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Journal

Biological Invasions, 10(7)

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Publication Date

2008-10-01

DOI

10.1007/s10530-007-9185-y

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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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Received: 21 May 2007 / Accepted: 15 October 2007 / Published online: 31 October 2007
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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

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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.cdffa.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; Travnicek 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 CO₂ and water exchange in coastal grasslands. The balance of CO₂ assimilation by plants and respiratory losses by plants and soil microbes is an important ecosystem function and can be quantified as net ecosystem CO₂ exchange (NEE). NEE is expressed as the sum of CO₂ assimilation by photosynthesis (gross ecosystem CO₂ exchange; GEE) and losses of CO₂ by plant and soil microbial respiration (collectively termed ecosystem respiration; R_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_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 CO₂ 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° N, 117.50° 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° N, 117.54° W, elev. 1 m) where mean annual temperature is 16.3°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 × 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 × 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

Fig. 1 (A) Daily average temperature for the period December 2005 through July 2006 in a coastal grassland near Irvine, CA. (B) Precipitation expressed in mm by event for the period December 2005–July 2006 in a coastal grassland near Irvine, CA. Arrows note sampling periods, asterisk notes timing of herbicide application

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:

$$M = aD^b \quad (1)$$

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 ($a = 9.51\text{E-}6$; $b = 3.6719$; $r^2 = 0.99$; $P < 0.01$) 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 (θ_{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 $\sim 75\%$ 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 CO₂ exchange in the absence of photosynthesis). The transparent chamber was removed from the plot, ventilated and resealed. 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 CO₂ concentration change through time was made. Linear changes in CO₂ concentration were observed during the measurement period, which implies that any declines in the partial pressure gradient of CO₂ between the soil and the chamber atmosphere were insufficient to affect rates of CO₂ diffusion from the soil to the chamber atmosphere. To estimate ecosystem fluxes, we analyzed CO₂ 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 CO₂ 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 CO₂ exchange (GEE) as the difference between midday NEE and midday R_e . Ecosystem water use efficiency (WUE_e), the efficiency of net ecosystem CO₂ 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 $\delta^{13}\text{C}$ 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” (δ) 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, θ_{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 CO₂ 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 CO₂ 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 $\delta^{13}\text{C}$ 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 $\times$ time). Consistent with patterns of aboveground live biomass, litter mass was greater in plots containing *Cynara* than in grassland plots (Fig. 2 inset).

Fig. 2 Inset mean ($\pm$ SE) mid-growing season (April 20) litter abundance (gm^{-2}). Main figure mean aboveground live biomass (gm^{-2}) in *Cynara*, *Cynara*-removal and grassland plots during the spring and summer of 2006 in a coastal grassland near Irvine, CA. On July 10, almost no live biomass was observed in *Cynara*-removal and grassland plots. Error bars indicate SE; lower case letters indicate significant, same-day differences in means (Tukey HSD, $P < 0.05$). For clarity, same day treatments are slightly offset from one another on the X-axis

Shallow soil moisture (θ_{15}) declined steadily during the growing season (Fig. 3, upper panel). Contrary to our prediction, growing-season declines in θ_{15} were not influenced by the presence of *Cynara* or its removal (Table 1, type $\times$ time). However, we observed greater θ_{15} among *Cynara*-removal plots in comparison with grassland plots on July 10 (Fig. 3A; Tukey's HSD, $P < 0.05$).

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

Fig. 3 (A) Volumetric soil moisture at 15-cm depth (θ_{15}) in *Cynara*, *Cynara*-removal and grassland plots during the spring and summer of 2006 in a coastal grassland near Irvine, CA. (B) Midday maximum evapotranspiration ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) 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

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

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

Factors	df	Biomass	θ_{15}	ET	NEE	R_e	GEE	WUE _c
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 $\times$ 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 $P < 0.01$

Fig. 4 (A) Midday maximum net ecosystem CO₂ exchange (NEE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in *Cynara*, *Cynara*-removal and grassland plots during the spring and summer of 2006 in a coastal grassland near Irvine, CA. Negative values note ecosystem CO₂ assimilation. (B) Midday maximum ecosystem respiration (R_e ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in *Cynara*, *Cynara*-removal and grassland plots during the spring and summer of 2006 in a coastal grassland near Irvine, CA. (C) midday maximum gross ecosystem CO₂ exchange (GEE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in *Cynara*, *Cynara*-removal and grassland plots during the spring and summer of 2006 in a coastal grassland near Irvine, CA. Negative values indicate increasing ecosystem CO₂ assimilation. Symbols follow Fig. 2

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 CO₂ 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 CO₂ exchange; GEE) associated with *Cynara* and its removal also contribute to patterns of net ecosystem CO₂ exchange (Fig. 4C). Calculated as the balance of NEE and R_e , GEE is expressed by negative values (indicating ecosystem CO₂ 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 CO₂ 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,

Fig. 5 Midday ecosystem water use efficiency (WUE_e ; $\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$) 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

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

Mid-growing season (April 20) leaf tissue stable carbon isotopes ($\delta^{13}\text{C}$) 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, $\delta^{13}\text{C}$ 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%, $SE = 0.075$,

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; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); negative values note

increasing ecosystem CO_2 assimilation. (B) Ecosystem respiration (R_e ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); positive values indicate increasing ecosystem CO_2 loss. (C) Gross ecosystem CO_2 exchange (GEE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); negative values note increasing ecosystem CO_2 assimilation. (D) Ecosystem water use efficiency (WUE_e ; $\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$); increasingly negative values note increasing efficiency

$n = 14$; 0.7%, SE = 0.10, $n = 7$ respectively; ANOVA, $F = 13.05_{1,19}$, $P = 0.0016$).

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 shifts in local and regional water balance (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 C₃ 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 $\delta^{13}\text{C}$ between *Cynara* and *Avena* suggest that shifts in NEE, GEE and WUE_e 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_e . 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_2O 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.

Acknowledgments We thank G. Winston, I. Ashton, L. Larios, S. Rifai, A. Rocha, D. Houdeshel, M. Ng, N. Gross, R. Winkleman and M. Whiteside for field and laboratory assistance. C. Holmgren, N. English and two anonymous reviewers provided insightful comments on earlier drafts of this manuscript.

References

- Archer S, Boutton TW, Hibbard KA (2001) Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze ED, Heimann M, Harrison S, Holland E, Lloyd J, Prentice I, Schimel D (eds) Global biogeochemical cycles in the climate system. Academic Press, San Diego, pp 115–138
- Arnone JA, Obrist D (2003) A large daylight geodesic dome for quantification of whole-ecosystem CO_2 and water vapour fluxes in arid shrublands. *J Arid Environ* 55:629–643
- Bhark EW, Small EE (2003) Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. *Ecosystems* 6:185–196
- Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. *Nature* 427:731–733
- Craig H (1957) Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. *Geochim Cosmochim Acta* 12:133–140
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- Diaz S, Symstad AJ, Chapin FS III, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. *Trends Ecol Evol* 18:140–146
- Dunkerley D (2000) Measuring interception loss and canopy storage in dryland vegetation: a brief review and evaluation of available research strategies. *Hydrol Process* 14:669–678
- Ehrenfeld JG (2003) Effects of exotic plant invasion on soil nutrient cycling processes. *Ecosystems* 6:503–523

- Enloe SF, DiTomaso JM, Orloff SB, Drake DJ (2004) Soil water dynamics differ among rangeland plant communities dominated by yellow starthistle (*Centaurea solstitialis*), annual grasses, or perennial grasses. *Weed Sci* 52:929–935
- Evimer VT (2004) Plant traits that influence ecosystem processes vary independently among species. *Ecology* 85:2215–2229
- Geiger EL, McPherson GR (2005) Response of semi-desert grasslands invaded by non-native grasses to altered disturbance regimes. *J Biogeogr* 32:895–902
- Gerlach JD (2004) The impacts of serial land-use changes and biological invasions on soil water resources in California, USA. *J Arid Environ* 57:365–379
- Gill RJ (ed) (1990) Noxious weeds of California. Part 2: distribution maps. B-rated weeds. *Calif Plant Pest Dis Rep* 9:74–125
- Goodale CL, Davidson EA (2002) Uncertain sinks in the shrubs. *Nature* 418:593–594
- Hibbert AR (1983) Water yield improvement potential by vegetation management on western rangelands. *Water Res Bull* 19:375–381
- Huxman TE, Cable JM, Ignace DD, Eilts AJ, English NB, Weltzin J, Williams DG (2004) Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141:295–305
- Huxman TE, Wilcox BP, Breshears DD, Scott RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB (2005) Ecohydrological implications of woody plant encroachment. *Ecology* 86:308–319
- Jackson RB, Banner JL, Jobbagy EG, Pockman WT, Wall DH (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418:623–626
- Jasoni RL, Smith SD, Arnone JA III (2005) Net ecosystem CO₂ exchange in Mojave Desert shrubland during the eighth year of exposure to elevated CO₂. *Glob Chang Biol* 11:749–756
- Kazakou E, Vile D, Shipley B, Gallet C, Garnier E (2006) Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Funct Ecol* 20:21–30
- Kremer RG, Hunt ER Jr, Running SW, Coughlan JC (1996) Simulating vegetational and hydrologic response to natural climatic variation and GCM-predicted climate change in a semi-arid ecosystem in Washington, USA. *J Arid Environ* 33:23–38
- Lacey CA, Lacey JR, Fay PK, Story JM, Zamora DL (1999) Controlling knapweed on Montana rangeland. Montana State University Extension Service, Bozeman, Montana, USA
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem function from plant traits: revisiting the Holy Grail. *Ecology* 16:545–556
- Le Maitre DC (2004) Predicting invasive species impacts on hydrological processes: the consequences of plant physiology for landscape processes. *Weed Technol* 18:1408–1410
- Litton CM, Sandquist DR, Cordell S (2006) Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. *For Ecol Manage* 231:105–113
- Marushia RG, Holt JS (2006) The effects of habitat on dispersal patterns of an invasive thistle, *Cynara cardunculus*. *Biol Invas* 8:577–593
- McCulley RL, Archer SR, Boutton TW, Hons FW, Zuberer DA (2004) Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology* 85:2804–2817
- McDowell SCL (2002) Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). *Am J Bot* 89:1431–1438
- Nagel JM, Griffin KG (2001) Construction cost and invasive potential: comparing *Lythrum salicaria* (Lythraceae) with co-occurring native species along pond banks. *Am J Bot* 88:2252–2258
- Newman BD, Wilcox BP, Archer SR, Breshears DD, Dahm CN, Duffy CJ, McDowell NG, Phillips FM, Scanlon BR, Vivoni ER (2006) Ecohydrology of water limited environments: a scientific vision. *Water Resour Res* doi:10.1029/2005WR004141
- Obrist D, Delucia EH, Arnone JA III (2003) Consequences of wildfire on ecosystem CO₂ and water vapour fluxes in the Great Basin. *Glob Chang Biol* 9:563–574
- Pacala SW, Hurt GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath L, Sundquist ET, Stallard RF, Ciais P, Moorcroft P, Casperson JP, Shevliakova E, Moore B, Kohlmaier G, Holland E, Gloor M, Harmon ME, Fan SM, Sarmiento JL, Goodale CL, Schimel D, Field CB (2001) Consistent land- and atmosphere based US carbon sink estimates. *Science* 292:2316–2320
- Parsons WT, Cuthbertson EG (1992) Noxious weeds of Australia. Inkata Press, Melbourne
- Patrick L, Cable J, Potts D, Ignace D, Barron-Gafford G, Griffith A, Alpert H, Van Gestel N, Robertson T, Huxman T, Zak J, Loik M, Tissue D (2007) Effects of an increase in summer precipitation on leaf, soil, and ecosystem CO₂ and H₂O fluxes in a sotol grassland in Big Bend National Park, Texas. *Oecologia* 151:704–718
- Potts DL, Huxman TE, Cable JM, English NB, Ignace DD, Eilts AJ, Mason MJ, Weltzin JF, Williams DG (2006a) Antecedent moisture and seasonal precipitation influence the responses of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. *New Phytol* 170:849–860
- Potts DL, Huxman TE, Scott RL, Williams DG, Goodrich DC (2006b) The sensitivity of ecosystem carbon exchange to seasonal precipitation and woody plant encroachment. *Oecologia* 150:453–463
- Prater MR, Obrist D, Arnone JA III, Delucia EH (2006) Net carbon exchange and evapotranspiration in postfire and intact sagebrush communities in the Great Basin. *Oecologia* 146:595–607
- Saleska SR, Harte J, Torn MS (1999) The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Glob Chang Biol* 5:125–141
- Schlesinger WH, Raikes JA, Hartely AE, Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77:364–374
- Seyfried MS, Wilcox BP (2006) Soil water storage and rooting depth: key factors controlling recharge on rangelands. *Hydrol Process* 20:3261–3275
- Sheley RL, Larson LL, Jacobs JS (1999) Yellow starthistle. In: Sheley RL, Petroff JK (eds) *Biology and management of*

- noxious rangeland weeds. Oregon State University Press, Corvallis
- Sheley RL, Mangold JM, Anderson JL (2006) Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. *Ecol Monogr* 76:365–379
- Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seemann JR, Nowak RS (2000) Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature* 408:79–82
- Suding KN, LeJeune KD, Seastedt TR (2004) Competitive impacts and response of an invasive weed: dependencies on nitrogen and phosphorous availability. *Oecologia* 141:526–535
- Tang J, Baldocchi DD, Xu L (2005) Tree photosynthesis modulates soil respiration on a diurnal time-scale. *Glob Chang Biol* 11:1298–1304
- Thomsen C, Barbe G, Williams W, George M (1986) “Escaped” artichokes are troublesome pests. *Calif Agric* 40:7–9
- Travinicek AJ, Lym RG, Prosser C (2005) Fall-prescribed burn and spring-applied herbicide effects on Canada thistle control and soil seedbank in a northern mixed-grass prairie. *Rangeland Ecol Manage* 58:413–422
- Vitousek PM, D’Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environment change. *Am Sci* 84:468–479
- White VA, Holt JS (2005) Competition of artichoke thistle (*Cynara cardunculus*) with native and exotic grassland species. *Weed Sci* 53:826–833
- Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol Evol* 16:454–459
- Zhang L, Dawes WR, Walker GR (2001) Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resour Res* 37:701–708