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LEAF-LEVEL GAS EXCHANGE AND FOLIAR CHEMISTRY OF COMMON OLD-FIELD SPECIES RESPONDING TO WARMING AND PRECIPITATION TREATMENTS

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We investigated the shifts in plant carbon (C) and water dynamics by measuring rates of photosynthesis, transpiration, and instantaneous water use efficiency (WUE) in three common species of "old-field" plants—two C_3 forb species (*Plantago lanceolata* and *Taraxacum officinale*) and one C_3 grass species (*Elymus repens*)—under 12 experimentally altered temperature and precipitation regimes at the Boston Area Climate Experiment (BACE) in Waltham, Massachusetts. We also measured shifts in foliar C and nitrogen (N) content to determine possible changes in plant C/nutrient balance. We hypothesized that the warming treatment would cause an increase in photosynthesis rates, unless water was limiting; therefore, we expected an interactive effect of warming and precipitation treatments. We found that warming and drought reduced leaf-level photosynthesis most dramatically when environmental or seasonal conditions produced soils that were already dry. In general, the plants transpired fastest when soils were wet and slowest when soils were dry. Drought treatments increased WUE relative to plants in the ambient and wet treatments but only during the driest and warmest background conditions. Leaf N concentration increased with warming, thereby indicating that future warming may cause some plants to take up more soil N and/or allocate more N to their leaves, possibly as consequences of increased nutrient availability. There were no significant interactive effects of the warming and precipitation treatments together across all seasons, indicating that responses were not synergistic or ameliorative.

Keywords: climate change, photosynthesis, transpiration, foliar chemistry, warming, precipitation.

Online enhancements: appendix tables.

Introduction

A plant's abilities to gain carbon (C) via photosynthesis and regulate water loss via transpiration are highly dependent on and sensitive to temperature and precipitation conditions (Berry and Björkman 1980; Fay et al. 2002). Changes in air temperature, humidity, solar radiation, and soil moisture directly influence the stomatal opening of plants (Kozlowski et al. 1991) and therefore affect leaf-level C fixation and water use efficiency (WUE). C uptake by plants also depends on the utilization of nutrients, such as nitrogen (N), to support new plant growth. Both leaf gas exchange and foliar C:N ratio serve as indicators of plant physiological performance and stress (Fay et al. 2002).

Previous studies investigating how leaf-level gas exchange rates respond to changes in temperature have found both increases and decreases in plant photosynthetic rates and net primary productivity (NPP; Battaglia et al. 1996; Rustad et al. 2001; Nemani et al. 2003; Welker et al. 2004; Ciais et al. 2005; Wu et al. 2011). Even slight warming may cause some plant species to exceed their metabolic optima, reducing photosynthetic output and decreasing plant survival (Niu et al.

2006; Sage et al. 2008). Warming can also suppress photosynthetic rates as a result of warming-induced soil moisture stress (De Valpine and Harte 2001). However, some plants can acclimate to temperature changes by altering their physiology, thereby retaining similar or potentially even higher photosynthetic rates in warmer conditions (Mooney and West 1964; Strain et al. 1976; Berry and Björkman 1980; Säll and Pettersson 1994; Zhou et al. 2007; Gunderson et al. 2009).

During drought conditions, most temperate, herbaceous species are vulnerable to temporary reductions in C fixation due to stomatal closure (Ingram and Bartels 1996; Chaves and Oliveira 2004). The effects of precipitation changes on individual plant performance are complex and depend on a number of factors, such as ambient rainfall conditions, initial soil water status, occurrence and seasonality of extreme heat stress or droughts (De Boeck et al. 2011), plant age (Law et al. 2003), the ability of the plant to shed wilted leaves (Chaves et al. 2009), and the diversity of the surrounding plant community (Kahmen et al. 2005). Previous studies have found that the photosynthetic responses of grassland plants to rainfall manipulations simulating drought conditions have ranged from negative to neutral (reviewed in Fay et al. 2002). Interestingly, in a recent meta-analysis, increased precipitation was found to stimulate ecosystem-level photosynthesis (i.e., gross primary production) far more than

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decreased precipitation reduced photosynthesis (40% increase, compared to 9% reduction; Wu et al. 2011). During the European heat wave of 2003, low NPP was better correlated with altered rainfall patterns than changes in summer temperature, indicating a dominant role of water limitation in plant performance (Ciais et al. 2005).

To survive drought conditions, plants either tolerate partial desiccation or change physiologically to avoid it. Water stress causes most plants to reduce their water use (Blum 2005). Although plants could reduce water use simply by decreasing transpiration, such an adjustment could also decrease photosynthesis and growth. WUE, the ratio of C assimilation to water loss, is an important indicator of plant function under different climate regimes. Higher WUE does not simply equate to higher photosynthesis levels under water-stressed conditions, however, except in specialized dryland conditions (Condon et al. 2002).

Changes in temperature and precipitation regimes can also have indirect effects on plant C exchange by affecting rates of plant nutrient uptake, allocation of nutrients to leaf tissue, or the ratio of C to N in leaves (BassiriRad 2000; Reich and Oleksyn 2004). Temperature and precipitation directly influence the uptake of nutrients by roots. Therefore, a shift in leaf tissue chemistry is predicted to occur if photosynthetic C gain is restricted more or less than root N uptake or allocation. Interestingly, previous studies have found that warming can either increase (Nijs et al. 1996; Oleksyn et al. 2003) or decrease (Yin 1993; Reich and Oleksyn 2004) a plant species' foliar N concentration. Altered foliar N concentration can feed back to affect photosynthesis levels, herbivore forage quality, plant litter chemistry, and ultimately C and nutrient pathways and ecosystem processes (Shaver et al. 2001; Welker et al. 2005; Aerts et al. 2009).

Here, we tested responses of leaf physiology and leaf tissue stoichiometry to climate using three herbaceous plant species common to old fields of New England. We manipulated canopy temperature and precipitation and measured changes in photosynthetic rates, transpiration rates, instantaneous WUE, and leaf tissue C and N concentration in three dominant herbaceous plants: *Plantago lanceolata* (English plantain), *Taraxacum officinale* (common dandelion), and *Elymus repens* (quack grass). Specifically, we tested the following four hypotheses: (1) Leaf-level photosynthesis rates of all species will increase in response to the warming treatment, unless limited by water availability. Therefore, we expect an interactive effect of warming and precipitation on photosynthesis rates. (2) Plant transpiration rates will increase when soil moisture levels are high (ambient or wet conditions) and decrease when soil moisture levels are low (drought or warmed conditions). (3) Plants with a strategy of dehydration avoidance will increase their WUE in drought or warming conditions, whereas plants with a strategy of dehydration tolerance will not change their WUE in low soil moisture conditions. (4) Foliar C : N ratio will decrease with greater warming and increased precipitation treatments because of warming-induced increases in N availability.

Material and Methods

Experimental Design

The Boston Area Climate Experiment (BACE) is located in Waltham, Massachusetts, and was designed to expose an old-

field community to a factorial combination of different heating and precipitation treatments. The BACE employs a complete randomized block design with 12 different climate regimes, each replicated three times for a total of 36 plots (2 m × 2 m in size, with 1-m spacing between plots). The 12 climate conditions consist of four temperature treatments (ranging within the Intergovernmental Panel on Climate Change predictions for the year 2100), using ambient temperature, low warming (target of +1.0°C), medium warming (+2.7°C), and high warming (+4.0°C) treatments, crossed with three precipitation treatments, consisting of ambient rainfall, 50% reduced rainfall (drought), and 50% increased rainfall (wet). The entire experiment took place under open greenhouse frames, and precipitation treatments were achieved using a roof of evenly spaced, clear polycarbonate slats that collected half of the precipitation over the drought treatments (year-round) and immediately delivered it to the wet treatments via an overhead sprinkler system (May–November). Soil moisture is fully recharged to water holding capacity during the winter months in all plots (Hoeppner and Dukes 2012). In order to adjust for the ~5% reduction in photosynthetically active radiation (PAR) imposed by the polycarbonate slats, the ambient and wet sections of the greenhouse frames were covered by deer fencing, which provided an identical reduction in PAR.

Plots were arranged in a split-plot design with the precipitation treatment as the whole-plot factor and the temperature treatments as subplot factors nested within the precipitation treatment. Warming treatments were applied year-round with infrared heaters (e.g., Nextthermal FSR) that were mounted 1 m above each corner of every plot and that varied in wattage by treatment (200-, 600-, and 1000-W heaters for the low, medium, and high warming treatments, respectively). Canopy temperatures of all unwarmed and high warming plots were monitored every 10 s by infrared radiometers (IRR-PN; Apogee Instruments, Logan, UT), and power to all heaters for each group of warming plots within a precipitation zone was adjusted on the basis of the temperature difference between the unwarmed and high warming plots (with a target temperature increase of 4°C). Drought treatments began in spring 2007, wet treatments in June 2008, and warming treatments on July 1, 2008. The vegetation within and around the plots was clipped twice per growing season. The BACE site has a loam topsoil (0–30 cm) over a gravelly sandy loam subsoil. Hoeppner and Dukes (2012) provide further details on the BACE experimental design.

Species

We chose *Plantago lanceolata*, *Taraxacum officinale*, and *Elymus repens* for this study because they were the most ubiquitous herbaceous plants throughout all treatments in 2009. *Plantago lanceolata* is a winter-active perennial C_3 forb and has a mean rooting depth of 18 cm (Mommer et al. 2010), with most activity in the top 5 cm (Tsialtas et al. 2001), and it has a medium drought tolerance (USDA 2010). *Taraxacum officinale* is a perennial C_3 forb, and, similar to *P. lanceolata*, *T. officinale* has a medium drought tolerance (USDA 2010) but generally grows with a minimum rooting depth of 15 cm and most root activity at a depth of 10–15 cm (Tsialtas et al. 2001). *Elymus repens* is a perennial, rhizomatous C_3 grass, and, in contrast to *P. lanceolata* and *T. officinale*, *E. repens* is not classified as a stress-

tolerant species: it has a low drought tolerance and is considered to be shade intolerant (USDA 2010). *Elymus repens* also has a much deeper rooting depth, with a maximum rooting depth greater than 100 cm, although over 80% of the root mass is located at a depth of 0–30 cm (Crush et al. 2005).

Response Variables and Sampling

Ambient daily rainfall and air temperature measurements were collected at the weather station adjacent to the BACE site. The daily rainfall values were averaged across the week including the two consecutive sampling days. Air temperature was measured every 10 min from 1000 to 1500 hours and averaged across the two consecutive sampling days. Measurements of soil moisture (0–30-, 45-, and 60-cm depth) were taken weekly in each plot during the growing season using permanently installed time-domain reflectometry waveguides and a Campbell TDR-100 (Campbell Scientific, Logan, UT).

We measured plant photosynthesis and transpiration rates using two cross-calibrated Li-6400 infrared gas analyzers with 6-cm^2 clamp-on leaf cuvettes (LiCOR, Lincoln, NE). Measurements were taken on cloud-free days between 1000 and 1500 hours (local time), and only fully expanded, whole green sun leaves were chosen for leaf gas exchange measurements. The 6-cm^2 leaf chamber was completely filled for each measurement. We measured one leaf per plant on each of three replicate plants per species per plot. In each plot, we randomly selected three plants of each species for our measurements. In plots where fewer than three plants were available, we took measurements from all plants that were available or noted that none were available. *Plantago lanceolata* and *T. officinale* were measured in both 2009 and 2010, and, with additional resources available, *E. repens* was added as the third species in 2010 only. Field measurements were made in early June and late July in both 2009 and 2010 in order to capture changes within the growing season. Gas exchange measurements for a species were all made within one day, and each group of samples were taken within two consecutive days. The average PAR reading at our field site between 1100 and 1400 hours on a typical day in early July was 1500 μmol m^{-2} s^{-1}. The Li-6400 infrared gas analyzers were set with specifications for light availability (1500 PAR), airflow rate (400 μmol s^{-1}), and control reference CO_2 (400 μmol mol^{-1}); otherwise, ambient conditions were used.

Green leaf tissue samples were collected from each of the plants measured during the late July sampling in each year. Leaf samples were dried to constant mass at 65°C, ground, and analyzed for C and N concentration on a Costech ECS 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA).

Statistical Analyses

Photosynthesis and transpiration rates were analyzed separately for each species in each year using a mixed-model ANCOVA for a split-split-plot randomized block design. Precipitation was analyzed as the whole-plot factor, and the temperature treatment was a subplot factor nested within the precipitation treatment. The different sampling dates within each year were analyzed as split-split plots in the design. The block effect was considered to be a random effect. Because infrared heating warms leaf surfaces, rather than the surrounding air (Kimball et al. 2008), we sought to remove the diurnal air temperature changes by incorporating air temperature as a covariate in the ANCOVA models of photosynthetic rates and transpiration rates. Therefore, any effect of the warming treatment would be the result of either plant acclimation or temperature effects on soil/leaf variables, such as soil moisture availability or leaf chemistry.

Instantaneous leaf-level WUE was calculated by dividing the photosynthetic rate by the transpiration rate. WUE was analyzed individually by species and year, using an ANOVA (using the same model structure as above). Leaf tissue C:N ratio, percent C by weight, and percent N by weight were analyzed using separate ANOVA models for each year, but species were combined, with two species in 2009 and three species in the 2010 field season. Contrast analyses were used to test a priori hypotheses.

To gauge the overall effect of soil moisture, leaf temperature, and leaf N content on photosynthesis, we used species-specific multiple regression models. The multiple regressions modeled plot-averaged photosynthesis values over both sampling years as a dependent variable and an a priori set of independent variables as linear predictors: soil moisture, plot-averaged leaf temperature, and plot-averaged leaf %N.

The ANOVA and ANCOVA model analyses used PROC mixed, and the regression analyses used PROC REG; all analyses were carried out using SAS statistical software (ver. 9.2; SAS, Cary, NC). Where necessary, data were transformed to better meet model assumptions. Post hoc pairwise comparisons were adjusted for multiple comparisons with the Tukey method, and all effects reported were significant at the $P < 0.05$ level.

To test whether there was predictable absence (i.e., plants were not present within certain treatments in a predictable manner), we ran exact logistic regressions (Derr 2000) of plant absences (<3 plants in a plot) by year with warming and precipitation treatments, as well as sampling season, as independent categorical predictors. Numerous plant absences indicate that effect estimates in those treatments are less robust.

Results

Field Conditions

Stark differences in ambient air temperature and rainfall produced substantially cooler and wetter growing conditions in 2009 than in 2010 (fig. 1). July 2009 was characterized by very high daily rainfall, with resulting high soil moisture availability (at 0–30-cm depth), but July 2010 had low daily rainfall with relatively high daily air temperatures, resulting in very low soil moisture (at 30-cm depth). Mean soil moisture levels at 45-cm depth followed similar patterns, with June 2009 at 9.79% ± 0.46%, July 2009 at 12.79% ± 0.78%, June 2010 at 12.53% ± 0.54%, and July 2010 at 7.80% ± 0.32%. The mean soil moisture readings at 60-cm depth had slightly less variation across sample points, with June 2009 at 10.06% ± 0.42%, July 2009 at 12.13% ± 0.83%, June 2010 at 11.53% ± 0.52%, and July 2010 at 8.25% ± 0.29%. In 2009, the cool, dry early June and hot, wet late July contrasted greatly with the cool, wet early June and hot, dry late July of 2010
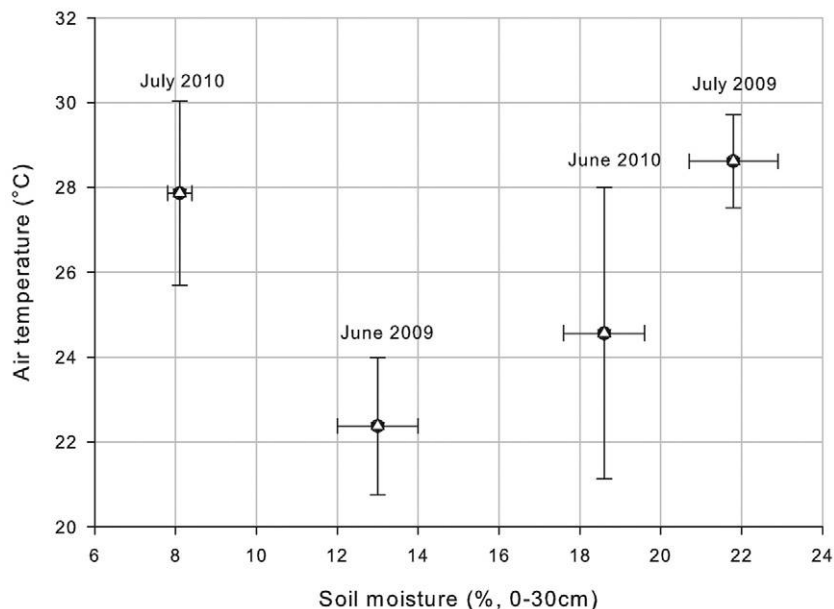
Fig. 1 Mean field conditions at the Boston Area Climate Experiment (BACE) site for each of the four sampling periods. Means and standard errors for air temperature are based on values measured between 1000 and 1500 hours on each sampling date at the nearby weather station; means and standard errors for soil moisture are based on weekly measurements within the 36 plots at BACE. Representative moisture stress is highest in the top left corner and lowest in the bottom right corner.

(fig. 1). These factors resulted in large ranges of what we considered to be ambient temperature and precipitation conditions.

Regression Analyses

Soil moisture availability, air temperature, and leaf chemistry affected the photosynthetic (A_{CO_2}) rates of the three species differently, and these patterns changed from June to July of each year. On the cooler June measurement dates, plot-level soil moisture availability and air temperature were significant predictors of plot-level A_{CO_2} rates for both *Plantago lanceolata* and *Taraxacum officinale* (table 1). Interestingly, A_{CO_2} rates of the grass, *Elymus repens*, were not influenced by either soil moisture or air temperature in June (table 1). On the warmer July measurement dates, A_{CO_2} rates of *P. lanceolata* and *E. repens* were both significantly affected by soil moisture availability. Leaf N content was a significant predictor of July A_{CO_2} rates only for *T. officinale* (table 1).

Shifts in Photosynthesis Rates

The warming treatments caused a decrease in A_{CO_2} rates of *P. lanceolata* in the first year of measurements, but this effect was not present in the second year (table 2; fig. 2a–2d). Although the precipitation treatment did not have an overall direct effect on the A_{CO_2} of *P. lanceolata*, in both years the cooler June measurements showed a clear separation of the three precipitation treatments, with the wet treatments resulting in higher A_{CO_2} rates than the ambient and drought treatments (table 2; fig. 2a, 2c). In 2010, A_{CO_2} rates of *P. lanceolata* were lower in July than they were in June, and in June the wet treatments resulted in higher A_{CO_2} rates than the drought treat-

ments in all the plots, except for the plots with the high warming treatment (table 2; fig. 2c, 2d). During the hot, dry late season of 2010, the precipitation and warming treatments had no effect on the A_{CO_2} rates of *P. lanceolata* (fig. 2d).

Using the contrast analyses, we found a number of significant partial effects and additional interaction effects, further explaining the patterns of *P. lanceolata* A_{CO_2}. In 2009, the response of A_{CO_2} to warming was more negative in the drought treatment than in the ambient and wet treatments together (contrast $P = 0.0120$; fig. 2a, 2b). In addition, A_{CO_2} was lower in the drought treatments as compared to the average of the ambient and wet treatments together only when soil moisture was relatively plentiful, as in July 2009 (contrast $P = 0.0055$) and June 2010 (contrast $P < 0.0001$). Therefore, the drought treatments resulted in lower A_{CO_2} later in the season (July) in 2009 but earlier in the season (June) in 2010 (fig. 2a, 2d).

The increasing levels of warming overall resulted in decreased rates of A_{CO_2} for *T. officinale* during the dry periods in June 2009 and July 2010, but this trend was reversed during the wet periods in July 2009 and June 2010 (fig. 2e–2h). Interestingly, the drought treatment reduced A_{CO_2} rates of *T. officinale* in June 2009, but supplemental precipitation reduced A_{CO_2} when soil moisture availability was already high in July 2009 (fig. 2e, 2f). Seasonal differences were also observed in the contrast analyses, where A_{CO_2} rates of *T. officinale* in the drought treatments were lower than the average of the ambient and wet treatments together in the cool, dry early season of 2009 (contrast $P < 0.0001$), but then the drought treatments resulted in higher A_{CO_2} rates than the ambient and wet treatments together in the hot and dry conditions of later season 2010 (contrast $P = 0.0001$; fig. 2e, 2h).

The A_{CO_2} of *E. repens* was faster in the cooler, wetter period of June than in the warmer and drier period of July

Table 1

Multiple Regression Results for Plot-Averaged Photosynthesis Values over Both Sampling Years, Separated by Season

	Early season					Late season				
Variable	Parameter estimate	Standardized estimate	P value	95% confidence limits		Parameter estimate	Standardized estimate	P value	95% confidence limits	
Plantago lanceolata (adjusted $R^2 = .2791$, $P < .0001$)						*P. lanceolata* (adjusted $R^2 = .1543$, $P = .0030$)				
Intercept	−15.976	0	.0854	−34.240	2.287	6.148	0	.389	−8.014	20.311
Soil moisture	30.092	.401	.0003	14.515	45.668	18.715	5.893	.0023	6.945	30.484
Air temperature	.822	.305	.0046	.263	1.382	.1411	.102	.3878	−.183	.465
% Leaf N						.871	.094	.4694	−1.519	3.260
Taraxacum officinale (adjusted $R^2 = .0803$, $P = .0291$)						*T. officinale* (adjusted $R^2 = .1235$, $P = .0165$)				
Intercept	19.500	0	<.0001	10.623	28.378	−7.210	0	.4492	−26.170	11.749
Soil moisture	15.212	.289	.0259	1.895	28.529	−11.228	−.206	.1171	−25.361	2.904
Air temperature	−.299	−.269	.0379	−.581	−.0173	.355	.198	.131	−.109	.820
% Leaf N						2.776	.288	.0236	.386	5.167
Elymus repens (adjusted $R^2 = .0063$, $P = .3546$)						*E. repens* (adjusted $R^2 = .1982$, $P = .0548$)				
Intercept	5.739	0	.6449	−19.642	31.120	−2.508	0	.8699	−33.966	28.951
Soil moisture	7.790	.262	.197	−4.323	19.904	52.564	.499	.0140	11.765	93.364
Air temperature	.329	.159	.429	−.515	1.172	.253	.121	.5375	−.587	1.093
% Leaf N						−.321	−.0563	.7705	−2.576	1.935

Note. Soil moisture and plot-averaged air temperature were used as linear predictors for the early season, and soil moisture, plot-averaged air temperature, and plot-averaged % leaf N were used as linear predictors for the late season. Each species (*P. lanceolata*, *T. officinale*, and *E. repens*) was analyzed separately. Values corresponding to $P < 0.05$ are underlined.

Table 2

ANCOVA Results for Light-Saturated Rate of Photosynthesis for *Plantago lanceolata*, *Taraxacum officinale*, and *Elymus repens* in Each Year

| | | *P. lanceolata* | | | | *T. officinale* | | | | *E. repens* | |
| | | 2009 (total $N = 193$) | | 2010 (total $N = 194$) | | 2009 (total $N = 155$) | | 2010 (total $N = 129$) | | 2010 (total $N = 155$) | |
	df	F	P	F	P	F	P	F	P	F	P
Precipitation (P)	2	2.61	.1871	.88	.4899	5.08	.0738	1.80	.2785	.78	.5318
Warming (W)	3	6.05	.0047	.29	.8332	2.59	.0907	1.31	.3093	2.11	.1550
P × W	6	2.44	.0645	.78	.5982	.83	.5670	.74	.6228	1.00	.4697
Season (S)	1	.20	.6666	56.94	<.0001	1.03	.3137	.28	.5993	28.00	<.0001
S × P	2	13.56	<.0001	11.78	<.0001	34.33	<.0001	10.76	<.0001	2.22	.1146
S × W	3	1.24	.2968	1.93	.1265	3.25	.0238	4.02	.0093	1.59	.1964
S × P × W	6	.94	.4718	4.13	.0007	1.76	.1125	3.08	.0078	1.00	.4311
T_{air}	1	10.75	.0326	.50	.4982	.69	.4086	1.41	.2413	.78	.3840

Note.   *Elymus repens* was measured only in 2010. Values corresponding to $P < 0.05$ are underlined.

2010, but it did not respond to precipitation treatments (table 2; fig. 2i, 2j). High and medium warming treatments reduced *E. repens* A_{CO_2} rates compared to the no and low warming treatments (contrast analysis, $P = 0.0405$).

Shifts in Transpiration Rates

Similar to the A_{CO_2} results for *P. lanceolata*, transpiration (E) rates were reduced by the warming treatment in 2009 but not in the hotter, drier year of 2010 (table 3; fig. 3a–3d). Overall E of *P. lanceolata* followed patterns of ambient soil moisture conditions, resulting in lower rates in June 2009, followed by higher rates in July but then higher rates in June 2010, followed by lower rates in July (table 3; fig. 3a–3d). There was an interactive effect of season with the precipitation treatment in both years. This resulted in high E rates in the wet treatments during the cooler season of June 2009 but low E rates in the drought treatments during the warmer July seasons. Similar to the A_{CO_2} results, the linear warming trends within the drought treatments were lower than the average trend seen in the ambient and wet treatments together (contrast $P = 0.0227$; fig. 3a, 3b). Not surprisingly, the lowest E rates observed for *P. lanceolata* were seen in July 2010 under drought conditions with a medium level of warming (fig. 3d).

Similar to those of *P. lanceolata*, overall E rates of *T. officinale* were lower in June 2009 than in the wet period of July 2009 (table 3; fig. 3e, 3f). Season had significant interactive effects with both the precipitation and warming treatments in 2009. In June 2009 the drought treatment caused declines in E, but this trend was not seen when soil moisture was plentiful in July 2009. Also in the drought treatment, warming reduced E, even with the low level of warming, in June 2009 (fig. 3e). Contrast analyses showed that E of *T. officinale* was lower in the drought treatment as compared to the average of the ambient and wet treatments together in both 2009 (contrast $P = 0.0284$) and 2010 (contrast $P = 0.0011$; fig. 3e–3h).

Transpiration rates for *E. repens* were lower in the drier July conditions than in the wetter June conditions of 2010 (table 3; fig. 3i, 3j). Season interacted significantly with precipitation, warming, and precipitation and warming together. This resulted in all June measurements being relatively uniform but the July measurements having lower E in the drought

treatments and lower rates also in the warmed treatments (fig. 3i, 3j). The highest E rates in July occurred in the wet plots with no warming (fig. 3i, 3j). Interestingly, the contrast analyses showed that the warming treatment reduced (contrast $P = 0.0241$) E of *E. repens* when the averages of the no and low warming treatments were compared to the averages of the medium and high treatments (fig. 3i, 3j).

Water Use Efficiency

All three species had higher WUE in the drought treatments, compared to the ambient and wet treatments, only during the driest and warmest conditions of July 2010 (fig. 4d, 4h, 4j). During the two drier measurement periods (June 2009 and July 2010), the drought treatment caused increases in WUE of *P. lanceolata* ($P = 0.0247$) compared to the ambient and wet treatments (fig. 4a, 4d). Interestingly, warming also significantly elevated the WUE of *P. lanceolata* in June 2009 (table 4; fig. 4a). The WUE of *E. repens* was not affected by treatments in June, but in July the drought treatment resulted in a significantly higher WUE than the average of the ambient and wet treatments together (contrast $P < 0.0001$; fig. 4j).

Supplemental precipitation reduced WUE of *T. officinale* ($P = 0.0382$) compared to the drought and ambient treatments (fig. 3e–3h). Contrast analyses indicated that in 2009 the wet treatment suppressed WUE of *P. lanceolata* (contrast $P = 0.0085$) and *T. officinale* (contrast $P = 0.0210$) as compared to the ambient and drought treatments (table 4; fig. 4a, 4b, 4e, 4f). *Taraxacum officinale* had lower WUE in the wet treatments than the ambient treatments during the wet conditions of July 2009 (contrast $P < 0.0001$; fig. 4f).

Leaf Tissue Stoichiometry

Leaf C:N ratios, as well as leaf C and N contents, differed significantly among the three species (table 5; fig. 5). The grass *E. repens* had higher leaf C and N contents but a lower leaf C:N ratio than either of the forbs (fig. 5). Of the two forbs, *T. officinale* had higher leaf C and N contents and a lower leaf C:N ratio than *P. lanceolata*. The species differences in leaf nutrient contents were often more pronounced than warming or precipitation effects (cf. figs. 5, 6). Nonetheless, leaf N contents in medium and high warming treatments were signifi-
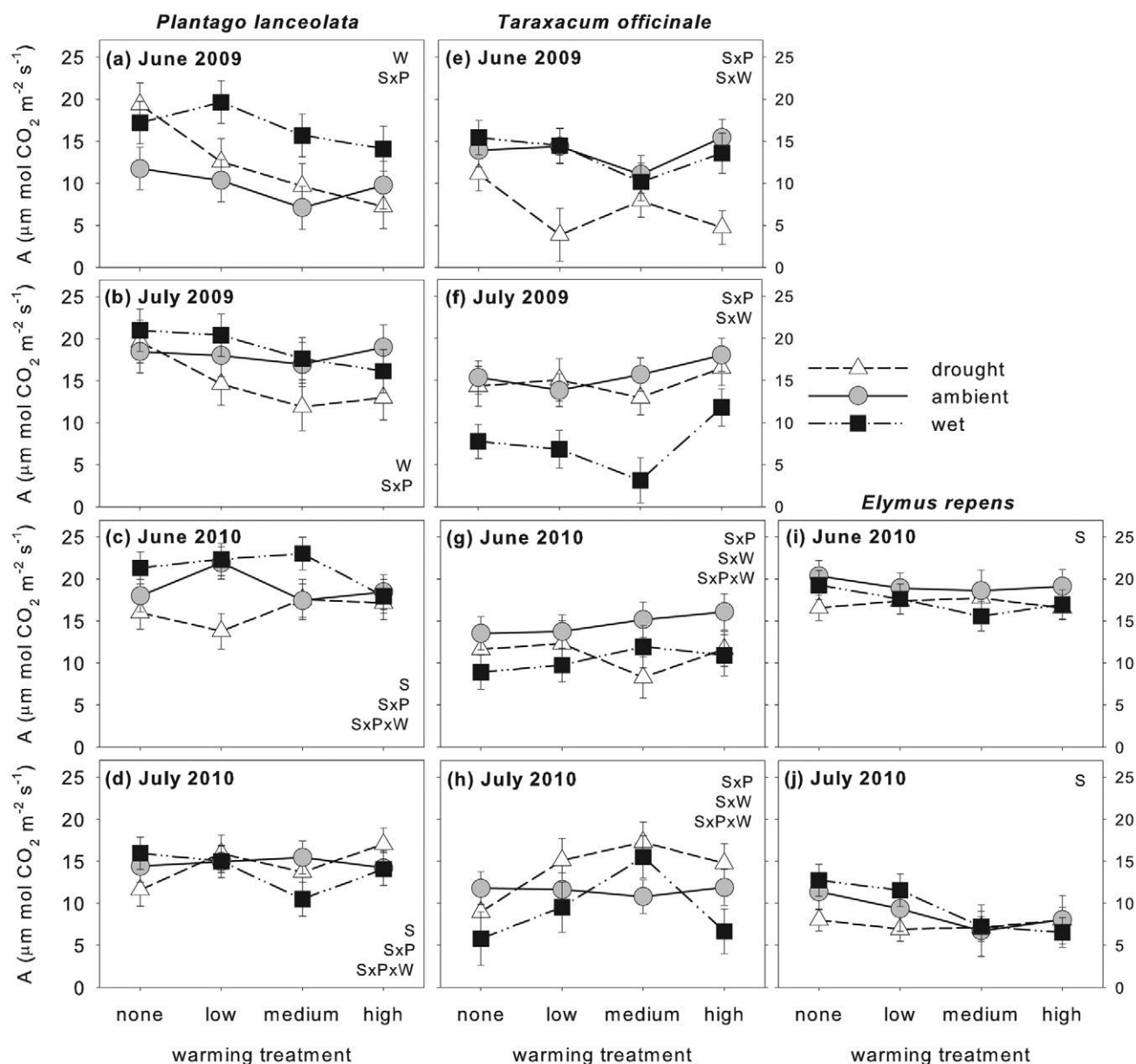
Fig. 2 Mean light-saturated rate of photosynthesis (*A*) ± SE for *Plantago lanceolata* (*a–d*), *Taraxacum officinale* (*e–h*), and *Elymus repens* (*i, j*) by warming treatment and precipitation treatment as measured in early June 2009 (*a, e*), late July 2009 (*b, f*), early June 2010 (*c, g, i*), and late July 2010 (*d, h, j*). Control plots received ambient conditions; low, medium, and high plots received heating treatments of +1.3°C (200 W m^{-2}), +2.7°C (600 W m^{-2}), and +4°C (1000 W m^{-2}), respectively. The drought treatment received 50% less precipitation than the ambient treatment, and the wet treatment received 50% more precipitation than the ambient treatment. Significant (*P* < 0.05) main treatment effects and interaction terms are indicated by capital letters within each panel. S, season; W, warming; P, precipitation.

cantly higher than in no and low warming treatments (fig. 6*c*) in both years, resulting in lower C : N ratios for all three species in the higher warming treatments (fig. 6*a*). During the hot, dry summer of 2010, leaf C content was greater for both *E. repens* and *T. officinale* within the drought treatment as compared to the wet treatment (not shown). Interestingly, this shift in C content did not significantly affect leaf C : N ratios (table 5). Precipitation treatments did not affect leaf C content of *P. lanceolata* in either year (fig. 6*b*).

Plant Abundance

The exact logistic regression analyses identified warming treatments as strong predictors of *P. lanceolata* absences (totals: 29/144 plots with absent plants, 14 plots in 2009, 15 in 2010) and precipitation treatments as strong predictors of *T. officinale* absences (totals: 52/144 plots with absent plants, 20 plots in 2009, 32 in 2010) and *E. repens* absences (totals: 25/72 plots with absent plants; tables A1, A2, available in the online edition of the *International Journal of Plant Sciences*).

Table 3

ANCOVA Results for Rate of Transpiration for *Plantago lanceolata*, *Taraxacum officinale*, and *Elymus repens* in Each Year

	df	*P. lanceolata* 2009 (total N = 193)[a]		2010 (total N = 195)[a]		*T. officinale* 2009 (total N = 155)		2010 (total N = 129)		*E. repens* 2010 (total N = 155)	
		F	P	F	P	F	P	F	P	F	P
Precipitation (P)	2	3.54	.0988	4.54	.0655	5.17	.0686	9.78	.0014	2.45	.2341
Warming (W)	3	8.85	.0007	.31	.8143	2.82	.0804	.24	.8707	3.50	.0521
P × W	6	1.76	.1622	1.03	.4456	2.89	.0521	1.59	.2129	1.51	.2603
Season (S)	1	97.07	<.0001	266.88	<.0001	24.82	<.0001	.40	.5487	42.46	<.0001
S × P	2	3.71	.0268	3.40	.0359	11.94	<.0001	.43	.6487	23.02	<.0001
S × W	3	1.4	.2447	1.28	.2820	3.71	.0132	1.76	.1597	4.72	.0038
S × P × W	6	.29	.9398	2.60	.0201	1.58	.1576	.99	.4353	2.61	.0205
T_{air}	1	3.62	.0744	5.21	.0329	5.05	.0397	1.03	.3155	5.93	.0171

Note.   *Elymus repens* was measured only in 2010. Values corresponding to $P < 0.05$ are underlined.

[a] Block effect removed from model due to infinite likelihood in estimation.

The odds of a *P. lanceolata* plant missing in a plot were 19 times (2009) and 10 times (2010) greater in the warmest plots compared to plots that were not warmed. The odds of *P. lanceolata* absences were also 13 times greater in medium-warmed plots than in unwarmed plots in 2010, the warmer of the two sampling years. *Taraxacum officinale* plant absences, by contrast, were better explained by precipitation treatments, such that both drought and wet treatments decreased the probability of finding a complete set of three plants per plot compared to ambient precipitation treatments (table A2). *Taraxacum officinale* plants were six times more likely to be absent in both drought or wet treatments in 2009, as well as four times more likely to be absent in drought plots and five times more likely to be absent in wet plots in 2010. The absence of *E. repens* was significantly less likely in drought plots, where the odds of plant absence were only 0.03 times that of plant absences in ambient precipitation plots (table A2).

Discussion

Leaf-level photosynthesis responded to warming or decreased precipitation primarily when soils were dry. Transpiration rates and instantaneous WUE responded strongly to shifts in soil moisture availability. Leaf N concentration increased and C : N ratio decreased with warming, likely because of warming-induced increases in N availability, but photosynthesis of only one species, *Taraxacum officinale*, was positively correlated with leaf percent N.

Shifts in Photosynthesis, Transpiration, and Water Use Efficiency

We found that soil moisture availability was a significant predictor of photosynthesis for *Plantago lanceolata* and *Elymus repens*, and both *P. lanceolata* and *T. officinale* were able to increase their instantaneous WUEs with warming. This suggests that *P. lanceolata* responded negatively to the warming treatment because of warming-induced soil moisture stress, rather than exceeding its photosynthetic temperature optimum. Similarly, Clark et al. (1999) found that low soil moisture markedly reduced the net leaf photosynthetic rate of *P. lanceolata*

in a pasture ecosystem. Using *P. lanceolata* in a Solardome experiment in the United Kingdom, Stirling et al. (1997) found that neither warming (+3°C) nor elevated CO_2 significantly affected the light-saturated rate of photosynthesis; however, water deficits and nutrient limitations were eliminated from this study by providing regular irrigation and nutrient additions. A recent study at BACE found that the aboveground biomass production of the total herbaceous plant community was not affected by warming alone but rather by an interaction of warming with drought conditions (Hoeppner and Dukes 2012). This mechanism could be a likely cause for our observations with *P. lanceolata*.

In our study, the precipitation treatments did not cause a significant shift in plant transpiration rates and instantaneous WUE. *Taraxacum officinale* was the only species to transpire less under the drought treatment, and this occurred only in 2010. The WUEs of all three species were highest in the drought treatments in the driest month of our study, July 2010. In a greenhouse experiment, Brock and Galen (2005) found that 6 d of imposed drought reduced the photosynthesis and transpiration rates of *T. officinale* compared to controls. Interestingly, this reduction was greater for *T. officinale* than for the congeneric *Taraxacum ceratophorum*.

The three species chosen for this study had a base level of intrinsic desiccation tolerance; plants persisted within most plots in 2009, even though the drought and warming treatments had been in place for 2 yr. Both forb species are known to have a medium level of drought tolerance, but the grass is less drought tolerant. However, we found that the grass was more likely to be within the drought treatment plots than the wet and ambient rainfall plots. One explanation for this is that our experimental site is not located within extreme drought conditions; rather, we are within the cool, moist spectrum for grasslands (Sala et al. 1988; Hoeppner and Dukes 2012). It is also possible that *E. repens* was able to avoid dehydration by accessing water at depths of 100 cm or greater, a depth at which the drought treatment may not affect soil moisture levels. Alternatively, the grass may have been more present within the drought plots, simply because the wet and ambient rainfall plots had greater aboveground biomass of other plants (Hoeppner and Dukes 2012) and therefore reduced the light availability for this shade-intolerant species.
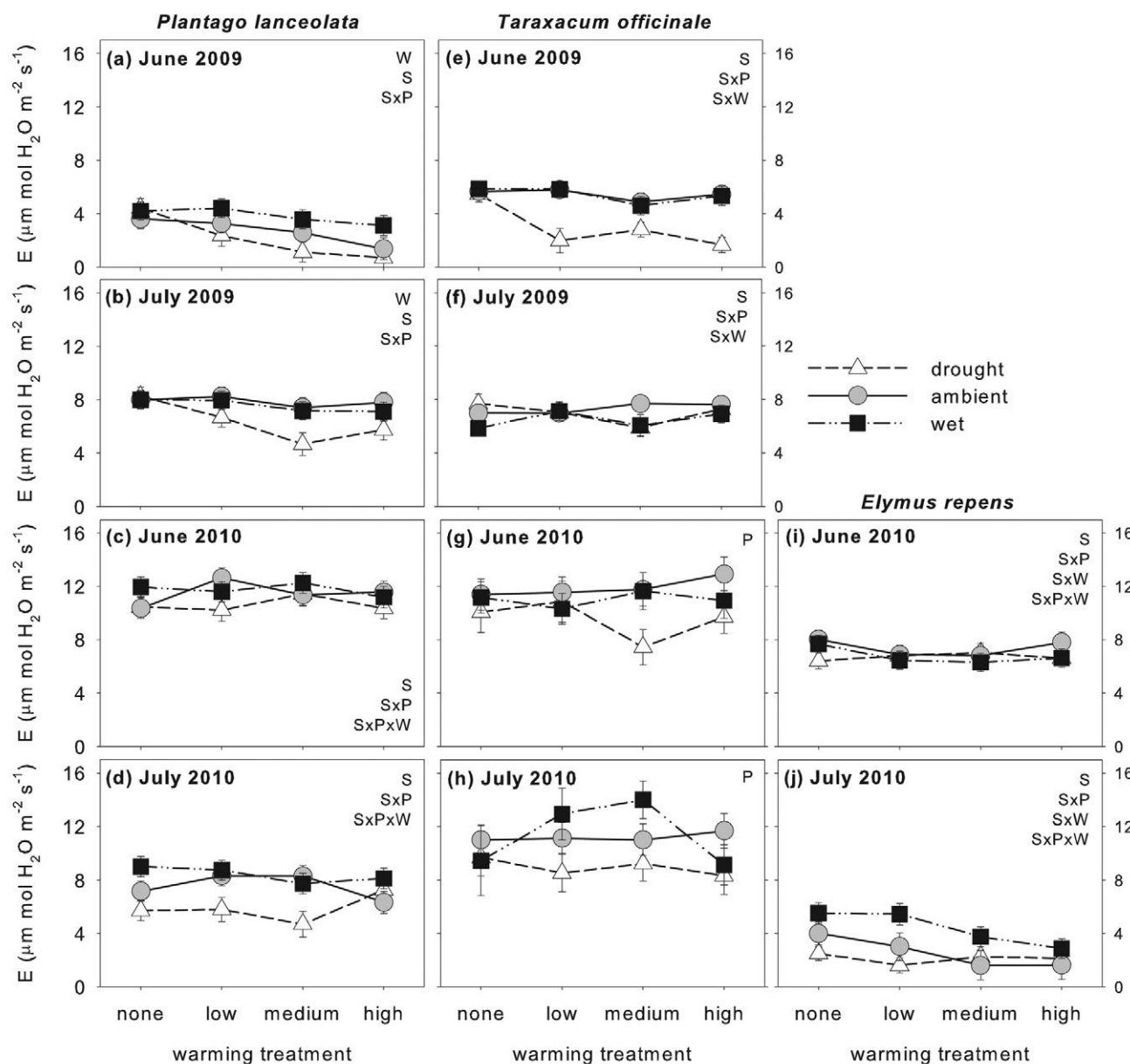
Fig. 3 Mean transpiration rate (E) $\pm$ SE for *Plantago lanceolata* (*a–d*), *Taraxacum officinale* (*e–h*), and *Elymus repens* (*i*, *j*) by warming treatment and precipitation treatment as measured in early June 2009 (*a*, *e*), late July 2009 (*b*, *f*), early June 2010 (*c*, *g*, *i*), and late July 2010 (*d*, *h*, *j*). Control plots received ambient conditions; low, medium, and high plots received heating treatments of +1.3°C (200 W m^{-2}), +2.7°C (600 W m^{-2}), and +4°C (1000 W m^{-2}), respectively. The drought treatment received 50% less precipitation than the ambient treatment, and the wet treatment received 50% more precipitation than the ambient treatment. Significant ($P < 0.05$) main treatment effects and interaction terms are indicated by capital letters within each panel. S, season; W, warming; P, precipitation.

Leaf Tissue Stoichiometry

Warming reduced foliar C:N in all of our study species; in both 2009 and 2010 we found that medium and high warming resulted in significantly lower foliar C:N ratios. The C content remained relatively stable across the warming treatment, but the percent N content was significantly greater. These results suggest warming may allow some plants to either take up more soil N or allocate more N to their leaves. Interestingly, Nijs et al. (1996) found a similar significant in-

crease in foliar N of a C$_3$ ryegrass exposed to experimental warming of 2.5°C in Switzerland, when compared to the ambient-grown grass. In their study, Nijs et al. (1996) also measured a drastic reduction in plant aboveground dry matter, suggesting that the N allocated to the leaf was simply concentrated into less dry matter, therefore enhancing N concentration on a mass basis (Nijs et al. 1996).

In our study, foliar C:N was not significantly affected by the precipitation treatment in either year of measurements. In response to experimentally reduced rainfall quantity, Fay
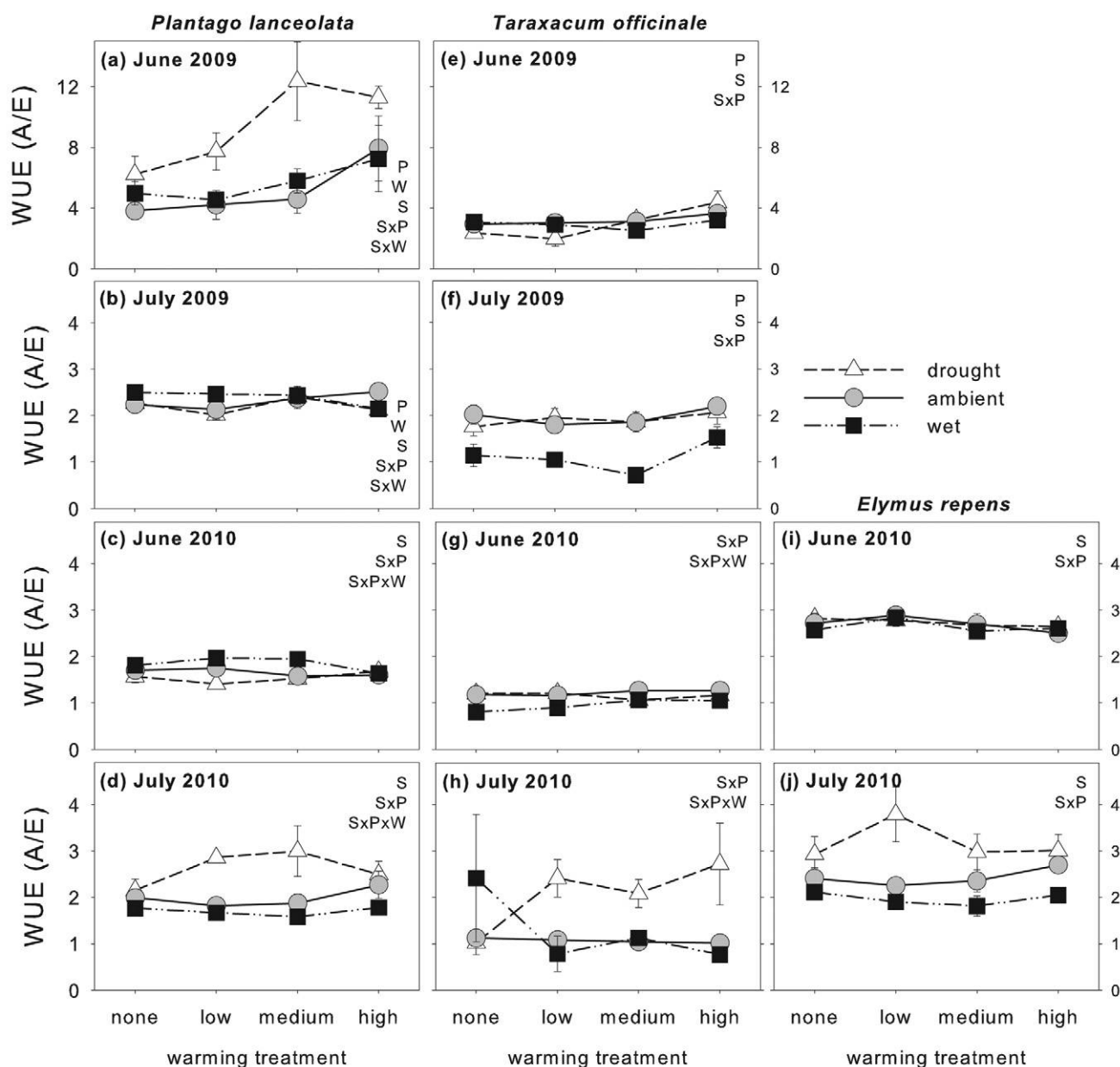
Fig. 4 Mean instantaneous water use efficiency (*A/E*) ± SE for *Plantago lanceolata* (*a–d*), *Taraxacum officinale* (*e–h*), and *Elymus repens* (*i, j*) by warming treatment and precipitation treatment as measured in early June 2009 (*a, e*), late July 2009 (*b, f*), early June 2010 (*c, g, i*), and late July 2010 (*d, h, j*). Control plots received ambient conditions; low, medium, and high plots received heating treatments of +1.3°C (200 W m^{-2}), +2.7°C (600 W m^{-2}), and +4°C (1000 W m^{-2}), respectively. The drought treatment received 50% less precipitation than the ambient treatment, and the wet treatment received 50% more precipitation than the ambient treatment. Significant (*P* < 0.05) main treatment effects and interaction terms are indicated by capital letters within each panel. S, season; W, warming; P, precipitation.

et al. (2002) found grassland species that were less deeply rooted than expected significantly increased their leaf C∶N ratio, thereby indicating their dependence on the rainfall to provide plant-available soil moisture and soil N. In our study, precipitation treatments did not affect foliar C∶N ratios (but warming treatments did), suggesting either that our species are more deeply rooted and therefore able to access deeper water reserves or that temperature plays a more dominant role than water availability in determining shifts in foliar chemistry dynamics. Hoeppner and Dukes (2012) found that the drought treatment increased belowground biomass production and that this was more pronounced in deeper (10–30 cm) soils.

Although we hypothesized that photosynthesis rates would be influenced by shifts in leaf chemistry, *T. officinale* was the only species to show a significant correlation between its leaf

Table 4

ANOVA Results for Water Use Efficiency for *Plantago lanceolata*, *Taraxacum officinale*, and *Elymus repens* in Each Year

| | | P. lanceolata | | | | T. officinale | | | | E. repens | |
| | | 2009 (total N = 179) | | 2010 (total N = 194)[a] | | 2009 (total N = 177) | | 2010 (total N = 149) | | 2010 (total N = 155) | |
	df	F	P	F	P	F	P	F	P	F	P
Precipitation (P)	2	9.45	.0247	.82	.4846	10.24	.0382	1.63	.3047	3.19	.1895
Warming (W)	3	3.98	.0230	.17	.9140	2.54	.0907	.88	.4725	.28	.8383
P × W	6	.81	.5732	.81	.5772	.94	.4942	.85	.5499	.11	.9933
Season (S)	1	364.10	<.0001	44.41	<.0001	169.21	<.0001	1.78	.1850	6.70	.0108
S × P	2	19.77	<.0001	32.91	<.0001	14.25	<.0001	16.34	<.0001	11.06	<.0001
S × W	3	6.98	.0002	.70	.5562	.98	.4019	1.32	.2725	.40	.7511
S × P × W	6	.83	.5471	3.23	.0052	1.75	.1137	2.95	.0104	1.04	.4025

Note. *Elymus repens* was measured only in 2010. Values corresponding to $P < 0.05$ are underlined.
[a] Log transformed.

N content and its photosynthesis rate. This indicates that the growth of *T. officinale* may be more strongly limited by its ability to take up N than the other two species, which had significant correlations with soil moisture availability but not foliar N.

Similar to the results of Aerts et al. (2009), our results indicate that species differences in leaf C and N contents are greater than the effects of experimental climate change treatments. These results are in line with the observation that plant functional group differences and differences among plant genera within functional groups explained more variation in leaf nutrient contents than either climate factors or soil nutrient concentrations across China (He et al. 2006; Han et al. 2011). On ecosystem or biome scales, it is likely, therefore, that shifts in species composition in response to climate change will have greater effects on nutrient turnover and forage quality than phenotypic changes in leaf nutrient concentrations. However, Craine et al. (2010) found that minimum crude protein values of forage grasses decreased by 2.0 mg g^{-1} for every 1°C increase in mean annual temperature. In addition, Craine et al. (2010) found that crude protein values peaked almost 2 d earlier in the season for every 1°C increase in mean annual temperature. Both of these observations suggest that even the relatively small changes in leaf nutrient contents may have significant im-

pacts on forage quality and phenology of available grassland resources.

Other Considerations

Experimental treatments had species-specific effects on missing data, which need to be taken into consideration in interpreting the observed treatment effects. For instance, *P. lanceolata* plants were significantly more likely to be absent in the warmest plots, which reduced our power to detect warming effects on the physiological responses of *P. lanceolata*. At the same time, these marked absences might indicate that these high-temperature conditions may be too stressful for *P. lanceolata*'s survival, recruitment, or successful competition against other plant species. Similarly, *T. officinale* was more likely to be absent from drought and wet precipitation treatments, thereby reducing our power to detect precipitation effects on physiological parameters while indicating that there may be a fairly narrow precipitation optimum at which *T. officinale* can survive and successfully compete with other old-field species. The increased likelihood of *E. repens*'s presence in drought treatments also weakens our statistical power to detect differences between the effects of the three precipitation treatments on *E. repens*'s physiological responses but suggests

Table 5

**ANOVA Results for Foliar Carbon to Nitrogen Ratio (C : N), Percent C by Weight, and Percent N by Weight for
All Three Species (*Plantago lanceolata*, *Taraxacum officinale*, and *Elymus repens*) Together**

| | C : N ratio | | | | % C (wt.) | | | | % N (wt.) | | | |
| | 2009 | | 2010 | | 2009 | | 2010 | | 2009[a] | | 2010 | |
Effect	df	Pr > F	df	Pr > F	df	Pr > F	df	Pr > F	df	Pr > F	df	Pr > F
Precipitation (P)	2, 4.09	.0628	2, 4.74	.2321	2, 3.88	.065	2, 4.36	.035	2, 3.56	.0044	2, 4.61	.2575
Warming (W)	3, 18.6	.0113	3, 16.6	.0028	3, 18.1	.7898	3, 17.8	.5137	3, 22.5	.0356	3, 19.2	.0006
P × W	6, 18.4	.4902	6, 16.4	.6454	6, 18	.1252	6, 17.7	.5343	6, 22.4	.3463	6, 18.9	.7736
Species (Sp)	1, 94.6	<.0001	2, 196	<.0001	1, 94.9	.1132	2, 192	<.0001	1, 95.1	<.0001	2, 198	<.0001
P × Sp	2, 94.4	.1934	4, 191	.3064	2, 94.8	.903	4, 190	.0016	2, 94.8	.1109	4, 192	.5167
W × Sp	3, 94.4	.2336	6, 197	.8629	3, 94.9	.3471	6, 196	.0151	3, 94.4	.1231	6, 198	.5772
P × W × Sp	6, 94.1	.1884	12, 196	.4198	6, 94.6	.8441	12, 194	.2026	6, 94.2	.4699	12, 197	.5619

Note. *Elymus repens* was measured only in 2010. Values corresponding to $P < 0.05$ are underlined.
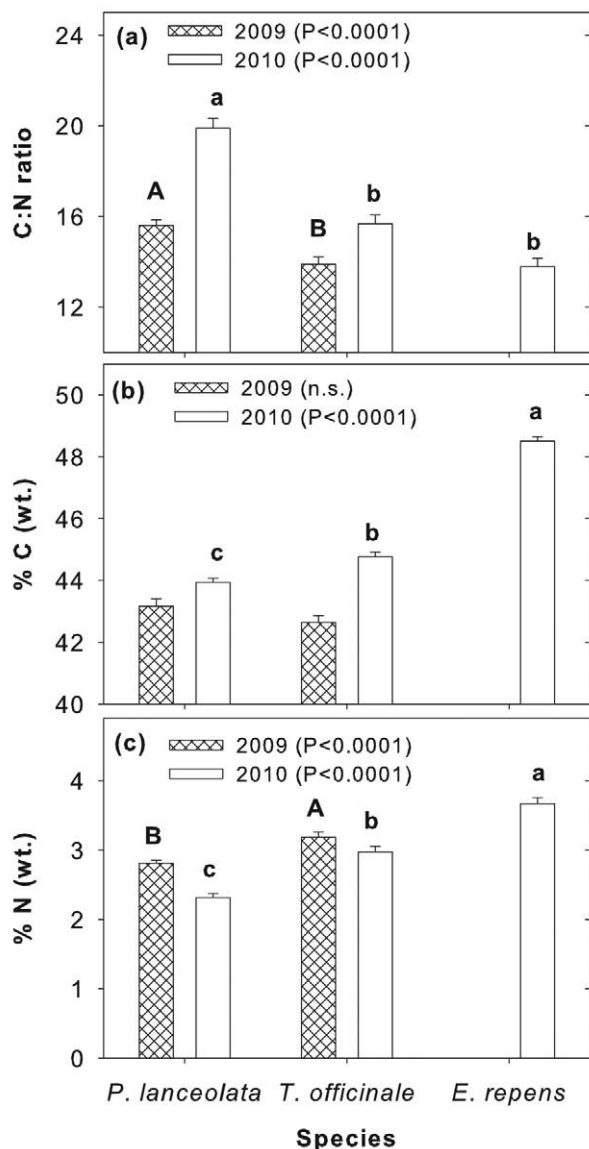[a] Estimation method is type 3 because REML did not converge.

Fig. 5 C : N ratio (*a*), percent C by weight (*b*), and percent N by weight (*c*) of each species (*Plantago lanceolata*, *Taraxacum officinale*, and *Elymus repens*) across the treatments, as collected in July 2009 and July 2010. Values represent means ± SE. Significant ($P < 0.05$) species differences are indicated in 2009 by different capital letters and in 2010 by different lowercase letters.

plots in both June 2009 and July 2010. Dry ambient conditions coupled with the drought treatment produced the lowest transpiration values for the two forb species in June 2009; substantially higher values in July 2010 suggest that these species may be more sensitive to a drought earlier in the season than later in the season. Similarly, De Boeck et al. (2011) found that negative effects of drought treatments on the C assimilation of an experimental perennial forb community in Belgium, including *P. lanceolata*, were exacerbated by heat stress to a greater extent in summer than in the spring and fall.
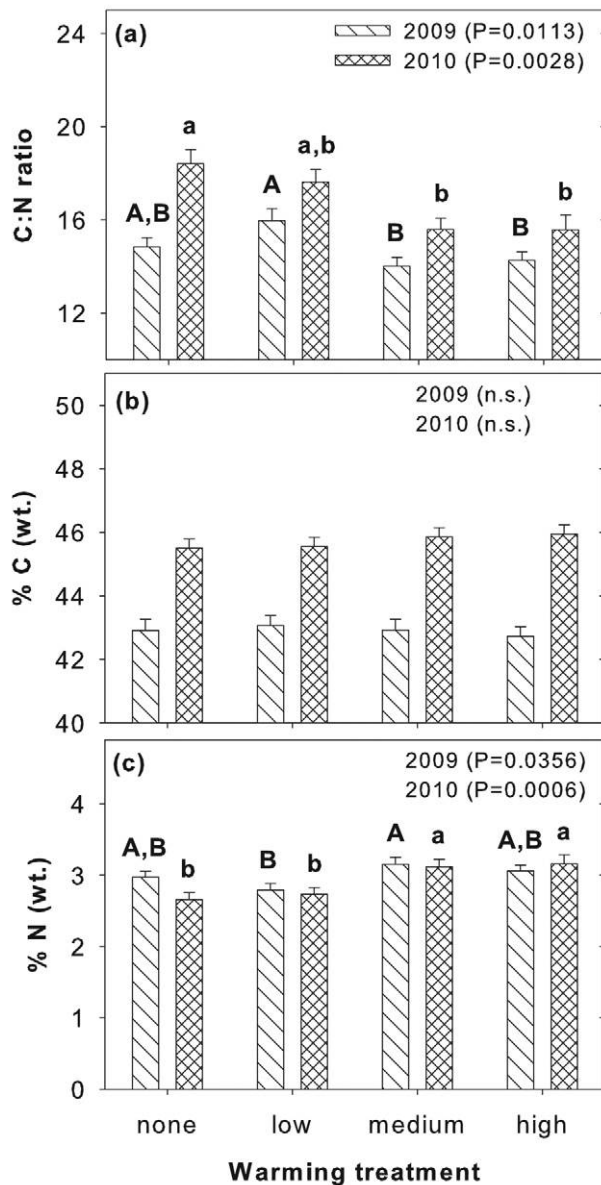
the possibility that *E. repens* might be competitively excluded from all but the most drought-stressed plots.

Our results indicate that season (i.e., measurement date) played a more dominant role in predicting significant changes in leaf-level gas exchange than either the warming or precipitation treatments. These findings make sense since the seasonal differences carried with them mean daily temperature changes of roughly 5°–7°C and mean daily precipitation changes of 2.5–5 mm, larger shifts than the imposed treatments. Ambient soils were dry, and severe soil moisture stress (volumetric water content <5%) was evident in the drought

Fig. 6 C : N ratio (*a*), percent C by weight (*b*), and percent N by weight (*c*) of the three species combined (*Plantago lanceolata*, *Taraxacum officinale*, and *Elymus repens*) by warming treatment, as collected in July 2009 and July 2010. Values represent means ± SE. Significant ($P < 0.05$) species differences are indicated in 2009 by different capital letters and in 2010 by different lowercase letters.

Future projections of climate change include higher temperatures and altered rainfall patterns but also increased atmospheric CO_2 concentrations and continued atmospheric N deposition. The multifactorial effects of climate change will have important implications for plant C-water relations and the overall ecosystem productivity of plant communities. Many modeling experiments and manipulated field ecosystems have been conducted to examine how these factors may interact to influence patterns of plant growth and photosynthesis (e.g., Cox et al. 2000; Chapin 2003; Nemani et al. 2003; Dukes et al. 2005; Luo et al. 2008; Wu et al. 2011). Interestingly, many of these studies suggest that interactive terms of these factors are either not significant or smaller than expected from additive, single-factor effects (Leuzinger et al. 2011). We found no significant interactive effects of the warming and precipitation treatments together across all seasons, indicating that the ecological responses of the plants studied here to these climate change treatments were not synergistic, nor did the responses ameliorate one another, as has been previously proposed (Niu et al. 2008). The warming treatment had the greatest effect on foliar chemistry; our results indicate that future warming may cause some plants to either take up more soil N or allocate more N to their leaves.

Acknowledgments

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