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REGULAR ARTICLE

How do elevated [CO_2], warming, and reduced precipitation interact to affect soil moisture and LAI in an old field ecosystem?

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Abstract Soil moisture content and leaf area index (LAI) are properties that will be particularly important in mediating whole system responses to the combined effects of elevated atmospheric [CO_2], warming and altered precipitation. Warming and drying will likely reduce soil moisture, and this effect may be exacerbated when these factors are combined. However, elevated [CO_2] may increase soil moisture contents and when combined with warming and drying may partially compensate for their effects. The response of LAI to elevated [CO_2] and warming will be closely tied to soil moisture status and may mitigate or exacerbate the effects of global change on soil moisture. Using open-top chambers (4-m diameter), the interactive effects of elevated [CO_2], warming, and differential irrigation on soil moisture availability were examined in the OCCAM (Old-Field Community Climate and Atmospheric Manipulation) experiment at Oak Ridge National Laboratory in eastern Tennessee. Warming consistently reduced soil moisture contents and this effect was exacerbated by reduced irrigation. However, elevated [CO_2] mitigated the effects of warming and drying on soil moisture. LAI was determined using an AccuPAR ceptometer and both the leaf area duration (LAD) and canopy size were increased by irrigation and elevated [CO_2]. Changes in LAI were closely linked to soil moisture status. The climate of the southeastern United States is predicted to be warmer and drier in the future, and this research suggests that although elevated [CO_2] will ameliorate the effects of warming and drying, losses of soil moisture will cause declines in the LAI of old field ecosystems in the future.

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Introduction

Increased global CO_2 concentrations, warming and reduced water inputs are some of the most important aspects of global change currently affecting ecosystems (Hanson et al. 2005; Norby and Luo 2004; Prather et al. 2001). While much progress has been made on understanding how elevated atmospheric [CO_2], warming and reduced precipitation alter ecosystems when applied in isolation, much less is known about how interactions between these factors will affect plants, communities and ultimately ecosystem functioning (Dermody 2006; Hanson et al. 2005; Shaw et al. 2002). The response of ecosystems to elevated atmospheric [CO_2], warming and altered precipitation will be mediated in part by spatial and temporal variation in soil moisture, but predicting how soil water contents will respond to interacting global change factors is difficult (Dermody 2006; Emmett et al. 2004; Norby and Luo 2004). Warming reduces soil moisture primarily by increasing evaporation, and this will be exacerbated when combined with lower precipitation inputs (Diffenbaugh 2005; English et al. 2005; Norby and Luo 2004). By reducing stomatal conductance and transpiration at the stand level, elevated [CO_2] has the opposite effect (Ainsworth and Rogers 2007; Drake et al. 1997; Hsieh et al. 2005; Nowak et al. 2004). However, it is not clear whether elevated [CO_2] will mitigate some of the effects of warming and drying (Ainsworth and Rogers 2007; Carter et al. 1997; Tschaplinski et al. 1995) or if the effects of drying and warming on soil moisture content will be stronger than those of elevated [CO_2] (Diffenbaugh 2005; Fuhrer 2003).

The plant canopy is the interface for the physiological and physical processes that control energy and water exchange between the atmosphere and terrestrial biosphere. Changes in the size of the canopy are often closely linked to soil moisture content (Murthy et al. 2005). For example, limited soil moisture often leads to decreased maximum LAI and earlier senescence (Harper et al. 2005; Wand et al. 1999). Although evapotranspiration may be reduced, such declines in LAI may actually exacerbate soil moisture losses, because of increased heat load and evaporation at the soil surface (Obrist et al. 2003; Wan et al. 2002). In elevated [CO_2], lower light compensation point, delayed senescence and increased number and size of leaves may all contribute to increased LAI (Dermody et al. 2006; Ferris et al. 2001; Hirose et al. 1996; Pearcy 1983). The responses of LAI will in turn affect soil moisture contents e.g. greater LAI in elevated [CO_2] may increase the surface for evapotranspiration (Phillips et al. 2006); alternatively, losses of soil moisture in warm and dry conditions may be slowed if declines in LAI also occur (Wan et al. 2002; Zavaleta et al. 2003). Knowing how LAI will respond and feedback to alter soil moisture contents when elevated [CO_2] and warming are combined with reduced precipitation, is crucial to model future ecosystem productivity (Cowling and Field 2003; Ewert 2004; Filella et al. 2004).

To determine how elevated [CO_2], warming and altered precipitation may interact to affect soil moisture content and LAI of ecosystems in the future, we placed open top chambers (OTCs) and rainout shelters over constructed, replicate old-field communities in eastern Tennessee, USA. The old-field ecosystem was chosen as a model system because of its stature, diversity and growth rate; old-fields, which encompass about 50,000 km^2 of the continental United States are also a dominant early successional ecosystem that represent a potentially significant pool for carbon storage (Caspersen et al. 2000; Schimel et al. 2001). We expected interactive effects to be important in driving the response of soil moisture and LAI to elevated [CO_2], warming and reduced water inputs in this system. Specifically, we expected that soil moisture content would decline in warm conditions, and that interactions between warming and drying would exacerbate losses of soil moisture, relative to warming alone. Because growth in elevated [CO_2] generally leads to reduced stomatal conductance (Ainsworth and Rogers 2007), we expected that soil moisture contents in this system would be greater in elevated [CO_2] and the effects of warming and drying on soil moisture would be partially mitigated when combined with elevated [CO_2]. We expected the responses of LAI to elevated [CO_2], warming and altered precipitation to be tightly linked to those of soil moisture. Specifically, we predicted that high soil moisture contents and elevated [CO_2] conditions would lead to the greatest values of LAI. We also expected that the duration of the canopy (leaf area duration, LAD) and thus the season long capacity for carbon gain to be greatest in well watered and elevated [CO_2] conditions.

Materials and methods

Site description

Research was conducted at the Old field Community, Climatic and Atmospheric Manipulation (OCCAM) experimental site at Oak Ridge National Laboratory (ORNL), Environmental Research Park in Oak Ridge, Tennessee (35° 54′ N; 84° 21′ W). At this site, precipitation is evenly distributed throughout the year with an annual mean of 1,322 mm; the mean July maximum temperature is 31.2°C and the mean January minimum temperature is −2.7°C. The soil is derived from floodplain alluvium, and is classified as Captina silt loam fine-silty, siliceous, mesic typic fragiudult, well drained, and is slightly acidic (Norby et al. 1997).

Experimental design and setup

Construction of plots was initiated in early summer 2002, when existing vegetation within each plot was killed with an application of glyphosate herbicide (Roundup (R) herbicide, Monsanto Company, Marysville, OH, 43041, mixed with water to manufacturer's specifications). To create a split-plot for the water treatment, each plot was trenched to a depth of 75 cm around its perimeter and along its diameter in a north–south direction. To minimize lateral flow of sub-surface water and heat into and out of the plot, trenches were lined with 4-mil polyvinyl chloride (PVC) film, insulating foam panels, and were backfilled with packed soil. Field soil within each trenched plot was otherwise left intact to maintain soil structure. Plots were planted with seven plant species common to old-field communities in the southeastern United States: *Andropogon virginicus* L., a C_4 grass, the C_3 grasses *Dactylis glomerata* L. and *Festuca pretense* L., the nitrogen-fixing legumes *Lespedeza cuneata* (Dum. Cours.) G. Don and *Trifolium pratense* L., and the herbaceous dicots *Plantago lanceolata* L., a weak biennial at this site, and the perennial *Solidago canadensis* L. The initial planting density was approximately 31 plants/m^2.

Open-top chambers were constructed of aluminum frames (4 m diameter, 2.2 m height) covered with clear PVC panels; the double-walled panel on the lower half of each OTC was perforated on the inner wall with 2.5 cm holes, through which air of the appropriate temperature and [CO_2] flowed (Norby et al. 1997). Chambers were equipped with evaporative coolers coupled to in-line heating coils to maintain desired temperatures. Temperature and [CO_2] control was achieved through a modification of methods described in Norby et al. (1997). The chamber material reduced PAR by approximately 30% (C. Campany pers. comm.). Rainout shelters over each OTC measured 6 m×5 m and were constructed of 6-mil PVC film stretched over 9 cm width, pressed steel greenhouse bows affixed to a steel frame, the shelters ranged in height from 2.2 m at their lowest point to approximately 3.3 m at their peak.

Warming and [CO_2] treatments were initiated in April 2003 and maintained 24 h d^{-1} throughout the year. Whole-plots received ambient and elevated [CO_2] (ambient + 300 ppm), and ambient and elevated temperatures (ambient + 3°C). Each whole-plot was split along its diameter into two 6.3 m^2 experimental units; each experimental unit, or plot, was assigned to one of two soil moisture treatments ('wet,' 'dry') created by differential irrigation. Each 6.3 m^2 plot represented a unique soil moisture, [CO_2], and warming treatment within one of three blocks that were located to account for potential variations in environmental conditions across the field site (n=3).

Mean air temperatures between 1st May 2004 and 30th September 2004 and for the same period in 2005, were 21.7±0.2 and 21.3±0.2°C in ambient temperature chambers and 24.5±0.2 and 23.5±0.2°C in warmed chambers. The difference between chamber air temperature and outside air temperature averaged 0.55±0.23 and 3.20±0.21°C in ambient and warmed chambers, respectively. The hourly-averaged temperature differentials were within 0.5°C of the mean, 74% of the time in ambient temperature chambers and 89% of the time in warmed chambers. The concentration of CO_2 within the chambers during daylight hours averaged 396±3 ppm in ambient [CO_2] chambers and 696±10.0 ppm in elevated [CO_2] chambers. The standard deviations represent the variation across the six chambers within a [CO_2] treatment; the standard deviations of the hourly observations over 2 years were 29 and 72 ppm in ambient and elevated [CO_2] chambers, respectively.

Irrigation treatments were initiated in June 2003 and were based on long-term mean weekly precipitation records from the Oak Ridge weather station, modified by ±50% to create ‘wet’ and ‘dry’ irrigation treatments. During the 2003 growing season, VWC at all soil depths differed little between wet and dry treatments; therefore, in September 2003, we modified our irrigation protocol to include weekly additions of 2 mm (dry) and 25 mm (wet) rainwater. Irrigation was performed with rainwater collected at the site in 10,000 liter tanks and applied to all plots using metered hoses and handheld sprinklers.

Measurement of soil moisture content

We used time domain reflectometry (TDR) to monitor soil volumetric water content (VWC) at six locations within each plot. Two probes with 15 cm long tines were installed vertically at the soil surface; these represent the integrated value of VWC from 0 to 15 cm. Two probes were also installed horizontally, each at depths of 30 and 55 cm along the outer perimeter of each plot. Soil VWC was recorded weekly during the growing season (i.e., March–October), and twice a month during the non-growing

Table 1 The effect of elevated [CO_2], warming and watering on soil moisture content expressed as soil volumetric water content (VWC) of an old-field mixed species community in the 2004 and 2005 water years (October–September)

Year	Effect	0–15 cm		30 cm		55 cm	
		F-stat	*P*	*F*-stat	*P*	*F*-stat	*P*
2004	[CO_2]	2.29	0.18	2.95	0.14	0.58	0.47
	warming	17.70	**0.01**	57.54	**≤0.0003**	8.00	**0.03**
	water	360.19	**≤0.0001**	49.41	**≤0.0001**	7.16	**0.01**
	date	112.39	**≤0.0001**	136.55	**≤0.0001**	104.90	**≤0.0001**
	[CO_2] × warming	0.15	0.71	0.23	0.65	0.36	0.57
	[CO_2] × water	1.44	0.23	0.17	0.68	3.31	**0.07**
	warming × water	3.09	**0.08**	21.88	**≤0.0001**	1.15	0.28
	[CO_2] × warming × water	5.01	**0.03**	4.10	**0.04**	1.48	0.22
	[CO_2] × date	1.70	**0.07**	0.24	0.99	0.85	0.59
	warming × date	1.14	0.33	4.49	**≤0.0001**	5.17	**≤0.0001**
	[CO_2] × warming × date	0.28	0.99	0.56	0.86	0.46	0.93
	water × date	3.54	**≤0.0001**	5.04	**≤0.0001**	1.68	**0.07**
	[CO_2] × water × date	0.16	1.00	0.12	1.00	0.18	1.00
	warming × water × date	0.79	0.65	1.07	0.39	0.58	0.84
	[CO_2] × warming × water × date	0.46	0.93	0.09	1.00	0.08	1.00
2005	[CO_2]	4.34	**0.08**	5.04	**0.07**	5.98	**0.05**
	warming	15.59	**0.01**	40.93	**≤0.0007**	17.71	**0.01**
	water	172.40	**≤0.0001**	28.25	**≤0.0001**	4.36	**0.04**
	date	140.22	**≤0.0001**	210.85	**≤0.0001**	152.97	**≤0.0001**
	[CO_2] × warming	0.02	0.88	0.62	0.46	0.03	0.87
	[CO_2] × water	1.39	0.24	0.00	0.96	1.43	0.23
	warming × water	1.41	0.24	42.62	**≤0.0001**	6.01	**0.01**
	[CO_2] × warming × water	0.06	0.81	1.49	0.22	0.00	0.98
	[CO_2] × date	0.86	0.59	1.16	0.31	1.29	0.22
	warming × date	1.51	0.12	2.36	**0.01**	3.71	**≤0.0001**
	[CO_2] × warming × date	1.80	**0.05**	0.63	0.82	0.71	0.74
	water × date	3.44	**≤0.0001**	4.81	**≤0.0001**	3.22	**≤0.0001**
	[CO_2] × water × date	0.15	1.00	0.36	0.98	0.81	0.64
	warming × water × date	1.17	0.30	1.30	0.21	1.41	0.16
	[CO_2] × warming × water × date	0.44	0.95	0.31	0.99	0.20	1.00

Each effect in the mixed model is shown with the corresponding *F*-statistic and *P*-value calculated from the repeated measures ANOVA (n=3). $P \leq 0.1$ are in bold text.

season (i.e., November–February). VWC data were averaged to obtain monthly mean soil VWC at each depth in each experimental plot. To obtain an estimate of the duration and amount of soil moisture from 0 to 15 cm, the area under the VWC plots was integrated to obtain VWCD (VWC duration), this is analogous to the leaf area duration (LAD).

Soil water recharge was defined as the increase in plot VWC between October and December, and drawdown was defined as the decrease in soil VWC between March and May. The rate of each of these processes was calculated as the slope of the decline between March and May (drawdown) or increase between October and December (recharge) in soil VWC.

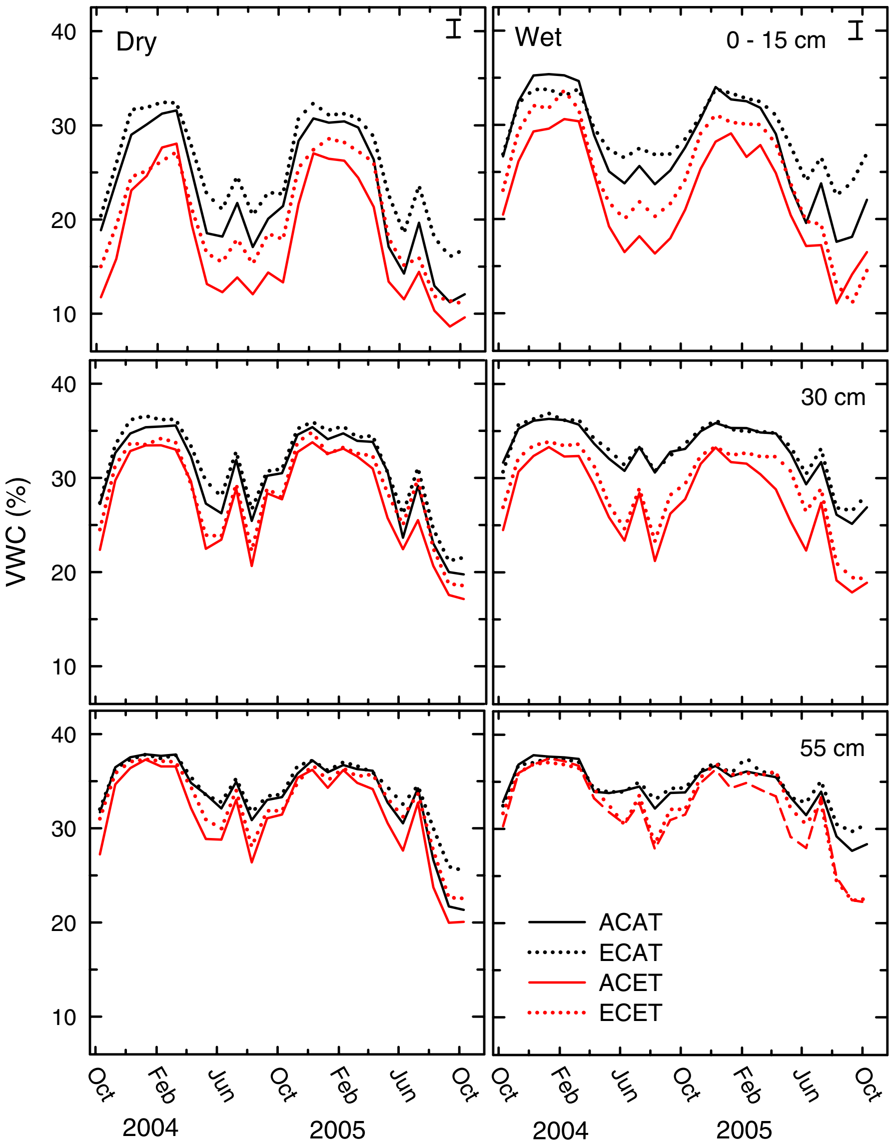


Fig. 1 The effect of elevated [CO_2], warming and watering on soil moisture content expressed as volumetric water content (VWC) of an old field mixed species community The three panels on the left side represent the dry plots and the three on the right represent the wet plots. The panels are arranged according to soil depth, with the top row corresponding to 0–15 cm and the second and third rows to 30 and 55 cm below the surface, respectively. Measurements span the 2004 and 2005 water years (October–September). Each point represents the least squared mean, the corresponding standard error calculated from the repeated measures ANOVA is represented by a bar in the upper right hand corner of the top two panels

Measurement of leaf area index

LAI was measured monthly (in October 2003, between March and October 2004, and between March and November 2005) using an AccuPAR line-integrating ceptometer (Decagon Devices Ltd, USA). The AccuPAR calculates LAI from measurements of intercepted photosynthetically active radiation. All measurements were performed within one hour of solar noon. In 2003 and 2004, we sub-sampled LAI at six locations within each plot on each sample date; in 2005, we reduced the number of sub-samples to four per plot. Leaf area duration (LAD) is a parameter that integrates both the duration and the size of the canopy; LAD was calculated for each experimental plot and for each year (2004,

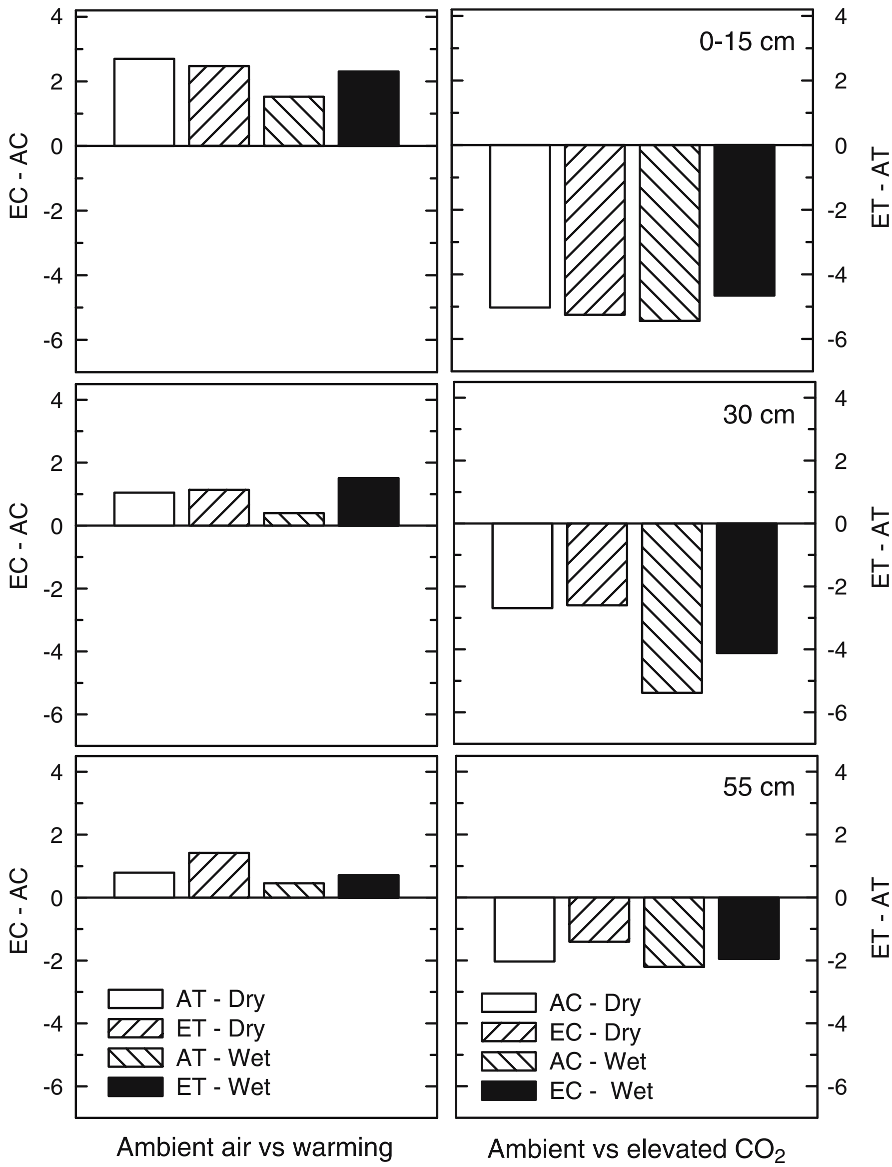


Fig. 2 The effect of elevated [CO_2], warming and watering on soil moisture content. The panels on the left represent the difference in soil VWC between ambient [CO_2] and elevated [CO_2] (EC-AC) and the difference between ambient and warmed conditions are represented (ET-AT) in the panels on the right. The panels are arranged according to soil depth, with the top row corresponding to 0–15 cm and the second and third rows to 30 and 55 cm below the surface, respectively. Measurements span the 2004 and 2005 water years (October–September)

2005), as the area under the LAI curve, using the trapezoidal rule (SigmaPlot Version 10, Systat Software Inc., Point Richmond, CA, USA).

Statistical analysis

Repeated measures analysis of variance (PROC MIXED; SAS, The SAS Institute; Version 8.1, Cary, NC.) was used to test for treatment effects on soil moisture content and LAI. The effects of elevated [CO_2], warming and water on LAD were analyzed in a mixed model ANOVA. All analyses were conducted on the plot means. The levels of [CO_2], warming and water treatment were fixed effects, and blocks and the interaction between blocks, [CO_2] and warming were included as random effects. A block was defined as one full replicate of a unique water, [CO_2], and warming treatment (n=3). Post hoc linear contrasts were performed to elucidate treatment effects within interaction terms. Analyses were separated according to water year (October–September). To determine whether elevated [CO_2], warming and reduced precipitation affected the rate of soil moisture drawdown and recharge, the slopes of the decline in soil moisture content between March and May (drawdown) or the increase in soil moisture content between October and December (recharge) were compared. To determine if LAI was dependent on VWC across the year, linear correlations between LAD and VWCD were performed in SigmaPlot. Least squared means are presented in all figures and tables and the associated variances are the standard errors from mixed model ANOVAs. Differences between treatments were considered significant at $p \leq 0.1$.

Results

Soil moisture content

Interactions between the effects of elevated [CO_2], reduced precipitation and atmospheric warming were important in determining soil moisture contents in 2004 and 2005, although the magnitude diminished with depth, and varied with time, (Table 1, Fig. 1). The effects of warming and drying both alone and in combination led to consistently low soil moisture, whereas the greatest soil moisture contents were measured in elevated [CO_2], wet and unwarmed plots (Table 1, Figs. 1 and 2). There was a consistent trend towards greater soil moisture content in elevated [CO_2] plots relative to those in ambient air (Fig. 1), although this was not statistically significant. In 2004, elevated [CO_2] significantly reduced

Table 2 The effect of elevated [CO_2], warming and watering on canopy size expressed as leaf area index (LAI) of an old field mixed species community

Effect	2004		2005	
	F-stat	P	F-stat	P
[CO_2]	12.82	**0.01**	0.01	0.91
warming	1.11	0.33	0.01	0.92
water	79.02	**≤0.0001**	59.33	**≤0.0001**
date	92.55	**≤0.0001**	250.46	**≤0.0001**
[CO_2] × warming	5.11	**0.06**	1.31	0.29
[CO_2] × water	5.00	**0.03**	0.06	0.79
warming × water	0.68	0.41	10.01	**0.0016**
[CO_2] × warming × water	1.01	0.32	0.54	0.46
[CO_2] × date	1.25	0.28	5.35	**≤0.0001**
warming × date	5.82	**≤0.0001**	1.55	0.17
[CO_2] × warming × date	2.12	**0.05**	1.16	0.32
water × date	3.96	**≤0.0001**	1.73	**0.12**
[CO_2] × water × date	0.85	0.53	0.47	0.79
warming × water × date	0.47	0.83	4.8	**≤0.0003**
[CO_2] × warming × water × date	1.05	0.39	1.38	0.22

Each effect in the mixed model is shown with the corresponding F-statistic and P-value (n=3) calculated from the repeated measures ANOVA. Effects significant at the $P \leq 0.1$ level are bolded the effects of warming and drying on soil moisture content (Table 1, Fig. 1). However, when averaged across the year, the effects of warming on soil moisture were generally stronger than those of elevated [CO_2] (Figs. 1 and 2).

Soil moisture drawdown and recharge

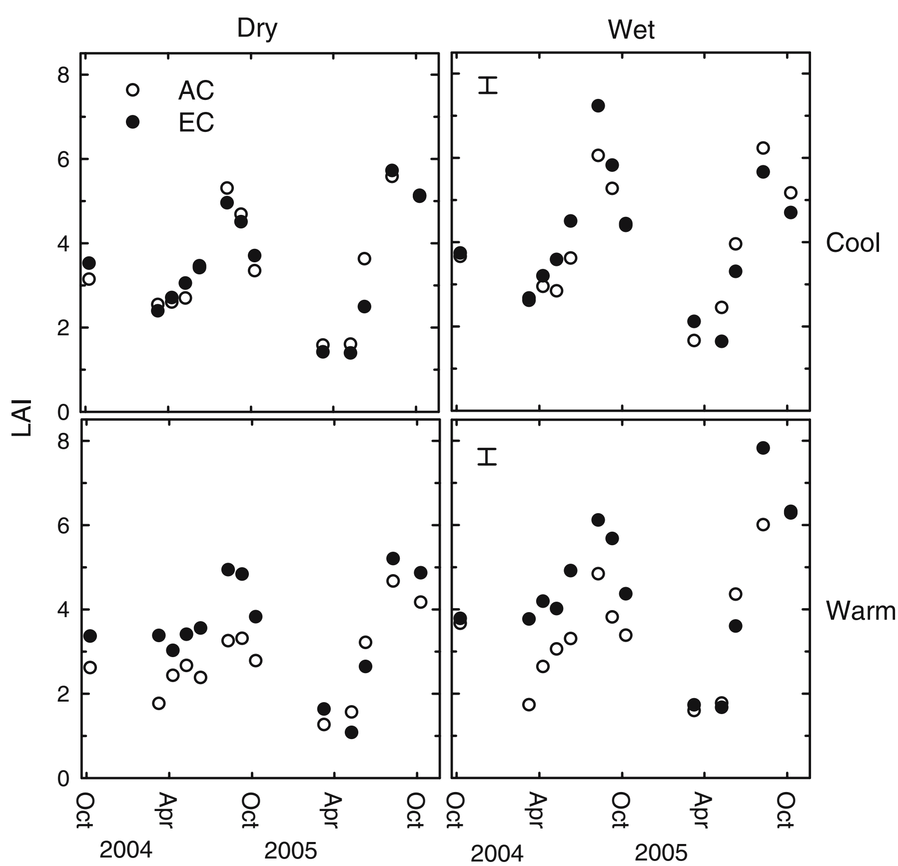
Although elevated [CO_2], warming and water were important in driving the rate of soil moisture drawdown and recharge in the Spring and Fall, no interactions between the treatments were detected (Fig. 1; e.g. in 2003, 0–15 cm, Oct–Dec. [CO_2] × warming × water, F-stat=1.33, $P\leq0.26$, n=3). Elevated [CO_2] reduced the rate of soil moisture drawdown (e.g. 2005, 0–15 cm, F-stat=10.9, $P\leq$ 0.01, n=3), whereas warming (e.g., 2005, 0–15 cm, F-stat=8.4, $P\leq0.01$, n=3) and drying (e.g. 2005, F-stat=13.8, $P\leq0.001$, n=3) had the opposite effect.

Although elevated CO_2 played a part in increasing VWC, these effects did not alter the rates of soil moisture recharge in the fall (e.g. 2004, 0–15 cm, F-stat=1.3, $P\leq0.35$, n=3). Warming also had no effect on the rate of soil moisture recharge between 0 and 15 cm (e.g. 2004, 0–15 cm, F-stat=2.5, $P\leq0.17$, n=3). However, drying increased the rate of recharge in both years (e.g. 2004, 0–15 cm, F-stat=22.2, $P\leq$ 0.001, n=3).

Leaf area index

Interactions between water and [CO_2] in 2004, and water and warming in 2005, were important in driving variation in LAI (Table 2, Fig. 3). Watering consistently increased LAI and the greatest LAI values were measured in wet and elevated [CO_2] plots, whereas the lowest LAI was measured in the dry and warm plots (Fig. 3). Not unexpectedly, the strength of these interactions varied with time, and the responses of LAI to water, warming and elevated [CO_2] varied both across the growing season and between 2004 and 2005 (Fig. 3, Table 2).

Fig. 3 Leaf area index (LAI) for an old field mixed species community. Dry plots are on the left hand side and wet plots are on the right hand side. The top row corresponds to the plots at ambient temperatures while the warmed plots are in the bottom panels. Measurements span the 2004 and 2005 water years (October–September). Each point represents the least squared mean ± standard error (n=3) calculated from the repeated measures ANOVA



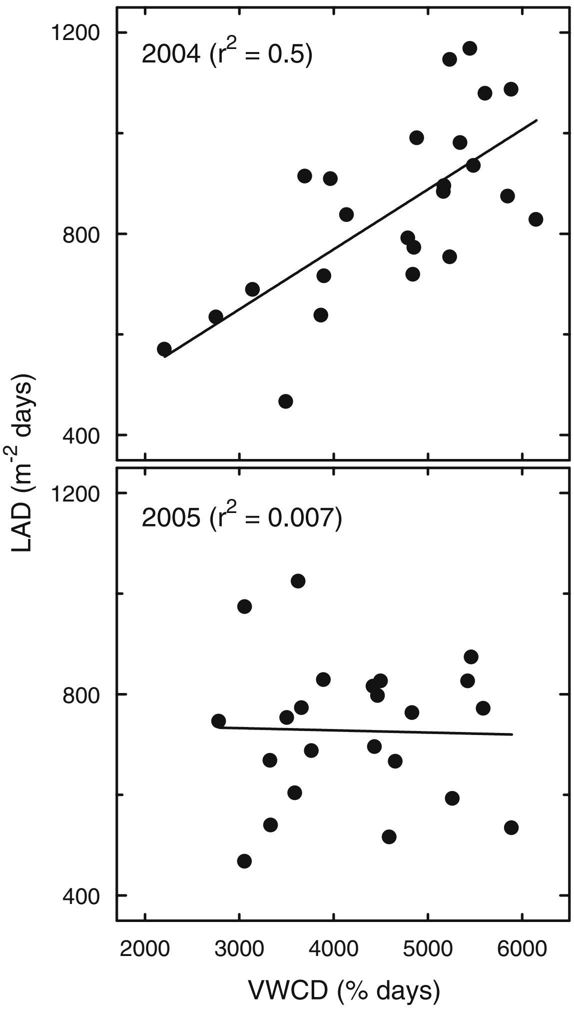


Fig. 4 Leaf area duration (LAD) versus volumetric water content duration (VWCD) for an old field mixed species community. Dry plots are on the left hand side and wet plots are on the right hand side. Measurements span the 2004 and 2005 water years (October–September). The points are not separated by treatment and each point represents the LAD and VWCD for a single experimental unit

Leaf area duration and VWC duration

There was a strong relationship between LAD and VWCD in 2004 (Fig. 4). However, this response was not detected in 2005. Elevated [CO_2] tended to increase LAD [CO_2] (ambient [CO_2]: 743±21 m^{-2} days; elevated [CO_2]: 823±21 m^{-2} days, *F*-stat=−3.4, $P \leq 0.009$, n=3) and drying reduced it (wet: 865±21 m^{-2} days; dry: 700±21 m^{-2} days, *F*-stat=−5.2, $P \leq 0.001$, n=3). There was a trend towards greater VWCD in elevated [CO_2] however, this effect was not significant (ambient [CO_2]: 5,072±303 days; elevated [CO_2]: 5,440±303% days, *F*-stat=2.1, $P \leq 0.15$, n=3). Warming reduced VWCD (warmed: 4,455±273% days; ambient temperature: 5,559±273% days, *F*-stat=15, $P \leq 0.004$, n=3) and drying had a similar effect (wet: 5,443±253% days; dry: 4,571±253% days, *F*-stat=21, $P \leq 0.001$, n=3).

Interactions between the treatments were important in determining the LAD and the difference in LAD between ambient and elevated [CO_2] was greater in warmed plots than in ambient temperature plots (LAD, ambient air and warm, 676±21 m^{-2} days, elevated CO_2 and warm, 845±21 m^{-2} days, *F*-stat=−4, $P \leq$ 0.0001, n=3). Interactions between the treatments were not important in determining the VWCD.

Discussion

The interactive effects of elevated [CO_2], warming and reduced irrigation on soil moisture and LAI were complex, however, some consistent patterns emerged. Warming and drying reduced soil moisture, and interactions between these factors exacerbated their individual effects. However, declines in soil moisture in warm and dry conditions were mitigated by elevated [CO_2]. While other factors were likely important, the response of LAI to warming and elevated [CO_2] closely corresponded to changes in soil moisture content. Community level LAI was consistently low in warm and dry plots, however, in 2004, elevated [CO_2] more than compensated for the effects of warming and drying when these factors were combined. Although the effect varied between years, elevated [CO_2] and irrigation increased both LAI and LAD. The strongest effects of elevated [CO_2] and warming on soil moisture occurred during the growing season, suggesting that physiological (transpiration) processes played a large role in driving ecosystem response to elevated [CO_2] and warming.

In 2004, when warming and drying were combined with elevated [CO_2] their effects on soil moisture were reduced. Stomatal conductance was measured on all species in 2004, and it was consistently lower on plants grown in elevated [CO_2] relative to ambient air (L.A. Souza, pers. comm.), this likely helped to mitigate the effects of warming and drying on soil moisture. While lower stomatal conductance is a common plant response to elevated [CO_2] (Ainsworth and Rogers 2007; Drake et al. 1997; Wand et al.

1999), subsequent increases in soil moisture content under elevated [CO_2] are rarer (Richter and Semenov 2005; Savabi and Stockle 2001). Previous research has shown that interactions between atmospheric warming and reduced irrigation are especially detrimental to soil water contents (Emmett et al. 2004; Filella et al. 2004; Richter and Semenov 2005); however, we extend these results by highlighting that expected reductions in transpiration will not compensate for soil moisture loss when warming and drying are combined with elevated [CO_2].

It is likely that elevated [CO_2] warming and drying impacted soil moisture drawdown and recharge primarily through their effects on evapotranspiration. Lower stomatal conductance in plants grown in elevated [CO_2] (L.A. Souza, pers. comm.), may have caused slower drawdown of soil moisture in the spring. Warming and drying had the opposite effect and not unexpectedly these factors increased the rate of soil moisture drawdown (Emmett et al. 2004; Mohseni and Stefan 2001; Seneviratne et al. 2002). Measurements of canopy green-up, estimated using normalized difference vegetation index (NDVI) did not reveal any effects of elevated [CO_2], warming or drying on early season community phenology (E.C. Engel, unpublished data) which also supports a critical role for evapotranspiration in driving changes in soil moisture.

Although not evident in 2005, elevated [CO_2] increased LAI, and fully mitigated the effects of warming and drying on canopy size in 2004. The inconsistent response of LAI to elevated [CO_2] may have been due in part to inter-annual variation in ambient temperatures. By suppressing photorespiration, elevated [CO_2] lowers the light compensation point (LCP) of photosynthesis, allowing leaves to maintain a positive carbon balance in deeper shade and thereby increasing LAI (Long and Drake 1991). The rate of photorespiration increases with temperature, and because air temperatures were higher in March to June 2004 than 2005, the positive effects of elevated [CO_2] on leaf level photosynthesis may have been more pronounced. In an agroecosystem, Dermody et al. (2006) found that increased maximum LAI in elevated [CO_2] was caused by a combination of greater leaf retention deep in the canopy and increased leaf size. Such mechanisms may also have been important here, but in more complex systems like old-fields, inter annual variation in species abundance and overall resource availability often prevent consistent increases in LAI under elevated [CO_2] (Hirose et al. 1996; Kammann et al. 2005).

In the future, global change may render ecosystems more sensitive to the effects of invasive species (Chornesky et al. 2005; Smith et al. 2000), and many invasive plant species already present in old-fields have the potential to dramatically alter biogeochemical cycling across large land areas (Ehrenfeld 2003; Strayer et al. 2006). The establishment and persistence of invasive plants in old-fields may be facilitated by features such as deep woody taproots, which confer a significant degree of drought tolerance (Blair and Fleer 2002). Here, we show how the interactive effects of atmospheric warming and lower precipitation led to decreased soil moisture content within 15 cm of the surface, even in association with elevated [CO_2]. However, deeper in the soil, the effects of warming and drying on soil moisture content were less. When surface moisture is depleted, deep-rooted exotic plants may have a significant competitive advantage over shallow rooted native grasses and forbs (Blair and Fleer 2002; DiTomaso et al. 2003) and such an advantage may facilitate their persistence in the warmer and drier conditions predicted for the future.

Ecosystems across the globe are already being exposed to altered atmospheric composition, reduced precipitation and temperature. This research shows that the effects of warming and drying on soil moisture content are magnified when they are applied simultaneously. Additionally, soil moisture losses in warmer and drier conditions were not completely compensated for by growth in elevated [CO_2]. The effects of global change on LAI will be determined by many interacting factors however, changes in soil moisture content will be particularly important and the corresponding effects on LAI may have significant impacts on material and energy exchange between the land surface and atmosphere (Cowling 1999; Gamon et al. 1995). By linking the results of empirical studies like this one into more theoretical experiments, it may be possible to predict how local changes may scale across landscape scales to dramatically alter energy exchange and biogeochemical cycling (Rowell and Jones 2006; Zeng et al. 2005).

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