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# LIVING IN THE PHANTOM GAS FIELD: PHYSIOLOGICAL RESPONSES OF ARTEMISIA TRIDENTATA TO EXPERIMENTAL-NOISE-INDUCED CHANGES IN ARTHROPOD HERBIVORY

by

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# Committee Approval

To the Graduate Faculty:

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#### ABSTRACT

Changes in soundscapes from human-caused noise disturbance alter avian and mammalian community assemblages, their foraging behavior, and reproductive success. Little is known, however, about how changes in insectivorous predators can directly, or indirectly, affect plant physiology and productivity. We continuously broadcasted (24-hrs /day) recordings of natural-gas compressor station extraction from April through October 2015 in sagebrush-steppe habitat in Idaho, USA. We hypothesized that effects of an altered soundscape would change existing insect abundances (via changes in avian predators; assessed in a separate study) and therefore insect herbivory on plant physiology and productivity in sagebrush shrubs (Artemisia tridentata ssp. wyomingensis). We predicted that we would observe increases in shrub herbivory at Noise-On sites, because of reductions in avian predation on herbivorous insects. We further predicted that we would observe decreased physiology and productivity in shrubs at Noise-On sites because of physiological costs associated with increased herbivory damage. Total arthropod abundance was not statistically significantly different between noise treatments; however, greater numbers (13.5%, n.s.) of insects from sap-sucking families occurred on shrubs in Noise-On sites. Stem elongation per cm during the growing season was 19.5% greater at Noise-On sites, contrary to our initial hypotheses. Noise significantly increased both shrub respiration ( $R_d$ ) and photosynthesis ( $A_{net}$ ), and a significant day×noise interaction occurred for light-reaction photochemistry ( $\Phi$ PSII) and  $A_{net}$ . We hypothesize that the increases in  $A_{net}$  and  $R_d$  that we observed—which were opposite our hypotheses—were compensatory responses from increased sap-feeding damage in sagebrush at Noise-On sites. Boosts in photosynthesis and growth because of

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modest increases in herbivory have been reported in previous studies, whereas more intense herbivory can lead to declines in photosynthesis. Collectively, our research indicates that chronic human noise has the capacity to affect ecosystem functioning at multiple trophic levels because of altered soundscapes.

Keywords: soundscape, energy development, herbivory, physiology, big sagebrush, respiration, photosynthesis, compensatory

#### **Chapter 1: Introduction**

In terrestrial ecosystems, insectivorous birds are primary or secondary consumers, and prey upon multiple arthropod groups (Marquis and Whelan 1994, Mooney et al. 2010, Maas et al. 2013). In turn, this avian consumption of herbivorous insects can indirectly influence overall plant biomass in ecosystems (Marquis and Whelan 1994, Bridgeland et al. 2010, Maas et al. 2013). Changes in arthropod populations and behavior affect plants and ecosystem dynamics, and manipulative changes in the activities of herbivorous insects have resulted in alterations of ecosystem functioning (Bridgeland et al. 2010, Mass et al. 2013, Strickland et al. 2013). To understand how predator-prey dynamics could affect surrounding plant communities, researchers have experimentally excluded insectivorous predators using bird netting or excluded herbivorous insects via the use of controlled insecticide applications (Sipura 1999, Takahashi and Huntly 2010, Maas et al. 2013). For example, Maas et al. (2013) reported a 31% reduction in cacao (Erythrina sp. and *Gliricidia* sp.) crop yields by excluding birds and bats from the cacao trees using netted exclosures. Those authors reported significant increases in the number and diversity of arthropod groups on trees inside exclosures. Takahashi and Huntly (2010) used insecticide treatments to remove insects from basin big sagebrush (Artemisia tridentata ssp. tridentata), and noted significant increases in seed and flower production, inflorescence growth, and significant decreases in leaf damage, compared with control plots of sagebrush with no insecticide treatments. Moreover, significantly fewer insects were observed on shrubs receiving the insecticide treatment compared with controls; significant differences were attributed to decreases in leaf damage.

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Increases in herbivory can negatively influence plant functioning in several ways. One mechanism is through the direct effects of herbivory damage, such as the removal of leaf tissue and thus photosynthetic area (Zangerl et al. 2002, Nabity et al. 2009). Herbivory damage also can sever vasculature, which disrupts water transport, and can lead to reduced gas exchange (i.e., photosynthesis, respiration, transpiration), and altered carbon source-sink dynamics (Nabity et al. 2009, Ferrieri et al. 2013). For example, Aldea *et al.* (2006) reported for several different categories of herbivory damage (chewing, fungal, gall infection) photochemical efficiency (ΦPSII) was reduced, this affects efficiency of the light reactions which drive photosynthesis, and this effect from herbivory extended beyond the initial damaged area in upwards of 25% of hardwood saplings (Quercus velutina and Cercis canadensis). Reductions in  $\Phi$ PSII and photosynthesis also were observed in another study on Arabidopsis (Tang et al. 2006) in response to chewing insect damage, in which effects of damage also extended greatly beyond the wound area. Damage from grasshoppers (Hesperotettix virid) on snakeweed (*Gutierrezia microcephala*) exhibited a significant long-term reduction in plant-water potentials, indicating that plant-water balance also can be indirectly influenced by herbivory (Parker 1985).

Herbivory also can affect plant growth and reproduction, through both direct and indirect pathways. Herbivory results in decreased growth (productivity), flower and seed production, and viability of seeds (thereby reducing the overall fitness of the plants) (Nabity *et al.* 2009, Takahashi and Huntly 2010, Maas *et al.* 2013, Gols *et al.* 2015). Takahashi and Huntly (2010) reported a 22% increase in inflorescence growth of big sagebrush when insect herbivores were removed, and almost a 1000% increase in seed

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production. Chronic, long term-damage from herbivory resulted in substantial reductions in mountain birch saplings (*Betula pubescens*), including vertical growth and leaf size (Zvereva *et al.* 2012). Furthermore, Bridgeleand *et al.* (2010) observed, under particular environmental conditions, cottonwood trees (*Populus spp.*) experienced an 18% reduction in trunk growth when insectivorous predators were excluded physically from the tree, leading to an increase in arthropod abundance of 67%. Although we know that physiological and morphological responses because of herbivory occur at leaf and organismal scales, little is known about how those plant responses are linked with changes in top-down predation at various ecosystem scales (Mooney *et al.* 2010, Strickland *et al.* 2013), including changes in the acoustic environment (Francis and Barber 2013, McClure *et al.* 2013).

The soundscape is the sum total of all acoustic energy present in an environment, and is recognized as an important driver of ecosystem structure and function (Francis and Barber 2013, Strickland *et al.* 2013). Numerous species use acoustic signaling as part of their life histories (e.g., birds and bats), and the location and behavior of many animals can be shaped through ecosystem soundscapes (Francis *et al.* 2009, Blickley *et al.* 2012, Francis and Barber 2013, McClure *et al.* 2013, Ware *et al.* 2015, Kleist *et al.* 2016). In the Intermountain West, USA, activities associated with urban growth and energy development have been increasing exponentially over the past 2 decades (Northrup and Wittemyer 2012). Changes in soundscapes through those human activities have altered assemblages of avian and mammalian communities, foraging behavior, and reproductive success (Blickley *et al.* 2012, Francis and Barber 2013, McClure *et al.* 2013, McClure *et al.* 2013, Ware *et al.* 2015, Kleist *et al.* 2016). Furthermore, changes in predator-prey dynamics, because of

[3]

human noise disturbance, have the potential to create "top-down" alterations in ecosystem functioning across trophic levels (Sinclair and Krebs 2002, Estes *et al.* 2011, Pierce *et al.* 2012). Few manipulative studies, however, have quantified how changes in avian, mammalian, and arthropod communities through increased anthropogenic noise, can directly or indirectly affect ecosystem functioning beyond those trophic levels, including plant morphology and physiology.

Herein, we report on the results of a sound-manipulation experiment (i.e., altered soundscape) on plant herbivory damage, physiology, and growth in sagebrush shrubs, via changes in songbird and arthropod communities. Using speakers, we broadcasted noise from recordings of a natural gas-well compressor station 24 hrs a day from April-October 2015. This approach isolates the direct effects of noise from associated indirect effects of human presence, such as automobiles, chemical pollutants, and infrastructure (e.g., roads and buildings, [Fahrig and Rytwinski 2009]). We focused on natural gas-well extraction noise because noise associated with natural gas-well operations have affected avian predators (Francis et al. 2009, Blickely et al. 2012, Kleist et al. 2016), and the spectral nature of this noise is broadly applicable to many types of anthropogenic noise (Francis and Barber 2013). In the Intermountain West, energy production doubled between 1990 and 2007 (Copeland *et al.* 2009), and is predicted to keep increasing at even greater rates (Allred *et al.* 2015). The World Energy Council (Northrup and Wittemyer 2012) predicts that extensive landscapes of shrub steppe are likely to be developed across the world as implementation of this new technology spreads. In the U.S. alone, estimated natural-gas development will affect no less than 3.7 million ha of sagebrush steppe (Copeland et al. 2009). The Great Basin region of the U.S., is considered an immense expanse of arid,

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sage-steppe wilderness, effected only occasionally by human noise near roads and urban centers. Since 2014, however, >5,900 gas-well leases have been generated in the Great Basin, which was approximately 5,267,527 ha under lease for California, Nevada, Utah, and Wyoming (USDI-BLM 2014). Sagebrush steppe is considered to be one of the most endangered ecosystems in North America (Noss et al. 1995, Miller et al. 2011), and provides crucial habitat for many animal species of conservation concern, including: pronghorn (Antilocapra americana [O'Gara and Yoakum 2004]), greater sage-grouse (Centrocercus urophasianus [Connelly et al. 2000]), mule deer (Odocoileus hemionus), North American elk (Cervus elaphus [Stewart et al. 2010]), and the pygmy rabbit (Brachylagus idahoensis [Rachlow et al. 2005]). The current range of sagebrush steppe, however, is less than one-half of its historical range, because of change in human landuse activities (including energy development), increasing wildfire regimes, and climate change (Copeland et al. 2009, Neely et al. 2009). Increases in energy development infrastructure dramatically alter the background sound levels for much of the vast 'Sagebrush Sea', and has the potential to interfere with important ecosystem services (e.g., carbon and water storage, habitat protection, and plant pollination).

We hypothesized that persistent human-noise would alter existing sagebrusharthropod interactions. We predicted that experimentally-broadcast noise would result in increases in arthropod herbivory on shrubs, because of decreases in avian predation on insects (Maas *et al.* 2013, McClure *et al.* 2013, Ware *et al.* 2015). We further hypothesized that disruption of these interactions would result in changes of sagebrush physiology and growth. We predicted that increases in herbivory damage to shrubs would result in decreased photosynthesis, photochemical efficiency, and shrub growth, because

[5]

of the increases in costs associated with plant-tissue repair and production of defense compounds (Nabity et al. 2009, Ferrieri *et al.* 2013). Understanding how recent increases in human- noise affect ecosystem structure and function is critical for land managers and stakeholders that strive to balance urban growth and energy development with the protection of vital ecosystem services.

#### **Chapter 2: Materials and methods**

#### Study Area

We conducted this study from March through October 2015, on the National Birds of Prey Conservation Area, southwest of Boise, ID, USA (approx. 97.7 km<sup>2</sup>, centered on  $43^{\circ}18'49.98"$ N and  $116^{\circ}09'57.42"$ W, with an average elevation of 966 m ± 26 SD). Annual precipitation is 25.3 cm, with an annual low temperature of  $3.1^{\circ}$  C, and annual high temperature of  $17.7^{\circ}$  C. Soil composition is sandy-clay loam, with clay composition ranging from 20-40% (USDANRCS 2015).

This area is dominated by Wyoming big sagebrush (*Artemisia tridentate ssp. wyomingensis*), with intermittent patches of green rabbit brush (*Chrysothamnus viscidiflorus*), and shadscale saltbush (*Atriplex confertifolia*). Common grasses include sandberg bluegrass (*Poa secunda*), and purple threeawn (*Astrida purpurea*). Forbs present include slickspot peppergrass (*Lepidium papilliferum*), which has a current conservation status of 'threatened' under the endangered species act (USDI-FWS 2016). Common mammals in the area include mule deer, pronghorn, coyote (*Canis latrans*), black-tailed jackrabbit (*Lepus californicus*), and Paiute ground squirrel (*Urocitellus mollis*). Common insectivorous birds include the Brewer's sparrow (*Spizella breweri*) and sage sparrow (*Artemisiospiza nevadensis*).

# Experimental design

This project was a collaboration with researchers at Boise State University, Boise, Idaho. We broadcasted recordings of noise produced from compressor stations from natural-gas well fields, 24 hrs per day from April through October 2015 (with 100 dB (A)

at 1m, and 70.5 dB (A) at 40 m from the source of the speakers, broadband of 20-8760 Hz), see Cinto Mejia (2017) for full speaker and playback file specifications. Briefly, we used an average of recordings taken from five currently operating natural gas-well compressor stations in New Mexico and Wyoming, USA (Appendix 1, Fig. 1). We used averaged recordings in order to account for the variability associated with recording just one compressor station. We broadcasted this noise at six randomly selected plots (hereafter "Noise-On" plots; each plot was 7,850 m<sup>2</sup> based off radius from the central speaker). We randomly selected six control plots of the same size with no noise broadcast (hereafter "Noise-Off" plots), but with dummy speaker systems in place. We set-up dummy speakers as five-gallon buckets similar in size, shape, and color to match the real speaker systems, with blue plexi-glass used to represent solar panels. At each Noise-On and Noise-Off site, we selected three pairs of sagebrush shrubs (six total) at a 50-m radius from the central speaker or dummy speaker, with each pair being located at three cardinal directions (W, N, E) from the speaker. We chose shrubs at the south direction for a separate study on sagebrush-tissue chemical analysis. Since it has been demonstrated that chemical compounds can be altered by damage to plant tissues (Karban et al. 2006), we did not use south shrubs for our insect collections, herbivory assessment, or shrub physiology studies. With these pairs of shrubs, one shrub received a netting treatment (for physical predator exclusion-i.e., positive controls) and the other shrubs remained unnetted (within 3 m of the netted shrubs, but >1 m away to avoid chemical signaling between un-netted and netted shrubs [Karban et al. 2006]). The netting treatment allowed us to examine the effects of a bird-predation-free environment on arthropod herbivory, and to determine if the noise treatments had a direct effect on the arthropod community.

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For example, significant differences in herbivory between netted shrubs at Noise-Off and Noise-On sites could indicate direct effects of noise treatments on arthropod assemblages, rather than indirect influences of noise on arthropod communities through noise-effects on birds.

To compare differences in habitat quality among sites, we quantified percent vegetation cover for each site using the program Sample Point (Version *1.59*, Booth et al. 2015). We established five 300m transects radially from the center speaker at each site, and 20,  $1-m^2$  photographs were taken 15 m apart along each transect (n = 100 photographs per site), with a Fujifilm FinePix XP70 16.4 Megapixel camera attached to a 2 m Sokkia 724290 Economy Aluminum 2-section GPS Rover Rod. We overlaid a 64-point grid on each photograph; with the main categories of interest being percent sagebrush, grass, forb, bare ground, and biological crust cover.

#### Birds and Arthropods

Detailed methods for avian and arthropod collection and analyses are provided in Cinto Mejia (2017). Briefly, for arthropods, netted and un-netted shrubs (separate from our shrubs selected for the herbivory and physiology study) were beat-netted in April, May, and June 2015, and we visited two netted and un-netted shrubs per site every other week. Arthropods were sorted, placed in vials in 95% ethanol, and further identified to lowest possible taxonomic group by the laboratory of A. Kawahara (University of Florida, Florida Museum of Natural History and McGuire Center for Lepidoptera and Biodiversity). We assigned arthropod counts into six main trophic groups (Grazers, Sapfeeders, Predators, Scavengers, Detritivores, and Parasites) modified from Davies *et al.* 

[9]

(2012). We excluded the subclass Acari, and the family Formicidea in our groupings because classification into a further trophic group was not possible; taxonomic groups that had <10 insects for the total collection period were also excluded from our trophic groupings. For bird community dynamics, detailed methods and analysis are reported in Cinto Mejia (2017). Briefly, we monitored five main species of focus (sagebrush sparrow, Brewer's sparrow, and sage thrasher [*Oreoscoptes montanus*], horned lark [*Eremophila alpestris*], and western meadowlark [*Sturnella neglecta*]) by bird point counts for each species April to June 2015 to estimate songbird abundance.

#### Shrub Herbivory and Growth

For each netted and un-netted shrub, we randomly tagged three vegetative stems (using clear sip-ties) in March (pre-experiment) for herbivory and growth measurements throughout summer (three stems per shrub per site). To quantify variation in herbivory, we assessed the amount of leaf damage (bite marks, holes, scrapes), and quantified per unit stem-length, biomass, leaf number, and leaf area—once at the beginning of the growing season, and then again at the end (March and October, respectively). We determined leaf area by photographing the stem and leaves from each sample with a ruler for scale, and we analyzed photographs using ImageJ software (1.46r, Scion Co., Fredrick, MD, USA). For stem elongation ("growth"), we measured the three-tagged stems to the nearest 1 mm with a ruler to determine total annual growth, as well as total number of leaves. At the end of the growing season, we randomly harvested three floral inflorescences from each netted and un-netted shrub, as sagebrush produce reproductive structures in the summer but do not produce them in early spring (Evans and Black 1993), when we initially tagged vegetative stems. We assessed the amount of flower

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damage (bite marks, holes), and quantified per unit stem-length (mm), biomass, and floret number. We placed samples in a drying oven at 78° C for 48hrs, and then weighed them to the nearest 0.01g.

#### Physiology

We collected all physiological measurements every other week April- July, and monthly August-October. We measured plant carbon (photosynthesis, respiration, chlorophyll fluorescence, <sup>13</sup>C isotope ratios) and water (stomatal conductance, transpiration, pre-dawn water potentials, intrinsic water use efficiency) relations. On each measurement date, we measured gas exchange (photosynthesis, respiration, stomatal conductance, and transpiration) on randomly selected intact shoots for each experimental shrub in each plot with a model LI-6400 portable photosynthesis machine (LI-COR Biosciences, Inc, Lincoln, NE, USA) equipped with a LED light chamber (model 6400-02B). We collected instantaneous gas-exchange measurements at midday, at approximately 10:00 AM-2:00 PM (MST), and shifted to 9:00 AM to 12:00 PM during mid-summer, so that we could make all measurements before plant midday depression in variables of interest (Depuit and Caldwell 1975). We set the LED light source within the chamber to 1,200  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> for midday photosynthesis (A<sub>net</sub> measurements), and the LED was set to  $0 \mu mol m^{-2} s^{-1}$  during dark respiration (R<sub>d</sub>) measurements. We acknowledge that  $R_d$  during the day may be different than at night (Krömer 1995), but assumed that differences in  $R_d$  in the light compared with the dark were similar between shrubs. By convention, R<sub>d</sub> is represented by negative numbers, with more negative numbers representing more respiration. We presented all gas exchange measurements on a silhouette leaf area basis, which is the most appropriate leaf area method for complex

[11]

shoots (Smith *et al.* 1991). We determined leaf area by photographing the stem sections that were in the chamber inside an empty chamber gasket (used for scale bar), and then analyzed with ImageJ software (1.46r, Scion Co., Fredrick, MD, USA). To examine if potential changes in midday A<sub>net</sub> were associated with stomatal or non-stomatal limitations, we used leaf chlorophyll fluorescence techniques. Specifically, we measured differences in photochemical efficiency ( $\Phi$ PSII) randomly selected intact shoots on each experimental shrub with a portable chlorophyll fluorometer (model MINI-PAM, Heinz Walz GmbH, Effeltrich, Germany).  $\Phi$ PSII represents the maximum quantum yield of photosystem II, and light captured for photosynthesis can take three different pathways; it can be used for photosynthesis, released as heat, or it can be re-emitted as fluorescence. Thus, a measurement of the yield of chlorophyll fluorescence can inform on the efficiency of photochemical reactions in plants, as a change in the efficiency of one pathway will change the efficiency of the other (Maxwell and Johnson 2000). The maximum theoretical yield for plants with un-stressed leaves is consistent at approximately 0.83 Fv/Fm or 83% (intrinsic efficiency of PSII, Murchie and Lawson 2013).

We measured pre-dawn water potentials of un-netted shrubs, with a portable pressure chamber (Model PMS-1000, PMS Instruments; Corvallis, OR, USA) and compressed N<sub>2</sub> gas. We conducted water-potential measurements at only 9 of 12 sites, because of logistical constraints associated with sampling the remaining three sites; only un-netted shrubs (not our originally selected un-netted shrubs; only those neighboring our un-netted shrubs) were sampled because we did not want to damage my netted shrubs. Between 3-6:00 AM, we randomly excised three stem-tips (~6 cm of distal ends) at each site from

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three un-netted shrubs; we then applied petroleum jelly to the cut end of the excised stem, and placed the stem in a plastic bag with a damp paper inside. We made all measurements <10 min after excision.

# <sup>13</sup>C Isotopes

Leaves from the vegetative stem that were monitored for growth and herbivory were collected along with inflorescences in October 2015, and further analyzed for stable carbon and nitrogen isotopes after assessing herbivory damage and biomass. We used vegetative leaves and florets of inflorescences from the same nine sites where we conducted pre-dawn water potential measurements, to provide another metric of water stress (water use efficiency, see below) in sagebrush shrubs. For plants, the amount of carbon gained relative to the amount of water lost over a growing season (water use efficiency, WUE<sub>i</sub>) can be quantified by measuring the  ${}^{13}C$ , carbon isotope ratio in plant tissue. WUE<sub>i</sub> can be indicative of the amount of stress that plants receive during the growing season, such as drought stress or potential stress from herbivore damage. In the case of drought stress, with less water available, plants discriminate against the heavier <sup>13</sup>C isotope less, resulting in a different <sup>13</sup>C/<sup>12</sup>C ratio. How insect herbivory can affect the <sup>13</sup>C:<sup>12</sup>C signature in sagebrush, however, is inconsistent and little studied (Takahashi 2012). We ground dried leaves from each shrub separately, and weighed ~4 mg  $\pm$  10% of each material into separate tin capsules. Samples were analyzed using a Thermo Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS), with a ConFlo IV interface and Costech Elemental Analyzer (EA) in the Stable Isotope Laboratory at the Center for Archaeology, Materials and Applied Spectroscopy (CAMAS) on the campus of Idaho State University, Pocatello ID, USA. Precision of measurement was  $\pm 0.2\%$  for  $\delta^{13}$ C and

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 $\pm 0.2\%$  for  $\delta^{15}$ N. All  $\delta^{13}$ C and  $\delta^{15}$ N isotopes were reported relative to the Vienna Pee Dee Belemnite (VPDB) (carbon) and atmospheric air (nitrogen) standards as:  $\delta$  (‰) =  $10^{3}$ [Rsample /Rstandard -1]. We calculated carbon isotope discrimination with equation (1):

$$\Delta(\%_0) = \frac{(\delta \operatorname{air} - \delta \operatorname{plant})}{(1000 + \delta \operatorname{plant})} \times 1000$$
(1)

where  $\Delta$  is the discrimination against <sup>13</sup>C during carbon fixation, and  $\delta$  is the <sup>13</sup>C/<sup>12</sup>C ratio (Duquesnay *et al.* 1998); We used -8.3 for  $\delta$  air (USDC-NOAA, 2012). We calculated WUE<sub>i</sub> using equation (2):

WUE<sub>i</sub> = 
$$\frac{A}{g} = \frac{C_a}{1.6} \left( \frac{(b - \Delta(\%_0))}{(b - a)} \right)$$
 (2)

where  $\frac{A}{g}$  = the ratio of net photosynthesis to stomatal conductance (i.e. intrinsic water use efficiency),  $\Delta$ = <sup>13</sup>C discrimination calculated from equation (1), Ca = 400 ppm CO<sub>2</sub> in the atmosphere, b=27‰, the discrimination associated with carboxylation, and a = 4.4‰ is the discrimination against <sup>13</sup>C through the stomata (Seibt *et al.* 2008).

#### Soil Moisture

To quantify variation in soil moisture across the growing season, and to compare site differences in soil water that might cause differences in physiology not related to the noise treatments, we measured soil volumetric water content (VWC) at each site with one EC-5 soil-moisture sensor (Decagon Devices). We installed sensors at each site at 30 cm depth using a shovel to excavate a hole, which was backfilled and tamped down after installation. We made soil moisture measurements on the same days as physiological

measurements using a Pro-Check hand reader (Decagon Devices, Pullman, WA, USA). We confirmed periodically that VWC measurements during the day were not affected by soil temperature by comparing pre-dawn VWCs on the same day.

#### Analyses

Our experimental design involved collecting measurements on the same shrubs during each sampling effort throughout the growing season (i.e., repeated measures). Consequently, we used a mixed-model ANOVA approach to analyze effects of noise and netting (fixed effects), the interaction of noise and netting (fixed effect), day and individual shrub (random effects), and the interaction of calendar date and noise (random effect) on our response variables —photosynthesis, transpiration, stomatal conductance, photochemical efficiency, stem-water potentials, and soil moisture. We defined the significance level to be  $\alpha = 0.05$ . We used an autocorrelation function test (in R [version 3.1.2; R Core Team 2015], package *nlme*, function "ACF" [Pinheiro *et al.* 2015]) at  $\alpha =$ 0.05 to determine the presence and form of temporal autocorrelation resulting from measuring the same shrubs over time. We addressed assumptions of constant variance using a Fligner-Killeen test (in R, base package, function "fligner.test"). In our initial analysis, we found netting and the interaction of noise to be insignificant (P>0.12 for all comparisons; Appendix II, Table 3), and we found no statistically significant differences for vegetative stems between netted and un-netted shrubs for herbivory damage,  ${}^{13}C$ isotopes, or physiology (P>0.11 for all comparisons, except  $\Phi$ PSII; Appendix IV Fig.1-2, Table 1-3). This prompted the elimination of netting as a factor, thus we pooled netted and un-netted shrubs for our main analysis of examining noise effects (noise and netted

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data: Appendix II, Fig.1-2, Table 1-4; and Appendix III for noise and un-netted data, Fig 1-2, Table 1-3).

We analyzed differences in beginning-of-season (pre-noise treatment) and end-ofseason herbivory damage, stem elongation, stem and leaf biomass, leaf area, percent cover of vegetation,  $\Delta$ ,  $\delta^{13}$ C,  $\delta^{15}$ N, C: N, and WUE<sub>i</sub> with t-tests (comparisons were made within the same time-point, e.g. differences in leaf area between noise treatments in October). All analyses were performed using JMP Pro<sup>®</sup> (Version *11.2.0.*, SAS Institute Inc., Cary, NC, USA), and R<sup>®</sup> software.

#### **Chapter 3: Results**

#### Vegetation Cover and Arthropod Data

No statistically significant difference in percent sagebrush cover (P = 0.719, mean percent 21.3 and 22.2 respectively), grasses (P = 0.566), and forbs (P = 0.250) were found between Noise-On and Noise-Off sites. Arthropods collected from beat-nettings showed that sap-feeders were the most abundant trophic group collected, followed by grazers, and then predators (Fig.1a, b; Table 1). No statistically significant differences occurred because of noise within any trophic comparison (e.g., comparing grazers at Noise-On vs. Noise-Off sites). Nevertheless, members of the sap-sucking families (Aphididae, Cercopidae, Cicadellidae, Miridae, Psyllidae, and Ortheziidae) were about 13.5% greater at our Noise-On sites compared with Noise-Off sites (Fig. 1a, Table 1), albeit not statistically so (P = 0.685). There were no statistically significant differences between insects in netted shrubs compared to un-netted shrubs between Noise-On and Noise-off sites, however sap-feeding insects were 16.7% greater in Nets at Noise-On sites (P=0.741, Table 2). Comparing only the effect of netting (no noise treatments), sapfeeding insects were 66.9% greater (P=0.105, Table 2) in netted shrubs than un-netted shrubs, and grazers were 36.1% greater (P=0.336, Table 2) in netted shrubs than unnetted shrubs.

# Herbivory Damage

Beginning-of-season (pre-experiment) herbivory damage on vegetative stems was not statistically different between Noise-Off and Noise-On sites for damage per number of leaves (P = 0.107), damage per stem length (P = 0.820), or damage per biomass (P = 0.107)

0.906). End-of-season herbivory damage on vegetative stems was not significant for either damage per number of leaves (P = 0.666, Fig. 2c), damage per stem length (P = 0.722, Fig. 2b), damage per leaf area (P= 0.652, Fig. 2e), or damage per biomass (P = 0.290). Despite the lack of statistically significant differences between treatments, damage per biomass for Noise-Off sites was about 29% greater than Noise-On sites (Table 3, Fig. 2d). Additionally, annual growth was marginally-statistically greater at Noise-On sites (19.5% greater, P = 0.073, Table 3, Fig. 2a). End-of-season herbivory damage was not significant for inflorescences between Noise-On and Noise-Off sites for either damage per number of florets (P = 0.440; Appendix V, Fig. 1c), damage per stem length (P =0.204; Appendix V, Fig. 1b), damage per biomass (P = 0.179; Appendix V, Fig. 1d), or inflorescence growth (P=0.457; Appendix V, Fig. 1a, Table 1).

#### Shrub Physiology

Noise had a significant effect on shrub photosynthesis and respiration ( $A_{net}$ ,  $R_d$ ; Table 4), and was greater regularly at our Noise-On sites compared with our Noise-Off sites (Table 5, Fig. 3a, b). The effect of Julian day across the growing season was significant for photosynthesis, respiration, transpiration (E), stomatal conductance ( $g_s$ ), photochemical efficiency ( $\Phi$ PSII), pre-dawn water potentials ( $\Psi$ ) and soil moisture (%, Table 4), which was expected for plants in a semi-arid environment across a growing season. Transpiration, stomatal conductance, and pre-dawn water potentials varied little between Noise-Off and Noise-On plots over the course of the experiment (Table 5, Fig. 4a, b, c). The variables that had a significant day × noise interaction were photochemical efficiency and photosynthesis (Table 4, Fig. 3a, 5). Transpiration and stomatal conductance had a statistically significant autocorrelation detected at the 3<sup>rd</sup>, and 4<sup>th</sup>

points in time, respectively. Consequently, a  $3^{rd}$  order ARIMA (for transpiration) and  $4^{th}$  order ARIMA (for stomatal conductance) were fitted for the repeated measures ANOVA. Pre-dawn water potentials and soil moisture also had statistically significant autocorrelation detected, at the  $3^{rd}$  (fitted to  $3^{rd}$  order ARIMA), and  $1^{st}$  (fitted to  $1^{st}$  order ARIMA) points in time, respectively. An interesting trend occurred over Julian Days 166 and 189, in which all physiology variables decreased at both Noise-On and Noise-Off sites. These variables began to increase again at Julian Day 261, but not completely back to levels observed before Julian Day 166, except for photochemical efficiency at Noise-Off sites only. The overall mean difference between netted and un-netted shrubs (not looking at noise treatments) across the growing season was statistically significant for  $\Phi$ PSII (P=0.012; Appendix IV, Table 1) with netted shrubs showing regularly greater photochemical efficiency than un-netted.

# <sup>13</sup>C Isotopes

No statistically significant differences occurred in vegetative stems between Noise-On and Noise-Off sites for either  $\Delta$  (P= 0.176, Fig. 6b),  $\delta^{13}$ C (P= 0.176, Fig. 6a,),  $\delta^{15}$ N (P= 0.347, Fig. 6d), or WUE<sub>i</sub> (P= 0.176, Fig. 6c). There was a marginally-statistical difference for C: N (P= 0.097, Fig. 6e), with the ratio higher for Noise-Off sites compared to Noise-On sites (Table 6). We found no statistically significant differences in inflorescences for either  $\Delta$  (P= 0.980; Appendix V, Fig. 2b),  $\delta^{13}$ C (P= 0.980; Appendix V, Fig. 2a),  $\delta^{15}$ N (P= 0.349; Appendix V, Fig. 2d), WUE<sub>i</sub> (P= 0.980; Appendix IV, Fig.2c), or C:N (P=0.195; Appendix V, Fig.2e) between Noise-On and Noise-Off sites (summary statistics: Appendix V, Table 1).

#### **Chapter 4: Discussion and Conclusion**

To our knowledge, this collaborative study is the first to quantify how changes in a soundscape can directly, or indirectly, affect ecosystem dynamics across multiple trophic levels. Collaborators at BSU focused on the effects of noise on bird abundance and arthropod community dynamics. We focused on quantifying the effects of noise on physiology of shrubs, through changes in arthropod herbivory. We originally hypothesized that experimental noise would alter existing sagebrush-arthropod interactions, which in turn would affect shrub physiology. We predicted that we would observe fewer birds at Noise-On sites, resulting in greater arthropod abundance (because of less avian predation) and thus greater herbivory damage to shrubs. We expected to observe reduced photosynthesis, because of reduced photosynthetic leaf area, vascular damage, reduced water transport, and reduced gas exchange (Nabity et al. 2009, Ferrieri et al. 2013). Nonetheless, we observed a significant increase in photosynthesis ( $A_{net}$ ) and respiration ( $R_d$ ) in shrubs at Noise-On sites, which is contrary to our original prediction. No significant differences were observed between treatments in plant water relations (E,  $g_s$ ,  $\Psi$ ), which also was reflected in my carbon isotope data and thus intrinsic water-use efficiency (integrated across the growing season). This indicated that shrubs at both Noise-Off and Noise-On sites were experiencing the same amount of water stress throughout the growing season, and those variables were not influenced by our noise treatment. Additionally, the decreases observed in all physiology variables at Noise-On and Noise-Off sites around Julian Day 189, corresponded to the hottest and driest time of the year (beginning of July) which has been well documented for sagebrush during the growing season (Evans and Black

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1993, Bates *et al.* 2006, Gilmanov *et al.* 2006). Interestingly, the significant day  $\times$  noise interaction for photosynthesis occurred at this same point in time. Noise-On sites were photosynthesizing more than Noise-Off sites until Day 189, and then values decreased to lower than those at Noise-Off sites. Noise-On sites remained lower than Noise-Off for the rest of July and August, then both sites reached equivalent levels for the remainder of the study.

The changes in physiology we observed did not seem to be related to changes in herbivory or total arthropod abundance. Although there was no statistically significant difference in herbivory damage, there was substantially more annual growth at our Noise-On sites (19.5%) compared with Noise-Off sites. We also observed greater amounts of herbivory damage per biomass (29%) on shrubs in Noise-Off sites, contrary to our original hypothesis. One explanation for this is that while total arthropod abundance was not different among sites, my analysis showed more sap-feeding insects (~13.5%) at Noise-On sites compared to Noise-Off sites (but not significantly so). Perhaps the total number of arthropods might not be affected by the noise treatment, but we observed changes within the community dynamics of arthropods. Visual detection of sap-sucking insects is particularly difficult, even for experts, and quantifying damage from sap-sucking insects can be more challenging compared with assessing damage from insect foliavores, and methodology for such remains inconclusive amongst the literature (see review by Zvereva et al. 2010). We acknowledge that there could have been more herbivory damage for which our methodology did not account. Our quantification through direct, visible damages to the leaves could have underestimated effects of the damage caused by families of xylem and phloem piercing insect (i.e.,

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there may have been more sap-piercing damage than we could observe). Nevertheless, the numbers we observed for amount of herbivore damage were smaller than what has been reported previously, making it additionally difficult to quantify or determine effects of treatments. For example, Takahashi and Huntly (2010) documented that for basin big sagebrush without insecticide, damage per number of leaves averaged 4.73%, whereas our average value at Noise-On sites was 2.26%. Our highest value for damage per leaf area at Noise-On sites was ~7%, compared with Sipura (1999), who reported for *Salix phylicifolia* that were caged from avian predators, leaf area damaged was almost 12%.

Cinto Mejia (2017) observed significantly fewer birds (~25%) within the 50m radius at Noise-On sites compared to Noise-Off sites, in support of our original hypothesis, which, in theory should have resulted in increased arthropod abundance at Noise-On sites, or changes in the arthropod community structure (Weins *et al.* 1991, Takahashi and Huntly 2010, Maas *et al.* 2013). We hypothesize that the significant reduction in bird abundance observed at Noise-On sites resulted in the increase in the abundance of sap-feeding families relative to the other families, because of altered avian-predation-dynamics among arthropod species. For example, songbirds at Noise-On sites might spend less time foraging for insects than they would at Noise-Off sites (Francis and Barber 2013, Shannon *et al.* 2015, Ware *et al.* 2015). Furthermore, phloem-feeding aphids (i.e., sap-feeding) have been reported to significantly increase in abundance following exclusion of avian and chiropteran predation in cacao trees (Maas *et al.* 2013). While we did not see any statistical difference between the netting treatments at our Noise-On and Noise-Off sites, overall, not including noise treatment,

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there was a substantial increase in sap-feeding insects in netted shrubs compared to unnetted shrubs (66.9% greater), which is consistent with previous findings of physical predator exculsion from vegetation (Bridgeland *et al.* 2010, Maas *et al.* 2013).

With no differences in direct leaf damage (herbivory), water stress, habitat quality or microclimate variables between noise treatments, but a significant increase in  $R_d$  and A<sub>net</sub>, we hypothesize that the increase in sap-feeding insect groups at our Noise-On sites could have elicited a compensatory photosynthetic and respiration response in big sagebrush. It has been demonstrated that insect herbivory can stimulate growth and/or photosynthetic responses ("compensatory growth" and "compensatory photosynthesis"; McNaughton 1983, Nowak and Caldwell 1984, Trumble et al. 1993, Messina et al. 2002, Thomson et al. 2003). Mechanistically, increases in photosynthesis can result from changes in carbon sink demand or reallocation of resources to growth (either vegetative, floral, root mass) to compensate for loss of tissue (Gifford and Evans 1981, Nowak and Caldwell 1984). Whether increased herbivory results in positive or negative effects on plants seems to depend, in part, on factors such as amount of herbivory damage, duration of herbivory, the plant species involved, and even the types of insects that are feeding on the plant. Differences in plant responses to certain guilds of insect herbivores such as members of the sap-sucking families compared to primary defoliating insect families have been reported (Rutuerto et al. 2004, Goggin 2007, Zvereva et al. 2010). Defoliating insects directly remove plant tissue, whereas sapsucking insects consume fluids from either the xylem or the phloem of the plant; each type of damage eliciting a potential different response from the injured plant (Zvereva et al. 2010). Wyoming big sagebrush is characterized as a long-lived, slow-growing,

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and hardy desert shrub with primary growth of vegetative structures in the spring followed by growth of reproductive structures in the summer (Evans and Black 1993). Messina *et al.* (2002) reported that changes in relative growth rate from different herbivory treatments on varieties of sagebrush was highly variable, and given the longevity of sagebrush, conducting a study over the course of a single season might not be enough to observe a difference from a herbivory treatment. Nonetheless, our data on photosynthesis supports the findings of Thompson *et al.* (2003), who reported a significant increase in photosynthetic capacity and efficiency in herbivore-damaged Cucumis sativus plants; moreover, Retuerto et al. (2004) demonstrated a significant increase in photosynthetic capacity of *Ilex aquifolium* trees after exposure to scale insect (sap-feeder) infestations. Our hypothesis regarding sap-sucking insects driving this potential compensatory response in sagebrush contradicts results from Meyer et al. (1992), and results from a large meta-analysis on sap-feeding insect studies conducted by Zvereva et al. (2010). Zvereva et al. (2010) reported a lack of consistency among methods for adequately determining effects of sap-feeding damage amongst currently published literature, and also concluded that compensatory plant responses to this form of damage was very rare, but not un-documented. Both Meyer et al. 1992 and Zvereva et al. 2010 stress the need for more consistent methodology, and more research on plant responses to sap-feeder insects. Given my inability to adequately measure damage from sap-sucking families on sagebrush during our study, the mechanism (either direct or indirect) behind the physiological and morphological responses I observed is unclear and in need of further investigation.
## Conclusions

Our research indicates that altered soundscapes do have the capacity to affect ecosystem functioning. The significant differences we observed in  $A_{net}$ ,  $R_d$ ,  $\Phi PSII$ , and the substantive differences in annual growth, indicate that noise does affect shrub physiology and morphology. Although our current arthropod dataset was not able to definitively explain the mechanisms for the changes we observed in our shrubs, we did observe differences in sap-sucking insect abundances on those shrubs. Furthermore, our collaborators at BSU also observed significant decreases in the sagebrush bird community at our study site.

This research and continuing studies will aid the efforts of land managers as we work to find the best strategies to mitigate damage from chronic human-caused noise pollution in these areas of critical habitat concern. Research about types of sound-barrier walls around compressor stations (or other sources of chronic noise, Code of Federal Regulations 2010) and their benefits in reducing the spatial extent of noise across a landscape have been reported by Francis *et al.* (2011), Francis and Barber (2013), and Kleist *et al.* (2016). Thus, managing for an acoustic landscape is not an improbable endeavor but one that is in need of greater publicity. Given our new evidence for the potential effects of human-caused noise on surrounding vegetation habitat, as well as the deleterious effects on sensitive animal species, it is clear that more mitigation is needed. Land managers in cooperation with energy companies should strive to enforce measures of noise control in areas of sensitive habitat concern currently under production, or slated for development in the future.

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Figures



Figure 1. Comparison of (A) mean number of grazers and sap-feeding arthropods. (B) mean number of predatory, parasitic, detritivore, and scavenging arthropod groups collected using beat-nets from Wyoming big sagebrush at Noise-On and Noise-Off sites, April- June 2015. Means were computed from total number of arthropods over total number of beat-net collections. The functional groups in panel B were plotted separately from the other functional groups in panel A due to large differences in scale. Error bars are  $\pm$ SE.



Figure 2. Comparison of the effects of Noise on stem elongation and herbivory in vegetative stems (n = 36 stems per treatment) of Wyoming big sagebrush at Noise-On and Noise-Off sites at the end of the growing season, October 2015. Panels are: (A) mean stem elongation, (B) mean total herbivory damage ("td", i.e., number of bites, holes, scrapes counted) per stem length, (C) mean td per number of leaves, (D) mean td per biomass, and (E) mean td per leaf area). Error bars are ±SE. In panels where no P-value is indicated, there were no marginal or statistical differences because of Noise.



Figure 3. Variation in mean midday (A) photosynthesis, and (B) respiration from April through October 2015 in Wyoming big sagebrush. Error bars are ±SE. Asterisks indicate dates when mean values were significantly different between Noise treatments ( $P \le 0.05$ ). P-values in the panels indicate the overall, across the summer differences because of the Noise treatment.



Figure 4. Variation in mean midday (A) transpiration, (B) stomatal conductance, and (C) pre-dawn stem xylem-pressure potentials from April through October 2015 in Wyoming big sagebrush. Error bars  $\pm 1$ SE. When bars are not visible, it is due to the bars being smaller than the graph symbol size. Asterisks indicate dates when mean values were significantly different between Noise treatments (P  $\leq 0.05$ ).



Figure 5. Variation in mean midday photochemical efficiency ( $\Phi$ PSII) from April through October 2015 in Wyoming big sagebrush. Error bars are ±1SE. Asterisks indicate dates when mean values were significantly different between Noise treatments (P ≤ 0.05). P-values in the panel indicate the overall, across the summer differences because of the Noise treatment.



Figure 6. Comparison of the effects of Noise on isotopic discrimination, intrinsic water use efficiency, and elemental ratios in leaves of vegetative stems in Wyoming big sagebrush at Noise-On (n=29, dark cyan bars) and Noise-Off (n=24, white bars) sites at the end of the growing season, October 2015. Panels are: (A) mean  $\delta^{13}$ C; (B) mean Discrimination ( $\Delta$ ); (C) mean intrinsic water use efficiency (WUE<sub>i</sub>); (D) mean  $\delta^{15}$ N; and (E) mean C:N values. Error bars are ±SE. In panels where no P-value is indicated, there were no marginal or statistical differences because of Noise.

## Tables

Table 1. Total number and means of arthropods collected from beat-nets April-June 2015 at Noise-On and Noise-Off sites, organized into trophic groupings: scavengers (n=1 family), parasites (n=4 families), detritivores (n=2 families), predators (n=6 families, grazers (n=7 families), and sap-feeders (n=6 families). Table was constructed excluding the subclass Acari and the family Formicidea because classification into a further trophic group was not possible by October 2016.

		Noise On			Noise Off	
Group	Count	Mean	SE	Count	Mean	SE
Sap-feeders	3202	94.177	22.421	2821	82.971	15.925
Grazers	230	6.765	1.397	247	7.265	1.741
Predators	105	3.088	0.491	111	3.265	0.435
Scavengers	4	0.118	0.07	7	0.206	0.125
Detritivores	20	0.559	0.203	19	0.588	0.199
Parasites	27	0.794	0.214	31	0.912	0.258

Table 2. Total number of sap-feeders (n=6 families) and grazer (n=7 families) arthropods collected from beat-nets April-June 2015 at Noise-On and Noise-Off sites, and within Netted and Un-netted Wyoming big sagebrush shrubs at those sites.

			Sapsuckers			Grazers	
		Count	Mean	SE	Count	Mean	SE
Noise Off		2821	82.971	15.925	247	7.265	1.741
	Netted	1738	102.235	29.903	148	8.706	2.985
	Un-netted	1083	63.706	10.275	99	5.824	1.826
Noise On		3202	94.177	22.421	230	6.765	1.397
	Netted	2028	119.294	41.445	127	7.471	2.125
	Un-netted	1174	69.059	16.645	103	6.059	1.862

Table 3. Summary of herbivory damage and seasonal growth in vegetative stems of Wyoming big sagebrush in March (preexperiment) and October 2015 at Noise On and Noise Off sites, "td" stands for the total damage of bite, holes, scrapes counted per variable. Numbers in italics indicate marginal differences in variables (0.05>P<0.10).

			March						October			
		Noise ON			Noise O	FF		Noise Of	1		Noise Ol	ŦF
Variable	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Damage per leaf number (#td/#leaves)	0.097	0.023	0.059-0.154	0.128	0.009	0.107-0.15	0.226	0.021	0.045-0.523	0.241	0.028	0.046-1.00
Damage per stem length (#td/cm)	1.033	0.375	0.5-2.0	1.01	0.06	0.875-1.167	2.137	0.224	0.465-5.273	2.283	0.341	0.583-12
Damage per biomass (#td/g)	33.683	7.514	15.83-61.539	32.448	6.093	24.72-50.360	73.183	7.223	13.889-216.981	94.42	18.325	19.499-692.308
Damage per leaf area (#td/cm <sup>2</sup> )	-	-	-	-	-	-	2.890	0.303	0.425-7.008	3.215	0.621	0.991-23.560
Seasonal growth (cm)	-	-	-	-	-	-	8.214	1.389	2.5-13.9	6.869	0.525	1.5-15.1

Table 4. Summary ANOVA table for the effects of Julian Day and Noise on response variables respiration ( $R_d$ ), transpiration (E), photosynthesis ( $A_{net}$ ), photochemical efficiency ( $\Phi$ PSII), stem water potentials ( $\Psi$ ), and % soil moisture (SM) in Wyoming big sagebrush across the growing season of April through October 2015. Bold indicates statistically significant differences (P<0.05).

			Julian Day			Noise		D	ay X Noise	
Variable	Optimum covariance structure	dF	$\chi^2$	Р	dF	$\chi^2$	Р	dF	$\chi^2$	Р
R <sub>d</sub> (µmol m <sup>-2</sup> s <sup>-1</sup> )	Ind.Cov, χ <sup>2</sup> =0.581, P=0.356	1	42.883	5.8e <sup>-11</sup>	8	7.771	0.021	1	0.313	0.576
$A_{net}(\mumolm^{-2}s^{1})$	Ind.Cov, $\chi^2$ =2.284, P=0.131	1	25.332	4.8e <sup>-07</sup>	7	4.376	0.036	1	3.917	0.048
E (mmol m <sup>-2</sup> s <sup>-1</sup> )	ARMA3, $\chi^2 = 23.331$ , P=<0.0001	1	172.468	<2e <sup>-16</sup>	9	0.124	0.725	1	0.750	0.386
$g_s \pmod{m^{-2} s^{-1}}$	ARMA4, $\chi^2$ =21.571, P=0.00002	1	196.52	<2e <sup>-16</sup>	11	0.091	0.763	1	1.765	0.184
$\Phi PSII(\%)$	Ind.Cov, $\chi^2$ =2.269, P=0.519	1	4.662	0.031	7	0.002	0.963	1	7.495	0.006
Ψ (MPa)	ARMA3, $\chi^2$ = 27.693, P=<0.0001	1	308.51	<2e <sup>-16</sup>	9	0.002	0.964	1	0.008	0.930
SM (%)	ARMA1, $\chi^2$ =14.205, P=<0.00002	1	36.033	2e <sup>-09</sup>	7	0.114	0.735	1	1.496	0.221

		Noise ON			Noise OF	F
Variable	Mean	SE	Range	Mean	SE	Range
$A_{net} \ (\mu mol \ m^{-2} \ s^{-1})$	7.031	0.237	0.183-23.370	6.423	0.219	0.146-19.457
$R_d \pmod{m^{-2} s^{-1}}$	-6.500	0.389	-19.754-(-0.174)	-4.966	0.45	-17.24-(-0.149)
E (mmol m $^{-2}$ s $^{-1}$ )	3.089	2.662	0.013-15.330	3.042	2.439	0.002-17.370
gs (mol m <sup>-2</sup> s <sup>-1</sup> )	0.141	0.008	0.0002-0.972	0.144	0.008	0.00008-0.808
$\Phi PSII(\%)$	0.717	0.042	0.566-0.794	0.722	0.039	0.565-0.807
Ψ (MPa)	-2.100	0.208	-5.287- (-0.35)	-2.062	0.203	-4.553- (-0.603)

Table 5. Summary statistics for physiological response variables for Wyoming big sagebrush, April through October 2015 at Noise On and Noise Off sites. Numbers in bold indicate statistically significant differences (P<0.05), and numbers in italics indicate marginal differences (0.05>P<0.10).

Table 6. Summary statistics for the response variables Discrimination ( $\Delta$ ),  $\delta^{13}$ C,  $\delta^{15}$ N, WUE<sub>i</sub>, and C: N in vegetative stem isotope samples collected from Wyoming big sagebrush in October 2015 at Noise On and Noise Off sites. Numbers in italics indicate marginal differences (0.05>P<0.10).

		Noise ON			Noise OFF	
Variable	Mean	SE	Range	Mean	SE	Range
Δ (°/ <sub>••</sub> )	18.368	0.132	17.018-19.927	18.659	0.169	17.184-20.441
$\delta^{13}C(^{\prime}/_{\circ\circ})$	-26.187	0.126	-24.894-(-27.676)	-26.464	0.162	-25.054-(-28.166)
$\delta^{15}N$ (°/ <sub>••</sub> )	3.208	0.226	0.941-6.489	2.848	0.316	0.140-6.671
WUE <sub>i</sub> (µmol mol <sup>-1</sup> )	95.484	1.458	78.242-110.427	92.271	1.874	72.551-108.583
C:N	23.953	0.395	20.125-27.848	24.997	0.483	21.045-28.773

## Appendixes

Appendix I



Figure 1. Power spectra of currently operating natural gas-well compressor stations in Wyoming and New Mexico, USA, plotted with the playback of our Phantom Gas Field project; recordings were taken at 40m from the central station. Our 2015 playback was an average of recordings taken from five compressor stations in those two states, in order to account for variability associated with recording just one compressor station.

Appendix II: Summary data for herbivory damage (Fig. 1b-e), growth (Fig.1a), and physiology (Table 1), summary ANOVA (Table 2), ANOVA for Noise and Netting treatment (Table 3), and vegetative stem isotopes (Fig. 2a-e, Table 4) in Netted Wyoming big sagebrush shrubs in October 2015.



Figure 1. Comparison of Noise treatments on stem elongation and herbivory in vegetative stems (n= 18 stems per treatment) of Netted Wyoming big sagebrush for Noise-On (dark cyan bars) and Noise-Off (white bars) sites at the end of the growing season, October 2015. Error bars are  $\pm$ SE. Panels are (A) mean stem elongation, (B) mean total herbivory damage ("td", i.e., number of bites, holes, scrapes counted) per stem length, (C) mean td per number of leaves, (D) mean td per biomass, and (E) mean td per leaf area). In panels where no P-values is indicated, there were no marginal or significant differences because of Noise.



Figure 2. Comparison of the effects of Noise on isotopic discrimination, intrinsic water use efficiency, and elemental ratios in leaves of vegetative stems in Netted Wyoming big sagebrush at Noise-On (n=12, dark cyan bars) and Noise-Off (n=14, white bars) sites at the end of the growing season, October 2015. Panels are: (A) mean  $\delta^{13}$ C; (B) mean Discrimination ( $\Delta$ ); (C) mean intrinsic water use efficiency (WUE<sub>i</sub>); (D) mean  $\delta^{15}$ N; and (E) mean C:N values. Error bars are ±SE. In panels where no P-value is indicated, there were no statistically significant differences because of Noise.

Table 1. Summary of herbivory damage, growth, and statistics for physiological response variables vegetative stems in Netted Wyoming big sagebrush, April through October 2015. Numbers in italics indicate marginal differences (0.05>P<0.10).

		Noise ON		No	oise OFF	
Variable	Mean	SE	Range	Mean	SE	Range
Damage per leaf number (#td/#leaves)	0.188	0.029	0.045-0.468	0.246	0.03	0.111-0.467
Damage per stem length (#td/cm)	1.804	0.357	0.465-5.273	2.11	0.304	0.583-5.138
Damage per biomass (#td/g)	59.344	9.13	13.889-143.791	76.411	9.967	31.7-147.959
Damage per leaf area (#td/cm <sup>2</sup> )	2.227	0.372	0.425-5.875	2.742	0.341	1.010-5.902
Seasonal growth (cm)	8.065	0.547	4.3-13.2	6.939	0.636	2.7-10.9
$A_{net} \ (\mu mol \ m^{\text{-2}} \ s^{\text{-1}})$	7.134	0.338	0.207-18.048	6.382	0.322	0.424-18.332
$R_d \ (\mu mol \ m^{-2} \ s^{-1})$	-7.116	0.676	-19.75-(-0.174)	-4.942	0.584	-17.236-(-0.149)
E (mmol m <sup>-2</sup> s <sup>-1</sup> )	3.171	0.226	0.013-15.330	3.069	0.213	0.002-17.3701
$g_s \pmod{m^{-2} s^{-1}}$	0.144	0.012	0.0002-0.972	0.142	0.010	0.0001-0.8077
ΦΡSII (%)	0.727	0.004	0.653-0.788	0.724	0.004	0.638-0.792

Table 2. Summary ANOVA table for the effects of Julian Day and Noise on response variables respiration ( $R_d$ ), transpiration (E), photosynthesis ( $A_{net}$ ), and photochemical efficiency ( $\Phi$ PSII) in Netted Wyoming big sagebrush across the growing season of April through October 2015. Bold indicates statistically significant differences (P<0.05), and numbers in italics indicate marginal differences (0.05>P<0.10).

			Julian Day		Noise		Day X Noise			
Variable	Optimum covariance structure	dF	$\chi^2$	Р	dF	$\chi^2$	Р	dF	$\chi^2$	Р
$A_{net} (\mu mol m^{-2} s^{-1})$	Ind.Cov, $\chi^2$ =1.819, P=0.178	1	4.911	0.027	7	3.293	0.070	1	0.201	0.654
$R_d \ (\mu mol \ m \ ^{-2} \ s^{-1})$	Ind.Cov, $\chi^2$ =0.235, P=0.628	1	17.738	2.5e <sup>-05</sup>	8	6.584	0.037	1	0.276	0.599
E (mmol m <sup>-2</sup> s <sup>-1</sup> )	ARMA4, χ <sup>2</sup> =14.192, Ρ=0.007	1	53.180	3e <sup>-13</sup>	10	0.306	0.580	1	0.165	0.685
$g_s \pmod{m^{-2} s^{-1}}$	ARMA2, $\chi^2$ =6.489, P=0.039	1	96.372	<2e <sup>-16</sup>	9	0.016	0.898	1	1.531	0.216
$\Phi PSII (\%)$	Ind.Cov, $\chi^2$ =0.352, P=0.552	1	3.356	0.067	7	0.492	0.483	1	2.406	0.121

Table 3. Summary ANOVA table for the effects of Netting treatment (Trt) and Noise on response variables respiration ( $R_d$ ), stomatal conductance ( $g_s$ ), transpiration (E), photosynthesis ( $A_{net}$ ), and photochemical efficiency ( $\Phi$ PSII) in Wyoming big sagebrush, across the growing season of April through October 2015.

		Trt X Noise		
Variable	Optimum covariance structure	dF	$\chi^2$	Р
$R_d \ (\mu mol \ m^{-2} \ s^{-1})$	Ind.Cov, $\chi^2$ =0.818, P=0.367	9	0.812	0.367
gs (mol $m^{-2} s^{-1}$ )	ARIMA4, $\chi^2$ =22.056, P=<0.0002	13	0.002	0.970
E (mmol $m^{-2} s^{-1}$ )	ARIMA3, $\chi^2$ =23.756, P=<0.0001	12	0.101	0.751
$A_{net} \left( \mu mol \ m^{-2} \ s^{-1} \right)$	Ind.Cov, $\chi^2$ =2.316, P=0.128	9	0.513	0.474
ΦPSII (%)	Ind.Cov, χ <sup>2</sup> =7.100, Ρ=0.131	10	2.425	0.119

Table 4. Summary statistics for the response variables Discrimination ( $\Delta$ ),  $\delta^{13}$ C,  $\delta^{15}$ N, WUE<sub>i</sub>, and C: N in vegetative stem isotope samples collected from Netted Wyoming big sagebrush in October 2015 at Noise-On and Noise-Off sites. Numbers in bold indicate significant differences (P>0.05)

		Noise ON	1	Noise OFF				
Variable	Mean	SE	Range	Mean	SE	Range		
$\Delta(\ ^{\circ}/_{\circ\circ})$	18.172	0.199	17.018-19.304	18.912	0.249	17.820-20.441		
$\delta^{13}C(\ ^{\circ}/_{\circ\circ})$	-25.999	0.19	-24.894-(-27.082)	-26.706	0.238	-25.663-(-28.166)		
$\delta^{15}N$ ( $°/_{\circ\circ})$	2.956	0.299	0.941-4.815	2.629	0.314	0.680-3.848		
$WUE_i(\mumolmol^{-1})$	97.658	2.196	85.129-110.425	89.470	2.757	72.551-102.547		
C:N	24.049	0.602	20.125-27.848	24.453	0.734	21.045-28.773		

Appendix III. Summary data for herbivory damage (Fig. 1b-e), growth (Fig. 1a), and physiology (Table 1), summary ANOVA (Table 2), and vegetative stem isotopes (Fig. 2a-e, Table 3) in Un-netted Wyoming big sagebrush shrubs in October 2015.



Figure 1. Comparison of Noise treatments on stem elongation and herbivory in vegetative stems (n= 18 stems per treatment) of Wyoming big sagebrush for Noise-On (dark cyan bars) and Noise-Off (white bars) sites at the end of the growing season, October 2015. Error bars are  $\pm$ SE. Panels are (A) mean stem elongation, (B) mean total herbivory damage ("td", i.e., number of bites, holes, scrapes counted) per stem length, (C) mean td per number of leaves, (D) mean td per biomass, and (E) mean td per leaf area).



Figure 2. Comparison of the effects of Noise on isotopic discrimination, intrinsic water use efficiency, and elemental ratios in leaves of vegetative stems in Un-netted Wyoming big sagebrush at Noise-On (n=15, dark cyan bars) and Noise-Off (n=12, white bars) sites at the end of the growing season, October 2015. Panels are: (A) mean  $\delta^{13}$ C; (B) mean Discrimination ( $\Delta$ ); (C) mean intrinsic water use efficiency (WUE<sub>i</sub>); (D) mean  $\delta^{15}$ N; and (E) mean C:N values. Error bars are ±SE. In panels where no P-value is indicated, there were no differences because of Noise.

Table 1. Summary of herbivory damage, growth, and statistics for physiological response variables vegetative stems in Un-netted Wyoming big sagebrush, April through October 2015 Numbers in italics indicate marginal differences (0.05>P<0.10).

	Ν	oise ON		Noise	e OFF	
Variable	Mean	SE	Range	Mean	SE	Range
Damage per leaf number (#td/#leaves)	0.226	0.021	0.045-0.523	0.241	0.028	0.046-1
Damage per stem length (#td/cm)	2.137	0.224	0.465-5.273	2.283	0.341	0.583-12
Damage per biomass (#td/g)	86.252	10.409	27.972-216.981	105.006	35.487	19.499-692.308
Damage per leaf area (#td/cm <sup>2</sup> )	3.533	0.432	0.815-7.008	3.687	1.202	0.991-23.560
Seasonal growth (cm)	8.356	0.882	2.5-13.9	6.800	0.855	1.5-15.1
$A_{net} \ (\mu mol \ m^{-2} \ s^{-1})$	6.935	0.332	0.183-23.370	6.463	0.299	0.146-19.457
$R_d (\mu mol \ m^{-2}  s^{-1})$	-5.834	0.580	-14.91-(-0.287)	-4.992	0.513	-12.743- (-0.179)
E (mmol m <sup>-2</sup> s <sup>-1</sup> )	3.012	0.211	0.168-14.614	3.045	0.186	0.133-13.434
$g_s \pmod{m^{-2} s^{-1}}$	0.138	0.011	0.005-0.685	0.150	0.011	0.004-0.759
ΦΡSII (%)	0.713	0.003	0.566-0.794	0.723	0.003	0.565-0.807

		Julian	Day		Nois	e		Day X N	oise
Optimum covariance structure	dF	$\chi^2$	Р	dF	$\chi^2$	Р	dF	$\chi^2$	Р
Ind.Cov, χ <sup>2</sup> =1.118, Ρ=0.290	1	21.991	2.70E-06	6	1.075	0.584	1	0.034	0.856
ARMA3, $\chi^2$ =16.794, P=<8e <sup>-04</sup>	1	98.875	<2e-16	9	0.005	0.944	1	0.737	0.391
AR1, $\chi^2 = 3.675$ , P= 0.055	1	20.08	7.40E-06	7	0.154	0.694	1	4.746	0.029
ARMA4, $\chi^2$ =16.847, P=0.002	1	115.819	<2e-16	11	0.159	0.690	1	0.629	0.428
ARMA4, $\chi^2$ = 10.352, P=0.035	1	2.615	0.106	11	0.260	0.610	1	5.777	0.016
	Optimum covariance structure Ind.Cov, $\chi^2$ =1.118, P=0.290 ARMA3, $\chi^2$ =16.794, P=<8e <sup>-04</sup> AR1, $\chi^2$ = 3.675, P= 0.055 ARMA4, $\chi^2$ =16.847, P=0.002 ARMA4, $\chi^2$ = 10.352, P=0.035	Optimum covariance structuredFInd.Cov, $\chi^2=1.118$ , P=0.2901ARMA3, $\chi^2=16.794$ , P=<8e <sup>-04</sup> 1AR1, $\chi^2=3.675$ , P=0.0551ARMA4, $\chi^2=16.847$ , P=0.0021ARMA4, $\chi^2=10.352$ , P=0.0351	JulianOptimum covariance structuredF $\chi^2$ Ind.Cov, $\chi^2$ =1.118, P=0.290121.991ARMA3, $\chi^2$ =16.794, P=<8e <sup>-04</sup> 198.875AR1, $\chi^2$ = 3.675, P=0.055120.08ARMA4, $\chi^2$ =16.847, P=0.0021115.819ARMA4, $\chi^2$ = 10.352, P=0.03512.615	Julian DayOptimum covariance structuredF $\chi^2$ PInd.Cov, $\chi^2=1.118$ , P=0.290121.991 <b>2.70E-06</b> ARMA3, $\chi^2=16.794$ , P=<8e <sup>-04</sup> 198.875< <b>2e-16</b> AR1, $\chi^2=3.675$ , P=0.055120.08 <b>7.40E-06</b> ARMA4, $\chi^2=16.847$ , P=0.0021115.819< <b>2e-16</b> ARMA4, $\chi^2=10.352$ , P=0.03512.6150.106	Julian Day   Optimum covariance structure dF $\chi^2$ P dF   Ind.Cov, $\chi^2=1.118$ , P=0.290 1 21.991 <b>2.70E-06</b> 6   ARMA3, $\chi^2=16.794$ , P=<8e <sup>-04</sup> 1 98.875 <2e-16	Julian DayNoisOptimum covariance structuredF $\chi^2$ PdF $\chi^2$ Ind.Cov, $\chi^2=1.118$ , P=0.290121.991 <b>2.70E-06</b> 61.075ARMA3, $\chi^2=16.794$ , P=<8e <sup>-04</sup> 198.875< <b>2e-16</b> 90.005AR1, $\chi^2=3.675$ , P= 0.055120.08 <b>7.40E-06</b> 70.154ARMA4, $\chi^2=16.847$ , P=0.0021115.819< <b>2e-16</b> 110.159ARMA4, $\chi^2=10.352$ , P=0.03512.6150.106110.260	Julian DayNoiseOptimum covariance structuredF $\chi^2$ PdF $\chi^2$ PInd.Cov, $\chi^2=1.118$ , P=0.290121.991 <b>2.70E-06</b> 61.0750.584ARMA3, $\chi^2=16.794$ , P=<8e <sup>-04</sup> 198.875< <b>2e-16</b> 90.0050.944AR1, $\chi^2=3.675$ , P= 0.055120.08 <b>7.40E-06</b> 70.1540.694ARMA4, $\chi^2=16.847$ , P=0.0021115.819< <b>2e-16</b> 110.1590.690ARMA4, $\chi^2=10.352$ , P=0.03512.6150.106110.2600.610	Julian DayNoiseOptimum covariance structuredF $\chi^2$ PdF $\chi^2$ PdFInd.Cov, $\chi^2=1.118$ , P=0.290121.991 <b>2.70E-06</b> 61.0750.5841ARMA3, $\chi^2=16.794$ , P=<8e <sup>-04</sup> 198.875< <b>2e-16</b> 90.0050.9441ARI, $\chi^2=3.675$ , P=0.055120.08 <b>7.40E-06</b> 70.1540.6941ARMA4, $\chi^2=16.847$ , P=0.0021115.819< <b>2e-16</b> 110.1590.6901ARMA4, $\chi^2=10.352$ , P=0.03512.6150.106110.2600.6101	Julian DayNoiseDay X NOptimum covariance structuredF $\chi^2$ PdF $\chi^2$ PdF $\chi^2$ PdF $\chi^2$ Ind.Cov, $\chi^2=1.118$ , P=0.290121.991 <b>2.70E-06</b> 61.0750.58410.034ARMA3, $\chi^2=16.794$ , P=<8e <sup>-04</sup> 198.875< <b>2e-16</b> 90.0050.94410.737AR1, $\chi^2=3.675$ , P=0.055120.08 <b>7.40E-06</b> 70.1540.69414.746ARMA4, $\chi^2=16.847$ , P=0.0021115.819< <b>2e-16</b> 110.1590.69010.629ARMA4, $\chi^2=10.352$ , P=0.03512.6150.106110.2600.61015.777

Table 2. Summary ANOVA table for the effects of Julian Day and Noise on response variables respiration ( $R_d$ ), transpiration (E), photosynthesis ( $A_{net}$ ), and photochemical efficiency ( $\Phi$ PSII) in Un-netted Wyoming big sagebrush across the growing season of April through October 2015. Bold indicates statistically significant differences (P<0.05).

Table 3. Summary statistics for the response variables Discrimination ( $\Delta$ ),  $\delta^{13}$ C,  $\delta^{15}$ N, WUE<sub>i</sub>, and C: N in vegetative stem isotope samples collected from Un-netted Wyoming big sagebrush in October 2015 at Noise On and Noise Off sites. Numbers in bold indicate significant differences (P>0.05)

		Noise ON			Noise OFF	
Variable	Mean	SE	Range	Mean	SE	Range
$\Delta$ (°/ <sub>••</sub> )	18.552	0.168	17.349-19.927	18.406	0.215	17.184-19.482
$\delta^{13}C(°/_{\circ\circ})$	-26.362	0.160	-25.211-(-27.676)	-26.222	0.206	-25.054-(-27.251)
$\delta^{15}N\left(^{\circ}/_{_{\circ\circ}}\right)$	3.444	0.334	1.527-6.489	3.067	0.557	0.140-6.671
$WUE_i \ (\mu mol \ mol \ ^l)$	93.454	1.853	78.242-106.763	95.072	2.378	83.160-108.582
C:N	23.863	0.536	20.710-27.162	25.540	0.620	21.506-28.751

Appendix IV: Summary data for herbivory damage (Fig.1b-e), growth (Fig.1a), and physiology (Table 1), ANOVA (Table 2), and vegetative stem isotopes (Fig. 2a-e, Table 3) in Netted and Un-netted Wyoming big sagebrush shrubs in October 2015



Figure 1. Comparison of Netting treatment on stem elongation and herbivory in vegetative stems (n= 18 stems per treatment) of Wyoming big sagebrush for Netted (dark gray bars) and Un-netted (white bars) sites at the end of the growing season, October 2015. Error bars are  $\pm$ SE. Panels are (A) mean stem elongation, (B) mean total herbivory damage ("td", i.e., number of bites, holes, scrapes counted) per stem length, (C) mean td per number of leaves, (D) mean td per biomass, and (E) mean td per leaf area). In panels where no P-values is indicated, there were no differences because of Noise.



Figure 2. Comparison of the effects of Netting treatment on isotopic discrimination, intrinsic water use efficiency, and elemental ratios in leaves of vegetative stems in Wyoming big sagebrush in Netted (n=26, dark cyan bars) and Un-netted (n=27, white bars) shrubs at the end of the growing season, October 2015. Panels are: (A) mean  $\delta^{13}$ C; (B) mean Discrimination ( $\Delta$ ); (C) mean intrinsic water use efficiency (WUE<sub>i</sub>); (D) mean  $\delta^{15}$ N; and (E) mean C:N values. Error bars are ±SE.

		Un-netted			Netted	
Variable	Mean	SE	Range	Mean	SE	Range
Damage per leaf number	0.249	0.029	0.046-1.0	0.218	0.021	0.045-0.468
Damage per stem length (cm)	2.453	0.332	0.583-12	1.961	0.231	0.465-5.273
Damage per biomass (g)	95.629	18.294	19.499-692.308	71.939	7.198	13.889-159.420
Damage per leaf area (cm <sup>2</sup> )	3.610	0.630	0.815-23.560	2.492	0.252	0.425-5.902
Seasonal growth (cm)	7.578	0.620	1.5-15.100	7.486	0.426	2.7-13.200
$A_{net} \ (\mu mol \ m^{-2} \ s^{-1})$	6.701	0.224	0.146-23.370	6.757	0.234	0.207-18.332
$R_d (\mu mol \; m^{\text{-}2} \; s^{\text{-}1})$	-5.435	0.221	-14.906-(-0.179)	-6.254	0.293	-23.616-(-0.149)
$E \pmod{m^{-2} s^{-1}}$	3.013	0.140	0.133-14.614	3.152	0.158	0.002-17.370
$g_s \pmod{m^{-2} s^{-1}}$	0.142	0.008	0.004-0.759	0.159	0.018	0.0001-4.94
ΦΡSII (%)	0.717	0.003	0.565-0.807	0.726	0.002	0.638-0.792

Table 1. Summary of herbivory damage, growth, and statistics for physiological response variables in vegetative stems in Netted and Un-netted Wyoming big sagebrush, April through October 2015. Numbers in bold indicate statistically significant differences (P<0.05).

Table 2. Summary ANOVA table for the effects of Julian Day and Netting treatment (Trt) on response variables respiration ( $R_d$ ), transpiration (E), photosynthesis ( $A_{net}$ ), and photochemical efficiency ( $\Phi$ PSII) in Netted and Un-netted Wyoming big sagebrush across the growing season of April through October 2015. Bold indicates statistically significant differences (P<0.05).

			Julian Day			Trt			Day X Trt	
Variable	Optimum covariance structure	dF	$\chi^2$	Р	dF	$\chi^2$	Р	dF	$\chi^2$	Р
$R_d (\mu mol m^{-2} s^{-1})$	Ind.Cov, χ <sup>2</sup> =0.931, P=0.335	1	39.570	3.20E-10	6	0.407	0.523	1	0.83	0.362
$A_{net} \ (\mu mol \ m^{-2} \ s^{\text{-1}})$	Ind.Cov, χ <sup>2</sup> =2.550, P=0.110	1	24.636	6.90E-07	8	2.691	0.836	1	2.69	0.101
g <sub>s</sub> (mol m <sup>-2</sup> s <sup>-1</sup> )	ARMA4, $\chi^2$ =23.283, P=0.00001	1	224.109	<2e-16	11	1.166	0.280	1	2.647	0.104
E (mmol m <sup>-2</sup> s <sup>-1</sup> )	ARMA3, χ <sup>2</sup> =25.257,P=<0.0001	1	171.3	<2e-16	9	0.789	0.375	1	2.047	0.153
$\Phi PSII(\%)$	Ind.Cov, $\chi^2$ =6.743, P=0.150	1	4.300	0.038	6	4.719	0.030	1	0.014	0.906

Table 3. Summary statistics for the response variables Discrimination ( $\Delta$ ),  $\delta^{13}$ C,  $\delta^{15}$ N, WUE<sub>i</sub>, and C: N in vegetative stem isotope samples collected from Netted and Unnetted Wyoming big sagebrush in October 2015.

		Un-netted			Netted	
Variable	Mean	SE	Range	Mean	SE	Range
$\Delta$ (°/ <sub>••</sub> )	18.486	0.131	17.184-19.927	18.513	0.171	17.018-20.441
$\delta^{13}C(\ \ \ )_{\ \ \circ})$	-26.3001	0.126	-25.054-(-27.676)	-26.325	0.163	-24.894-(-28.166)
$\delta^{15}\!N\left(^{\circ}/_{\scriptscriptstyle \circ\circ}\right)$	3.276	0.305	0.141-6.671	2.805	0.215	0.680-4.815
$WUE_i~(\mu mol~mol^{-1})$	94.173	1.454	78.242-108.582	93.879	1.887	72.551-110.425
C:N	24.609	0.430	20.709-28.751	24.235	0.461	20.125-28.773

Appendix V. Summary data for herbivory damage, growth, and floral stem isotopes for treatments: Noise-On and Noise-Off (Fig.1- 2, Table 1), Netted and Noise (Fig.3-4, Table 2), Un-netted and Noise (Fig.5-6, Table 3), and Netted-Un-netted (Fig.7-8, Table 4), for floral inflorescences of Wyoming big sagebrush collected in October 2015.



Figure 1. Comparison of Noise treatments on stem elongation and herbivory in floral stems of Wyoming big sagebrush for Noise-On (n=28, dark cyan bars) and Noise-Off (n= 23, white bars) sites at the end of the growing season, October 2015. Error bars are  $\pm$ SE. Panels are (A) mean stem elongation, (B) mean total herbivory damage (bites, holes, scrapes counted) per stem length, (C) mean td per number of florets, and (D) mean td per biomass.



Figure 2. Comparison of the effects of Noise on isotopic discrimination, intrinsic water use efficiency, and elemental ratios in floral stems in Wyoming big sagebrush at Noise-On (n=28, dark cyan bars) and Noise-Off (n=23, white bars) sites at the end of the growing season, October 2015. Panels are: (A) mean  $\delta^{13}$ C; (B) mean Discrimination ( $\Delta$ ); (C) mean intrinsic water use efficiency (WUE<sub>i</sub>); (D)  $\delta^{15}$ N; and (E) mean C:N values. Error bars are ±SE.



Figure 3. Comparison of Noise treatments on stem elongation and herbivory in floral stems of Netted Wyoming big sagebrush for Noise-On (n=13, dark cyan bars) and Noise-Off (n= 12, white bars) sites at the end of the growing season, October 2015. Error bars are  $\pm$ SE. Panels are (A) mean stem elongation, (B) mean total herbivory damage (bites, holes, scrapes counted) per stem length, (C) mean td per number of florets, and (D) mean td per biomass. In panels where no P-value is indicated, there were no marginal or statistical differences because of Noise.


Figure 4. Comparison of the effects of Noise on isotopic discrimination, intrinsic water use efficiency, and elemental ratios in floral stems in Netted Wyoming big sagebrush at Noise-On (n=13, dark cyan bars) and Noise-Off (n=12, white bars) sites at the end of the growing season, October 2015. Panels are: (A) mean  $\delta^{13}$ C; (B) mean Discrimination ( $\Delta$ ); (C) mean intrinsic water use efficiency (WUE<sub>i</sub>); (D)  $\delta^{15}$ N; and (E) mean C:N values. Error bars are ±SE. In panels where no P-value is indicated, there were no marginal or statistical differences because of Noise.



Figure 5. Comparison of Noise treatments on stem elongation and herbivory in floral stems of Un-netted Wyoming big sagebrush for Noise-On (n=15, dark cyan bars) and Noise-Off (n= 11, white bars) sites at the end of the growing season, October 2015. Panels are (A) mean stem elongation, (B) mean total herbivory damage (bites, holes, scrapes counted) per stem length, (C) mean td per number of florets, and (D) mean td per biomass. Error bars are  $\pm$ SE.



Figure 6. Comparison of the effects of Noise on isotopic discrimination, intrinsic water use efficiency, and elemental ratios in floral stems in Un-netted Wyoming big sagebrush at Noise-On (n=15, dark cyan bars) and Noise-Off (n=11, white bars) sites at the end of the growing season, October 2015. Panels are: (A) mean  $\delta^{13}$ C; (B) mean Discrimination ( $\Delta$ ); (C) mean intrinsic water use efficiency (WUE<sub>i</sub>); (D)  $\delta^{15}$ N; and (E) mean C:N values. Error bars are ±SE.



Figure 7. Comparison of netting treatments on stem elongation and herbivory in floral stems of Wyoming big sagebrush for Netted (n=25, dark gray bars) and Un-netted (n= 26, white bars) sites at the end of the growing season, October 2015. Panels are (A) mean stem elongation, (B) mean total herbivory damage (bites, holes, scrapes counted) per stem length, (C) mean td per number of florets, and (D) mean td per biomass. Error bars are  $\pm$ SE.



Figure 8. Comparison of the effects of netting on isotopic discrimination, intrinsic water use efficiency, and elemental ratios in floral stems for Netted (n=25, dark cyan bars) and Un-netted (n=26, white bars) Wyoming big sagebrush at the end of the growing season, October 2015. Panels are: (A) mean  $\delta^{13}$ C; (B) mean Discrimination ( $\Delta$ ); (C) mean intrinsic water use efficiency (WUE<sub>i</sub>); (D)  $\delta^{15}$ N; and (E) mean C:N values. Error bars are ±SE. In panels where no P-value is indicated, there were no marginal or statistical differences because of Noise.

Table 1. Summary of herbivory damage, growth, and Discrimination ( $\Delta$ ),  $\delta^{13}$ C,  $\delta^{15}$ N, WUE<sub>i</sub>, and C:N in floral stem isotope samples collected from Wyoming big sagebrush at Noise-On and Noise-Off sites in October 2015. "Td" stands for the total damage of bite, holes, scrapes counted per variable.

		Noise ON			Noise OFF		
Variable	Mean	SE	Range	Mean	SE	Range	
Damage per floret number (td/#)	0.072	0.029	0-0.571	0.045	0.015	0-0.323	
Damage per inflorescence length (td/cm)	0.596	0.236	0-6.240	0.254	0.052	0-0.807	
Damage per floral biomass (td/g)	23.548	9.017	0-186.158	9.676	2.235	0-36.610	
Annual inflorescence growth (cm)	12.004	0.646	6.9-20.700	12.722	0.709	6.7-19.70	
Δ( °/ <sub>••</sub> )	17.713	0.189	15.771-19.499	17.720	0.201	15.995-19.257	
δ <sup>13</sup> C ( °/ <sub>••</sub> )	-25.56	0.181	-23.698-(-27.268)	-25.566	0.192	-23.912-(-27.037)	
δ <sup>15</sup> N ( °/ <sub>••</sub> )	3.500	0.244	1.024-6.340	3.130	0.311	0.796-6.755	
$WUE_i ( \circ/_{\circ\circ})$	102.73	2.09	82.973-124.206	102.652	2.223	85.651-121.741	
C:N	29.021	0.875	22.762-38.922	30.965	1.237	22.480-47.056	

Table 2. Summary of herbivory damage, growth, and Discrimination ( $\Delta$ ),  $\delta^{13}$ C,  $\delta^{15}$ N, WUE<sub>i</sub>, and C:N in floral stem isotope samples collected from Netted Wyoming big sagebrush at Noise-On and Noise-Off sites in October 2015. "Td" stands for the total damage of bite, holes, scrapes counted per variable. Bold indicates statistically significant differences (P<0.05), numbers in italics indicate marginal differences between treatments (0.05>P<0.10).

	Noise ON			Noise OFF		
Variable	Mean	SE	Range	Mean	SE	Range
Damage per floret number (td/#)	0.073	0.043	0-0.571	0.052	0.027	0-0.323
Damage per inflorescence length (td/cm)	0.489	0.190	0-2.174	0.254	0.083	0-0.806
Damage per floral biomass (td/g)	21.712	11.785	0-155.039	9.616	3.555	0-38.610
Damage per floret number (td/#)	11.439	0.820	7.6-17.800	13.525	0.824	8.6-17.900
$\Delta( \ \circ/_{\circ \circ})$	17.701	0.275	16.27-19.270	18.256	0.221	17.058-19.257
δ <sup>13</sup> C ( °/ <sub>••</sub> )	-25.548	0.264	-24.177-(-27.049)	-26.079	0.211	-24.933-(-27.037)
$\delta^{15}$ N ( °/ <sub>••</sub> )	3.423	0.279	1.718-5.310	2.669	0.235	1.315-4.142
$WUE_i( \circ/_{\circ\circ})$	102.865	3.044	85.509-118.697	96.730	2.439	85.651-109.976
C:N ( °/ <sub>••</sub> )	28.655	1.500	22.762-38.351	31.921	2.131	22.480-47.056

Table 3. Summary of herbivory damage, growth, and Discrimination ( $\Delta$ ),  $\delta^{13}$ C,  $\delta^{15}$ N, WUE<sub>i</sub>, and C:N in floral stem isotope samples collected from Un-netted Wyoming big sagebrush at Noise-On and Noise-Off sites in October 2015. "Td" stands for the total damage of bite, holes, scrapes counted per variable.

Variable	Noise ON			Noise OFF		
	Mean	SE	Range	Mean	SE	Range
Damage per floret number (td/#)	0.071	0.040	0-0.542	0.037	0.014	0-0.150
Damage per inflorescence length (td/cm)	0.688	0.419	0-6.240	0.254	0.065	0-0.597
Damage per floral biomass (td/g)	25.138	13.755	0-186.158	9.741	2.795	0-28.571
Annual inflorescence growth (cm)	12.493	0.983	6.9-20.700	11.845	1.161	6.7-19.700
$\Delta$ ( °/ <sub>••</sub> )	17.724	0.267	15.772-19.499	17.136	0.249	15.995-18.576
$\delta^{13}C(\ ^{\circ}/_{\circ\circ})$	-25.57	0.257	-23.698-(-27.268)	-25.007	0.239	-23.912-(-26.386)
$\delta^{15}N(~^{\circ}/_{_{\circ\circ}})$	3.564	0.396	1.02-6.340	3.634	0.574	0.796-6.755
WUE <sub>i</sub> (°/ <sub>••</sub> )	102.612	2.972	82.973-124.206	109.113	2.757	93.189-121.741
C:N	29.338	1.034	25.9-38.922	29.932	1.177	25.1-37.075
C.N	29.336	1.034	23.9-38.922	29.932	1.177	25.1-57.07.

Table 4. Summary of herbivory damage, growth, and Discrimination ( $\Delta$ ),  $\delta^{13}$ C,  $\delta^{15}$ N, WUE<sub>i</sub>, and C:N in floral stem isotope samples collected from Netted and Un-netted Wyoming big sagebrush in October 2015. "Td" stands for the total damage of bite, holes, scrapes counted per variable. Numbers in italics indicate marginal differences in variables (0.05>P<0.10).

		Noise ON		Noise OFF		
Variable	Mean	SE	Range	Mean	SE	Range
Damage per floret number (td/#)	0.057	0.024	0-0.542	0.063	0.026	0-0.571
Damage per inflorescence length (td/cm)	0.505	0.241	0-6.240	0.376	0.107	0-2.174
Damage per floral biomass (td/g)	18.624	8.047	0-186.158	15.906	6.357	0-155.039
Annual inflorescence growth (cm)	12.219	0.738	6.7-20.7	12.44	0.608	7.6-17.9
$\Delta$ ( °/ $_{\circ\circ}$ )	17.967	0.183	16.270-19.270	17.475	0.193	15.772-19.499
δ <sup>13</sup> C ( °/".)	-25.803	0.175	-24.177-(-27.049)	-25.332	0.185	-23.698-(-27.268)
$\delta^{15}$ N ( $^{\circ}/_{\circ\circ}$ )	3.061	0.195	1.315-5.310	3.594	0.326	0.796-6.755
$WUE_i ( \circ/_{\circ\circ})$	99.92	2.027	85.509-118.697	105.633	2.134	82.973-124.206
C:N	30.219	1.302	22.480-47.056	29.589	0.764	25.1-38.922