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# HOW DO LONG-TERM CHANGES IN PRECIPITATION SEASONALITY AFFECT DRYLAND CARBON DYNAMICS? EVIDENCE FROM A 21-YEAR MANIPULATIVE CLIMATE-CHANGE EXPERIMENT

by

Kathryn McAbee

A thesis

submitted in partial fulfillment

of the requirements for the degree of

Master of Science in the Department of Biological Sciences

Idaho State University

Spring 2015

# **Committee Approval**

To the Graduate Faculty:

The members of the committee appointed to examine the thesis of Kathryn McAbee find it satisfactory and recommend that it be accepted.

Keith Reinhardt, Major Advisor

Kathleen Lohse, Committee Member

Matthew Germino, Committee Member

Laura Ahola-Young, Graduate Faculty Representative

#### ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor, Dr. Keith Reinhardt, for his unwavering patience, support, and encouragement. His insight, spirit, and dedication were instrumental in the completion of my thesis research. I would also like to thank the other members of my graduate committee, including my Graduate Faculty Representative, Laura Ahola-Young, as well as Dr. Kathleen Lohse and Dr. Matthew Germino, whose invaluable guidance has strengthened my skills as a scientist. The statistical expertise and advice of Ken Aho has also been of great help during this study. I received tremendous personal and professional support from students - including Lindsay Curran, Maria Pacioretty, Harmandeep Sharma, and David Huber – to whom I am especially grateful. I would additionally like to thank Idaho State University and the Geological Society of America for their financial support.

I would also like to thank the individuals who assisted me with field work and data analysis, including Ryann Mata and Cassidy Howarth. I am exceedingly grateful for the assistance of Andrew Bosworth, whose encouragement, effort, and stimulating conversation made even the most difficult field work possible and enjoyable. I would also like to thank Gonzales-Stoller Surveillence, particularly Roger Blew, whose patience and effort enabled this study to be conducted at the INL Ecohydrology Experiment. I would also like to thank those responsible for the funding, maintenance, and continuation of the INL Ecohydrology Experiment, who enabled research by myself and many others.

I would also like to thank my fiancé, Alex, without whose support this academic pursuit would have been impossible. I would also like to thank my parents, whose lifelong support has been essential in my personal and professional growth.

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## ABSTRACT

Semi-arid shrublands of the Intermountain West have been identified as potential carbon (C) sinks, contingent on precipitation amount and timing. Increases in wintertime precipitation relative to summertime are predicted for this region. To quantify the effects of altered precipitation amount and seasonality on aboveground C storage and turnover, I measured C pools and fluxes at leaf, soil, and ecosystem scales during the 2014 growing season, at a 21-year ecohydrological experiment site. I hypothesized that increases in winter precipitation would stimulate aboveground C uptake and storage relative to ambient conditions. This hypothesis was generally supported: winter-irrigated and summer-irrigated plots exhibited greater ecosystem C uptake and long-term biomass accumulation than plots under ambient precipitation conditions. Our findings suggest that expected shifts in precipitation seasonality could result in increased aboveground C uptake and storage in shrubland communities in cold deserts of western North America.

## **Chapter I: Introduction**

Rangelands cover between 30 and 50% of the land surface of the Earth (Booker et al. 2013; IPCC 2013). Those ecosystems, including grasslands and shrublands, support at least 938 million people – or about 17% of the world's population (World Resources Institute Report, 2000; cited by IPCC 2007). One important ecosystem service rangelands provide is carbon (C) storage (Svejcar et al. 2011, Booker et al. 2013). Rangelands store approximately 30% of the world's terrestrial C (Booker et al. 2013), in both vegetation and soil, underscoring rangelands as an important component of global C stocks (IPCC 2000). However, many rangeland ecosystems are water-limited, and thus, their C-storage capacity is quite sensitive to precipitation inputs. Changes in precipitation timing and/or magnitude are predicted in many dryland systems worldwide (IPCC 2013). This leaves us with an unclear picture of how C storage capacity in dry rangelands will vary with changing precipitation regimes.

In the North American Intermountain West, arid and semi-arid sagebrush-steppe rangelands occupy approximately 4.5 x 10<sup>6</sup> ha total land area (Angell et al. 2001), and have been identified as possible future C sinks (C capture and storage exceeds C release, annually) (Svejcar et al. 2011, Gilmanov et al. 2006). The capacity of net C storage in these water-limited ecosystems, however, is contingent on precipitation amount and timing (Svejcar et al. 2011, Kwon et al. 2008, Gilmanov et al. 2006, Huxman et al. 2004, Ivans et al. 2006), pulse patterns (Chen et al. 2009, Huxman et al. 2004), and vegetation community composition. Precipitation in semi-arid environments is highly variable, both spatially and temporally (Svejcar et al. 2011). Consequently, studies of water-limited rangelands in North America have demonstrated wide variability in annual ecosystem C

balance. In these ecosystems, short periods of high C uptake are often counterbalanced by long periods of C loss (Svejcar et al. 2011). Thus, conditions that lengthen and maintain periods of active C uptake, while minimizing respiratory C loss, are critical to increasing potential C sequestration in native rangelands (Svejcar et al. 2011). This could occur if, for example, increased precipitation occurred in winter, which would benefit spring and summertime plant photosynthesis (resulting from increased soil moisture storage), while minimizing soil respiration losses, which are related to soil temperature. Cold-desert sagebrush steppe sites, which receive most precipitation during winter months, generally are C sinks on an annual basis (Gilmanov et al. 2003, Gilmanov et al. 2006, Svejcar et al. 2011), storing an average of 78 g C m<sup>-2</sup> yr<sup>-1</sup> (Svejcar et al. 2011). Conversely, warm deserts, which can receive comparable amounts of precipitation primarily during the growing season, generally are C sources, releasing an average of 126 g C m<sup>-2</sup> yr<sup>-1</sup> (Svejcar et al. 2011). Ultimately, the degree of C storage or release in waterlimited systems depends on the amount and timing of precipitation, which has not been adequately addressed by previous manipulative research, especially over long time scales.

The tight coupling of precipitation patterns with C balance in arid systems necessitates understanding how forecasted changes in precipitation seasonality will influence future C-storage capacity. Specifically, a 10-20% increase in cool-season (November – March) precipitation is expected in the northern latitudes of western North America over the next fifty years (Abatzoglou & Kolden 2011, IPCC 2013). These precipitation changes could be accompanied by a 30-60% increase in the frequency of wet cool-season conditions, coupled with slight decreases in summer precipitation (Abatzoglou & Kolden 2011). Such changes reflect a shift in precipitation seasonality

that is likely to affect the structure and function of rangeland ecosystems in nuanced ways.

Despite the need to understand the effects of current and future precipitation dynamics on rangeland C balance, a dearth of knowledge currently exists regarding the long-term effects of altered precipitation seasonality on C storage in water-limited rangelands. Prior studies have generally been observational with respect to precipitation (Jasoni et al 2005, Gilmanov et al. 2003, Gilmanov et al. 2004, Kwon et al. 2008, Svejcar et al. 2011), have implemented large-scale Bowen ratio or eddy covariance techniques (Svejcar et al. 2011, Gilmanov et al. 2003, Gilmanov et al. 2004, Kwon et al. 2008), or were not of sufficient duration to discern long-term effects (Bates et al. 2006, Chen et al. 2009). Interpolated from hourly, daily, and annual rates, net ecosystem exchange of sagebrush-steppe averaged 0.21  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> over the calendar year (Svejcar et al. 2011),  $0.95 \,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$  during the growing season (Gilmanov et al. 2003), and ranged from -2.31  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> to 6.44  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> during two growing seasons in dry and wet years (mid-day, Kwon et al. 2008). The inter-annual variation in net ecosystem exchange observed by Kwon et al. (2008) suggests that increases in winter or springtime precipitation will drive increases in C uptake during the growing season. Bates et al. (2006) found that the cover and density of a foundational Great Basin shrub, Artemisia *tridentata*, did not respond to precipitation manipulations during a 7-year experiment, but that herbaceous plants were detrimentally affected by enhancements of summer precipitation. Given the observational nature and relatively short timescales of these studies, their results cannot adequately forecast how C storage and fluxes in semi-arid ecosystems will respond to predicted changes in precipitation seasonality.

Herein, we report on the variation in aboveground C pools and fluxes following 20 years of manipulated precipitation seasonality. We focus on natural sagebrush-steppe and crested wheatgrass (Agropyron cristatum) monoculture communities, both of which occur extensively throughout western North America (USDA 2015), and represent important natural and managed systems. We hypothesized that increases in winter or summer precipitation would lead to increases in soil-water storage and plant production, resulting in greater net ecosystem C uptake compared to ambient conditions. However, we predicted that the combination of warm and moist soil conditions resulting from increases in summer precipitation would stimulate soil respiration to a greater extent, and result in less net ecosystem C uptake compared with increases in winter precipitation. This hypothesis is supported by prior findings indicating that ecosystems are able to store C most efficiently by extending the period of greatest net C uptake, which occurs in spring and early summer, when soil water is available and soil and air temperatures are neither limiting C assimilation nor facilitating copious soil respiration (Svejcar et al. 2011). Because plant functional type and community composition have demonstrated influence on C storage, we additionally hypothesized that C storage would be influenced by differences in vegetation type and cover. Specifically, we predicted that sagebrushsteppe communities would have greater C-storing capacity than A. cristatum monoculture communities. To address these hypotheses, we quantified aboveground C fluxes (net ecosystem exchange (NEE), soil respiration ( $R_{soil}$ ), and leaf-level photosynthetic assimilation  $(A_{net})$ , and C pools (biomass) under altered precipitation regimes, and determined in which environmental circumstances and community compositions these ecosystems function as C sinks or sources.

#### **Chapter II: Methodology**

#### Study Area

Our study was conducted at the Idaho National Laboratory Ecohydrology Experiment (IEE), Idaho, USA (43.602' N, 112.904' W; approximate elevation 1500 m). The IEE has a mean annual temperature of 5.6°C, and a frost-free period of about 90 days (Anderson & Forman 2002). The climate is typical of "cold desert" ecosystems of western North America: summertime daytime maximum temperatures range from 19.2 – 30.6 °C, with low humidity (average monthly humidity ranges from 35% - 53%) (Anderson & Forman 2002). Minimum daily winter temperature averages range from 0.6 °C in October and March down to -17.2 °C in January, with snow cover persisting for a few weeks to over two months (Anderson & Forman 2002). Mean annual precipitation is 213 mm, with ~ 54% occurring during the dormant season, between October and May.

#### Experimental Design

Initiated in 1993, the IEE design manipulates precipitation amount and timing, plant community composition, and soil depth. Our study focuses on only one of these soil depths (2-m deep soils). Soils at the IEE have a silty clay loam texture (Huber 2014, personal communication). Three irrigation treatments are (1) ambient precipitation with no supplemental irrigation, (2) supplemental irrigation applied during the growing season, and (3) supplemental irrigation applied during the dormant season. The growing-season ("summer") irrigation treatment consists of four 50-mm irrigations applied biweekly beginning in mid-June (200 mm total) (Germino & Reinhardt 2014). These treatments are intended to simulate large summer-monsoon rainfall events that wet soils down to ~4 m depth (Germino & Reinhardt 2014). The dormant-season ("winter")

irrigation treatment supplies 200 mm of water during a 2-week period occurring in October or April, preceding or following winter snowpack when plants are assumed to be dormant (Germino & Reinhardt 2014). Drip irrigation is applied using line emitters, with drip lines spaced at 0.5-m intervals and non-functioning irrigation lines arranged identically on control plots (Janzen 2009).

The three irrigation treatments (ambient, summer, and winter) are applied across two vegetation communities – Agropyron cristatum monoculture and native sagebrushsteppe. The native vegetation treatment originally consisted of 12 species, including shrubs, grasses, and forbs, similar to the natural vegetation at the INL. That community was characterized by a shrub overstory, dominated by great basin sagebrush (Artemisia tridentata), and an understory of grasses and forbs, including Hedysarum boreale (Northern sweetvetch), Chrysothamnus sp. (rabbitbrush), and Leymus cinerus (Great Basin wildrye). An extensive list of these species is provided in Anderson & Forman 2002. The vegetation treatments were established in 1993, when forb species were seeded and all other species transplanted from local sagebrush-steppe communities (Germino & Reinhardt 2014). Some replacement of failed transplants occurred within the first year, but no subsequent vegetation manipulations have occurred since 1994 (Germino & Reinhardt 2014). The IEE design is a split-plot randomized block design, consisting of 9 plots subdivided into 18 subplots ( $8 \times 8$  m each), with irrigation as the among-plot factor and vegetation-community-type the within-plot factor. A 1-m buffer zone on the four sides of each subplot was established, and measurements were only recorded within the resulting  $6 \times 6$ -m area within each subplot.

#### Net Ecosystem Exchange, leaf- and soil-level gas exchange

Diel measurements of net ecosystem exchange (NEE), leaf- and soil-level gasexchange were made biweekly throughout the growing season (May 1 - September 14) to capture daily and seasonal patterns. NEE was measured across the day at dawn (beginning of photoperiod, approximately 6:00 MDT), mid-day (approximately 11:30 MDT), and in the late afternoon or early evening (approximately 17:00 MDT) to encompass a range of evaporative demand and sunlight conditions. Occasional late afternoon/early evening NEE measurements were missing due to high-wind conditions that made our equipment inoperable. Absence of NEE,  $A_{net}$ , and  $R_{soil}$  measurements at a single date were often the result of equipment failure. Dawn and mid-day measurements were averaged as a proxy of "mean daily" NEE. Interpolated "mean daily" values have been reported in other studies, including Jasoni et al. (2005), in which NEE was not measured continuously throughout the day. Measurement campaigns that occurred between mid-June and mid-August were conducted at least 3 days after summer irrigations to avoid transient bursts in A. tridentata productivity (Loik et al. 2007) or ecosystem respiration (Chen et al. 2009).

We used a closed-chamber "tent" design to measure NEE. The tent was composed of translucent woven rip-stop fabric (Shelter Systems, Menlo Park, CA). The fabric has high tensile strength, is very resistant to tearing, and transmits approximately 90% of incident light radiation (Shelter Systems, Menlo Park, CA, USA). The diameter of our tent was 2.44 m, with a height of approximately 2 m, and a footprint area of 4.65 m<sup>2</sup> in a roughly hexagonal shape (Shelter-Systems, Menlo Park, CA, USA). That basic design was identical, except in size, to that used in NEE studies by Arnone & Obrist (2003) and Jasoni et al. (2005).

Several modifications to the original tent design were needed to address challenges of our study site. To enhance stability and maintain a consistent ground area, we installed a PVC base on three alternating bottom edges of the hexagonal tent, and added PVC bracings to the remaining three sides, approximately 0.5 m above the base of the tent. That design allowed for rapid assembly and easy repair of the tent base and minimized weight, enabling safer and quicker transport between measurements and more rapid placement of the tent during measurements. To prevent leaks during measurement periods, polyethylene skirting was attached to the interior of the tent with white duct tape approximately 0.5 m above the base of the tent. During tent placement, this skirting was tucked out from underneath the base, and was overlaid with 10-mm-diameter chain outside the tent to prevent diffusion of air at the tent base. The seams between rip-stop fabric panels were additionally sealed with duct tape to prevent leaks. Previous analyses determined that "chamber leakage" for this tent-chamber-design was very minimal (Arnone & Obrist 2003).

Net ecosystem exchange was measured by infrared gas analysis over two minutes following tent placement (after allowing a ~30 s equilibration period). Carbon dioxide (CO<sub>2</sub>) drawdown and other environmental variables (water vapor content, temperature, and atmospheric pressure) were measured by a LI-COR LI-7500 open-path infrared gas analyzer (IRGA), which was mounted on a metal frame and placed in the center of the tent during measurement, and data recorded in a LI-7500 control box (Li-Cor Biosciences, Lincoln, NE). A small clamp fan was attached to the LI-COR apparatus to

circulate air within the tent. The fan, IRGA, and control box were operated by a 12-volt battery that was also mounted on the metal frame.

We calculated NEE from the 2-min changes in CO<sub>2</sub> concentration using equation 1, provided by Jasoni et al. (2005), and originally derived from LI-COR Inc, 2004:

$$F_c = \frac{V P_{av} (1000 - W_{av})}{RS(T_{av} + 273)} \times \frac{dC'}{dt} ; \qquad \text{Eq. 1}$$

 $F_c$  is defined as the CO<sub>2</sub> flux, *V* is the volume of the dome (m<sup>3</sup>),  $P_{av}$  the average pressure (kPa) during the measurement period,  $W_{av}$  the average water mole fraction (mmol/mol) during the measurement period, *R* the ideal gas constant, *S* the surface area covered by the dome,  $T_{av}$  the average temperature (degrees C) during the measurement period, and dC'/dt the slope of least squares linear regression of C' on time (Jasoni et al. 2005). C' is an estimate of the mole fraction of CO<sub>2</sub>, adjusted for influence of humidity; C' = C / (1-(W/1000)), where C is the mole fraction of CO<sub>2</sub> (µmol/mol), and W is the mole fraction of water vapor (mmol/mol) (Jasoni et al. 2005).

Tent placement sites within each subplot were carefully selected with regard to several criteria. Excluding areas in which NEE measurements would interfere with other experiments, we selected areas in which the relative abundance of *A. tridentata* (where applicable), *A. cristatum*, and *H. boreale* were representative of the whole subplot. Among native vegetation treatments specifically, our tent placement sites included a single *A. tridentata* shrub, and surrounding grasses and forbs. The shrubs contained within the tent area were similar in size between the three irrigation treatments to maintain consistency in canopy size and total leaf area.

We additionally measured leaf-level photosynthesis as net CO<sub>2</sub> assimilation ( $A_{net}$ ) with an LI-6400 photosynthesis machine (Li-Cor Biosciences, Lincoln, NE, USA). A clear-top chamber was used to measure leaf photosynthesis, with an internal CO<sub>2</sub> concentration of 400 µmol/mol. Measurements of leaf-level photosynthesis were taken four times daily: at dawn, mid-morning, mid-afternoon, and late afternoon, at roughly 4-hour intervals. "Mid-day"  $A_{net}$  was calculated as the average of mid-morning and mid-afternoon  $A_{net}$ .  $A_{net}$  was measured on live, intact tissues of each dominant plant species within the tent footprint.  $A_{net}$  was then scaled to the sunlit (silhouette) area of the leaves contained within the chamber – a metric especially appropriate for geometrically complex shoots (Carter & Smith, 1985). Silhouette leaf area was determined with ImageJ software (National Institutes of Health, Bethesda, MD, USA).

 $R_{soil}$  was measured concurrently with leaf photosynthesis, with a PP Systems EGM-4 connected to a SRC-1 soil respiration chamber (PP Systems, Amesbury, MA, USA). "Daily"  $R_{soil}$  was estimated as the average of dawn and mid-afternoon  $R_{soil}$ , with mid-afternoon  $R_{soil}$  used as an approximate of "mid-day"  $R_{soil}$ . Soil moisture at 0.2, 0.5, and 1.0-m depths was measured with EC-5 soil moisture sensors, and was recorded with EM-50 dataloggers (Decagon Devices, Pullman, WA, USA) in inter-shrub spaces in native vegetation plots.

#### Aboveground Biomass and C Pools

In June 2014, we quantified variation in above-ground biomass and C pools among plots using vegetation surveys and biomass harvests. We measured 2-dimensional plant cover using photometric point-intercept vegetation surveys with a digital camera mounted on a pole 4-m above each subplot (i.e., "down-plot photos"). We overlaid grids at 0.25 m<sup>2</sup>-spacing on each image using ImageJ software (U.S. National Institutes of Health, Bethesda, MD, USA). Photometric cover estimates derived from down-plot photos were similar to in-field surveys of plant cover (Germino & Reinhardt 2014, Janzen 2009). We then scaled 2-D plant-cover measurements to 3-D plant bio-volumes using allometric equations developed from *in situ* biomass measurements.

We harvested biomass of the three most abundant species among all treatments (Artemisia tridentata, Agropyron cristatum, Hedysarum boreale) to calculate biovolumes, and thus, aboveground C pools. A. cristatum and H. boreale were collected from winter- and summer-irrigated plots in June, and from ambient plots in July. Three individuals from each irrigation treatment were harvested from each experimental rep (27 samples for each species). Plants selected at each sampling date were chosen to represent the range of plant sizes present in each plot when possible (based on crown area). Standing plant height and crown circumference were measured on each plant. The plants were then clipped to the crown and any dead material from previous growing seasons was removed. Live material was partitioned into stem, leaf and reproductive biomass. All plant material was placed in paper bags, oven-dried at 80° C for 24 hours, and weighed (A. Bosworth, unpublished data). To minimize disruption of the experimental plots, three A. tridentata plants were selected for harvest from buffer areas surrounding the experiment. These individuals were chosen as most visually representative of A. tridentata biomass in the experimental plots. Prior to harvesting, crown diameter was measured in two directions. The first direction represented the maximum diameter of the shrub and the second measurement was perpendicular to the first at the maximum diameter. Plant height was also recorded, and each shrub was then harvested. Biomass

was partitioned into large stems, small stems, live vegetative, reproductive and senesced material. All plant material was placed into paper bags and oven-dried at 80° C for 72 hours, and weighed (A. Bosworth, unpublished data).

#### Statistical Analysis

NEE, *R*<sub>soil</sub>, and *A*<sub>net</sub> measurements were made at the same within-plot locations. Consequently, the effects of time, irrigation, and plant community type on these variables were analyzed with repeated measures MANOVA, with post-hoc Tukey tests conducted to discern among-subject effects within each measurement interval (Zar 1999). Missing NEE data (due to occasionally windy conditions that prevented using the tent chamber), initially prevented assessment of among-subject effects (irrigation, plant community type) and within-subject effects (time) by repeated measures MANOVA. We addressed this by interpolating averaged data from identical treatments at the same measurement interval. Treatment effects on biomass production were also assessed with ANOVA tests and post-hoc Tukey tests for pairwise comparisons. All statistical procedures were completed in JMP 10.0 and JMP Pro 11.2 (SAS Institute, Cary, NC, USA).

#### **Chapter III: Results**

#### Hydroclimate

*Ambient Precipitation* We observed irregular precipitation patterns at our study site during the 2014 growing season. Substantially below-average precipitation occurred during the early and mid-growing season (May – July; 39.9% of average (Fig. 1)), but significantly above-average levels of precipitation were observed during the late growing season (NCDC 2014). Specifically, a total of 123.4 mm of rain was recorded in August and September, 2014; by contrast, these months generally receive an average of 36.5 mm of rain (NCDC, 2014). Although total precipitation during the 2014 water-year (October 1, 2013 through September 30, 2014) was 97% of the 30-year average, only 51% of this precipitation fell between October 1 and May 31, whereas 71% of yearly precipitation typically falls during this period (NCDC, 2014).

*Soil moisture*. Soil water storage in native plots at depths of 0.2, 0.5, and 1.0 m followed anticipated patterns in response to irrigation treatments (Fig. 2). Soil water storage declined over the growing season in plots supplemented with winter irrigation. Summer irrigation treatments were initiated on June 13<sup>th</sup>, 2014, and immediately resulted in dramatic increases in shallow (0.2-m) soil water content. Increases in 0.5- and 1.0-m soil water following summer irrigations were not observed until early July, with lesser increases at 1-m depths. Plots exposed to ambient precipitation conditions maintained low and relatively stable levels of soil water storage, except in September, when shallow soil water increased, likely in response to large late-summer rain events and associated vegetation growth (Fig. 2). Averaged across the growing season and all soil depths,

volumetric water content was  $11.98 \pm 0.01\%$  in ambient plots,  $15.54 \pm 0.24\%$  in summer plots, and  $13.36 \pm 0.36\%$  in winter plots.

#### C Fluxes

*Net Ecosystem Exchange (NEE)* Overall, both winter and summer irrigations stimulated NEE during the growing season, but at varying times and magnitudes among the native vegetation and *A. cristatum* monoculture treatments (Fig. 3). Peak daytime (mid-day and cumulative mean daily) NEE was generally greatest in winter-irrigated plots for the first half of the growing season, until early July, at which point NEE declined in winter plots and increased in summer-irrigated plots. Summer plots maintained relatively greater NEE until the end of the growing season, when NEE was similar among all three irrigation treatments (Fig. 3).

Specific trends in NEE were observed among different diurnal intervals and vegetation treatments. Dawn NEE of native-vegetation plots averaged  $-0.24 \pm 0.13 \mu$ mol m<sup>-2</sup> s<sup>-1</sup> across the growing season and among irrigation treatments (Fig. 3a). Across the growing season, "irrigation" was the only treatment to affect dawn NEE (Table 1). Dawn NEE was generally less in summer-irrigated plots compared with winter-irrigated and non-irrigated (ambient) plots during the mid-late growing season, following application of "summer" irrigation treatments (Fig. 3a, Table 2). Summer irrigation also resulted in decreased dawn NEE in late July relative to winter irrigation (Table 2).

Mid-day NEE of native-vegetation plots averaged  $0.85 \pm 0.21 \ \mu mol \ m^{-2} \ s^{-1}$  across the growing season and among irrigation treatments (Fig. 3b). Across the growing season, mid-day NEE was influenced independently by irrigation and vegetation

treatments, and these effects did not appear to be interactive (Table 1). Specifically, NEE among native vegetation plots was substantially greater than NEE among *A. cristatum* plots – but only among summer-irrigated plots. Mid-day NEE peaked at  $4.65 \pm 0.32$  µmol m<sup>-2</sup> s<sup>-1</sup> in winter-irrigated plots in mid-June, whereas summer-irrigated plots observed a similar maximum NEE ( $4.67 \pm 1.08 \mu$ mol m<sup>-2</sup> s<sup>-1</sup>) in late July (Fig. 3b).

Evening NEE of native-vegetation plots averaged  $-0.1 \pm 0.21 \,\mu$ mol m<sup>-2</sup> s<sup>-1</sup> across the growing season and among irrigation treatments (Fig. 3c). Similar to the dawn time interval, evening NEE was only affected by irrigation treatments (Table 1). Marginal seasonal variation existed between irrigation treatments; indeed, no significant seasonal effects were detected within any irrigation or vegetation treatment (Fig 3c, 3f). Similar to dawn and mid-day measurements, evening NEE declined in mid-August in response to irregular rain events, but this drop in NEE was substantially more pronounced in the winter-irrigated and ambient plots than in summer-irrigated plots (Fig 3c, 3f).

Vegetation treatments only had a significant effect on NEE during mid-day (P = 0.021). Dawn NEE of *A. cristatum* monoculture plots averaged  $-0.35 \pm 0.11 \mu$ mol m<sup>-2</sup> s<sup>-1</sup> across the growing season and among irrigation treatments (Fig 3d). Mid-day NEE of *A. cristatum* plots averaged 0.39 ± 0.19 across the growing season and among irrigation treatments (Fig 3e). Winter irrigation treatments resulted in higher NEE, relative to summer and ambient treatments, during the first half of the growing season (Fig. 3e, Table 2). These relationships shifted during late July, resulting in significantly higher NEE under summer irrigation treatments than ambient irrigation treatments (Fig. 3e, Table 2). Evening NEE of *A. cristatum* plots averaged 0.13 ± 0.22 µmol m<sup>-2</sup> s<sup>-1</sup> across the growing season and among irrigation treatments (Fig. 3f). As observed in native-

vegetation plots, no significant irrigation treatment effects on evening NEE emerged (Fig 3f).

Growing-season cumulative NEE of native-vegetation plots averaged  $3.54 \pm 0.26$ µmol m<sup>-2</sup> s<sup>-1</sup> among winter-irrigated plots,  $4.37 \pm 0.27$  µmol m<sup>-2</sup> s<sup>-1</sup> among summerirrigated plots, and  $0.12 \pm 0.24$  µmol m<sup>-2</sup> s<sup>-1</sup> among plots receiving no supplemental irrigation (Fig 4). Cumulative NEE of *A. cristatum* monocultures averaged  $3.41 \pm 0.27$ µmol m<sup>-2</sup> s<sup>-1</sup> among winter-irrigated plots by the end of the growing season,  $-1.27 \pm 0.27$ µmol m<sup>-2</sup> s<sup>-1</sup> among summer-irrigated plots, and  $-0.99 \pm 0.21$  µmol m<sup>-2</sup> s<sup>-1</sup> among plots receiving no supplemental irrigation (Fig 4).

We estimated gross ecosystem productivity (GEP) across the growing season by adding rates of night-time ecosystem respiration (Dawn NEE, expressed as a positive respiratory rate) from mid-day and evening NEE rates (Appendix 1). Averaged across the growing season, mid-day GEP was nearly identical in native vegetation plots irrigated in the summer or winter. Despite this similarity, the patterns of GEP in these treatments differed temporally; GEP was positive in winter plots throughout the growing season, but did not reach a comparably great peak magnitude as did summer-irrigated plots. The summer plots achieved a higher peak GEP rate which was offset by negative rates of GEP (net C efflux) during the early growing season (Appendix 1).

*Leaf-Level Photosynthesis* ( $A_{net}$ ). Across all plant species, irrigation treatments had only a marginal effect on  $A_{net}$  (Table 3, Fig. 5). Slight increases in mid-day and evening  $A_{net}$ of irrigated CWG plots were observed relative to ambient CWG plots (Fig. 5, Appendix 3). Diurnal time interval was the only variable determined to significantly affect  $A_{net}$ across the growing season, and this was observed within only native vegetation

treatments (P = 0.0036). Between-species comparisons indicated only two significant differences in  $A_{net}$ : across the growing season, *Hedysarum boreale* had greater mid-day  $A_{net}$  than *Artemisia tridentata* (P = 0.0061), and *Agropyron cristatum* had greater dawn  $A_{net}$  than *A. tridentata* (P = 0.0061) (i.e. dark respiration was higher among *A. tridentata* than *A. cristatum*). No significant influence of irrigation treatment was detected on  $A_{net}$ of *A. tridentata*. Similar to the pattern observed across all plant species,  $A_{net}$  of *A. tridentata* was significantly lower at dawn than during mid-day or evening (P < 0.0001).

Averaged across the growing season, irrigation treatments, and vegetation treatments,  $A_{net}$  of *H. boreale* and *A. cristatum* was generally higher than  $A_{net}$  of *A. tridentata* (Appendix 2, Appendix 4). Differences between those species were most pronounced during mid-day, when  $A_{net}$  averaged 17.36 ± 2.05 µmol m<sup>-2</sup> s<sup>-1</sup> among *H. boreale*, 11.83 ± 0.72 µmol m<sup>-2</sup> s<sup>-1</sup> among *A. cristatum*, and 7.55 ± 0.97 µmol m<sup>-2</sup> s<sup>-1</sup> among *A. tridentata* (Appendix 4). Significant differences were observed in  $A_{net}$  of all species during this time interval (P < 0.0038).  $A_{net}$  of *A. cristatum* at dawn was significantly greater (i.e. dark respiration was significantly lower) than  $A_{net}$  of *A. tridentata* (P = 0.0021). No differences in  $A_{net}$  of *A. cristatum*, *H. boreale*, or *A. tridentata* were observed during the evening (Appendix 4).

Soil Respiration ( $R_{soil}$ ). Irrigation treatments had a strong influence on dawn, mid-day, and evening soil respiration (Table 4, Fig. 6). Supplemental irrigation stimulated soil respiration relative to ambient conditions throughout the growing season, regardless of the seasonal timing of irrigation. The magnitude of stimulation, however, was generally greater in summer plots in the mid-late growing season, especially in native-vegetation plots. In winter plots, mid-day  $R_{soil}$  was greater than in ambient and summer plots during early June (Table 5, Fig. 6). "Daily"  $R_{soil}$  of winter plots peaked to  $1.17 \pm 0.06 \ \mu mol CO_2 \ m^{-2} \ s^{-1}$  during mid-July.  $R_{soil}$  was greatest among summer plots beginning in early-mid July and persisting through the growing season (Table 5). Summer-plot daily  $R_{soil}$  peaked to  $2.53 \pm 0.39 \ \mu mol CO_2 \ m^{-2} \ s^{-1}$  during late July. Daily  $R_{soil}$  was greatest among ambient plots during mid-May, peaking at  $0.42 \pm 0.004 \ \mu mol CO_2 \ m^{-2} \ s^{-1}$ . Excluding data collected in mid-August, when rain events occurred within 6 hours prior to measurements, daily  $R_{soil}$  averaged  $0.96 \pm 0.05 \ \mu mol CO_2 \ m^{-2} \ s^{-1}$  in winter plots,  $1.29 \pm 0.15 \ \mu mol CO_2 \ m^{-2} \ s^{-1}$  in summer plots, and  $0.18 \pm 0.03 \ \mu mol CO_2 \ m^{-2} \ s^{-1}$  in ambient plots (Fig. 6).

## C Pools as Biomass

Biomass production was greatest in plots irrigated during the winter, and least in plots receiving no supplemental irrigation (Fig. 7). Plots irrigated during summer experienced a slight increase in biomass production relative to ambient plots. Generally, irrigation did not appear to affect how biomass was allocated between vegetation types (Fig. 7). Irrigation treatment influenced the mass of *A. tridentata* and "other" species (live and senesced *A. cristatum* and *H. boreale*); among both of these groups, winter-irrigated plots produced significantly more biomass than ambient plots (P = 0.039, P = 0.009; Fig. 7). Live plant cover in native and *A. cristatum* plots, during peak biomass in June, was greatest in winter plots ( $69.7 \pm 5.1\%$ ), and similarly low in summer and ambient plots ( $5.1 \pm 1.8\%$ ,  $5.8 \pm 5.0\%$ ) (data not shown).

# **Chapter IV: Discussion**

#### C Fluxes

Our hypothesis of greater ecosystem C uptake in plots receiving supplemental irrigation was supported by significantly greater mid-day NEE (Fig. 3) and greater cumulative NEE across the growing season (Fig. 4) in nearly all irrigated plots. An exception to those patterns was observed in cumulative and mid-day NEE of Agropyron cristatum monocultures early in the growing season, when NEE was lower compared with control (ambient precipitation) plots (Fig. 3, 4). Our hypothesis of greater ecosystem C uptake in dormant-season-irrigated ("winter") plots relative to growingseason-irrigated ("summer") plots, however, was generally not supported by ecosystemlevel C fluxes among native vegetation communities. The influence of winter and summer irrigation appeared to be similar in magnitude across all photoperiod intervals, but the seasonal timing of peak midday NEE was offset between the irrigation treatments (Fig. 3). This similarity in peak and cumulative NEE was unexpected, considering the cover and size of A. tridentata shrubs and the relatively greater historical soil-water storage in winter plots compared with summer plots (Germino & Reinhardt 2014). However, this discrepancy may be due to constraints in the NEE tent size that affected selection of measurement areas within winter plots, but not summer or ambient plots. Because many of the shrubs within winter plots were larger than the polyethylene tent and NEE apparatus could accommodate, flux measurements centered on the smaller shrubs present in winter plots, and may therefore be under-representative of whole-plot fluxes, particularly compared with summer and ambient whole-plot C flux estimates.

Dormant-season precipitation is a driver of NEE in sagebrush steppe (Kwon et al. 2008). Conversely, growing-season precipitation has been demonstrated to stimulate both C-uptake and -release responses, including ecosystem photosynthesis (Wu et al. 2011), and ecosystem respiration (Wu et al. 2011, Chen et al. 2009). The extent to which each of those components are stimulated varies depending on the functional type of dominant plants and the pulse size of precipitation events (Huxman et al. 2004, Chen et al. 2009). For example, Huxman et al. (2004) assert that arid ecosystems act as C sources immediately after rainfall because microbial respiration responds quickly to even small precipitation events, but that larger rain events can cause arid systems to become sinks due to increases in photosynthetic activity. In the summer, it is more likely that small rain events may be quickly evapotranspired from the soil, resulting in short periods of wetting in shallow soil – conditions which stimulate microbial activity but limit plant productivity. Collectively, our data suggest that precipitation amount, and not seasonal timing, contributes most heavily to ecosystem C flux, in our cold-desert experiment doubling precipitation pulse sizes.

Another unexpected finding was the effect of vegetation community type on midphotoperiod and cumulative NEE levels. Specifically, *A. cristatum* communities in summer-irrigated plots exhibited much lower NEE than summer-irrigated native vegetation communities, whereas only marginal differences existed between vegetation treatments in ambient and winter-irrigated plots (Fig. 3, Fig. 4). These cumulative NEE findings suggest that the amount of precipitation, rather than seasonal timing, may be responsible for differences in C exchange among native communities, whereas both factors heavily influenced C exchange of *A. cristatum* monocultures (Fig. 4). These

communities are generally similar, except for the presence of *A. tridentata*, and the data may thus reflect a variable capacity for growing-season soil-water use, influenced by the presence or absence of shrubs. Bates et al. (2006) observed lower herbaceous production among plots receiving irrigation primarily between April and July, due to lower "effective" precipitation resulting from high evapotranspiration of water delivered in June and July. In our study, summer irrigation was delivered exclusively in June and July, and thus may have resulted in less soil moisture available for new growth *A. cristatum*. Indeed, Germino and Reinhardt (2014) observed that summer irrigations only increased soil moisture for 7-14 days following application, and only in the top 0.5-m of soil.

Average leaf-level photosynthesis ( $A_{net}$ ) across species, including within *A*. *tridentata* specifically (the dominant plant in native plots), was not affected by irrigation or vegetation treatments. Nonetheless, Germino and Reinhardt (2014) found that crown sizes of individual *A. tridentata* shrubs, in addition to plot-level canopy cover, were more than twofold greater in plots receiving winter irrigation compared to both summerirrigated and ambient plots. This suggests that influences of precipitation seasonality on plant productivity act on a whole-plant or canopy level, rather than effecting leaf-level physiological adjustments, or that precipitation seasonality primarily affects C allocation (Fig. 5). Whether sagebrush steppe species were making physiological or structural adjustments is unknown, but studies of *Pinus ponderosa* have indicated that short-term shifts in photosynthesis and gas exchange are balanced by changes in above-ground structure, resulting in greater canopy- and leaf-level photosynthesis over time (McDowell et al. 2006). In this case, more robust metrics of canopy-level photosynthesis are needed, as difficulties exist in scaling  $A_{net}$  from leaf- to canopy-scales (Smith et al. 2004).

Diurnal measurement interval was the only variable determined to influence  $A_{net}$  across plant species. Within this variable, differences in  $A_{net}$  between species emerged; *A. tridentata* had a generally lower photosynthesis, than *A. cristatum* and *H. boreale* at all time points, and  $A_{net}$  of *H. boreale* was more than twofold higher than  $A_{net}$  of *A. tridentata* during mid-day (Appendix 4). In order to determine the relative contribution of each species to plot-level  $A_{net}$ , it is necessary to consider the abundance of each species, as well as species-level differences in physiological growth patterns.

All three species – *H. boreale, A. cristatum, and A. tridentata* – are perennial, but exhibit different patterns of growth during the growing- and dormant-season. H. boreale, for example, emerges at different times during the growing season in the summer and winter plots, and it is missing entirely in ambient plots. It grows, flowers, and senesces between early June and mid-August, and has the shortest period of active C uptake of the three most abundant plant species observed. A. cristatum is present among all irrigation treatments, generally emerges in May and June, and senesces in late August and September. Unlike H. boreale and A. cristatum, A. tridentata maintains photosynthetic tissue year-round. The shrub develops ephemeral leaves in the early spring, which senesce during the summer, and perennial leaves in the late spring, which persist through the growing and dormant seasons, and are shed the following spring (Evans and Black 1993). Floral heads emerge on A. tridentata in the mid-summer, and bloom in the late summer and early autumn (Evans and Black 1993). Considering the growth patterns and observed leaf-level photosynthetic rates of *H. boreale*, *A. cristatum*, and *A. tridentata*, it can be inferred that *H. boreale* sustains a high photosynthetic rate for only a short period of time, A. tridentata maintains a lower photosynthetic rate for a much greater period of

time, and *A. cristatum* is intermediate between these two species – sustaining moderately high photosynthetic rates over a somewhat short period of time. This temporal variability suggests that ecosystem-level C uptake is likely to vary considerably over the growing season, depending on the relative abundance of each of these species, and that the factors controlling distribution and abundance of these plants may be of critical importance in assessing current and future ecosystem C uptake.

Despite a lack of irrigation-seasonality effect on NEE of native vegetation, both irrigation magnitude and seasonality exerted influence on soil respiration ( $R_{soil}$ ). As anticipated, supplemental irrigation stimulated  $R_{soil}$  relative to ambient conditions, and the boost in  $R_{soil}$  was significantly greater (by 34%) in summer plots relative to winter plots (Fig. 6). This supports our prediction that summer plots would experience greater C loss through  $R_{soil}$  than winter plots. However, the comparable NEE between winter and summer plots suggests that greater soil C-effluxes in summer plots were balanced by increases in canopy-level C uptake, which our leaf-level data did not capture.

In order to discern the contribution of  $R_{soil}$  to ecosystem C exchange and balance, as well as predict trends under future climate scenarios, it is essential to understand the environmental and biological factors regulating  $R_{soil}$ . These controls vary on the partitioning of  $R_{soil}$  into microbial decomposition (heterotrophic,  $R_h$ ) and root respiration (autotrophic,  $R_a$ ) (Carbone et al. 2008, Hanson et al. 2000). Research in warm, arid or semiarid ecosystems suggests that at least half of total soil respiration is autotrophic (Carbone et al. 2008, Chen et al. 2009), and that the apportionment of respiration into autotrophic and heterotrophic components is dependent on seasonal timing and plant functional type, and the influences of those factors on soil water distribution (Carbone et al. 2008).

al. 2008). Plant functional type can influence  $R_a$  through differences in root phenology and distribution (Carbone et al. 2008, Jackson et al. 2000), and  $R_h$  through differences in nutrient availability (Jackson et al. 2000), and litter quality and quantity. Although we did not observe any effects of vegetation treatment on  $R_{soil}$ , except at dawn, we were unable to partition  $R_{soil}$  measurements into  $R_a$  and  $R_h$ . It is possible that land-use changes resulting in shifts in vegetation community composition will influence the relative contribution of  $R_a$  and  $R_h$  to  $R_{soil}$ . Because  $R_a$  and  $R_h$  respond to precipitation at different time scales and magnitudes (Huxman et al. 2004, Chen et al. 2009), it is likely that vegetation community changes will influence patterns of soil C efflux in response to precipitation events.

In addition to seasonal timing, the size of rain events also regulates the balance and magnitude of R<sub>h</sub> and R<sub>a</sub>. Chen et al. (2009) observed that the contribution of R<sub>h</sub> and R<sub>a</sub> to ecosystem-level respiration varied temporally in response to rain pulses, with R<sub>h</sub> primarily responsible during the early stage of the pulse response, and R<sub>a</sub> more important during the later stage. This tiered response to rain pulses strengthened as pulse size increased, and was most dramatic following rain events of 50-75 mm (Chen et al. 2009). This effect may partly result from variation in spatial distribution of soil microorganisms and plant root systems. Whereas microorganisms tend to be concentrated in shallow, quickly drying horizons of topsoil, plant roots distributed over a wider range of depth integrate available water resources throughout the soil profile (Schwinning & Sala, 2004). This spatiotemporal variability in the distribution of microorganisms, roots, litter, and nutrients suggests that ecosystem-scale C efflux from soils is likely to respond to changes in precipitation seasonality in varied ways.

## C Pools

Aboveground biomass and C storage were greatest in winter plots and least in ambient plots (Fig. 7). The greater biomass production in A. tridentata in winter plots relative to summer and ambient suggest that this species may be a more important driver of C uptake and storage relative to other species. The contribution of A. tridentata to aboveground C storage may be particularly critical during mid-summer, or when other plants are dormant, as demonstrated by the strong vegetation effect observed in cumulative NEE among summer plots (Fig. 4). Though irrigation effects were only significant on production of A. tridentata and "other" species, our results lend support to both our original hypotheses by suggesting that irrigation stimulates aboveground biomass production relative to ambient precipitation, and that long-term increases in dormant-season precipitation lead to the most substantial C storage gains. Together with leaf- and ecosystem-level C flux data, these results indicate that changes in precipitation seasonality may affect aboveground C dynamics primarily through changes in community structure, rather than through physiological responses. Whereas our instantaneous C flux measurements encapsulate a small range of time and environmental and biological factors, C pools reflect the integrated, long-term biological changes resulting from shifts in C fluxes, and thus, may be more indicative of future C storage. This is supported by the findings of Polley et al. (2010), who indicate that the response of C exchange to altered precipitation can be influenced by concurrent changes in biological factors that regulate photosynthesis and respiration, such as canopy size or mineralization rates (functional change). Polley et al. (2010) further assert that the capacity to predict ecosystem-level C exchange from inter-annual variation in environmental factors

decreases with decreasing mean precipitation and increasing precipitation variability, and functional change plays a greater role in explaining variability in ecosystem C flux. Because these two hydroclimatic features – low mean precipitation and high precipitation variability – characterize arid and semi-arid ecosystems in the intermountain west, it is especially critical that studies of future C storage in these regions incorporate the effects of functional change over time (such as biomass production), in addition to the instantaneous responses of C flux.

#### Hydroclimate

Soil moisture patterns during the 2014 growing season differed from the longterm, average patterns reported by Germino and Reinhardt (2014) between 2002 and 2007, but largely reflected seasonal ambient precipitation trends (Fig. 1). Across the 2014 growing season and soil depths, moisture was greatest among summer plots. Contrarily, Germino and Reinhardt observed the greatest soil moisture among winter plots at all depths. In 2014 (this study), we observed increases in soil moisture content as deep as 1.0 m in summer plots following irrigations, beginning in July and persisting through mid-September (Fig. 2). This contradicts the findings of Germino and Reinhardt, who determined that summer irrigation treatments only increased water storage in the top 0.4 m of soil, and these gains were lost as evapotranspiration within two weeks of irrigation applications (2014). Our hypotheses were based on soil moisture conditions consistent with Germino and Reinhardt (2014) and long-term precipitation trends (Fig. 1). Thus, lack of support for these hypotheses may be primarily the result of inter-annual precipitation variability, and not indicative of long-term trends in C flux or storage.

Variation in natural precipitation, including differences in inter-annual precipitation and pulse sizes, has been demonstrated to have a considerable effect on C uptake and storage in rangeland ecosystems (Chen et al. 2009, Kwon et al. 2008, Svejcar et al. 2011). Schwinning and Sala (2004) assert that, across a variety of arid and semi-arid ecosystems, inter-annual variability in total precipitation is primarily a function of pulse size: larger rain events (e.g. > 10 mm) dominate differences in precipitation among years, while small events (< 5 mm) contributed to total precipitation more consistently among years. During the 2014 growing season, we observed atypical precipitation patterns at our study site; below-average precipitation was recorded during much of the winter and through mid-growing-season, and substantially more precipitation occurred during the late growing-season (especially August) compared with long-term trends (NOAA NCDC 2015). Approximately 95% of the precipitation measured in August occurred during rain events larger than 10 mm (NOAA FRD 2015), suggesting that associated ecosystem responses are likely to be uncharacteristic of long-term trends.

Precipitation pulse experiments have demonstrated how the distribution of large and small rain events influences the magnitude and duration C flux specifically. Central to this relationship is the fact that effects on C storage and exchange cannot simply be scaled; different ecosystem components respond to different precipitation thresholds (Huxman et al. 2004, Chen et al. 2009, Schwinning & Sala 2004). Specifically, smaller precipitation pulses have been demonstrated to stimulate productivity to a lesser amount relative to respiration, whereas larger pulses generally facilitate greater increases in productivity and net C uptake (Huxman et al. 2004, Chen et al. 2009). This effect may be due, in part, to the concentration and activity of microorganisms in shallow horizons of

topsoil, which dry out earlier than deeper soil horizons (Schwinning & Sala 2004). Thus, periods of microbial activity are expected to be shorter than plant responses due to spatial differences in soil water use (Schwinning & Sala 2004). Chen et al. (2009) also found that the drivers of C flux following large precipitation events varied temporally – with peak ecosystem C uptake following peak ecosystem C efflux by 1-3 days. This spatiotemporal effect on ecosystem photosynthesis and respiration suggests that C flux can be highly variable within and between years, and that measurements of C flux alone are insufficient to predict long-term trends. Instead, the combination of C fluxes and pools information reveals both the integrative history of C dynamics in addition to current change in C balance.

#### **Conclusions**

It has been suggested that cold deserts could be significant C sinks under predicted climate change scenarios (Svejcar et al. 2011). The potential for a cold-desert C-sink under future climate scenarios in western North America is generally supported by observational studies (Svejcar et al. 2011, Meyer 2011, Kwon et al. 2008), and by our manipulative data. Our results indicate that sagebrush steppe and *A. cristatum* communities both have the potential to be C sinks under future precipitation conditions (Fig 2). However, the C-sink strength of these plant communities most likely will be less than observed in our experiment, in which precipitation was doubled (100% increase) compared to long-term annual averages, whereas only 10-20% increases in dormantseason precipitation are forecasted for our study area (Abatzoglou & Kolden 2011). Additionally, our estimates address C fluxes during the growing season only. Within the Idaho National Laboratory specifically, Gilmanov et al. (2004) observed a mean

dormant-season daily ecosystem efflux of  $0.32 \pm 0.31 \,\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. It is unclear how these fluxes, interpolated from a day-time rate, will offset cumulative uptake or nighttime loss of C during the growing season (interpolated from a per-second rate). Changes in precipitation amount and seasonality, and the long-term functional changes reflected in biomass production will further influence these fluxes. The long-term C sink strength of sagebrush steppe ecosystems will, therefore, depend on the balance of dormant- and growing-season fluxes, and how these fluxes will respond to changes in precipitation and resultant functional change.

The independent and interactive effects of precipitation amount, seasonal timing, pulse-size distribution, and inter-annual variability can have a large effect on ecosystem C exchange (Svejcar et al. 2011, Huxman et al. 2004, Chen et al. 2009, Kwon et al. 2008). Over time, those effects can cause functional changes in the factors that regulate photosynthesis and respiration, which then influence ecosystem response to climatic variability (Polley et al. 2010). We demonstrated that C flux in native sagebrush steppe is primarily dependent on amount, rather than timing, of precipitation, whereas both factors influence C flux in *A. cristatum* monocultures (Fig. 4). We also found that both amount and timing of precipitation influenced aboveground C storage as biomass. We also hypothesize that our findings were influenced, to some degree, by inter-annual variability in precipitation, resulting in climatic conditions contrary to long-term trends. Although our experimental design is relatively robust to natural precipitation variation, this observation underscores the need for long-term experiments to accurately predict future C-storage patterns in these cold-desert ecosystems.

# Figures



**Fig 1**. 30-year monthly mean precipitation in the upper Snake River Plain compared to monthly precipitation during the 2014 water year (Oct 1, 2013 – Sep 31, 2014). Error bars represent an approximate of standard deviation, based on published 30-year anomalies (NOAA NCDC 2015).



**Fig. 2.** Mean soil water content of ambient, summer, and winter plots at 0.2-m, 0.5-m, and 1-m depths. Data were collected from native plots in two replicates; points therefore represent mean soil water content in one or two plots (n = 1, n = 2). Error bars represent one standard error of the mean.



**Fig. 3.** Mean net ecosystem exchange (NEE) of native sagebrush steppe (a-c) and *Agropyron cristatum* monocultures (d-f) during pre-photoperiod (dawn) (a,d), mid-photoperiod (mid-day) (b,e), and late-photoperiod (evening) (c,f). NEE was measured between May 1 and September 12, 2014, and exhibited substantial diel and seasonal variation. Asterisks indicate dates at which NEE differed significantly between at least two precipitation treatments (p < 0.05). Each point represents an average across either two or three replicates. Error bars represent one standard error of the mean.



**Fig. 4.** Cumulative mean daily net ecosystem exchange (NEE) of native sagebrush steppe and *A. cristatum* monocultures. Daily NEE was calculated as the average of dawn and mid-day measurements within vegetation and irrigation treatments at each seasonal time point. NEE was measured between May 1 and September 12, 2014. Cumulative seasonal NEE was highest among vegetation communities receiving supplemental irrigation in winter ("Winter"), and native vegetation communities receiving supplemental irrigation in summer ("Native – Summer"). Error bars represent one standard error of the cumulative mean.



**Fig. 5.** Mean leaf-level photosynthesis ( $A_{net}$ ) of *A. cristatum* monocultures (a-c) and native sagebrush steppe (d-f) and during pre-photoperiod (dawn) (a,d), mid-photoperiod (mid-day) (b,e), and late-photoperiod (c,f).  $A_{net}$  was measured between June 4 and September 12, 2014. Asterisks indicate dates at which  $A_{net}$  differed significantly between at least two precipitation treatments (p < 0.05). Sample sizes vary between 1 and 21. Significant effects of irrigation, indicated by asterisks, were only assessed for comparisons with n  $\geq$  2. Error bars represent one standard error of the mean, except where data represent a single measurement (n = 1).



**Fig. 6.** Mean soil respiration ( $R_{soil}$ ) of native sagebrush steppe (a-c) and *A. cristatum* monocultures (d-f) during pre-photoperiod (dawn) (a,d), mid-photoperiod (mid-afternoon) (b,e), and late-photoperiod (c,f).  $R_{soil}$  was measured between May 15 and September 12, 2014. Asterisks indicate dates at which  $R_{soil}$  differed significantly between at least two precipitation treatments (p < 0.05). Each point represents an average across either two or three replicates. Error bars represent one standard error of the mean.



**Fig 7**. Biomass accumulations of different species and functional groups in ambient (AMB), summer (SUM), and winter (WIN) plots. Error bars represent one standard error of the mean.

Time		Irrigati	on	Vegetation			Irrigation*Vegetation		
Interval	df	F	Р	df	F	Р	df	F	Р
Dawn	2,12	11.95	0.0014	1,12	1.07	0.32	2,12	1.77	0.21
Mid-Day	2,12	30.7	< 0.0001	1,12	7.01	0.02	2,12	2.84	0.10
Evening	2,12	6.12	0.015	1,12	1.72	0.21	2,12	1.4	0.28

 Table 1.
 Summary Repeated-Measures ANOVA table for NEE.

**Table 2**. One-Way ANOVA of the effects of irrigation treatments on NEE within each campaign date, with post-hoc Tukey comparisons. Only dates at which an overall effect (P < 0.05) was detected are recorded. No evening data are included in this table due to a lack of irrigation treatment effect detected in post-hoc Tukey comparisons.

Time		Campaign			Post-Hoc	Tukey's
Interval	Vegetation	Date	Overall F	Overall P	Comparison	Р
		1-Jul	12.22	0.0077	AMB > SUM	0.0062
	Native	29-Jul	25.49	0.0012	AMB > SUM	0.0010
					WIN > SUM	0.0133
Dawn		4-Jun	12.45	0.0073	AMB > WIN	0.0095
	CWG				SUM > WIN	0.0152
	0110	12-Aug	20.61	0.0177	AMB > SUM	0.0164
					WIN > SUM	0.0488
		1-May	5.5	0.0440	All two-way P	> 0.05
		15-May	5.71	0.0409	WIN > SUM	0.0365
	Native	18-Jun	98.53	0.0018	WIN > AMB	0.002
					WIN > SUM	0.0033
		29-Jul	15.64	0.0042	SUM > AMB	0.0049
					SUM > WIN	0.0109
		12-Aug	5.94	0.0378	SUM > AMB	0.0442
Mid-Day		15-May	6.41	0.0324	WIN > SUM	0.0335
		4-Jun	31.05	0.0007	WIN > SUM	0.0011
					WIN > AMB	0.0013
	CWG	18-Jun	33.96	0.0087	WIN > SUM	0.0096
	Cwu				WIN > AMB	0.0149
		1-Jul	8.73	0.0167	WIN > AMB	0.0170
					WIN > SUM	0.0490
		29-Jul	6.16	0.0351	SUM > AMB	0.0322

**Table 3**. One-Way ANOVA of across-species  $A_{net}$  within each campaign date, with posthoc Tukey comparisons. Statistical figures only provided for comparisons with n  $\geq 2$  at each treatment level.

Time		Campaign			Post-Hoc	
Interval	Vegetation	Date	Overall F	Overall P	Comparison	Tukey's P
Dawn	Nativo	15-Jul	5.086	0.0234	AMB > SUM	0.0220
	Native	12-Sep	5.02	0.0227	SUM > WIN	0.0293
	CWG	15-Jul	4.24	0.0465	All two-way P > 0.05	
Mid-Day	Native	1-Jul	3.85	0.0308	WIN > AMB	0.0264
		29-Jul	3.90	0.0288	AMB > WIN	0.0278
	CWG	29-Jul	4.11	0.0350	SUM > AMB	0.0384
Evening	CWG	12-Sep	32.12	0.0034	WIN > AMB	0.0030
	CWG				WIN> SUM	0.0146

Time Interval		Irrigation			Vegetation			Irrigation*Vegetation		
	df	F	Р	df	F	Р	df	F	Р	
Dawn *	2,6	50.40	0.0002	1,6	2.45	0.17	2,6	0.58	0.59	
Mid-Day	2,4	14.83	0.0141	1,4	1.35	0.31	2,4	0.84	0.50	
Evening <sup>†</sup>	2,12	34.87	< 0.0001	1,12	1.25	0.29	2,12	2.94	0.09	

Table 4. Summary Repeated-Measures ANOVA table for Rsoil.

\* Excludes data from mid-September, when missing data impeded repeated-measures analysis.

<sup>†</sup> Excludes data from mid-May, early June, mid-July, and mid-September, when missing data impeded repeated-measures analysis.

Time		Campaign			Post-Hoc	
Interval	Vegetation	Date	Overall F	Overall P	Comparison	Tukey's P
		1-Jul	11.71	0.0085	WIN > AMB	0.0086
	Native				SUM > AMB	0.0277
	Tutive	29-Jul	39.27	0.0004	SUM > WIN	0.0017
					SUM > AMB	0.0004
Dawn *		4-Jun	20.31	0.0021	WIN > SUM	0.0021
2					WIN > AMB	0.0089
	CWG	1-Jul	8.61	0.0173	WIN > AMB	0.0152
	Cwd	15-Jul	9.16	0.0150	SUM > AMB	0.0123
		29-Jul	9.90	0.0126	SUM > WIN	0.0448
					SUM > AMB	0.0121
Mid Day		4-Jun	11.33	0.0092	WIN > SUM	0.0364
		15-Jul			WIN > AMB	0.0087
	Native		44.46	0.0003	SUM > WIN	0.0015
	Tutive				SUM > AMB	0.0002
Wild-Day		29-Jul	16.51	0.0036	SUM > WIN	0.0118
					SUM > AMB	0.0039
-	CWG	15-Jul	34.14	0.0012	SUM > WIN	0.0019
	CWU				SUM > AMB	0.0023
Evening *† —	Nativa	29-Jul	52.08	0.0002	SUM > WIN	0.0006
	TVative				SUM > AMB	0.0002
	CWG	29-Jul	32.09	0.0006	SUM > WIN	0.0027
	CWG				SUM > AMB	0.0006

**Table 5.** One-Way ANOVA of  $R_{soil}$  within each campaign date, with post-hoc Tukey<br/>comparisons.

\* Excludes data from campaign dates specified in Table 4 footnotes.

† SUM  $R_{soil}$  marginally greater than AMB  $R_{soil}$  in Native (P = 0.0543) and CWG plots (P = 0.0513) on July 1.

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# Appendixes



**Appendix 1**. Gross Ecosystem Productivity (GEP) of native vegetation (a, b) and A. cristatum monoculture treatments (c, d) during mid-day (a, c) and evening (b, d). Conceptually, GEP represents the productivity inputs to NEE, but does not include ecosystem-level respiration as NEE does (NEE =  $GEP - R_{ecosystem}$ ). To estimate GEP, we added mid-day or evening NEE to Recosystem (dawn NEE), expressed as a positive respiratory rate. Averaged across the growing season, mid-day GEP was nearly identical in native vegetation plots irrigated in the summer or winter. Despite this similarity, the patterns of GEP in these treatments differed temporally; GEP was positive in winter plots throughout the growing season, but did not reach the same peak magnitude as in summerirrigated plots. These summer plots, despite achieving a higher peak GEP rate, had negative rates of GEP (net C efflux) during the growing season. Winter-irrigated A. cristatum plots had a higher seasonal rate of GEP than summer-irrigated plots. Among both time intervals and vegetation types, ambient plots had the lowest rates of seasonal GEP. Evening GEP of summer-irrigated A. cristatum plots was substantially greater than in winter-irrigated plots, but these irrigation treatment differences in GEP were less prominent in native vegetation plots.



**Appendix 2**. Mean  $A_{net}$  of native vegetation plots, separated by three most abundant plant species within native vegetation plots (*Agropyron cristatum*, a-c; *Hedysarum boreale*, d-f; *Artemisia tridentata*, g-i).



**Appendix 3**. Mean *A<sub>net</sub>* of *A. cristatum* monoculture plots, separated by two most abundant plant species within *A. cristatum* monoculture plots (*Agropyron cristatum*, a-c; *Hedysarum boreale*, d-f). Vegetative cover in plots is dominated by *A. cristatum*, with *H. boreale* accounting for less than 25% of vegetative cover during peak growth.



**Appendix 4.** Dawn, mid-day, and evening leaf-level photosynthesis ( $A_{net}$ ) of the three most abundant plant species (*Agropyron cristatum*, *Hedysarum boreale*, and *Artemisia tridentata*) at the IEE. Letters indicate which species groups are significantly different from others (P < 0.05) within a single diurnal interval. Error bars represent one standard error of the mean. Because  $A_{net}$  means do not vary significantly across the growing season, or between vegetation and irrigation treatments, these data represent means across those variables.