The impact of invasion and subsequent removal of an exotic thistle, *Cynara cardunculus*, on CO₂ and H₂O vapor exchange in a coastal California grassland

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Abstract Changes in vegetation structure and composition, particularly due to the invasion of exotic species, are predicted to influence biosphere-atmosphere exchanges of mass and energy. Invasion of *Cynara cardunculus* (cardoon or artichoke thistle), a perennial, non-native thistle in coastal California grasslands presently dominated by non-native annual grasses, may alter rates of ecosystem CO₂ exchange and evapotranspiration (ET). During spring and summer 2006, we compared midday maximum net ecosystem CO₂ exchange (NEE) and ET among adjacent grassland plots where *Cynara* was present and where it was absent. Measurements of NEE supported the prediction that deeply-rooted *Cynara* increase midday ecosystem C-assimilation. *Cynara*-mediated shifts in NEE were associated with increases in ecosystem photosynthesis rather than changes in ecosystem respiration. Furthermore, the presence of *Cynara* was associated with increased ET during the growing season. An increase in aboveground live biomass (a proxy for leaf area) associated with *Cynara* invasion may underlie shifts in ecosystem CO₂ and water vapor exchange. Following mid-growing season sampling during April, we removed *Cynara* from half of the *Cynara*-containing plots with spot applications of herbicide. Three weeks later, midday fluxes in removal plots were indistinguishable from those in plots where *Cynara* was never present suggesting a lack of biogeochemical legacy effects. Similar to woody-encroachment in some semi-arid ecosystems, *Cynara* invasion increases midday ecosystem CO₂ assimilation and evapotranspiration rates and has the potential to increase C-storage in California coastal grasslands.

Keywords Cardoon · Evapotranspiration · Net ecosystem CO₂ exchange · Species removal experiment

Introduction

Human-mediated introductions of non-native plants are a ubiquitous global change factor affecting the composition of plant communities and the function of terrestrial ecosystems (Vitousek et al. 1996). The introduction and spread of non-native plants may increase the frequency of disturbance (D’Antonio and Vitousek 1992), alter soil nutrient availability (Ehrenfeld 2003), influence soil biota (Callaway et al. 2004) and modify the population structure of native species (Litton et al. 2006). These impacts suggest that shifts in plant community structure and composition associated with the spread of non-native
plants may interact with other human-mediated global change factors to further impact patterns and rates of ecosystem processes (Smith et al. 2000; Zavaleta et al. 2001; Geiger and McPherson 2005). However, the effects of invasive, non-native plants on the cycling of carbon and water remains poorly understood in many ecosystems (Obrist et al. 2003; Le Maitre 2004; Litton et al. 2006; Potts et al. 2006a; Prater et al. 2006; Newman et al. 2006).

In cases where non-native species represent novel plant functional traits or otherwise alter the distribution of plant functional traits in a community, invasion may substantially alter ecosystem properties such as net primary production and litter decomposition (Lavorel and Garnier 2002; Eviner 2004; Kazakou et al. 2006). For example, the invasion of species possessing traits such as rapid growth in response to resource availability (Suding et al. 2004), high photosynthetic rates (McDowell 2002) and high photosynthetic energy-use efficiency (Nagel and Griffin 2001) have the potential to alter patterns of ecosystem carbon cycling. Likewise, increased active rooting depth (Enloe et al. 2004) and increased water use efficiency (McDowell 2002) are traits associated with successful plant invaders that may potentially affect patterns of ecosystem water cycling.

*Cynara cardunculus* L. is a non-native, herbaceous, perennial thistle which has successfully invaded thousands of hectares of California grasslands presently dominated by invasive annual grasses (Gill 1990). *Cynara* was introduced to California from the Mediterranean region of Europe during the 19th century (Thomsen et al. 1986) and is recognized by the state of California as a noxious plant (http://www.cdfa.ca.gov). Similar to other successful invasive thistles, *Cynara* possesses wind dispersed seeds, is capable of rapid growth, has an extensive root system and is an effective competitor for both above- and below-ground resources (White and Holt 2005; Marushia and Holt 2006). *Cynara* canopies may approach 2 m in diameter and 2 m in height, growing much larger than the annual grasses it frequently displaces. In addition to potentially altering light availability to surrounding plants, this large canopy produces an abundant litter layer that may differ in nutrient quality and influence soil nutrient cycles (Parsons and Cuthbertson 1992). In these ways, the invasion of *Cynara* offers a non-woody analog to increasing abundances and range expansions of trees and shrubs observed in other semi-arid ecosystems.

Species removal experiments have been utilized to document effects of invasive species on entire ecosystems, including as a means to better understand the contribution of species to ecosystem function (Diaz et al. 2003). Removal experiments are also an opportunity to observe the biogeochemical legacy effects of invasive species and to assess the potential for an ecosystem to return to its pre-invasion condition. In the case of deeply-rooted perennial thistles (including *Cynara*), herbicide application is a widely-utilized and effective short-term control strategy (Sheley et al. 1999; Travinicek et al. 2005; Sheley et al. 2006). Combined with monitoring carbon and water fluxes in existing grassland and *Cynara*-occupied patches, experimental removal of *Cynara* using herbicide provides an opportunity to better understand the impact of this invasive plant on coastal grassland ecosystem function including the potential for biogeochemical legacy effects after its removal.

In the present study, we used a combination of removal and comparative approaches to determine how *Cynara* invasion affects midday CO\textsubscript{2} and water exchange in coastal grasslands. The balance of CO\textsubscript{2} assimilation by plants and respiratory losses by plants and soil microbes is an important ecosystem function and can be quantified as net ecosystem CO\textsubscript{2} exchange (NEE). NEE is expressed as the sum of CO\textsubscript{2} assimilation by photosynthesis (gross ecosystem CO\textsubscript{2} exchange; GEE) and losses of CO\textsubscript{2} by plant and soil microbial respiration (collectively termed ecosystem respiration; R\textsubscript{e}). Similarly, evapotranspiration (ET) represents the sum of stomata-mediated transpiration and evaporation from soil and canopy surfaces and is an important link in the movement of water between ecosystems and the atmosphere. Chamber-based measurements of NEE and ET have been used to demonstrate the impacts of invasive plants on above- and below-ground carbon cycling and ecosystem water balance in semi-arid grasslands of southern Arizona (Huxman et al. 2004; Potts et al. 2006a) and in the Great Basin (Prater et al. 2006).

We hypothesized that because *Cynara* is larger and more deeply rooted than the non-native annual grasses it displaces, its invasion should increase ET by transpiring greater amounts of water from deeper in the soil profile while intensifying ecosystem carbon cycling by increasing both NEE and R\textsubscript{e}, with the net effect of increasing ecosystem carbon storage.
and ecosystem water use efficiency. Moreover, we predicted that herbicide removal of *Cynara* would result in a reduction in ET, while declines in $R_e$ would exhibit a lagged response with the decomposition of above- and below-ground thistle biomass. Finally, we predicted that a mid-growing season comparison of leaf tissue stable carbon isotopes and nitrogen content of *Cynara* and the co-occurring, exotic annual grass *Avena fatua* would reveal differences in integrated plant water status and leaf quality consistent with patterns of ecosystem CO$_2$ and water vapor exchange. Specifically, we predicted that *Cynara* leaf tissue would possess less negative carbon isotope ratios and greater nitrogen content than *Avena* leaf tissue.

### Methods and materials

#### Site description

We conducted our investigation within a grassland on the campus of the University of California in Irvine, California ($33.38^\circ$ N, $117.50^\circ$ W, elev. 80 m). Historically, this site was grazed by cattle and sheep; however, for approximately the past 10 years no active management has been conducted. The site is situated on gentle slopes (<5%) located approximately 6 km from the Pacific Ocean. Soil at the site is classified as a fine, montmorillonitic, thermic Typic Chromoxerert clay derived from shale and sandstone parent material (California Soil Resource Lab, http://casoilresource.lawr.ucdavis.edu). *Cynara* has established at this site within a continuous matrix of non-native, annual grasses (primarily *Avena fatua* (L.)) and scattered, non-native forbs (e.g. *Brassica nigra* (L.) and *Vicia* spp.) at a density of approximately 5,000 individuals per hectare. Canopies of mature *Cynara* individuals present at the site range from 0.5 to 2 m in diameter.

The site experiences a Mediterranean climate with warm, dry summers and cool, moist winters. The nearest climate data is recorded approximately 7 km away at Newport Harbor, CA ($33.36^\circ$ N, $117.54^\circ$ W, elev. 1 m) where mean annual temperature is 16.3$^\circ$C and mean annual precipitation is 287 mm. Precipitation for the period December 2005–July 2006 was 179 mm (Fig. 1).

### Methods

During the spring of 2006, we designated 14 plots containing a single *Cynara* and a mix of annual grasses and forbs and 7 plots containing only annual grasses and forbs. All plots were 1 m $\times$ 1.5 m. The primary selection criteria for plots containing *Cynara* were that the thistle appeared in healthy condition and had a canopy diameter of approximately 1 m (mean = 0.92 m, SE = 0.03, $N$ = 14). The plots not containing *Cynara* (hereafter referred to as grassland plots) were selected based on the criteria that their vegetation canopy was dominated by *Avena* and that their borders were at least 1.5 m from the nearest *Cynara* canopy.

Immediately following our initial ecosystem and plant community sampling on April 20, we randomly selected half of the *Cynara*-containing plots for spot applications of the broadleaf herbicide 2,4-D (Ortho Weed-B-Gon Max, Marysville, OH USA). Herbicide was applied according to the manufacturer’s instructions. We selected 2,4-D because of its specificity to forbs, demonstrated short-term effectiveness in the control of other perennial thistle species and because of its low soil residual (Lacey et al. 1999). We returned on May 16 to compare the effects of the herbicide treatment and dominant vegetation type on ecosystem function at the time of peak biomass. To assess whether or not the ecosystem effects of *Cynara* and its removal persisted into the summer dry season, we made a final series of measurements on July 10.

#### Aboveground live biomass, litter mass and soil moisture

We estimated aboveground live biomass of annual grasses and annual forbs in each experimental plot using a $7 \times 100$ cm strip harvest sampled from the plot edge immediately following sampling on April 20 and May 16. Clipped biomass samples were oven dried, weighed and plot biomass was reported on a per area basis. For plots containing *Cynara*, we estimated aboveground live biomass as the sum of *Cynara* biomass and the biomass of the annual grasses and forbs in the remaining area (area not occupied by *Cynara* canopy) of each plot. We estimated aboveground biomass of *Cynara* during each sampling period using an allometric relationship.
between mean canopy diameter (determined with a meter stick on the canopy’s major and minor axes) and aboveground dry-weight biomass of 10 Cynara individuals harvested from an adjacent patch growing on similar slopes and soil during mid-March 2006.

Untransformed canopy diameter and dry-weight biomass data were analyzed using nonlinear regression in the form:

\[ M = aD^b \]

where \( M \) was aboveground dry-weight biomass, \( D \) was canopy diameter and \( a \) and \( b \) were the scaling coefficients derived from the regression fit to the empirical data using the curve fitting function in Sigmaplot (Systat Software Inc. Point Richmond, CA). The resulting nonlinear regression equation relating canopy diameter with aboveground biomass (\( a = 9.51E-6; b = 3.6719; r^2 = 0.99; P < 0.01 \)) was then used to estimate the biomass of Cynara within our experimental plots. Next, litter mass in each plot was estimated by collecting litter from a representative 10-cm diameter patch in the center of each plot at the beginning of the experiment in mid-April. In the case of plots containing Cynara, litter was sampled from a representative 10-cm diameter patch beneath the thistle’s canopy. We estimated volumetric soil moisture to 15-cm depth (\( \theta_{15} \)) using time-domain reflectometry (MiniTrase, Soilmoisture Equipment Corp., Santa Barbara, CA USA) in a single, central location in each plot on April 20, May 16 and July 10.

Ecosystem CO\(_2\) exchange and evapotranspiration measurements

To measure the impact of Cynara and Cynara-removal on ecosystem carbon and water exchange, we measured midday (11:00–14:00) net ecosystem CO\(_2\) exchange (NEE) and evapotranspiration (ET) under clear sky conditions. We used a closed static chamber (1.5 m long, 0.97 m wide, 1.44 m tall) temporarily seated over each plot with an open-path infrared gas exchange analyzer (LI-7500, Li-Cor Inc., Lincoln, NE) placed inside on April 20, May 16 and July 20 (Arnone and Obrist 2003; Huxman et al. 2004; Potts et al. 2006a; Prater et al. 2006). The infrared gas exchange analyzer was mounted on a tripod fit with two 15-cm-diameter electric fans to promote 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). The transparent material used for chamber construction allowed ~75% of photosynthetically-active radiation to pass into the plots, while allowing thermal radiation to escape the chambers.

After the transparent chamber was seated and a loose fringe of polyethylene sheet around the chamber’s base was secured to the ground surface with a heavy steel chain to prevent chamber leaks, 20 s elapsed during which the chamber atmosphere was thoroughly mixed by the tripod-mounted fans before measurements were begun. Carbon dioxide and water vapor concentrations were allowed to build up or decline while a computer recorded the transient changes in the chamber atmosphere. We observed consistent linear changes in CO\(_2\) and water vapor concentrations during the 2 min measurement period, indicating 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. 2004). Air temperatures within the chamber during a typical measurement period increased less than 1°C.
Following the transparent chamber measurement, a second measurement of ecosystem gas exchange was made using an opaque, polyethylene cover (Shelter Systems, Santa Cruz, CA) to estimate ecosystem respiration ($R_e$, net ecosystem CO$_2$ exchange in the absence of photosynthesis). The transparent chamber was removed from the plot, ventilated and reseated. The opaque cover was immediately placed over the transparent chamber, the chain securing the chamber to the ground surface was replaced and a second measurement of CO$_2$ concentration change through time was made. Linear changes in CO$_2$ concentration were observed during the measurement period, which implies that any declines in the partial pressure gradient of CO$_2$ between the soil and the chamber atmosphere were insufficient to affect rates of CO$_2$ diffusion from the soil to the chamber atmosphere. To estimate ecosystem fluxes, we analyzed CO$_2$ and water vapor concentration data according to Jasoni et al. (2005). Because we focused on relative differences among experimental treatments, we did not assess the potential influence of leaks or pressure effects on estimates of ecosystem CO$_2$ and water vapor exchange (Saleska et al. 1999). To avoid potentially confounding treatment effects with sampling errors associated with changing sun angle, wind and temperature conditions, we stratified the order of our sampling. We measured ecosystem photosynthesis by estimating midday gross ecosystem CO$_2$ exchange (GEE) as the difference between midday NEE and midday $R_e$. Ecosystem water use efficiency ($WUE_e$), the efficiency of net ecosystem CO$_2$ assimilation to water vapor loss, was calculated as NEE divided by ET. Greater negative values indicate increasing $WUE_e$ whereas smaller negative values (values closer to zero) indicate a decline in $WUE_e$.

Leaf carbon isotope and %N analysis

Mature, sun-lit leaves of *Cynara* and *Avena* were collected on April 20. Leaf samples were stored in paper envelopes and air dried in the laboratory. We homogenized individual leaf samples with a mortar and pestle. Leaf tissue was analyzed for $\delta^{13}C$ on a continuous flow gas-ratio mass spectrometer (Delta Plus, Finnigan MAT Inc., San Jose, CA) coupled to an elemental analyzer (NA 1500, Fisons, Dearborn, MI) at the University of California, Irvine Department of Earth Systems Sciences. Data are reported relative to the PDB carbonate standard using “delta” ($\delta$) notation in parts per thousand (‰) (Craig 1957). In addition to reporting carbon isotope values, we report the nitrogen content (%N) of leaf and homogenized litter samples measured using the same instrumentation.

Data analyses

While biomass, $\theta_{15}$ and ecosystem gas exchange measurements met the parametric assumptions of normality, we performed logarithmic transformations on GEE and $R_e$ to meet the assumptions of normality for these variables. For these measures, we used repeated-measures analysis of variance (ANOVA) and post-hoc Tukey’s HSD tests (JMP, SAS Institute, Cary, NC) to examine the influence of *Cynara* and *Cynara*-removal on grassland ecosystem CO$_2$ exchange and ET. To better understand how *Cynara* mediates the linkage between carbon and water cycles in this system, we compared mid-growing season (April 20) aboveground live biomass and ecosystem CO$_2$ exchange and $WUE_e$ using linear regression (JMP, SAS Institute, Cary, NC). In the case of data only collected on April 20 (litter mass, leaf $\delta^{13}C$ and %N and litter %N) we compared experimental plots using an ANOVA model.

Results

Aboveground live biomass, litter mass and shallow soil moisture content

During the mid-growing season and prior to spot applications of herbicide (April 20), aboveground live biomass was slightly greater in plots containing *Cynara* than in plots containing only annual grasses (Fig. 2 main). The influence of *Cynara* on biomass persisted through the peak growing season before declining during the summer (Table 1, type). Herbicide treatment of *Cynara* caused biomass in those plots to decline so that by May 16 they were more similar to grassland plots (Table 1, type × time). Consistent with patterns of aboveground live biomass, litter mass was greater in plots containing *Cynara* than in grassland plots (Fig. 2 inset).
Shallow soil moisture ($\theta_{15}$) declined steadily during the growing season (Fig. 3, upper panel). Contrary to our prediction, growing-season declines in $\theta_{15}$ were not influenced by the presence of Cynara or its removal (Table 1, type × time). However, we observed greater $\theta_{15}$ among Cynara-removal plots in comparison with grassland plots on July 10 (Fig. 3A; Tukey’s HSD, $P < 0.05$). For clarity, same-day treatments are slightly offset from one another on the X-axis.

Evapotranspiration and ecosystem CO$_2$ exchange

Throughout the experiment, midday ET declined from a peak on April 20 (Fig. 3B). This pattern is consistent with declines in soil moisture during the same period and with declines in leaf gas exchange associated with the progression of annual grasses from initiation of flowering on April 20 to grain-filling on May 16 to senesced on July 10. In comparison with grassland plots, plots of Cynara tended to have greater ET throughout the course of the experiment (Table 1, type). Cynara removal was associated with a decline in late-growing season (May 16) midday ET to values similar to those observed in grassland plots (Fig. 3B; Tukey HSD, $P < 0.05$). The influence of Cynara removal on ET did not persist into the summer dry season.

During the growing season (April 20 and May 16 measurements), we observed negative values of midday net ecosystem CO$_2$ exchange (NEE) consistent with net CO$_2$ uptake by the various experimental treatments (Fig. 4A). Throughout the mid- and late-growing season (April 20 and May 16 measurements), we observed negative values of midday net ecosystem CO$_2$ exchange (NEE) consistent with net CO$_2$ uptake by the various experimental treatments (Fig. 4A). Throughout the mid- and late-growing season (April 20 and May 16 measurements), we observed negative values of midday net ecosystem CO$_2$ exchange (NEE) consistent with net CO$_2$ uptake by the various experimental treatments (Fig. 4A). Throughout the mid- and late-growing season (April 20 and May 16 measurements), we observed negative values of midday net ecosystem CO$_2$ exchange (NEE) consistent with net CO$_2$ uptake by the various experimental treatments (Fig. 4A). Throughout the mid- and late-growing season (April 20 and May 16 measurements), we observed negative values of midday net ecosystem CO$_2$ exchange (NEE) consistent with net CO$_2$ uptake by the various experimental treatments (Fig. 4A).

Table 1 Degrees of freedom (df) and F-statistics from the statistical analysis of the influence of vegetation type (Cynara, Cynara-removal, annual grassland) and time on standing crop biomass (biomass), 15-cm volumetric soil moisture ($\theta_{15}$) and midday maximum ecosystem gas-exchange variables in a coastal grassland near Irvine, California

| Factors          | df  | Biomass | $\theta_{15}$ | ET  | NEE  | $R_e$ | GEE  | WUE$_e$
|------------------|-----|---------|---------------|-----|------|-------|------|--------
| Type             | 2, 18 | 10.42** | 1.26 | 4.36* | 4.56* | 3.26 | 3.24 | 0.14
| Time             | 2, 17 | 136.0** | 65.25** | 221.3** | 100.4*** | 127.4** | 191.6** | 5.45**
| Type × time      | 4, 34 | 4.38** | 1.17 | 1.23 | 5.91** | 0.47 | 3.30 | 1.89

F-statistics with a single asterisk (*) indicate significance at $P < 0.05$; a double asterisk (**) indicates $P < 0.01$
late-growing season, the presence of *Cynara* was associated with more negative NEE values (Table 1, type). *Cynara* removal was associated with late-growing season (May 16) NEE more similar to grassland plots than plots where *Cynara* remained intact. However, the influence of *Cynara* and its removal on NEE did not persist into the summer dry season (July 10).

By convention, ecosystem respiration ($R_e$) is expressed as positive values (indicating ecosystem CO$_2$ loss). We observed a decline in $R_e$ among all treatments during the experiment (Fig. 4B). Consistent with our prediction, the presence of *Cynara* was associated with greater $R_e$, however this trend was not statistically significant (Table 1, type, $P = 0.062$). Likewise, *Cynara*-removal plots had late-growing season values of $R_e$ similar to those where *Cynara* remained intact and to grassland plots. Values of $R_e$ near zero in all of the plots during the last measurement on July 10 reflected low levels of metabolic activity by biota, consistent with low levels of soil moisture observed during the same period.

Like $R_e$, patterns of ecosystem photosynthesis (gross ecosystem CO$_2$ exchange; GEE) associated with *Cynara* and its removal also contribute to patterns of net ecosystem CO$_2$ exchange (Fig. 4C). Calculated as the balance of NEE and $R_e$, GEE is expressed by negative values (indicating ecosystem CO$_2$ gain). Throughout the growing season, *Cynara* plots consistently had more negative GEE fluxes than grassland plots (Table 1; type). The influence of *Cynara* on GEE appeared strongest during the mid-growing season (April 20; Fig. 4C; Tukey’s HSD, $P < 0.05$). *Cynara* removal was associated with a decline in late-growing season (May 16) GEE to values more closely matching those of the grassland plots (Fig. 4C; Tukey’s HSD, $P < 0.05$).

Grassland and non-removal *Cynara* plots used water most efficiently (WUE$_e$ tended to be most negative) during May 16 (Fig. 5). As the ratio of NEE to ET, a peak in WUE$_e$ during the late-growing season is consistent with a decline in soil surface evaporation and an increasing contribution of transpiration to ET. However, in contrast with our prediction, *Cynara* did not increase in WUE$_e$ by increasing the contribution of transpiration to ET over annual forbs and grasses (Table 1, type).

To further explore ecosystem functional shifts associated with the presence of *Cynara* we correlated mid-growing season (April 20) aboveground live biomass with ecosystem CO$_2$ exchange and WUE$_e$ measured on April 20 (Fig. 6A–D). Biomass, regardless of treatment, was negatively correlated with NEE during the mid-growing season (Fig. 6A). In contrast,
specific regressions did not explain significant additional variance, suggesting that aboveground biomass is more suitable for predicting mid-growing season fluxes than any species-specific trait.

Leaf $\delta^{13}C$, %N of leaves and litter

Mid-growing season (April 20) leaf tissue stable carbon isotopes ($\delta^{13}C$) did not vary between Cynara and Avena growing in the same plot ($-29.9^{0}/00$, $SE = 0.14$, $n = 14$; $-29.7^{0}/00$, $SE = 0.21$, $n = 14$ respectively). In addition, $\delta^{13}C$ of Avena leaves growing with Cynara did not differ from Avena growing in plots where Cynara was absent ($-29.7^{0}/00$, $SE = 0.21$, $n = 14$; $-29.4^{0}/00$, $SE = 0.16$, $n = 14$ respectively). Leaf tissue nitrogen content (%N) did not vary between Cynara and among Avena growing in plots where Cynara was present or absent (2.39%, $SE = 0.07$, $n = 14$; 2.46%, $SE = 0.10$, $n = 14$; 2.61%, $SE = 0.15$, $n = 7$ respectively). In contrast, litter nitrogen content was greater in Cynara plots than in grassland plots (1.17%, $SE = 0.075$).

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**Fig. 5** Midday ecosystem water use efficiency ($WUE_e$; µmol CO$_2$ mmol H$_2$O$^{-1}$) in Cynara, Cynara-removal and grassland plots during the spring and summer of 2006 in a coastal grassland near Irvine, CA. Symbols follow Fig. 2

$R_e$ was not influenced by biomass (Fig. 6B). Patterns of ecosystem photosynthesis in relation to biomass (GEE; Fig. 6C) were consistent with those observed for NEE. Similarly, increases in aboveground live biomass were associated with increases in $WUE_e$ (increasing negative values; Fig. 6D). In the case of each gas exchange variable considered, plant-type

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**Fig. 6** Mid-growing season (April 20) aboveground live biomass versus midday maximum ecosystem CO$_2$ exchange parameters and ecosystem water use efficiency in a coastal grassland near Irvine, CA. Open symbols indicate plots containing Cynara, closed symbols indicate plots containing only annual grasses and forbs. (A) Net ecosystem CO$_2$ exchange (NEE; µmol CO$_2$ m$^{-2}$ s$^{-1}$); negative values note increasing ecosystem CO$_2$ assimilation. (B) Ecosystem respiration ($R_e$; µmol CO$_2$ m$^{-2}$ s$^{-1}$); positive values indicate increasing ecosystem CO$_2$ loss. (C) Gross ecosystem CO$_2$ exchange (GEE; µmol CO$_2$ m$^{-2}$ s$^{-1}$); negative values note increasing ecosystem CO$_2$ assimilation. (D) Ecosystem water use efficiency ($WUE_e$; µmol CO$_2$ mmol H$_2$O$^{-1}$); increasingly negative values note increasing efficiency.

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\( n = 14; \ 0.7\%, \ \text{SE} = 0.10, \ n = 7 \) respectively; ANOVA, \( F = 13.051_{19}, P = 0.0016 \).

**Discussion**

We predicted that *Cynara* would act to increase NEE as well as \( R_e \). Indeed, the presence of *Cynara* was associated with greater aboveground live biomass (Fig. 2) and GEE (Fig. 4C), resulting in more negative NEE (Fig. 4A). Likewise, the presence of *Cynara* was associated with enhanced litter quantity (Fig. 2 inset) and nitrogen content than plots where *Cynara* was absent. In these ways, the invasion of *Cynara*, a large, non-native, extensively-rooted perennial thistle into coastal California grasslands represents a non-woody analog to the well-studied phenomenon of increasing densities and range expansions of woody-plants in semi-arid ecosystems (termed “woody-encroachment”; Goodale and Davidson 2002). The effects of woody-encroachment on ecosystem carbon balance are unresolved (Pacala et al. 2001; Archer et al. 2001; Jackson et al. 2002), but may include the formation of “islands of fertility” (e.g. Schlesinger et al. 1996) and intensification of carbon cycling through increases in aboveground biomass, soil organic carbon and increased soil respiration rates (McCulley et al. 2004). Surprisingly, an increase in aboveground live biomass and an increase in litter quantity and quality in plots containing *Cynara* did not influence a larger increase in \( R_e \) (Fig. 4B).

In addition to altering patterns of ecosystem carbon dynamics, woody-encroachment is associated with greater aboveground live biomass (Zhang et al. 2001; Huxman et al. 2005). Canopies of woody-plants may increase interception of rainfall (Dunkerley 2000), increase infiltration (Bhark and Small 2003) and alter the balance between evaporation and transpiration (Huxman et al. 2005). We observed that the presence of *Cynara* was associated with greater growing-season ET (Fig. 3B), a finding consistent with the predictions of Zhang et al. (2001) for woody-encroachment scenarios in Mediterranean-type ecosystems. Differences in ET associated with *Cynara* invasion could be attributable to shifts in leaf area, stomatal conductance and/or canopy and soil surface evaporation. However, shallow soil moisture data do not support the hypothesis that differences in ET were driven by soil surface evaporation (Fig. 3A).

Overall declines in ET were similar among *Cynara* removal and non-removal treatments, consistent with the drying of shallow soil layers during the transition from the spring growing season to the summer dry season. However, the removal of *Cynara* resulted in lower ET than in plots where *Cynara* remained intact (May 16, Fig. 3B). The effects of woody-plant removal on local hydrological processes are complex (Hibbert 1983; Seyfried and Wilcox 2006) and likely vary with soil infiltration characteristics, rainfall regime and physiographic setting (Huxman et al. 2005). The consequences of removing deeply-rooted, perennial thistles from rangelands on local hydrologic budgets are likely equally complex (Lacey et al. 1989; Enloe et al. 2004; Gerlach 2004). Nevertheless, these findings suggest that *Cynara*-removal is associated with a decline in growing season ET and has, at least in the short-term, the potential to increase water yields in rangelands.

Few studies have addressed the mechanisms through which invasive plants alter the linkage between carbon and water cycling in semi-arid ecosystems (Kremer et al. 1996; Huxman et al. 2004; Potts et al. 2006a; Prater et al. 2006). Our findings suggest that during the mid-growing season, an increase in aboveground live biomass (a proxy for leaf area) underlies observed shifts in carbon and water cycling. That *Cynara* and the annual grasses it commonly displaces (including *Avena*) share a common \( C_3 \) photosynthetic pathway supports the existence of a common functional relationship between ecosystem gas exchange and aboveground biomass (Fig. 6A, C, D). Furthermore, regression analysis of the influence of aboveground live biomass on ecosystem gas exchange were based on mid-growing season measurements, a period of abundant soil moisture when plant functional-type differences in rooting depth would have less influence on ecosystem gas exchange. Likewise, similarities in leaf tissue \( \%N \) and \( \delta^{13}C \) between *Cynara* and *Avena* suggest that shifts in NEE, GEE and WUEe were driven by shifts in leaf area and/or canopy architecture rather than a change in leaf-level photosynthetic rates and water use efficiency. Finally, the observation that \( R_e \) did not correlate strongly with aboveground live biomass (Fig. 6B) suggests the important contribution of microbial respiration to ecosystem respiration during the mid-growing season.
Experiments that examine the influence of species removal on ecosystem function require careful evaluation (Diaz et al. 2003). For example, the effects of Cynara-removal on ecosystem carbon and water fluxes represent the balance of three component effects. First and most straightforward, removal of Cynara reveals the direct influence of this deeply-rooted perennial thistle on ecosystem function. Secondly, removal reveals the responses of other species to the loss of Cynara. For example, it is possible that the removal of Cynara during the mid-growing season may have eased nutrient and water limitation among remaining annual grasses, thereby boosting performance later in the season. The effect of Cynara removal is also a function of the removal method itself. In this case, above- and below-ground Cynara biomass remained in the plots following herbicide application, possibly influencing subsequent rates of ET and $R_c$. Pre-existing microsite factors such as soil texture could potentially confound the results of this experiment. However, the effects of Cynara removal were consistent with contrasts between grassland and Cynara plots, suggesting that this was not the case. The lack of a legacy effect of Cynara on fluxes of CO$_2$ and H$_2$O following its removal suggests that the biological activity of Cynara, rather than changes in plant community structure, canopy architecture or soil processes, underlay the effects we observed.

Our scope of inference on the impacts of Cynara on net ecosystem productivity (NEE integrated through time) is limited because we measured only midday ecosystem gas exchange. For example, diel tent-based measurements of NEE in a Chihuahuan desert grassland revealed midday depression of ecosystem CO$_2$ assimilation with implications for net ecosystem productivity (Patrick et al. 2007). Furthermore, daytime measurements of ecosystem respiration may not be representative of nighttime ecosystem respiration, particularly in regards to the contribution of autotrophic respiration (Tang et al. 2005). Future investigations on the ecosystem-level impacts of Cynara should consider how this large, deeply-rooted perennial plant alters diurnal patterns of ecosystem CO$_2$ exchange.

This research demonstrates the impacts of Cynara and its removal on aboveground biomass, litter quality and ecosystem CO$_2$ exchange and ET in a coastal California grassland. In addition to increasing aboveground biomass and ecosystem photosynthesis, the presence of Cynara is associated with growing season increases in ecosystem water use efficiency. Cynara-mediated shifts in ecosystem function at the patch-scale suggest the potential for this invasive thistle to influence watershed hydrologic cycling, landscape-level ecosystem carbon storage and the sensitivity of ecosystem function to climate variability (Potts et al. 2006b). In addition to addressing broader spatial and temporal impacts of Cynara invasion, future research should consider the potential for Cynara-mediated impacts on soil microbial communities as well as nutrient and water feedbacks that potentially reinforce a performance advantage of this invasive, perennial thistle over annual grasses and forbs in coastal California grasslands.

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