Postdefoliation ecosystem carbon and water flux and canopy growth dynamics in sagebrush steppe bunchgrasses

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Abstract. Developing land-use practices that lead to sustainable net primary productivity in rangelands are important, but understanding their consequences to population and community processes is not often accounted for in basic ecosystem studies. Grazed and ungrazed upland ecosystems generally do not differ in net ecosystem CO_2 exchange (NEE), but the underlying mechanisms and the concurrent effects of defoliation to vegetative and reproductive biomass allocation are unclear. To address this, we measured evapotranspiration (ET), NEE, and its constituent fluxes of ecosystem respiration (R_{eco}) and gross ecosystem photosynthesis (GEP) with live canopy leaf area index (LAI_{live}; m² live leaf area/m² ground area) and aboveground leaf, culm, and reproductive biomass in plots of clipped and unclipped squirreltail (*Elymus elymoides*) and bluebunch wheatgrass (*Pseudoroegneria spicata*) growing in intact sagebrush steppe. Clipping reduced LAI_{live} by 75%, but subsequent re-growth rates in clipped plots was similar to LAI_{live} accumulation in unclipped plots. Concurrently, ET and NEE was similar between clipped and unclipped plots, with NEE primarily determined by GEP. GEP was initially lower in clipped plots, but then converged with unclipped GEP even as LAI_{live} continued to increase in both treatments. GEP convergence was driven by higher whole-plant photosynthesis (GEP_{live} = GEP/LAI_{live}) in clipped plots. Ecosystem water use efficiency (GEP/ET) was reduced by 16% with clipping, due to low GEP/ET 2 weeks following defoliation, but GEP/ET converged before GEP levels did. Proportional reproductive biomass was higher in *E. elymoides* (21.4% total biomass) than in *P. spicata* (0.5% total biomass) due to lower allocation to specific leaf and culm mass. Clipping reduced reproductive effort in *E. elymoides*, in terms of total reproductive biomass (−56%), seed mass per unit leaf area (−64%), and seed mass per flowering head (−77%). We concluded defoliation increased canopy-level light penetration, facilitating rapid recovery of ecosystem fluxes, but that allocation to vegetative regrowth supporting this led to lower reproductive effort in these range grasses. Insights from studies such as this will be useful in formulating systems-based land management strategies aimed at maintaining annual productivity and long-term population and community goals in semiarid rangeland ecosystems.

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INTRODUCTION

Maintaining ecosystem productivity in water-limited rangelands under developing climate change is a critical scientific and societal challenge (Briske et al. 2015). While grazing occurs in almost all arid and semiarid ecosystems, we still do not have a clear understanding on the impacts

of defoliation on ecosystem level carbon and water flux (Asner et al. 2004). In intensively managed and more mesic grazing systems, reductions in live aboveground biomass and leaf area index (LAI) generally reduce gross ecosystem photosynthesis (GEP) to a greater extent that ecosystem respiration (R_{eco}), resulting in more positive net ecosystem CO_2 exchange (NEE), increasing the likelihood such ecosystems act as a net atmospheric carbon sources (Welker et al. 2004, Nieveen et al. 2005, Schmidt et al. 2010, Boyd and Svejcar 2012). In addition, defoliation can reduce plant transpiration contributions to evapotranspiration (ET) (Asner et al. 2004), affecting ecosystem water use efficiency (GEP/ET) (Hu et al. 2008, Fu et al. 2009).

Given the evidence of strong direct effects of grazing to NEE in more mesic systems, it is surprising that most ecosystem-level flux research in arid and semiarid grazing systems—the bulk of global rangelands (Briske et al. 2015)—rarely address defoliation effects, and focus primarily on the role of environmental drivers or shifts in community composition to seasonal and interannual variation in ecosystem carbon and water flux (Flanagan et al. 2002, Nakano et al. 2008, Hu et al. 2008, Niu et al. 2008, Svejcar et al. 2008, Fu et al. 2009, Bowling et al. 2010, Polley et al. 2010, Scott et al. 2010, Hamerlynck et al. 2013). There are notable exceptions to this: experimental clipping has been found to have little effect on steppe or grassland NEE in central Asia (Niu et al. 2010), consistent with Risch and Frank (2006), who found no differences in NEE in grazed and ungrazed temperate grasslands along a riparian to upland moisture gradient in Yellowstone National Park, or in North American mixed grass prairie, where grazing rarely affected total NEE, but did reduce R_{eco} to a greater extent than GEP, thereby altering the interannual sensitivity of NEE to environmental drivers such as soil moisture and temperature (Polley et al. 2008).

Valuable as these studies have been, considerable uncertainty still exists regarding the mechanisms underlying the "NEE neutral" responses to aboveground biomass loss in arid and semi-arid grazing lands. Many rangeland grass species show both compensatory increases in leaf-level photosynthesis and whole-plant regrowth in response to grazing (Caldwell et al. 1981, McNaughton 1983, Detling and Painter 1983, Senock et al. 1991, Doescher et al. 1997, Loeser

et al. 2004, Walling and Zabinski 2006, Haubensak et al. 2009), though this is by no means consistent across all rangeland species or ecosystems (Ferraro and Oesterheld 2002). The impact such responses to the constituent fluxes underlying NEE in rangeland systems is currently unknown.

Moreover, there is a largely unmet research challenge calling for studies linking ecosystem flux dynamics to ecological processes that are of importance to rangeland managers and land users, many of which play out at the individual plant scale (Asner et al. 2004). Measuring carbon and water fluxes in small, whole-plant level plots is an effective approach to address this challenge, in that the spatial dimension of measurement (0.5–1.0 m^2) and inclusion of soil and plant components to carbon and water fluxes make measurement at this level readily generalizable to resolving whole-ecosystem processes, but are small enough to assess the effects of whole-plant or community-level manipulations that cannot be readily performed in large ecosystem-level flux measurements (Huxman et al. 2004, Potts et al. 2006, Boyd and Svejcar 2012, Hamerlynck et al. 2014). In our study system, the sagebrush steppe of the Intermountain West US, the establishment of self-sustaining native bunchgrass populations is critical for restoring and conserving sagebrush steppe (Davies et al. 2011, Morris et al. 2011). Demographic-based approaches have the potential to improved sagebrush steppe restoration efforts, in part through identification and manipulation of demographic bottlenecks that limit successful establishment and development of native species (James et al. 2011, Mangla et al. 2011). This work has led to the development of a strategic, systems-based approach to sagebrush steppe restoration (James et al. 2013), which, in addition to seed and seedling demography, recognizes how variation in parental plant performance and seed production is a critical component to sagebrush steppe conservation and restoration. Parental plant performance can greatly affect allocation to reproductive effort, seed quality, and seedling success (Huxman et al. 1999, He et al. 2005). We believe, therefore, quantifying defoliation effects to vegetative and reproductive biomass production of desirable native forage species within a whole-plant and ecosystem level context gives a more complete picture on the ecological costs and benefits associated

with any land-use practices, including grazing, used to retain the integrity of these economically and ecologically important ecosystems under changing climate conditions (Svejcar et al. 2014, Briske et al. 2015).

To address this, we present here a study addressing the effects of experimental clipping on canopy growth and concurrent whole-plant, ecosystem CO_2 and H_2O exchange in plots dominated by one of two important North American sagebrush steppe bunchgrasses, bottlebrush squirreltail (*Elymus elymoides*), and bluebunch wheatgrass (*Pseudoroegneria spicata*). While experimental defoliation such as clipping or mowing is not an ideal proxy for grazing (Collins et al. 1998, Socher et al. 2012), for small-plot and individual plant studies, such experimental defoliation can provide invaluable insight on ecosystem processes and whole-plant reproductive and vegetative allocation patterns (Senock et al. 1998, Gutman et al. 2001, Li et al. 2015). Both grasses are cool season C_3 tussock bunchgrasses, fairly tolerant of grazing and fire (Miller et al. 1994, Doescher et al. 1997, Haubensak et al. 2009), and are highly desirable in conservation and restoration efforts in sagebrush steppe degraded by invasive annual grasses (Jones 1998, Young and Mangold 2008, Stevens et al. 2014). *Pseudoroegneria spicata* is capable of compensatory photosynthesis following defoliation (Caldwell et al. 1981), and though this has not been documented in *E. elymoides*, both species display aboveground compensatory regrowth following defoliation (Busso et al. 1990, Loeser et al. 2004, Walling and Zabinski 2006, Haubensak et al. 2009). In addition, as tussock grasses, both have canopies with considerable amount of standing dead biomass in the absence of grazing or fire (Miller et al. 1994, Davies et al. 2010). In addition, *E. elymoides* is smaller, shorter lived, and with an open canopy (Jones 1998). Variation in canopy structural characteristics may modulate how carbon and water fluxes respond to defoliation and subsequent regrowth (Caldwell et al. 1983, Ryel et al. 1994). Both species also vary reproductive effort in response to grazing, and generally show an increase in relative reproductive biomass following early-season grazing, though this depends on grazing intensity, fire regime, as well as prevailing soil moisture and temperature conditions (Anderson and Frank

2003, Bates et al. 2009, Bates and Davies 2014). We therefore also quantified vegetative allocation (leaf and culm area, biomass and specific mass) and reproductive allocation (seed head number, reproductive mass, and seed mass per seed head) in clipped and unclipped plants in order to better link whole-plant gas exchange and ecosystem flux dynamics to potential population processes. Based on previous work comparing grazed and ungrazed upland systems (Risch and Frank 2006, Polley et al. 2008, Niu et al. 2010), compensatory growth responses (Loeser et al. 2004, Walling and Zabinski 2006), and vegetative and reproductive biomass allocation studies (Miller et al. 1994, Anderson and Frank 2003), we specifically expected:

(1) Overall, response of NEE of our small plots to be consistent with ecosystem-flux findings in other upland semiarid systems, specifically that NEE would be relatively unaffected by defoliation.
(2) Plots with similar NEE would exhibit consistent proportional reductions and increases in R_{eco} and GEP.
(3) Sensitivity of R_{eco} to soil moisture and GEP to total live canopy would be higher in clipped plots than in and unclipped controls.
(4) Accelerated, compensatory regrowth in clipped plants would cause GEP to become similar between clipped and unclipped plots.
(5) Proportional reproductive biomass would increase in response to experimental defoliation.

Materials and Methods

This study took place at the USDA-ARS Northern Great Basin Experimental Range (119°43′ W, 43°29′ N), located approximately 70 km west of Burns, Oregon at 1402 m ASL. Mean annual precipitation is 278.4 mm, with the bulk of this (70.6%) distributed fairly evenly through the cool season (November–May), primarily in the form of rain, with occasional snowfall over the coldest months, and with some years having additional early (October) and/or late (June) rainfall. Mean annual temperature is 14.8°C, ranging from average daily maximums in July (28.7) to daily minimum of −7.1°C in January. Sampling activities took place over an 8-week period, from May 1 to July

Table 1. Monthly precipitation (P) and average maximum and minimum temperatures (T_{max} and T_{min}) encompassing the 2015 study period, and long-term (1937–2012) summaries of these for the Northern Great Basin Experimental Range study site. Standard deviations are presented parenthetically for long-term data.

Month	2015 P (mm)	Long-term P (mm)	2015 T_{max} (°C)	Long-term T_{max} (°C)	2015 T_{min} (°C)	Long-term T_{min} (°C)
April	7.1	20.8 (16.0)	13.7	13.4 (1.15)	−0.8	−1.4 (0.14)
May	26.2	33.0 (22.1)	15.6	18.2 (1.32)	4.4	2.1 (0.18)
June	0.0	25.1 (20.3)	27.4	22.9 (1.34)	12.2	5.8 (0.46)

3, 2015; previous ecosystem flux results from this location has shown most of the annual CO_2 uptake occurs across this period (Svejcar et al. 2008). Monthly conditions for this period (April through June), and long-term averages for this period are presented in Table 1 (NCDC-NOAA Co-op Station #358029-7). Most of the May, 2015 precipitation fell from 18 to 21 May, over four consecutive 24-h rainfall accumulation periods (Western Regional Climate Center, http://www.wrcc.dri.edu/ Summary of the day graph (SOD-TD3200)).

The study site was located in intact sagebrush steppe enclosed and protected from livestock grazing since 1994 (Svejcar et al. 1999). To quantify plant community structure, five 30-m transects, spaced at 15-m intervals, and were used to measure plant community characteristics in June, 2015. Herbaceous canopy cover was estimated and density was measured by species inside 40 × 50-cm quadrats (0.2 m²) located at 3-m intervals on each transect line, resulting in 10 quadrats per transect and 50 quadrats per plot. Cover was visually estimated based on marking that divided the quadrats into 1%, 5%, 10%, 25%, and 50% segments. Shrub cover by species was measured by line intercept along the five 30 m transect lines per plot. Shrub density by species was measured by counting all individuals rooted in five 2 × 30 m belt transects. Plant community data are summarized in Table 2; the exotic annual grass, Bromus tectorum is infrequent and sparsely distributed (0.014% cover and less than 1 plant/m²).

Plant and ecosystem functional measurements

Soil moisture and attendant whole-plant and ecosystem functional dynamics were measured in eight 0.75 × 0.75 m plots, each dominated by one to two individual bottlebrush squirreltail (*Elymus elymoides*) or bluebunch wheatgrass (*Pseudoroegneria spicata*) plants. Four weeks prior to water relations, canopy, and gas exchange measurements (see below), all plants that were not the target species were removed from the plot, and small trenches were dug tangentially to the major basal diameter axis of the largest plant in each plot, and 5-cm-long time-domain-reflectometry (TDR) volumetric soil moisture probes (ECH2O-5, Decagon Devices, Pullman, WA, USA) were inserted into the trench face into soil under the plant canopy at 5 and 15 cm depths. Volumetric soil moisture (θ, mol/mol) data were recorded every 4 h on a datalogger (EM5b, Decagon Devices) and averaged to give a daily estimate of θ at each depth.

Plant functional measurements were made weekly from May 8, to June 25, 2015, with the May 8th measurements taken prior to clipping to establish baseline plant condition and function. This 8-week period covered peak canopy growth, commencement of flowering and reproductive effort. Half of the eight plots for each species were randomly selected for clipping. All aboveground structures were clipped to ca. 2 cm height, and all harvested material wrapped in moist paper towels, transported to the laboratory and stored in a refrigerator prior to determining live and dead biomass, and the surface area of live culms and leaves (see *Biomass and specific mass*, below). Predawn water potentials (ψ_{pd}, MPa) were measured early the morning (04:00–05:30 PDT), prior to midmorning measurements of gas exchange (10:00–13:30 PDT). ψ_{pd} of whole culms were measured for each plant monitored for canopy growth and whole-plant gas exchange immediately after harvesting with a Scholander pressure chamber (PMS, Corvallis, Oregon, USA).

Canopy projected leaf area index (LAI; m²/m²) was measured with a Decagon LP-80 line ceptometer (Decagon Devices) with an above-canopy

Table 2. Plant community cover and density characteristics of the Northern Great Basin Experimental Range study site, and the percent proportional contributions of the two study species, bluebunch wheatgrass (*Pseudoroegneria spicata*) and squirreltail (*Elymus elymoides*) to total perennial grass, total perennial species, and total vegetative cover for the 2015 study period.

Cover type	% Cover	% *P. spicata*	% *E. elymoides*	Density (no./ m^2)
Perennial grasses	15.0	45.5	1.5	21.5
Perennial forbs	4.9	—	—	11.8
Annual forbs	1.6	—	—	259
Shrub	9.6	—	—	0.5
Total perennial	29.5	23.2	0.75	33.8
Total plant	31.1	22.0	0.71	298.8

PAR sensor to estimate canopy LAI, and calculation of plot-level leaf LAI (LAI_{plot} = canopy projected LAI/plot area). Four to eight canopy LAI measurements were made on each plot on each sampling date, with these averaged to give LAI_{plot}. Leaf angle distribution was set to 1.2, similar to the value for wheat provided by manufacturer. Concurrent with LAI measurements, the relative proportions of live and dead leaves and culms were determined for each plant in the plot. Four line contact transects were established per plant, two running parallel to main axis of the canopy, two at 90° to these. For each transect, leaves and culms were pressed against a 20-cm-long thin metal rod at the height LAI was measured. Total live (green) and dead (brown and gray) leaves and culms in contact with the rod were counted, then summed across all four transects to estimate live and dead canopy fractions. These data were used to correct LAI_{plot} by live fraction to get total live LAI (LAI_{live} = LAI_{plot} × live fraction).

Midmorning (10:00–13:00 PDT) measurements of ecosystem (soil and plant) H_2O and CO_2 fluxes were made every week from May 8 to June 25, 2015 at each 0.75 × 0.75 m plot centered around plants monitored for θ and ψ_{pd} using an open-path infrared gas analyzer (IRGA; Li-7500, LiCOR Instruments, Lincoln, Nebraska, USA) under PC control. A 0.75 × 0.75 × 0.75 m (0.422 m^3) chamber of tightly sewn polyethylene held taut within a frame of PVC pipe (Shelter Systems, Santa Cruz, California, USA) was placed over the plot following ca 10 s of aeration and sealing the chamber base with a heavy chain. Changes in [CO_2] and [H_2O] were measured every 1 s for a minimum sampling time of 60 s, following an initial 20–30 s of air mixing provided by a small fan placed under the tripod holding the IRGA, and oriented 70–90° from the soil surface. Chamber material allowed 92% of photosynthetically active radiation (PAR) to pass into the chamber, while allowing infrared radiation (IR) to escape, maintaining chamber air temperatures within 1–2°C of external conditions (Potts et al. 2006). External ambient PAR levels were measured adjacent to the tent chamber every 5 s with a leveled PAR sensor (Apogee Instruments, Logan, Utah, USA) at 1 m above the soil surface on a tripod, with these observations averaged across the flux sampling period. After ambient light measurement, the chamber was removed, aerated, and replaced over the plot in same orientation, sealed, and covered with a cover made of reflective mylar safety blankets to repeat flux measurements in the dark. Ambient light measures provided estimate of net ecosystem CO_2 exchange (NEE) and evapotranspiration (ET); dark measurements estimate ecosystem respiration (R_{eco}), and, by subtraction, gross ecosystem photosynthesis (GEP = NEE − R_{eco}). We followed the sign conventions for NEE typically used in eddy-covariance studies, with negative values indicating ecosystem carbon uptake (GEP > R_{eco}) and positive values indicating ecosystem carbon loss (R_{eco} > GEP). Plot-level GEP was divided by LAI_{live} to estimate leaf-level photosynthesis integrated across the whole canopy (GEP_{live}). Instantaneous ecosystem water use efficiency was estimated as GEP/ET.

Biomass and specific mass

One week after the last gas exchange measurement, when flowering and seed set had occurred in all plots, all plants were harvested for determining biomass and specific mass

(g/m^2) of canopy constituents. Prior to clipping to the basal crown, total flowering culms were counted, clipped and placed into a paper bag for curing. Reproductive biomass was separated into structural reproductive support fractions (i.e., terminal culm, rachilla, and glumes) and seed fractions (palea, lemma, awn, and endosperm), with the latter further subdivided into filled (successful) and unfilled (aborted) seed fractions. The vegetative portion of the plant was then harvested, wrapped in moist paper towels, and transported back to the laboratory and stored in a refrigerator to await further processing. Live (green) and dead (yellow and gray) biomass were separated; dead biomass was then dried and weighed. Live vegetative biomass was then separated into culms and leaves, and then scanned on a flatbed scanner. Scanned images were analyzed using WhinRhizo software (Regent Instruments, Chateau Ste. Foy, Quebec, Canada) to determine the area (cm^2) of leaf and culm fractions; leaf area was estimated from the projected silhouette area, culm area was calculated of a cylinder using the culm diameter determined by the software. All vegetative tissue was then dried at 60°C for 48 h, and then weighed. Dry weights were used to provide plant biomass (g/plant), and the specific mass of leaves and culms (g/m^2).

Statistical analysis

We analyzed all preclip canopy, ψ_{pd}, daily θ_{5cm} and θ_{15cm}, ET, NEE, R_{eco}, GEP, GEP_{live}, and GEP/ET with two-way analysis of variance (ANOVA; Statistix v8.0, Analytical Software, Tallahassee, Florida, USA) to determine baseline differences between species and the plots selected for controls and experimental clipping before we clipped. After this, we used a split-plot, repeated-measures ANOVA (RM-ANOVA) to test for postclip differences in these between species, clipping treatment, and species-by-clipping interaction over the 7-week regrowth period. The whole-plot (between treatment) effects were species, clipping treatment, and the species-by-clipping interaction, using the species-by-clipping-by-replicate interaction as the whole-plot F-test error term. Sub-plot (within treatment) effects were date, date-by-species, date-by-clipping, and date-by-species-by-clipping treatment interactions, using the

species-by-clipping-by-date-by-replicate interaction effect as the sub-plot F-test error term. For the final harvest data, two-way ANOVA was used to test for species, clipping treatment, and species-by-clipping interaction effects. All percent data were arcsine transformed to meet ANOVA data distribution assumptions, post hoc means testing for all ANOVA was made using via α-corrected LSD. All final harvest and growing season environmental, canopy growth, and plant functional data are provided (Appendices S3 and S4, respectively), along with metadata (Appendix S1) and column descriptions (Appendix S2) for these.

Linear regression (Statistix v8.0) was used to determine the strength of the relationships of GEP with LAI_{live}, and R_{eco} with θ_{5cm} and θ_{15cm} to see which soil depth moisture most strongly affected R_{eco}, then using an F-test to see if slopes of clipped and unclipped controls significantly differed within each species. To detect compensatory regrowth over the postclipping period, we regressed LAI_{live} data against day of year (DOY), starting with the first DOY after clipping, and used an F-test to compare the slopes of clipped and unclipped controls within each species.

Results

Prior to clipping, *P. spicata* and *E. elymoides* plots had significantly different whole-plot LAI ($F_{1,12}$ = 9.31; P = 0.010), with *P. spicata* plots having higher LAI_{plot} (0.61 m^2/m^2 ± 0.052 SE) than *E. elymoides* plots (0.43 m^2/m^2 ± 0.028 SE). There were no differences in LAI_{plot} between plots selected for unclipped and clipped treatments (Fig. 1). Species differences were also apparent θ_{15cm} ($F_{1,12}$ = 4.77; P = 0.049), with θ_{15cm} higher under *P. spicata* (0.17 mol/mol ± 0.010 SE) than *E. elymoides* (0.14 mol/mol ± 0.010 SE), again with no difference between plots assigned to the two clipping treatments (Fig. 2). Plots selected for clipping also differed in R_{eco} ($F_{1,12}$ = 4.78 P = 0.049), and were higher (1.81 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ± 0.133 SE) than those assigned to be unclipped (1.37 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ± 0.156 SE). There were no differences between species or plots selected for clipping treatments in LAI_{live} (Fig. 1), θ_{5cm}, ψ_{pd} and ET (Fig. 2), NEE and GEP (Fig. 3), or GEP_{live} and GEP/ET (Fig. 4).
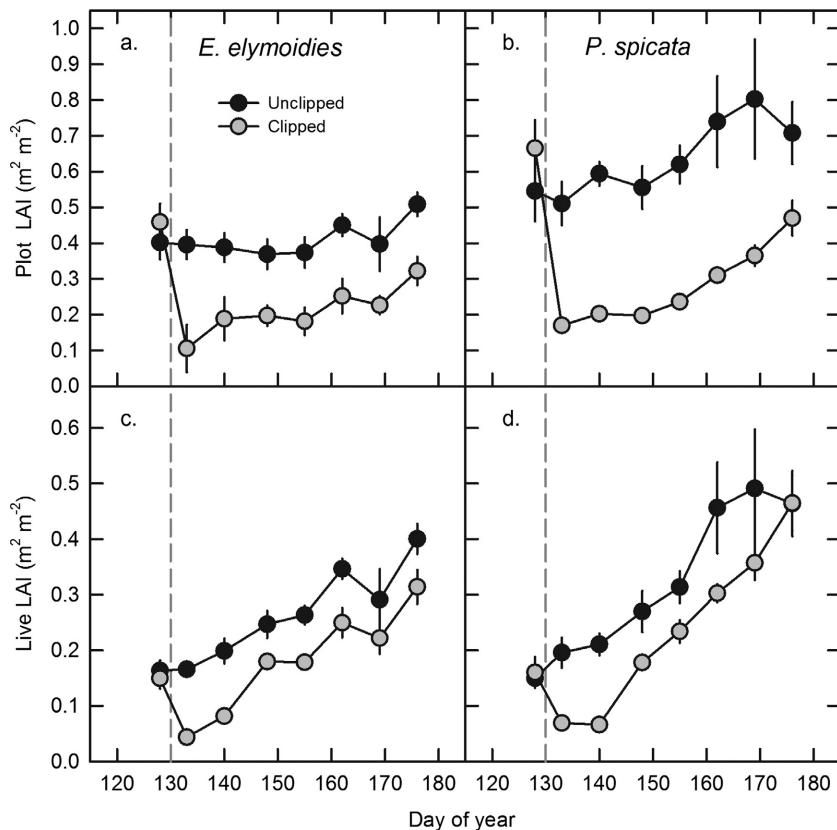
Fig. 1. Total plot leaf area index (LAI$_{plot}$) in unclipped (black) and clipped (gray) plots dominated by (a) *Elymus elymoides* and (b) *Pseudoroegneria spicata*, and live LAI (LAI$_{live}$) of unclipped and clipped (c) *E. elymoides* and (d) *P. spicata* plots. Each symbol is the mean of four measurements; error bars are ± 1 SE. Dashed line delineates pre and postclipping sampling.

LAI$_{plot}$ and LAI$_{live}$ were significantly lower in clipped plots than unclipped plots pooled over the study (Table 3). Clipping reduced LAI$_{plot}$ by 74%, and LAI$_{live}$ by 71% in *E. elymoides* and 57% in *P. spicata* plots (Fig. 1). *P. spicata* and *E. elymoides* plots differed in LAI$_{plot}$ and LAI$_{live}$ (Table 3), with *P. spicata* plots having higher levels in both variables (Fig. 1). Clipping did not significantly alter proportional differences in LAI$_{plot}$ or LAI$_{live}$ between the species, as indicated by lack of significant species-by-clipping interactions (Table 3). There was a significant species-by-time interaction in LAI$_{plot}$ and LAI$_{live}$, indicating species-specific differences in canopy development (Table 3). LAI$_{plot}$ in *E. elymoides* did not change markedly until last week of sampling (Fig. 1a), whereas *P. spicata* LAI$_{plot}$ stared

increasing the 3rd week after clipping (Fig. 1b), with proportionally more LAI$_{live}$ development in *P. spicata*, especially in unclipped controls (Fig. 1d) than in unclipped *E. elymoides* (Fig. 1c), and in clipped plots later in the study (Fig. 1d).

LAI$_{live}$ had a significant positive linear relationship with time for *E. elymoides* ($R^2 = 0.58$; $F_{1,54} = 76.19$; $P \leq 0.001$) and *P. spicata* plots ($R^2 = 0.64$; $F_{1,54} = 97.15$; $P \leq 0.001$). The slopes from these regressions did not show significant differences in the rate of LAI$_{live}$ increase, either between clipped and unclipped *E. elymoides* ($F_{1,52} = 1.01$; $P = 0.32$) or *P. spicata* plots ($F_{1,52} = 1.39$; $P = 0.24$), or between unclipped and clipped plots pooled across species ($F_{1,108} = 1.72$; $P = 0.19$). Fitted intercepts differed between clipping treatments for *E. elymoides* ($F_{1,53} = 53.94$; $P \leq 0.001$) and *P. spicata*
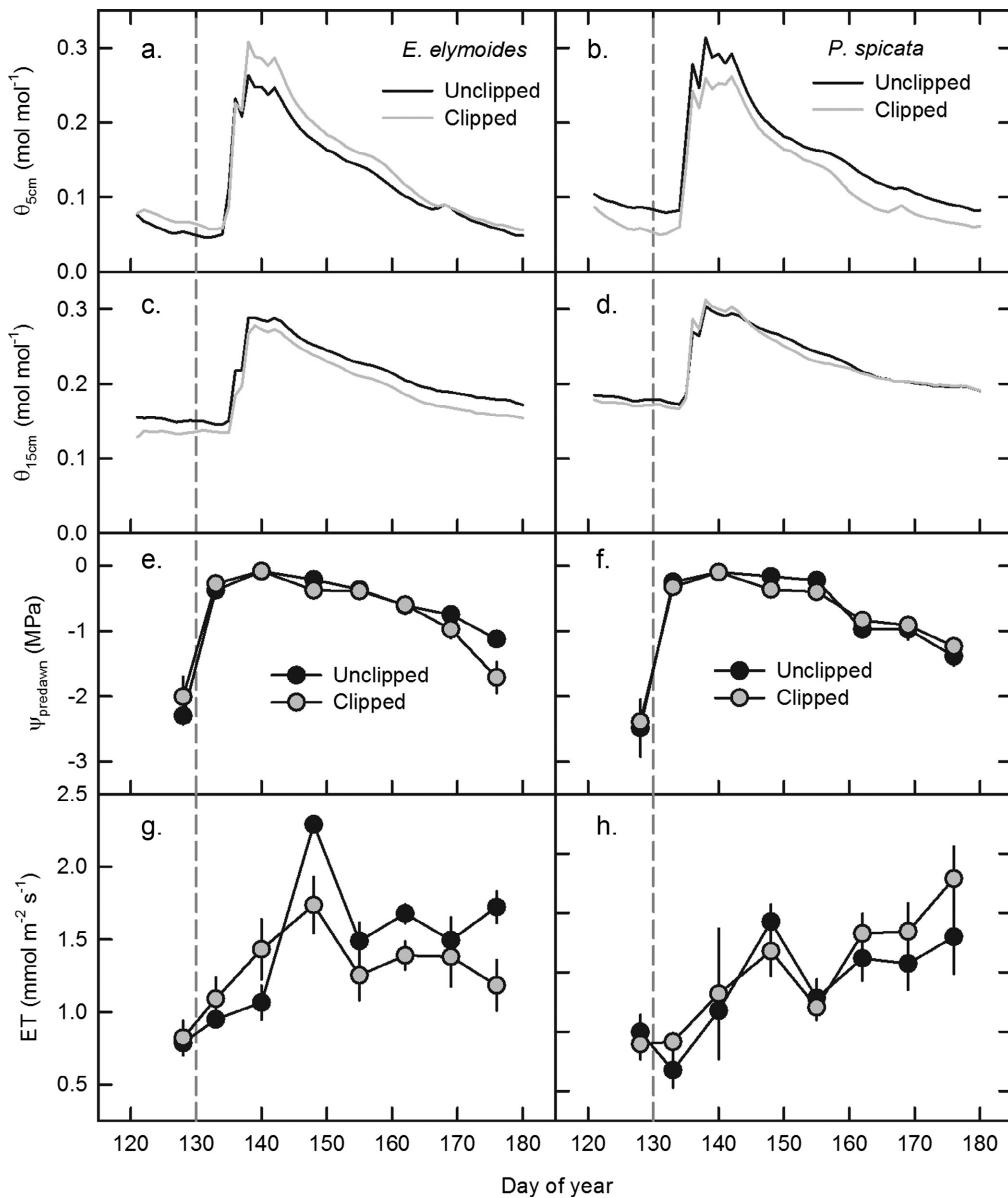
Fig. 2. Volumetric soil moisture (θ) at 5 cm under unclipped (black) and clipped (gray) (a) *Elymus elymoides* and (b) *Pseudoroegneria spicata*, and θ_{15cm} under unclipped and clipped (c) *E. elymoides* and (d) *P. spicata*. Predawn water potential (ψ_{pd}) of unclipped and clipped (e) *E. elymoides* and (f) *P. spicata*, and plot-level evapotranspiration (ET) for unclipped and clipped (g) *E. elymoides* and (h) *P. spicata* plots. Each symbol is the mean of four measurements; error bars are ±1 SE; dashed line delineates pre and postclipping sampling.

($F_{1,53} = 25.15$; $P \leq 0.001$), indicated by higher initial LAI$_{live}$ in unclipped controls (Fig. 1c, d).

Volumetric soil moisture (θ) at 5 cm did not differ between species ($F_{1,12} = 0.29$), or clipping treatments ($F_{1,12} = 0.16$), as was the case for θ_{15cm} ($F_{1,12} = 2.40$ and $F_{1,12} = 0.45$ for species

and clipping effects, respectively). There were also no species-by-time interactions for θ_{5cm} ($F_{1,12} = 2.21$) or θ_{15cm} ($F_{1,12} = 0.21$). Volumetric soil moisture only showed significant variation between sampling dates (θ_{5cm}: $F_{6,72} = 265.09$; $P \leq 0.001$, and θ_{15cm}: $F_{6,72} = 442.27$; $P \leq 0.001$),

following marked increases in θ following 3 d of rain in May (Fig. 2a, b). Predawn water potential (ψ_{pd}) did not differ between species, but did between clipping treatments, with significant species-by-time and species-by-clipping-by-time interactions (Table 3). Overall ψ_{pd} in clipped plants (−0.61 MPa ± 0.063 SE) was lower than in unclipped plants (−0.54 MPa ± 0.058 SE). The species-by-time interaction stemmed from divergence in ψ_{pd} over last three sampling dates, with *P. spicata* ψ_{pd} showing marked declines compared to levels in *E. elymoides* (Fig. 2e, f). The three-way interaction arose from greater differences in ψ_{pd} between clipped and unclipped *E. elymoides* plants, whereas clipped and unclipped *P. spicata* had similar ψ_{pd} over the last two sampling dates (Fig. 2e, f). The low ψ_{pd} in clipped *E. elymoides* also drove the significant clipping effect (Table 3). Evapotranspiration (ET) had significant species-by-time and clipping-by-time interaction effects (Table 3); the latter due to higher ET in unclipped plots on the third week after clipping, especially in unclipped *E. elymoides* (Fig. 2g, h). This, in addition to *P. spicata* having higher ET than *E. elymoides* plots over the last three sampling dates (Fig. 2h), drove the species-by-time interaction.

Net ecosystem CO_2 exchange (NEE) differed significantly between *E. elymoides* and *P. spicata* plots and across sampling dates, and was not affected by clipping, with no significant interaction effects (Table 3). NEE in *P. spicata* plots was more negative (−1.64 μmol · m^{-2} · s^{-1} ± 0.225 SE) than in *E. elymoides* plots (−0.83 μmol·m^{-2}·s^{-1} ± 0.195 SE). This reflected differences in gross ecosystem photosynthesis (GEP), not ecosystem respiration (R_{eco}), which did not differ between *E. elymoides* and *P. spicata* plots (Table 3). Indeed, linear regression analysis showed NEE did not significantly vary with R_{eco}, but had a strong, negative linear relationship with GEP (NEE = 1.73−0.77 × GEP; $R^2 = 0.77$; $P \leq 0.001$; data not shown), indicating GEP was the primary determinant of NEE in our study. Neither of the constituent fluxes differed between clipping treatments, or had a significant species-by-clipping interaction (Table 3). GEP and R_{eco} did show significant species-by-time interactions, with GEP also having a clipping-by-time interaction (Table 3). The species-by time-interaction in R_{eco} was due to higher R_{eco} in *P. spicata* over the last three

sampling dates compared to *E. elymoides* plots (Fig. 3c, f). In GEP, this interaction arose from higher GEP rates in *P. spicata* plots over the last four sampling periods, mainly from higher in GEP unclipped *P. spicata* plots (Fig. 3f). The GEP clipping-by-time interaction reflected lower clipped plot GEP from weeks 1 to 3, after which GEP were similar between clipping treatments over the rest of the study (Fig. 3e, f).

LAI$_{live}$-corrected GEP (GEP$_{live}$) did not differ between species, but did between clipped and unclipped plots, with no significant interaction effects (Table 3). GEP$_{live}$ was higher in clipped plots (17.5 μmol·m^{-2}·s^{-1} ± 0.73 SE) than unclipped treatments (14.0 μmol·m^{-2}·s^{-1} ± 0.61 SE), underlain by consistently high GEP$_{live}$ in clipped *P. spicata* plots (Fig. 4a, b). GEP$_{live}$ was highest in weeks three and four (Fig. 4a, b), when PAR levels were markedly higher than over the previous two sample dates (data not shown), and then reduced with increasing LAI$_{live}$ (Fig. 1c, d) and declining θ and ψ_{pd} (Fig. 2). Ecosystem water use efficiency (GEP/ET) differed significantly between species and clipping treatments, with a significant clipping-by-time interaction (Table 3). *P. spicata* plots had higher overall GEP/ET (2.94 μmol/mmol ± 0.137 SE) than *E. elymoides* plots (2.27 μmol/mmol ± 0.118 SE), mainly from higher GEP/ET over the last three sampling periods (Fig. 3c, d). Unclipped plots had higher overall GEP/ET (2.83 μmol/mmol ± 0.108 SE) compared to clipped counterparts (2.38 μmol/mmol ± 0.152 SE), which had very low GEP/ET over the two sampling periods after defoliation (Fig. 4c, d). After this, GEP/ET increased and converged between unclipped and clipped plots (Fig. 4c, d), giving rise to the clipping-by-time interaction (Table 3).

Ecosystem respiration (R_{eco}) had a stronger linear relationship with volumetric soil moisture at 15 cm (θ_{15cm}) in *E. elymoides* ($R^2 = 0.55$; $P \leq 0.05$) and *P. spicata* plots ($R^2 = 0.25$; $P < 0.05$) compared to θ_{5cm} ($R^2 = 0.47$ and $R^2 = 0.16$; $P \leq 0.05$ for *E. elymoides* and *P. spicata*, respectively). Clipping reduced the strength and degree of slope of the R_{eco}/θ_{15cm} relationship in *E. elymoides* (Fig. 5a) and *P. spicata* (Fig. 5b), but these changes were not significant for either ($F_{1,52} = 3.04$; $P = 0.09$ and $F_{1,52} = 0.93$; $P = 0.34$ for *E. elymoides* and *P. spicata*, respectively), or between clipped and unclipped controls
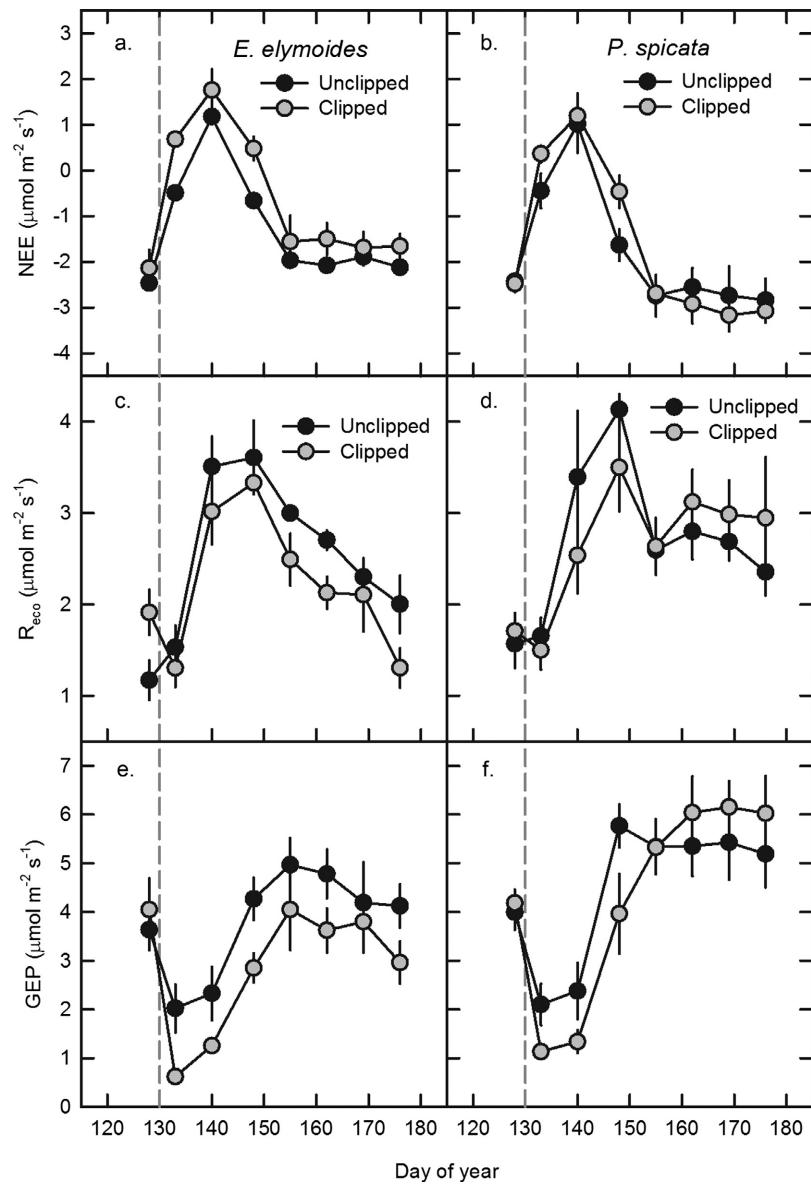
Fig. 3. Unclipped (black symbols) and clipped (gray symbols) plot-level net ecosystem carbon dioxide exchange (NEE) of (a) *E. elymoides* and (b) *P. spicata* plots, ecosystem respiration (R_{eco}) in (c) *E. elymoides* and (d) *P. spicata* plots, and gross ecosystem photosynthesis (GEP) for (e) *E. elymoides* and (f) *P. spicata* plots. Positive NEE indicate ecosystem carbon loss (R_{eco} > GEP), negative NEE indicate ecosystem carbon uptake (GEP > R_{eco}). Each symbol is the mean of four measurements; error bars are ±1 SE; dashed line delineates pre and postclipping sampling.

pooled across species ($F_{1,108}$ = 1.95; P = 0.16). LAI_{live} explained a similar amount of variance in GEP in *E. elymoides* (R^2 = 0.52; $P \leq 0.05$) and *P. spicata* plots (R^2 = 0.52; $P \leq 0.05$). Slopes of clipped and unclipped *E. elymoides* GEP/LAI_{live} relationships were similar (9.7 and 11.2, respectively; Fig. 5c) ($F_{1,52}$ = 0.21; P = 0.64). *P. spicata*

plots had more pronounced slope differences between clipped (12.5) and unclipped controls (8.2; Fig. 5d); however, these were not strongly significantly different ($F_{1,52}$ = 3.10; P = 0.08). Pooled across both species, clipped plots had significantly steeper GEP/LAI_{live} relationships (12.9) than unclipped controls (8.7; $F_{1,108}$ = 5.22;

Table 3. Split-plot, repeated-measures analysis of variance (RM-ANOVA) *F*-test results testing for differences between clipped and unclipped *Elymus elymoides* and *Pseudoroegneria spicata* plots over the 7-week postdefoliation period. Variables are total plot and live leaf area index, plant predawn water potential (ψ_{pd}), evapotranspiration (ET), and carbon dioxide fluxes of net ecosystem CO_2 exchange (NEE), ecosystem respiration (R_{eco}), gross ecosystem photosynthesis (GEP), live LAI-corrected GEP (GEP_{live}), and instantaneous water use efficiency (GEP/ET); effect subscripts are degrees freedom for each *F*-test.

$Effect_{df}$	LAI_{plot} (m^2/m^2)	LAI_{live} (m^2/m^2)	ψ_{pd} (MPa)	ET (mmol· $m^{-2}·s^{-1}$)	NEE (µmol· $m^{-2}·s^{-1}$)	R_{eco} (µmol· $m^{-2}·s^{-1}$)	GEP (µmol· $m^{-2}·s^{-1}$)	GEP_{live} (µmol· $m^{-2}·s^{-1}$)	GEP/ET (µmol/ mmol)
$Spp_{1,12}$	14.80*	7.00*	0.65	0.37	10.58*	3.09	10.14*	2.01	37.87*
$Clip_{1,12}$	52.10*	16.58*	6.22*	0.01	2.39	1.72	3.09	10.56*	17.86*
$S \times C_{1,12}$	4.49	0.06	3.94	1.93	1.00	1.01	1.49	3.28	0.01
$Week_{6,72}$	26.96*	94.67*	127.13*	25.99*	89.05*	33.59*	78.71*	15.37*	37.43*
$W \times S_{6,72}$	4.75*	7.11*	2.91*	5.00*	1.57	3.66*	4.83*	1.91	1.88
$W \times C_{6,72}$	1.55	2.03	1.80	2.73*	1.93	1.11	3.03*	1.68	6.90*
$W \times S \times C_{6,72}$	2.08	1.27	3.99*	2.12	0.21	1.75	1.59	0.20	0.79

*$P < 0.05$.

P = 0.02). Clipping markedly strengthened the relationship between GEP and LAI_{live} in both *E. elymoiodes* (Fig. 5c) and *P. spicata* plots (Fig. 5d).

Total plant biomass (live + dead + reproductive) significantly differed between species and clipping treatments, with no interaction effect (Table 4). *Pseudoroegneria spicata* had greater total plant biomass (31.7 g/plant ± 7.07 SE) compared to *E. elymoides* (10.9 g/plant ± 1.99 SE), whereas unclipped plants (30.8 g/plant ± 7.29 SE) had higher total biomass than clipped plants (11.8 g/plant ± 2.41 SE). Differences in total biomass were not consistent across biomass components; live biomass mass did not significantly differ between clipping treatments (Table 4; Fig. 6a), whereas dead biomass showed significant clipping and species-by-clipping interaction effects, with reproductive biomass was significantly affected only by clipping (Table 4). Dead biomass was lower in clipped (0.7 g/plant ± 0.13 SE) than in unclipped plants (14.4 g/plant ± 4.99 SE), with the species-by-clipping interaction arising from lower dead mass in control *P. spicata* compared to clipped plants that was not apparent in *E. elymoides* (Fig. 6a). Overall differences in reproductive biomass between *E. elymoides* (2.3 g/plant ± 0.49 SE) and *P. spicata* (0.13 g/plant ± 0.086 SE) were consistent between clipped and unclipped plants (Fig. 6a), thus, even though *P. spicata* reproductive biomass did not differ between clipping treatments (Fig. 6a), there was

no significant species-by-time interaction effect (Table 4).

Proportional biomass had markedly different patterns of significance compared to those from absolute values (Table 4). Percent live biomass did not differ between species, but did show significant clipping and species-by-clipping interaction effects (Table 4). Clipped plants had more live biomass (81.2% ± 5.96 SE) compared to unclipped (51.2% ± 2.62 SE). *E. elymoides* percent live biomass did not differ between clipped and unclipped plants, whereas proportions in *P. spicata* did (Fig. 6b). Dead biomass proportions differed between species and clipping, with a species-by-clipping interaction (Table 4). In *P. spicata*, dead biomass contributed more to total biomass (29.5% ± 9.26 SE) than in *E. elymoides* (16.2% ± 3.12 SE), and unclipped plants had more dead (38.4% ± 5.96 SE) than clipped counterparts (7.3% ± 1.87 SE). Species differences in percent dead biomass were apparent in unclipped plants, whereas clipped plants had similar proportions of dead material (Fig. 6b); hence the two-way interaction. Total proportional reproductive biomass (seeds + support structures) differed only between species (Table 4), and were higher in *E. elymoides* (21.0% ± 2.15 SE) than in *P. spicata* (0.5% ± 0.34 SE). The patterns of significance in the proportions of the two reproductive fractions to total biomass differed from total biomass proportions (Table 4). Seed and support structures showed significant
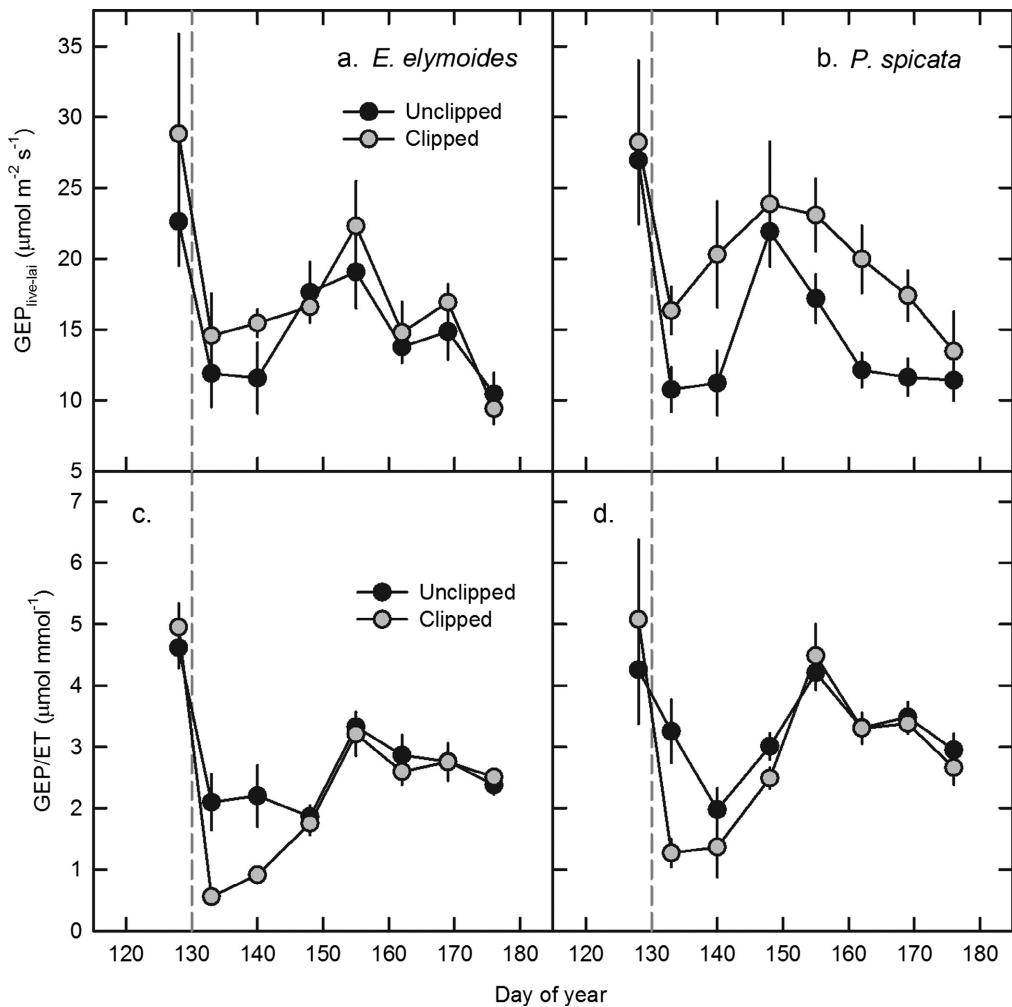
Fig. 4. Live leaf area index corrected gross ecosystem photosynthesis (GEP$_{live}$) in unclipped (black symbols) and clipped (gray symbols) in (a) *Elymus elymoides* and (b) *Pseudoroegneria spicata* plots, and ecosystem water use efficiency (GEP/ET) in (c) *E. elymoides* and (d) *P. spicata* plots. Each symbol is the mean of four measurements; error bars are ±1 SE; dashed line delineates pre and postclipping sampling.

responses to clipping, and had significant species by clipping interactions (Table 4). The proportion of biomass in seeds in *E. elymoides* (9.2% ± 2.32SE) and support structures (11.8% ± 2.98 SE) were dramatically higher than in *P. spicata* (0.26% ± 0.193 SE and 0.28% ± 0.205 SE for seed and support structures, respectively). The interaction effects in these two fractions were due to different reasons. In *E. elymoides*, proportional seed contributions in controls were significantly higher than in clipped plants, whereas proportions of support structures were significantly lower than in clipped plants (Fig. 6c).

Total surface area per plant differed between species and clipping treatments, with no interaction effect (Table 5). Control and clipped *P. spicata* had similar total surface area (1367.3 cm^2 ± 280.26 SE and 1167.6 cm^2 ± 174.83 SE, respectively), significantly higher than *E. elymoides*, which also had significant differences between unclipped (971.5 cm^2 ± 37.03 SE) and clipped plants (423.2 cm^2 ± 58.37 SE). Total leaf area and culm area per plant significantly differed between *E. elymoides* and *P. spicata*, but neither were significantly affected by clipping (Table 5). *P. spicata* had higher overall leaf (752.5 cm^2/plant
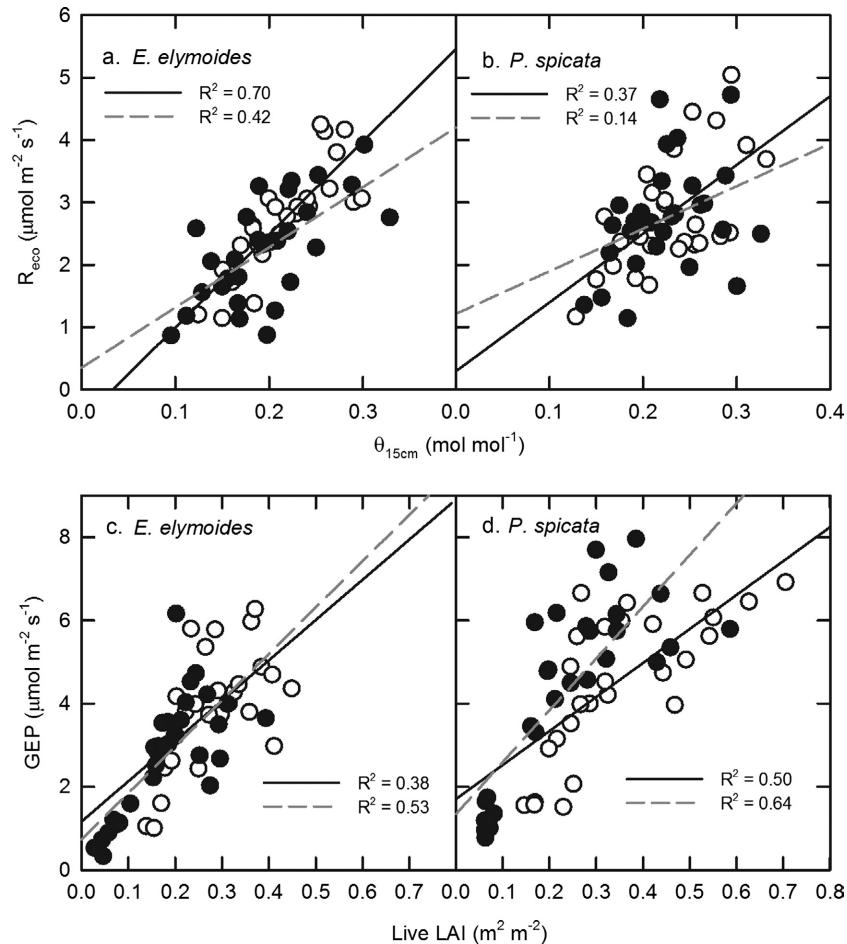
Fig. 5. Relationship between ecosystem respiration (R_{eco}) and volumetric soil moisture (θ_{15cm}) in unclipped (white symbols, solid line) and clipped (black symbols, dashed line) (a) *Elymus elymoides* and (b) *Pseudoroegneria spicata* plots, and relationship of gross ecosystem photosynthesis (GEP) with live leaf area index (LAI_{live}) in unclipped and clipped (c) *E. elymoides* and (d) *P. spicata* plots. All R^2 are significant at $P \leq 0.05$.

± 85.46 SE) and culm area (515.1 cm²/plant ± 81.82 SE) than *E. elymoides* (468.8 cm²/plant ± 74.92 SE and 228.5 cm²/plant ± 51.51 SE, for leaf and culm areas, respectively). Post hoc means testing did show significantly lower total leaf area in clipped (298.2 cm²/plant ± 30.92 SE) and control (639.5 cm²/plant ± 76.32 SE) *E. elymoides*, and a similar trend in culm area (Fig. 7a). Overall, clipping effects on leaf area ($P = 0.083$) and culm area ($P = 0.064$) were not strongly significant, but were sufficient for clipping to significantly reduce overall photosynthetic area (Table 5). Specific leaf mass (SLM) was also not vary significantly between clipping treatments, but did differ between species (Table 3), with *P. spicata* having greater SLM

(163.1 g/m² ± 3.67 SE) than *E. elymoides* (97.1 g/m² ± 5.24 SE). In contrast to SLM, specific culm mass significantly differed between species and clipping treatments, with no significant interaction effect (Table 3). Specific culm mass in *P. spicata* (124.3 g/m² ± 9.93 SE) exceeded *E. elymoides* (90.5 g/m² ± 2.91 SE). Pooled across species, specific culm mass in unclipped plants (118.1 g/m² ± 11.71 SE) were greater than in clipped plants (96.7 g/m² ± 4.39 SE). Though post hoc means testing showed clipped and control *E. elymoides* did not differ significantly in specific culm mass (Fig. 7b), these proportional differences were consistent with those in *P. spicata* counterparts, which did have significantly different specific

Table 4. Two-way ANOVA *F*-test results testing for differences between clipped and unclipped *Elymus elymoides* and *Pseudoroegneria spicata* total plant biomass and biomass constituents and their percent contributions to total plant biomass; effect subscripts are degrees freedom for each *F*-test, results from proportional results are from arcsine transformed data.

Effect$_{df}$	Total	Live veg.	Dead veg.	Repro.	% Live	% Dead	% Repro.	% Seed	% Repro. support
Species$_{1,12}$	17.23*	30.66*	12.72*	28.36*	3.52	37.88*	81.25*	25.11*	27.83*
Clip$_{1,12}$	14.41*	4.10	19.83*	5.43*	59.75*	206.87*	0.43	5.56*	6.75*
Spp × Clip$_{1,12}$	3.70	0.01	12.03*	4.51	24.94*	66.87*	0.41	6.29*	7.32*

*$P < 0.05$.

culm mass between treatments (Fig. 7b), giving rise to the significant clipping effect and lack of a strong species by species-by-clipping interaction ($P = 0.077$; Table 5).

Overall, *E. elymoides* produced more seed heads (35.5 heads/plant ± 8.07 SE) than *P. spicata* (2.6 heads/plant ± 2.11 SE) ($F_{1,12} = 23.64$; $P = 0.0004$), with a significant species-by-clipping interaction ($F_{1,12} = 5.69$; $P = 0.034$) driven by significant differences between control and clipped *E. elymoides* (Table 6). Also, proportional differences between clipped and unclipped *E. elymoides* (Table 6) were not enough to result in a significant clipping effect ($F_{1,12} = 3.63$; $P = 0.081$). Clipping reduced seed mass per live biomass ($F_{1,12} = 6.39$; $P = 0.026$), seed mass per live area ($F_{1,12} = 4.76$; $P = 0.050$) and seed mass per seed head ($F_{1,12} = 12.41$; $P = 0.004$), with significant species-by-clipping interactions for these parameters ($F_{1,12} = 6.65$; $P = 0.024$ for seed mass per live biomass, $F_{1,12} = 5.08$; $P = 0.044$ for seed mass per live area, and $F_{1,12} = 7.89$; $P = 0.016$ for seed mass per seed head). All of these effects were driven by the fact that unclipped *E. elymoides* plants had much higher seed mass per biomass, live area, and per seed head than all other species-treatment combinations (Table 6).

Discussion

As hypothesized, NEE in our study was similar between clipping treatments pooled across species, in agreement with larger scale studies showing grazed and ungrazed upland rangelands did not differ substantially in NEE (Risch and Frank 2006, Polley et al. 2008, Niu et al. 2010). However, this was not due to parallel decreases and increases in R_{eco} and GEP over the postclipping period. In contrast to grazed and ungrazed North American mixed grass prairie (Polley et al. 2008), clipping did not affect R_{eco} more than GEP; in fact, R_{eco} did not differ between species or clipping treatment and only responded to variation in soil moisture. Thus, similar NEE between clipped and unclipped plots was primarily driven by variation in GEP, in contrast to Polley et al. (2008). Though GEP did not differ between clipped and unclipped plots, GEP in clipped plots remained below unclipped plot levels over the first three weeks of regrowth, after which GEP between treatments converged to similar overall GEP. Contrary to our expectations, the convergence in GEP was not driven by accelerated compensatory regrowth. LAI$_{live}$ did not increase at a faster rate compared to LAI$_{live}$ in control plants, which started with higher LAI$_{live}$, and maintained this throughout the study. Clipping did enhance LAI$_{live}$-corrected GEP (GEP$_{live}$), especially in *P. spicata*, and the sensitivity of GEP to LAI$_{live}$, supporting our hypothesis. It is notable that GEP$_{live}$ was higher in clipped plants over the first 2 weeks after clipping, when LAI$_{plot}$ and LAI$_{live}$ did not change markedly in either species. This higher GEP$_{live}$ could reflect a transient period of compensatory photosynthetic upregulation in the remaining live tissue. As observed previously, this did not follow improved plant water status (Senock et al. 1991, Doescher et al. 1997); clipped plants either had the same, or slightly lower ψ_{pd} compared to controls (Fig. 2). Other studies have suggested grazing leads to increased volumetric soil moisture that can support compensatory responses (Doescher et al. 1997, Asner et al. 2004, Loeser et al. 2004). However, this was not the case in our study, though such differences may require
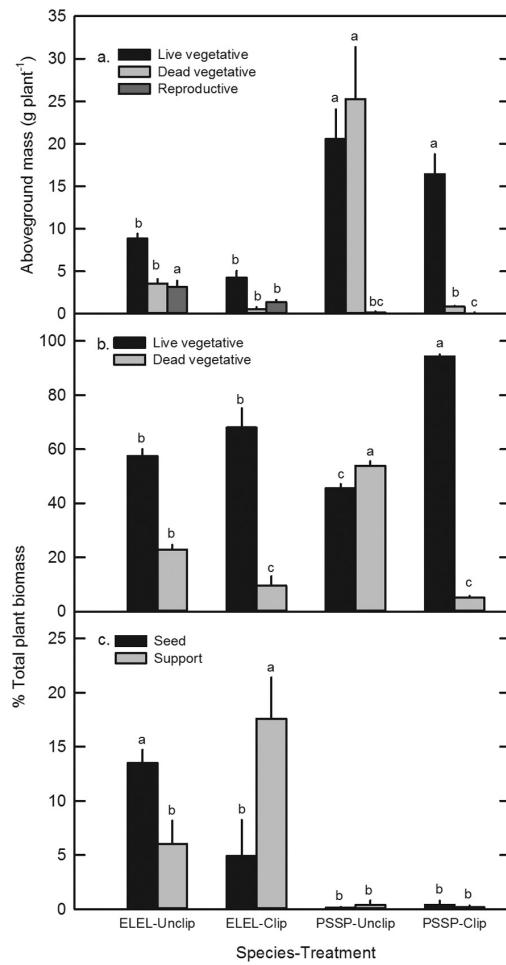
Fig. 6. Components of total live aboveground biomass (a), and percent contributions of (b) live and dead vegetative and (c) seed and reproductive support structures to total biomass of unclipped and clipped *Elymus elymoides* (ELEL) and *Pseudoroegneria spicata* (PSSP) plants. Each bar is the mean of four measurements, error bars are +1 SE; letters differ significantly within structures at $P \leq 0.05$ (α-adjusted LSD from two-way ANOVA; Table 4).

longer time scales to emerge than in our study (Asner et al. 2004).

The relative insensitivity of GEP_{live} to soil moisture strongly suggests clipping stimulated GEP_{live} primarily by increasing canopy-level light penetration. The first two sampling periods were very cool and cloudy, with low prevailing PAR (data not shown). We found PAR above 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was sufficient for maximum NEE and GEP (data not shown). Clipping

Table 5. Two-way ANOVA *F*-test results testing for differences clipped and unclipped *Elymus elymoides* and *Pseudoroegneria spicata* total plant leaf and culm area and specific mass (SM) of leaves and culms at the end of the 2015 study period; effect subscripts are degrees freedom for each *F*-test.

Effect$_{df}$	Leaf area (cm²)	Culm area (cm²)	Leaf SM (g/m²)	Culm SM (g/m²)
Spp$_{1,12}$	7.93*	10.19*	116.22*	17.32*
Clip$_{1,12}$	3.59	4.16	1.21	6.92*
Spp × Clip$_{1,12}$	2.23	0.07	3.73	3.73

*$P < 0.05$.

may have increased the penetration of diffuse light into the canopy, stimulating GEP_{live} at this time, augmenting any compensatory photosynthesis. Diffuse light is highly effective in driving canopy-level photosynthesis, as it increases integrated canopy PAR interception (Alton et al. 2007). Note the marked increase in *P. spicata* control plant GEP_{live} the third week after clipping (Fig. 4), which corresponded to the onset of clear, dry conditions and sustained increases in LAI_{live}. This suggests higher light levels and the increasing contribution of new leaves with higher photosynthetic capacity (Whitehead et al. 2011), contributed to higher GEP_{live} in control plants. After this peak, GEP_{live} declined over the latter part of study despite consistently higher LAI_{live}. It is likely the larger dead fraction in control plants coupled with increasing live leaf and culm growth, imposed greater self-shading, which can limit bunchgrass whole-plant carbon uptake and growth (Caldwell et al. 1983, Ryel et al. 1994, Tomlinson et al. 2007). However, self-shading could result in cooler leaf temperatures and lower stomatal conductance (Caldwell et al. 1983, Ryel et al. 1994), which could reduce leaf-level water loss at higher LAI_{live}, but still result in unclipped plots attaining similar GEP to their clipped counterparts. Self-shading is likely not as prevalent in *E. elymoides* plants, as these were smaller in stature and had lower LAI_{plot}. As a result, clipped and control *E. elymoides* plants generally attained similar GEP_{live}, and had more similar sensitivity of GEP to LAI_{live} compared to *P. spicata*. Thus, though there was some evidence of transient compensatory photosynthesis early in the study when LAI_{live} were low, convergence in GEP and greater sensitivity of GEP to LAI_{live}
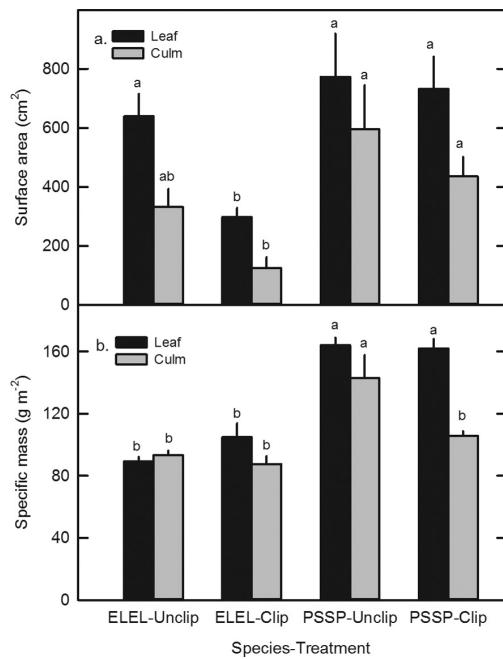
Fig. 7. Leaf and culm (a) surface area and (b) specific mass from unclipped and clipped *Elymus elymoides* (ELEL) and *Pseudoroegneria spicata* (PSSP) plants. Each bar is the mean of four measurements; error bars are +1 SE; letters indicate significant differences within structures at $P \leq 0.05$ (α-adjusted LSD from two-way ANOVA; Table 5).

was most likely due to enhanced light penetration into the canopy, and not proportionally faster regrowth compared to unclipped controls.

Contrary to our hypothesis, clipping did not significantly change the sensitivity of R_{eco} to θ. This suggests aboveground contributions to R_{eco} are small compared to soil contributions, and that autotrophic contributions to soil respiration was unaffected by defoliation. This may reflect the amount roots from surrounding grass and

shrubs (Knapp et al. 1998, Hamerlynck et al. 2013) in addition to those from our study plants, which might also explain the decreased goodness of fit in the obtained R_{eco}:θ relationship in clipped plants. We concluded that soil moisture is the principal driver of soil respiration, and this is likely the dominant component of R_{eco} in our system, as in other rangeland ecosystems (Flanagan and Johnson 2005, Barron-Gafford et al. 2011, Hamerlynck et al. 2013).

Ecosystem CO_2 flux recovered from defoliation much more quickly than did canopy development for these two arid land bunchgrasses. GEP in clipped and control plots converged the 4th week after clipping, when increasing LAI_{live} had just commenced. After this point, LAI_{live} continued to increase, and in fact nearly doubled in both species, whereas GEP was relatively invariant and did not differ between treatments. Colder temperatures early in the study likely restrained active regrowth. At this time, soil and plant water status were favorable for high photosynthetic activity, as the photosynthetic temperature optimum of these C_3 plants spans a broad range of temperatures (Smith et al. 1997), kept GEP_{live} high in clipped plants. By the 4th week, warmer temperatures released temperature-limitations to growth, whereas increased self-shading and decreasing ψ_{pd} started to limit GEP_{live}, driving similar GEP between clipped and unclipped plots. This is quite similar to findings in whole-plant gas exchange dynamics in warm desert shrubs, in which whole-plant photosynthesis is first limited by low leaf area then by increasing water stress as canopy growth reaches its maximum (Comstock and Ehleringer 1986), but with the added contribution of self-shading, which is generally not strong in desert shrubs (Smith et al. 1997). From a management perspective, our data suggest there might be a threshold level of

Table 6. Mean total number of seed heads per plant, seed mass per unit live biomass, unit live area (leaf + culm), and per seed head in clipped and unclipped *Elymus elymoides* (ELEL) and *Pseudoroegneria spicata* (PSSP).

Metric	ELEL-Control	ELEL-Clipped	PSSP-Control	PSSP-Clipped
Seed heads (no./plant)	50.0[a] (±7.88)	21.0[b] (±10.08)	1.0[b] (±1.00)	4.2[b] (±4.25)
Seed mass per live biomass (g/g)	0.239[a] (±0.0313)	0.081[b] (±0.0532)	0.003[b] (±0.0018)	0.004[b] (±0.0042)
Seed mass per live area (mg/cm^2)	2.19[a] (±0.342)	0.79[b] (±0.528)	0.04[b] (±0.028)	0.06[b] (±0.062)
Seed mass per seed head (mg)	42.5[a] (±1.27)	9.7[b] (±5.97)	7.5[b] (±7.49)	3.8[b] (±3.79)

Note: Means are from four plants, ±1 SE; letters differ significantly at $P \leq 0.05$ (α-adjusted LSD from two-way ANOVA).

LAI_{live} between 0.2 to 0.3 m^2/m^2 that could be maintained such that GEP and NEE may not be strongly affected.

Ecosystem water use efficiency is an integrative measure of rangeland ecosystem resiliency to environmental variation (Hu et al. 2008, Hamerlynck et al. 2014). Clipping induced a significant transient decrease in ecosystem water use efficiency, with lower GEP in clipped plots when ET and soil moisture was high. These immediate reductions in GEP/ET were strong enough to reduce GEP/ET in clipped plots pooled across the study, suggesting decreased resiliency in ecosystem function to disturbance. However, by the third week, before LAI_{live} began to increase and GEP had still not converged between clipped and unclipped plants, GEP/ET had converged, and stayed remarkably consistent over the rest of the study. When soils are moist, soil E contributions are the dominant component of ET; hence, under very wet conditions early in the study, ET was relatively unaffected by clipping, probably because T contributions to ET was already small, as is generally the case shortly after rainfall in rangelands (Moran et al. 2009). In contrast, GEP was strongly affected by tissue removal, leading to decline in GEP/ET. Once GEP/ET converged between clipped and unclipped controls, it was rarely as high as levels attained prior to clipping. This suggests that even over the fairly prolonged dry down after clipping, higher surface soil θ supported greater soil E, thereby reducing GEP/ET from preclip levels, when soils were drier and T represented a greater proportion of the overall ET flux (Moran et al. 2009). These, and the findings above showing more rapid convergence of GEP at low LAI_{live} between clipped and unclipped plots, suggest that the grass component of sagebrush steppe ecosystems can be remarkably resilient to disturbance, even one that removed ca. 75% of aboveground biomass. However, it should be noted that our study spans only a single growing season, and from a location at the cooler, wetter northern edge of Great Basin sagebrush steppe largely unaffected by invasive annual grasses (Svejcar et al. 2008). It is very likely the level of LAI_{live} needed to maintain NEE, GEP, and ecosystem WUE varies considerably from year to year, and could be affected by both the amount and form of antecedent winter precipitation as well as rainfall and abundance of competitive exotic annual grasses over the spring plant active period, which vary markedly with elevation and latitude across the Great Basin region (Smith et al. 1997).

Specific mass is indicative of energetic allocation to plant functional traits that reflect a species overall ecological strategy (Wilson et al. 1999). Our two study species fundamentally differed in allocation to their canopy components (Fig. 7). *P. spicata* had considerably larger and denser canopies, and within these, produced leaves and clums of high specific mass, suggesting greater energetic investment to these structures. In contrast, *E. elymoides* had smaller, more open canopies, made up of leaves and culms with lower specific masses. *E. elymoides* is likely shorter lived than *P. spicata*, but is considered more fire and grazing tolerant (Miller et al. 1994, Jones 1998). Thus, its habit of producing greater reproductive biomass and a smaller canopy of energetically less costly culms and leaves appears to fit its growth strategy. Defoliation losses of tissue with overall higher energetic costs in *P. spicata* were met in part by maintaining allocation to leaves, at the expense of reduced allocation to photosynthetic culms. Photosynthetic structures such as culms and branches typically have much lower photosynthetic capacity (Smith et al. 1997), so the return on investment in producing culms as compared to leaves after clipping may have driven this response in *P. spicata*. Such carbon allocation dynamics may be related to the relative grazing tolerances of these species, but we would need to quantify concurrent belowground growth responses to fully assess their importance in regards to grazing and climate variability (Osterheld 1992, Wilcox et al. 2015).

These differences in allocation to vegetative structures likely contributed to differences overall reproductive effort, which was considerably higher in *E. elymoides*. Production of energetically less costly photosynthetic tissues likely facilitated higher overall reproductive effort in *E. elymoides* as compared to the very low reproductive effort apparent in *P. spicata* (Dyer and Rice 1999, Huxman et al. 1999). But, by all metrics and contrary to our expectation, reproductive effort, even within *E. elymoides,* decreased with clipping. Prior to our study, winter conditions were relatively warm, with near normal levels of precipitation, but very low snow pack (NOAA

data). Therefore, soil moisture conditions when our plants initiated growth were likely drier than under more typical conditions. Thus, the increase in soil moisture in our study represents a rainfall pulse following dry antecedent conditions. Our ecosystem gas exchange results show that both species effectively utilized this pulse to sustain carbon uptake; however, this did not translate into successful reproductive effort. Second, seed set and filling typically occurs in June in these grasses (USDA Plants data base), and June conditions were abnormally warm and dry (Table 1). These likely induced plants to abort their seeds; indeed, most of our obtained seed mass came from unfilled seeds, with only 0.25 g total of filled seeds produced, with these distributed randomly across our treatments (data not shown). If future climate models are correct, there will be a shift from snow to rain for cool season water inputs across Pacific Northwest with ongoing climate change, especially at middle elevations such as NGBER (Mote 2003, Nolin and Daly 2006). Species and ecosystems can adjust net primary productivity to in response altered precipitation event sizes and their seasonal distribution (Potts et al. 2006, Heisler-White et al. 2009, Evans et al. 2012, Wilcox et al. 2015), but our work suggest these factors do not account for shifts in important population-level responses critical to the long-term viability of water-limited grazing systems.

Understanding both productivity and population-level processes will be important in effective management of semiarid grazing systems. In the face of ongoing climate change, managers of arid and semiarid rangeland ecosystems will have to use all available tools to develop novel approaches to address the often conflicting ecological and economic needs placed on rangelands (Svejcar et al. 2014). Developing land-use practices that lead to sustainable net primary productivity are always an important and desirable goal, but understanding the consequences of such practices to population and community processes is also of critical importance, and is not often accounted for in basic ecosystem studies. The best approach to addressing these management needs is to take a systems-based approach (James et al. 2013). While net primary productivity may recover quickly from defoliation, seed production for recruitment of new individuals

may require periodic rest from defoliation. Data such as from this study, gathered over a wider range of environmental conditions, will improve such efforts by providing detailed mechanistic information about the processes controlling net primary productivity and reproductive effort.

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SUPPORTING INFORMATION