

Ecosystem responses to water and nitrogen amendment in a California grassland

W. STANLEY HARPOLE*, DANIEL L. POTTS† and KATHARINE N. SUDING*

*Department of Ecology and Evolutionary Biology, University of California, Irvine, 321 Steinhaus Hall, Irvine, CA 92697, USA,

†Department of Biology, Buffalo State College, 1300 Elmwood Ave. Buffalo, NY 14222, USA

Abstract

The world's ecosystems are experiencing simultaneous changes in the supply of multiple limiting resources. Two of these, water and nitrogen (N) can strongly limit grassland production and can affect community composition and biogeochemical cycles in different ways. Grassland ecosystems in California may be particularly vulnerable to current and predicted changes in precipitation and N deposition, and ecosystem responses to potential interactive effects of water and N are not well understood. Here, we show strong colimitation of plant production resulting from factorial addition of water and N. In addition, water and N addition in combination led to increased dominance of the two most abundant grass species, while N addition regardless of water availability led to decreased species diversity. Late season carbon (C) flux response to water addition depended on N. Only plots that received additional water, but not N, still showed net ecosystem C uptake at the end of the experiment. Our results suggest that grassland ecosystem response to N deposition will be strongly dependent on future precipitation patterns.

Keywords: California, colimitation, ecosystem carbon flux, evapotranspiration, global change, grassland, net ecosystem CO₂ exchange, nitrogen, nitrogen deposition, precipitation, soil moisture, water

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Introduction

Anthropogenic-driven global change is impacting natural ecosystem structure and function (Field *et al.*, 1992; Vitousek *et al.*, 1997b; Sala *et al.*, 2000; Nemani *et al.*, 2003; Weltzin *et al.*, 2003), yet the interactive effects of global change factors remain largely unknown (Dukes *et al.*, 2005). The Earth's ecosystems are experiencing increased inputs of nitrogen (N) (Tilman *et al.*, 2001), and N deposition has been shown to impact ecosystem production, diversity and carbon (C) cycling in consistent ways (Vitousek *et al.*, 1997a; Bobbink *et al.*, 1998; Stevens *et al.*, 2004). In conjunction with increased N availability in many terrestrial ecosystems, changes in the amount and timing of precipitation associated with global climate change are expected to have particularly large impacts on the structure and function of arid ecosystems (Weltzin *et al.*, 2003; Huxman *et al.*, 2004b; Suttle *et al.*, 2007). It has been suggested that in these ecosystems, soil moisture mediates the influence of

other environmental factors, including elements of anthropogenic global change such as N deposition, at several scales of organization (Weltzin *et al.*, 2003).

Mediterranean ecosystems such as California grasslands may be particularly vulnerable to impacts from N deposition and climate change (Parton *et al.*, 1994; Sala *et al.*, 2000). N deposition rates as high as 90 kg ha⁻¹ yr⁻¹ have been recorded in southern California (Fenn *et al.*, 2003b), and increased N inputs to California ecosystems have been shown to have negative consequences for plant and soil communities (Fenn *et al.*, 2003a). Precipitation can also strongly control grassland ecosystem processes (Burke *et al.*, 1997; Knapp & Smith, 2001; Knapp *et al.*, 2001; Huxman *et al.*, 2004b; Potts *et al.*, 2006) and different climate change models for California predict changes in annual precipitation ranging from -30% to +200% (Hayhoe *et al.*, 2004).

N and water have been shown to be important limiting resources in California grasslands (Seabloom *et al.*, 2003; Zavaleta *et al.*, 2003; Dukes *et al.*, 2005; Harpole & Tilman, 2007). N limitation is common in Californian grasslands: in a meta-analysis, eight of nine N-addition experiments surveyed found a significant positive

Correspondence: W. Stanley Harpole, tel. +949 824 1559, fax +949 824 2181, e-mail: wharpole@uci.edu

response of plant productivity to N (Harpole *et al.*, 2007). In addition, California grasslands are, by definition, water limited due to California's Mediterranean climate: most precipitation occurs during the winter and drought conditions occur during the summer when temperatures are more optimal for growth. Although water is an important limiting resource in this system, there have been few experimental studies of water limitation (Dukes *et al.*, 2005; Harpole & Tilman, 2007; Suttle *et al.*, 2007; Harpole *et al.*, 2007). Because of the vast area represented by California grasslands (nearly 10 million ha) combined with their economic importance, there is a critical need for empirically based understanding of how these ecosystems may respond to projected climate change.

Water and N can colimit arid grassland productivity (Kirchner, 1977; Hooper & Johnson, 1999), further supporting the prediction that the effects of N deposition and precipitation change will be interdependent. Wet N deposition increases with increasing precipitation (Fenn *et al.*, 2003b). Soil inorganic N is dissolved in the soil water solution, and water affects its mobility and loss. Soil microbial activity (e.g. litter decomposition, N mineralization, nitrification and denitrification) is dependent on soil moisture (Jackson *et al.*, 1989; Schimel *et al.*, 1989; Burke *et al.*, 1997). Soil N availability influences plant photosynthetic rates through its positive influence on leaf N content. In turn, increased photosynthetic rates are associated with greater transpiration and more rapid depletion of soil moisture in the rooting zone. At the canopy scale, N deposition may increase plant productivity thereby increasing canopy light interception, reducing rates of evaporation at the soil surface and causing a decline in canopy conductance of water vapor.

In addition to effects on plant production and leaf-level gas exchange, changes in the supply of water and N can affect ecosystem level processes through their effects on plant community composition and phenology. Changes in water and N availability can have strong effects on plant species numbers and relative abundance (Hobbs & Mooney, 1991). If plants differ in their traits associated with water and N use, then changes in their relative abundance should affect whole-community ecosystem processes. Because plant physiology and development depend on both water and N (McIntyre, 2001), changes in the precipitation regime or N deposition could change the timing and intensity of plant growth and could either promote senescence or prolong seasonal growth (Cleland *et al.*, 2006). Such temporal changes in plant growth should affect net ecosystem C exchange and the ability of ecosystems to respond to precipitation (Potts *et al.*, 2006).

Here, we experimentally test the dependence of plant community composition and ecosystem processes to N

deposition and precipitation increases in a southern California grassland. To test this we applied water and N, alone and in combination. In addition, we took advantage of an unusually large, late growing-season storm to explore ecosystem gas exchange responses in relation to prior additions of water and N.

Materials and methods

Our experiment was located within the Irvine Ranch Land Reserve in Orange County, CA, USA (33.624°N, 117.755°W). Average annual rainfall is 325 mm and average temperatures during the growing season range from 6.2 to 23 °C (NOAA, Laguna Beach Station; 1928–2006). Annual precipitation in 2006 was 226 mm, 70% of the average. Soils are classified as Myford sandy loam (USDA soil survey). In November 2004, before the growing season, we prepared our site by mowing and then applying an herbicide (Roundup, Monsanto Corp., St Louis, MO, USA) to control a late-summer perennial noxious weed: artichoke thistle (*Cynara cardunculus*). Early in the following growing season (February 2005), we established five replicate blocks of four 1 m × 1.5 m plots, separated by 1.5 m aisles. *Lolium multiflorum* and *Avena fatua*, both annual grasses, were the dominant species at this site. All species present at the site were of annuals of exotic origin except for occasional occurrences of the native perennial grass *Distichlis spicata* (<2% average cover) and native annual forbs *Trichostema lanceolatum* and *Eremocarpus setigerus* (each <1% cover). Annual grasses and forbs present at the site were allowed to complete their life cycle during the 2005 growing season before we imposed factorial N × water addition treatments. We added N in January and March 2006, as Ca(NO₃)₂, in dry form in two applications totaling 10 g m⁻² N. Adjacent to our experimental plots, we constructed rainfall collectors using 0.65 m × 2.4 m corrugated fiberglass panels mounted on 1 m tall timber frames and angled to drain into a collection bucket. We applied the collected rainwater to plots within 1–3 days following major precipitation events. In total, 69 mm of additional water was added to experimental plots in five irrigation events during late-March to late-May 2006. Supplemental irrigation of experimental plots resulted in a 30% increase in rainfall amount over the ambient annual (July 2005 through June 2006) precipitation of 226 mm.

We sampled peak aboveground biomass on May 24, 2005 and May 18, 2006 by clipping a 7.5 cm × 1.5 m strip, sorting clipped plants to species and litter, drying the samples for 48 h at 50 °C and weighing (total live biomass was used as an estimate of current year's production). Because water addition extended plant growth in those plots, our single annual harvest in

2006 may have tended to underestimate aboveground production in watered plots. We sampled root biomass on May 26, 2006 by taking four 2.5 cm diameter \times 10 cm deep cores from each clipped area, washing the roots, drying and weighing. We measured the percent photosynthetically active radiation (% PAR) reaching the soil surface in the center of each plot on May 17, 2006 using a SunScan light meter (Delta-T Devices, Cambridge, UK), averaging across 64 quantum sensors. We installed permanent 0.635 cm diameter \times 15 cm long stainless-steel probes in each plot in April 2006 and measured soil moisture approximately weekly using time domain reflectometry (TDR, MiniTrase, Soil Moisture Inc., Santa Barbara, CA, USA). Changes in species abundance in response to treatments were determined by calculating the change in species biomass between the post- and pretreatment sampling years (2005 and 2006).

Under clear sky conditions, on May 17, 2006 and May 24, 2006, we measured midday (11:00–14:00 hrs) ecosystem carbon dioxide (CO_2) and water exchange using a closed static chamber (1.5 m long, 0.97 m wide, 1.44 m tall) seated over each plot with an open-path infrared (IR) gas exchange analyzer (LI-7500, Li-Cor Inc., Lincoln, NE, USA) installed inside (Arnone & Obrist, 2003; Huxman *et al.*, 2004a; Potts *et al.*, 2006). The IR gas exchange analyzer was mounted on a tripod fit with two 15 cm diameter electric fans to promote atmospheric mixing within the chamber. The chamber consisted of a 3.2 cm diameter PVC pipe frame covered by a tightly sewn polyethylene sheet (Shelter Systems, Santa Cruz, CA, USA). The transparent material used for chamber construction allowed $\sim 75\%$ of PAR to pass into the plots, while allowing IR radiation to escape the chambers. To avoid the development of soil-atmosphere pressure gradients in the enclosed atmosphere of the chamber, the chamber was vented appropriately. This lightweight and rugged chamber design allowed us to effectively capture relative differences among treatments.

To measure net ecosystem CO_2 exchange (NEE) and evapotranspiration (ET), the transparent chamber was seated and secured to the ground surface with a heavy steel chain. We allowed 20 s to elapse, during which the chamber atmosphere was thoroughly mixed by the tripod-mounted fans, before measurements were begun. CO_2 and water vapor concentrations were allowed to build up or decline while a computer recorded the transient changes in the chamber atmosphere. Following the transparent chamber measurement, the chamber was removed from the plot, ventilated and resealed. To measure ecosystem respiration (R_e), an opaque polyethylene cover (Shelter Systems) was immediately placed over the transparent chamber, the heavy chain was refit, and the gas exchange measurement was repeated in the absence of sunlight.

Consistently linear changes in CO_2 and water vapor concentrations during the 90-s measurement period indicated that changes in concentrations of water vapor were insufficient to significantly alter plant stomatal conductance, canopy photosynthesis or soil CO_2 efflux (Huxman *et al.*, 2004a). Air temperatures within the chamber during an average measurement period increased $< 1^\circ\text{C}$. CO_2 and water vapor concentration data were analyzed according to Jasoni *et al.* (2005) to estimate fluxes. Finally, we calculated gross ecosystem exchange (GEE) as the balance of NEE and R_e . By convention, ecosystem CO_2 assimilation is expressed as negative fluxes; ecosystem CO_2 efflux is expressed as positive fluxes. Because we observed significant plant senescence following our initial gas exchange measurements, we estimated the percent live (nonsenesced) vegetation in each plot on May 24, 2006, and used this to estimate standing live biomass at the time of our second ecosystem gas exchange measurements to use as a phenological covariate.

We fit mixed linear models using maximum likelihood, including block as a random effect. Data met assumptions of constant variance and normality. We log-transformed root and live biomass. We used repeated measures analysis for biomass and species number responses using pre- and posttreatment measurements (i.e. 2005 and 2006) and testing for significant time by treatment effects. We used preplanned contrasts to test for differences between treatment and control plots and adjusted *P*-values for multiple tests using Bonferroni's correction. Changes in species abundance between pre- and posttreatment measurements were calculated as the difference between 2006 and 2005 abundance and tested using contrasts between treatment combinations and controls (*P*-values were not adjusted in this case). We tested the May 17 responses of ecosystem CO_2 exchange to water and N addition using mixed linear models. We additionally tested ecosystem response to a late season rain event using both the May 17 and 24 gas exchange data using repeated measures with plot nested in block as the random subject. We used ANCOVA to test the response of ET to resource treatments using live biomass as a covariate. All analyses were performed using the R statistical language (<http://www.r-project.org>).

Results

Soil moisture

Overall, shallow soil moisture in our experimental plots decreased from 22.3% to 9.8% over time (repeated measures time effect; $F_{1,137} = 131.26$, $P < 0.01$) in response to plant water use and increasing vapor

pressure deficits associated with increasing daily temperatures during the growing season (Fig. 1). Water addition increased soil moisture, as intended ($F_{1,13} = 48.52$, $P < 0.01$), whereas N addition resulted in decreased soil moisture ($F_{1,13} = 5.80$, $P = 0.032$) and their combined effect was additive (i.e. no significant interaction) (Fig. 1). Soil moisture differences were attributable primarily to water and N addition treatments rather than differences in biomass (ANCOVA including water, N addition and biomass effects; biomass effect $F_{1,51} = 0.60$, $P = 0.44$). In response to a natural, late season 12 mm rain event that occurred on May 22, 2006, soil moisture increased significantly from 12.3% to 19.0% ($F_{1,117} = 211$, $P < 0.01$). Differences in percentage soil moisture among watering treatments persisted until July, well after the senescence of annual grasses and forbs in late-May (10.6% in watered vs. 9.0% in unwatered plots; $P < 0.01$). No such differences were observed among N treatments.

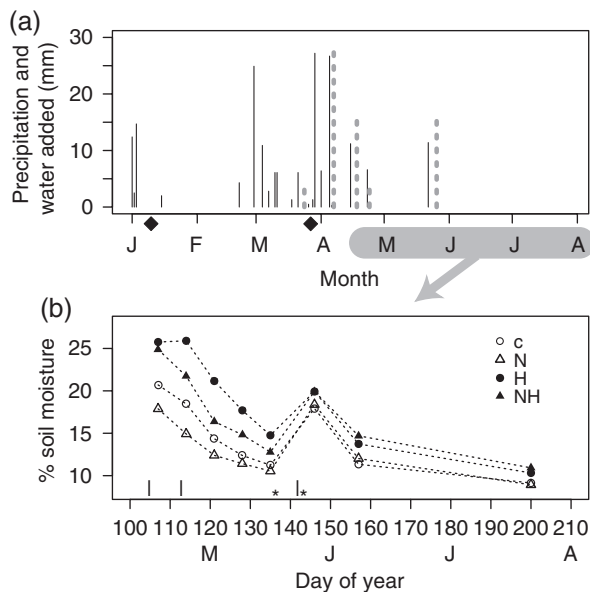


Fig. 1 (a) Temporal water patterns in plots receiving factorial addition of water and nitrogen (N). Dates are indicated by month abbreviations. Vertical solid lines represent precipitation events and dotted vertical lines represent water additions. Diamonds represent the two N additions. Period of sampling is highlighted and data are shown in (b): note the differences in scale of the x-axes. (b) Temporal patterns of percent volumetric soil moisture measured using time domain reflectometry. c, control plots; N, N addition; H, water addition; NH, addition of both water and N. Short vertical lines indicate occurrences of natural rain events [their magnitude is shown in (a)]. Day of year and month abbreviations are shown on the x-axis. The asterisks (*) indicate the two dates ecosystem gas exchange measurements were made (they occurred before and after a natural rain event of 11.4 mm, but before the final water addition).

Productivity and composition

Plant aboveground productivity response to water and N addition showed significant additive colimitation by both resources (Fig. 2a, repeated measures time \times water and time \times N effects; $F_{1,17} = 6.73$, 9.68 , $P = 0.02$, < 0.01 , respectively; water \times N interaction not significant). The only treatment combination that significantly increased production was the addition of both water and N (treatment vs. control contrast; $t = 3.64$, $P < 0.01$). Plants responded mainly by increasing aboveground production; we found no significant treatment effect on root biomass (Fig. 2b). Consistent with increased aboveground production, addition of N and water reduced light levels at the soil surface although only the effect of N addition was significant (Fig. 2c, N addition; $F_{1,13} = 5.74$, $P = 0.03$. Water addition; $F_{1,13} = 4.43$, $P = 0.055$).

Water and N addition influenced plant community composition through effects on species richness and species-specific patterns of abundance. N addition was associated with a decline in species number following treatment (Fig. 2d, repeated measures time \times N; $F_{1,17} = 8.53$, $P = 0.01$). Shifts in ANPP were primarily associated with biomass increases by two dominant annual grasses, *A. fatua* and *L. multiflorum*, both of which increased significantly with the combined addition of water and N (Fig. 3, $t = 3.14$, 2.22 , $P < 0.01$, $P = 0.04$, respectively). Two other species showed

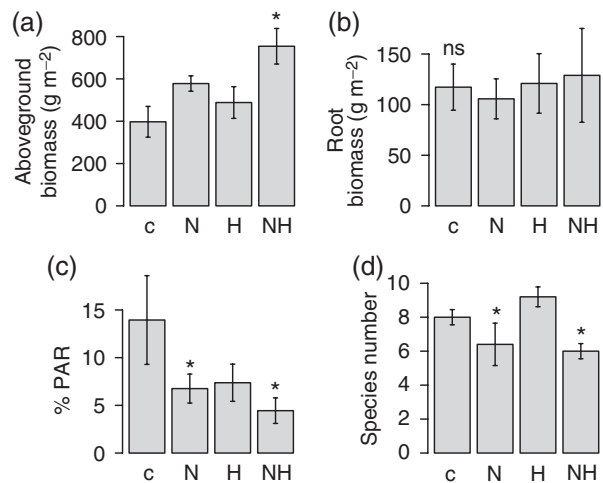


Fig. 2 Response of (a) aboveground biomass, (b) root biomass, (c) photosynthetically active radiation (PAR) (% ambient light reaching the soil surface) and (d) species number by treatment combination. c, control plots; N, nitrogen (N) addition; H, water addition; NH, addition of both water and N. For aboveground biomass, asterisks (*) indicate significant contrast differences between treatments and control ($P < 0.05$); for PAR and species number the main effect of N addition was significant but not individual contrasts. Means \pm SE are shown.

significant responses to treatments: *Bromus hordeaceus* decreased with water addition (Fig. 3, $t = -2.31$, $P = 0.04$) and *Erodium botrys* increased with N addition relative to the control plots (Fig. 3, $t = 2.36$, $P = 0.03$). Results for the remaining, less abundant, species showed treatment-specific trends that were not significant (Fig. 3). There was no treatment effect on the absolute abundance of forbs ($P = 0.85$).

In addition to impacts on ANPP, we observed phenological effects of water and N addition on annual grasses and forbs (Fig. 4). N addition promoted earlier leaf senescence, resulting in reduced live biomass (i.e. green leaf tissue on May 24, 2006) late in the growing season ($F_{1,13} = 12.73$, $P < 0.01$), whereas water addition tended to increase live biomass, but not significantly ($F_{1,13} = 3.62$, $P = 0.08$). The percentage live biomass was not dependent on aboveground production ($F_{1,13} = 3.06$, $P = 0.11$) and total variance in a model including both terms was primarily explained by water and N treatments (59%) rather than production (7%).

Ecosystem gas exchange

Predictably, the abundance of late season live biomass and the water addition treatment were both positively

related to midday ET (Fig. 4, ANCOVA, live biomass: $F_{1,16} = 39.88$, $P < 0.01$; water addition: $F_{1,16} = 6.21$, $P = 0.021$). ET rates were higher with water addition and lower with N addition before a late season rain event (Fig. 5a, May 17 ET; $F_{1,13} = 14.80$, 6.40 ; $P < 0.01$, 0.025 , respectively). Consistent with treatment-mediated differences in ET, late season ecosystem CO_2 exchange was influenced by both water and N addition treatments. Growing season water addition increased rates of ecosystem respiration (R_e) on May 17 (Fig. 5b, $F_{1,12} = 9.20$, $P = 0.01$). Water addition during the growing season strongly increased rates of late growing season ecosystem photosynthesis (GEE) (Fig. 5c, $F_{1,12} = 7.41$, $P = 0.019$). In contrast, N addition tended to reverse this effect (Fig. 5c, water \times N; $F_{1,12} = 3.47$, $P = 0.087$). Patterns of midday late-growing season NEE were consistent with those observed for GEE. N and water addition interacted such that N addition reversed increases in NEE due to water addition (Fig. 5d, water \times N; $F_{1,12} = 5.70$, $P = 0.034$).

Ecosystem response to a late season rain event

ET rates for all treatments, except N addition alone, increased following a late season rain event (Fig. 5a,

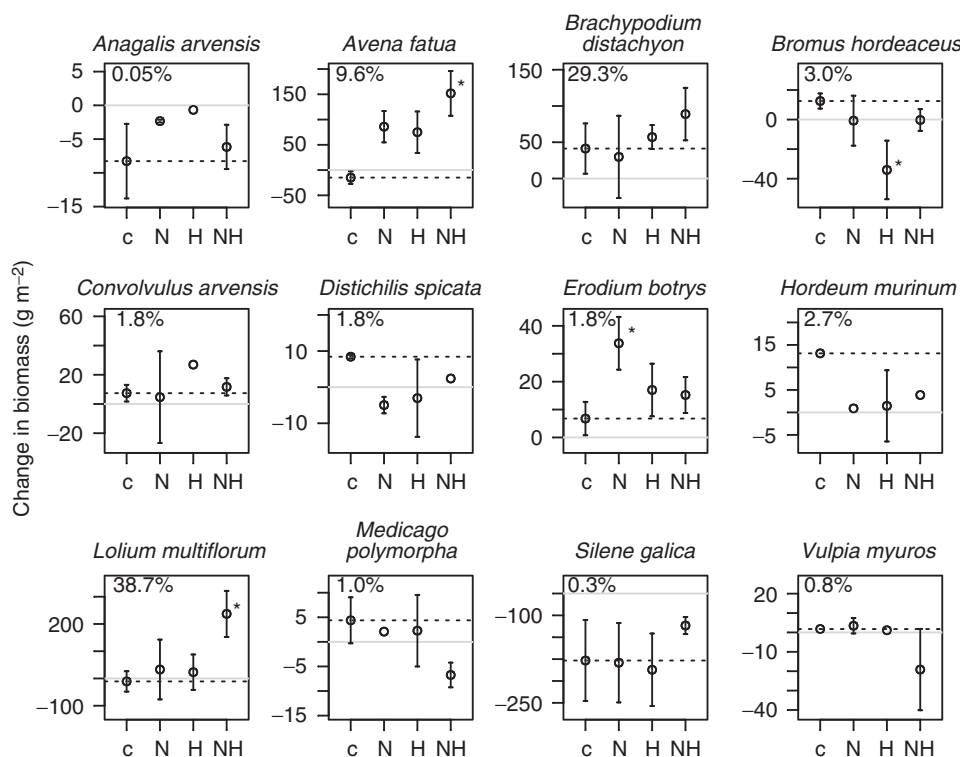


Fig. 3 Individual species response to treatments as measured by their change in biomass between posttreatment and pretreatment sample dates (2006 and 2005). Zero change is indicated by a horizontal gray line, and temporal change in control plots by a horizontal dashed line. Significant differences between treatment and control are indicated by an asterisk (*) ($P < 0.05$). c, control plots; N, nitrogen (N) addition; H, water addition; NH, addition of both water and N. Means \pm SE are shown.

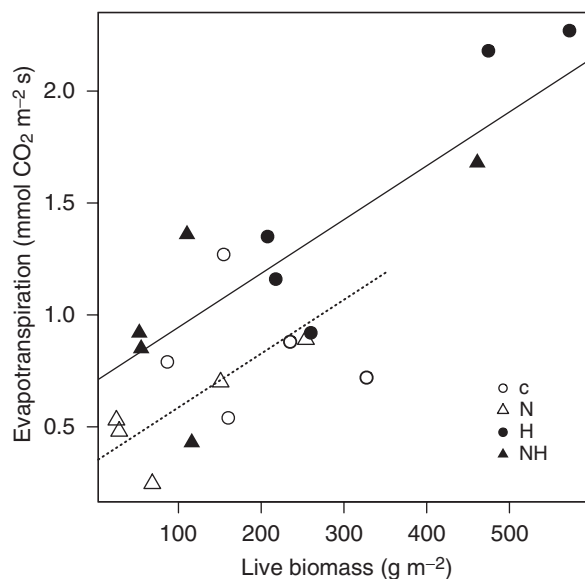


Fig. 4 Rates of canopy-level evapotranspiration indicate that plant physiological activity is a function of live biomass at the time of measurement (May 24, 2006) and water addition treatment. Solid line is ANCOVA fit through water addition plots and dashed line through plots not receiving water. c, control plots; N, nitrogen (N) addition; H, water addition; NH, addition of both water and N.

repeated measures time effect: $F_{1,17} = 13.20$, $P < 0.01$; $N \times \text{water}$: $F_{1,12} = 4.88$, $P = 0.047$). We found no significant response of R_e to late season rainfall (repeated measures time effect; $F_{1,19} = 2.26$, $P = 0.15$). Despite a 12 mm rainfall event on May 20, GEE continued to decline with time (repeated measures time effect; $F_{1,19} = 14.69$, $P < 0.01$) consistent with progression of annual plant leaf senescence. NEE similarly declined among all treatments also consistent with a decline in biological activity associated with overall patterns of annual plant senescence (Fig. 5, repeated measures time effect; $F_{1,19} = 49.07$, $P < 0.01$). Only plots receiving added water alone had significantly negative NEE rates following the late season rainfall event on May 22 (Fig. 5, $t = -2.79$, $P = 0.013$).

Discussion

Water and N had mixed effects on patterns of soil moisture and patterns of late-growing season ecosystem CO_2 and water vapor exchange. N addition led to decreased soil moisture, whereas water addition increased soil moisture as intended. Effects of N amendment on soil moisture have been demonstrated in other grasslands (Zavaleta *et al.*, 2003). Soil moisture levels at the end of the growing season were attributable to N addition but not to variation in ANPP suggesting that

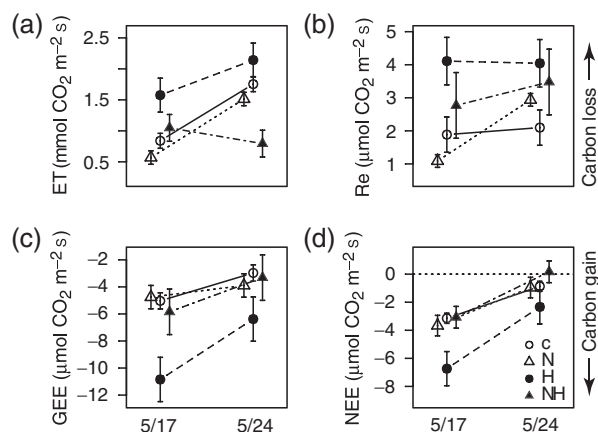


Fig. 5 Ecosystem gas flux in response to water and nitrogen (N) addition before (May 17) and after (May 24) a late season rain event on May 22. (a) Greater values of evapotranspiration (ET) represent greater loss of water due to plant activity (transpiration) and evaporation. (b) More positive respiration (R_e) values mean greater carbon (C) loss. (c) More negative values of gross ecosystem exchange (GEE) indicate greater C gain due to photosynthesis. (d) Negative values of net ecosystem CO_2 exchange (NEE) represent net ecosystem C gain. c, control plots; N, N addition; H, water addition; NH, addition of both water and N. Means \pm SE are shown.

plant effects on soil moisture were related to increases in leaf-level gas exchange rates associated with increased N availability (Field *et al.*, 1992) rather than simply greater aboveground biomass.

Water and N colimited productivity of our grassland system. Simultaneous increases in both resources were necessary to significantly increase production. Increased supply of these two colimiting soil resources acted to increase aboveground biomass but not root biomass, consistent with predicted decreased root allocation relative to shoot allocation in response to decreased light levels (Tilman, 1988; Lane *et al.*, 2000). Our results are consistent with patterns of colimitation by water and N in grasslands across a large range of precipitation (Hooper & Johnson, 1999).

We observed a decline in species richness associated with N addition. Similar declines in species diversity have been observed in a variety of other terrestrial ecosystems (Gough *et al.*, 2000; Stevens *et al.*, 2004; Suding *et al.*, 2005). In contrast to N addition, increases in soil moisture may have positive effects on species diversity (Cornwell & Grubb, 2003; Harpole & Tilman, 2007) although we found no significant effect of water addition on species diversity here.

Patterns of ANPP in response to water and N addition were driven primarily by the positive responses of two dominant annual grasses, *A. fatua* and *L. multiflorum*. Variation in the magnitude and timing of pre-

cipitation has been shown to strongly affect community composition (Murphy, 1970; Duncan & Woodmansee, 1975). In particular, forbs and grasses often respond differently to water vs. N addition (Zavaleta *et al.*, 2003). In our experiment, N and water addition affected functional group composition (i.e. grasses and forbs) by increasing the abundance of grasses, in particular the two dominant grasses but had no effect on forbs. A few other species in our experiment showed water- or N-specific responses suggesting alternative outcomes for community composition and diversity depending on how precipitation changes with expected increases in N deposition.

N addition increased production but also promoted earlier leaf senescence, possibly due to effects on leaf-level photosynthesis and rates of resource acquisition. These changes in phenology could reduce ecosystem flux differences of high N systems relative to ecosystems experiencing lower rates of N supply. Estimates of late-growing season R_e and GEE revealed the opposite phenological effect of water addition on ecosystem function. Water addition, particularly under conditions of ambient N supply, extended the period of both plant and soil microbe activity. Among these plots, midday net ecosystem assimilation of CO_2 (negative NEE fluxes) continued through at least the last measurement period on May 24. Our data also showed increased ET and R_e with water addition. Our results suggest that increases in ANPP associated with N deposition may be offset by precipitation-mediated shifts in ecosystem respiration with negative consequences for the strength of the terrestrial ecosystem C sink. N fertilization has also been shown to lead to C loss in Alaskan tundra, despite increased ANPP (Mack *et al.*, 2004).

The ability of annual grasslands to respond to late season precipitation will also be dependent on changes in N deposition and annual precipitation. Our results suggest that increased N deposition will decrease the ability of these systems to sustain net CO_2 assimilation later in the growing season due to increased water use and earlier leaf senescence. Thus, annual grasslands experiencing higher rates of N deposition may provide lower than expected C storage. The rate of N addition in our experiment ($10 \text{ g m}^{-2} \text{ yr}^{-1}$), while high, is representative of deposition rates observed near urban areas in California (Fenn *et al.*, 2003b). How C storage responds to N deposition will depend on longer-term changes in precipitation, species composition and litter decomposition rates. Short-term effects of increased precipitation have been shown to differ from longer-term results due to lagged species composition responses and changes in trophic structure (Suttle *et al.*, 2007).

Our results support the prediction that community and ecosystem responses to N deposition will be

mediated by changes in precipitation (Weltzin *et al.*, 2003). Because of the colimiting nature of these two resources, studies of the effects of N deposition should take into account potential precipitation change scenarios and vice versa. Additionally, changes in the mean and variance of precipitation can have different effects on ecosystem productivity and C cycling (Knapp *et al.*, 2002), but how these might interact with N addition is not clear. Because of expected changes in precipitation due to global climate change (Jackson *et al.*, 2001), priority should be given to control regional emissions of N in order to minimize the impacts of multiple interacting global change factors.

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