) 1998–1999, when nearly all (93%) seedlings were consumed and herbivory rate is expressed as number of days to 50% mortality by herbivores; and (b) 1999–2000, for which herbivory rate is expressed as the total percentage of seedlings surviving herbivory in each quadrant ( $n = 8$  for each of the four soil resource treatments). Error bars are  $\pm 1$  SE.

and Hobbs 1989). *Baccharis*' nearly complete failure to establish across all of our treatments indicates that either our modest enhancements of moisture and temperature were insufficient to overcome unfavorable ambient conditions in both years, or our seeding numbers were insufficient to overcome generally high herbivory and low germination and survival rates in the species.

The marked increase in germination and decline in herbivory under elevated CO<sub>2</sub> indicates a potential pathway to greater shrub recruitment under future climate and atmospheric conditions. Additional studies would be needed to evaluate whether these early-stage benefits of elevated CO<sub>2</sub> would translate into increased *Baccharis* establishment during an episodic recruitment year, such as during an El Niño-Southern Oscillation event (Williams and Hobbs 1989). Elevated CO<sub>2</sub> effects could also depend on the degree of soil resource limitation at a site, because, in this study, CO<sub>2</sub>

effects varied across soil moisture and N treatments. The scant *Baccharis* establishment that did occur in our plots suggests that warming and increased moisture availability also have the potential to increase early establishment under certain conditions.

Conditions that enhance germination, growth, and early survival of seedlings could reasonably be expected to also enhance establishment. As a group, the successfully established shrubs germinated earlier and grew more rapidly aboveground than failed shrubs. However, water and warming, the treatments associated with early establishment in Year 2, had at best mixed effects on emergence and earlier demographic stages. Added water increased early germination, but what little effect warming had on germination occurred only in the absence of added water rather than when both treatments were applied together. Neither warming nor water addition enhanced resistance to herbiv-

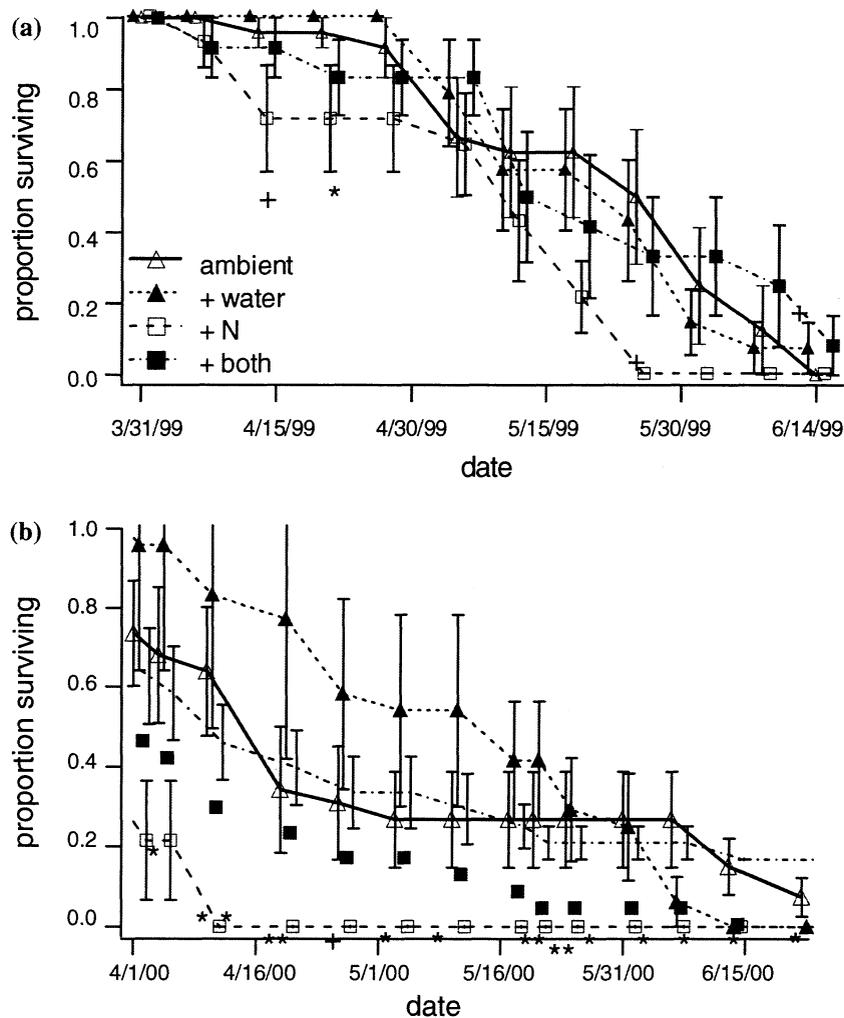


Figure 5. The effects of water and N additions on *Baccharis* survival during the period of seasonal drought onset in (a) 1998–1999 ( $n=7$ ) and (b) 1999–2000 ( $n=7$ ), at ambient  $\text{CO}_2$  and temperature levels. Measurements taken on the same date are offset for clarity. Significant differences in survival rate between ambient and elevated soil resource treatments are shown for  $p < 0.1$ , 0.05, and 0.01 as +, \*, and \*\*, respectively. Symbols below bars indicate an effect of N; symbols above bars indicate an effect of water. Error bars are  $\pm 1$  SE.

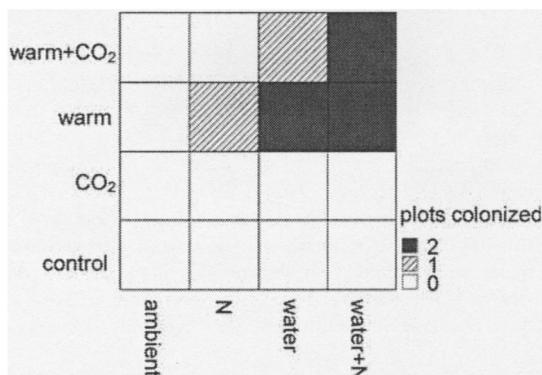
ory, drought-onset survival, or growth. Warming and water addition treatments actually contained smaller seedlings than the control treatment, though this might have reflected delayed mortality of small seedlings under these treatments rather than suppression of growth. Conditions seedlings faced in late spring and early summer therefore overwhelmed modest changes in winter and early spring performance. In particular, the positive effect of water addition on *Baccharis* establishment but not on March–June seedling survival indicates that water limitation may have become an important determinant of survival only very late in the

drought onset period, after soil moisture levels had neared their summer minima.

The results of this study suggest a model of shifting constraints on recruitment during the spring and early summer. Previous studies have shown that reduced herbaceous biomass and corresponding increases in light availability benefit *Baccharis* (DaSilva and Bartolome 1984; Williams and Hobbs 1989) as well as other shrubs (Knoop and Walker 1985; Brown and Archer 1989; Eliason and Allen 1994) in grasslands. Other studies make clear that drought-season moisture availability is a key controller of recruitment of *Baccharis* (Williams

Table 1. Treatment effects on *Baccharis* seedling size, May, 2000 (Year 2).

Treatment	Resource levels	<i>N</i>	<i>F</i>	<i>p</i>	Nature of effect
Elevated CO <sub>2</sub>	Ambient	6	3.94	0.039	Weak shift in allocation from stems to leaves (NS)
	+N	0			
	+Water	6	11.58	0.011	Total leaf area increased from 0.24 ± 0.072 to 0.70 ± 0.12 cm <sup>2</sup> ( <i>F</i> = 10.278, <i>p</i> <sub>corr</sub> = 0.045)
	+Both	0			
Elevated warming	Ambient	8	6.90	0.007	Leaf number reduced from 5.0 ± 0.36 to 2.5 ± 0.38 ( <i>F</i> = 24.00, <i>p</i> <sub>corr</sub> < 0.001), height from 1.0 ± 0.11 to 0.58 ± 0.11 cm ( <i>F</i> = 8.651, <i>p</i> <sub>corr</sub> = 0.033), total leaf area from 0.35 ± 0.06 to 0.11 ± 0.07 ( <i>F</i> = 7.37, <i>p</i> <sub>corr</sub> = 0.054)
	+N	0			
	+Water	5	8.42	0.021	Total leaf area reduced from 0.74 ± 0.12 to 0.19 ± 0.080 cm <sup>2</sup> ( <i>F</i> = 13.15, <i>p</i> <sub>corr</sub> = 0.024)
	+Both	0			

Figure 6. Number of plots in which *Baccharis* successfully established in each of the 16 treatment combinations (*n* = 8 quadrants per treatment).

et al. 1987; Williams and Hobbs 1989) as well as other woody species in California grasslands (Gordon et al. 1989). This study indicates that low germination rates and high susceptibility to herbivory also strongly limit *Baccharis* recruitment. The findings reported here suggest that germination and herbivory rates are responsive to resource conditions – notably, CO<sub>2</sub> concentrations – and that future shifts in resource availability could affect *Baccharis* through effects on germination and herbivory as well as on light and moisture availability.

The results of this study, while brief in duration, are consistent with past speculation that climate change and elevated CO<sub>2</sub> could underlie some of the

recent acceleration of woody invasion. The mechanisms underlying woody invasion in this ecosystem, however, are varied and should be applied cautiously to other systems. Longer-term investigation of climate and atmospheric CO<sub>2</sub> effects on the demography of woody plants in herb-dominated ecosystems will help clarify whether these global changes have influenced and will continue to affect the composition of grassland-woodland systems. The findings reported here, produced under conservative temperature and CO<sub>2</sub> treatments, underscore the need to study the implications of global change-accelerated shifts in successional trajectories and vegetation type at larger spatial and longer temporal scales.

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