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Cover-based allometric estimate of aboveground biomass of a non-native, invasive annual grass (*Bromus tectorum* L.) in the Great Basin, USA

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ABSTRACT

Cheatgrass (*Bromus tectorum* L.) presence in the Great Basin is associated with an increase in fire frequency and size, likely due to increased spatial continuity of fine fuel biomass. Measurements of the extent and cover of cheatgrass are steadily improving, but the strength of the relationship between cover and aboveground biomass (AGB) is unclear. An allometric equation that can reliably convert cover to AGB of cheatgrass would allow for improved incorporation of regional estimates of cover into models of fire activity, carbon storage, and net primary productivity, all of which rely on biomass. We measured cover and AGB of cheatgrass at 60 locations in the north-central Great Basin and used these measurements to model the relationship. We found a strong, linear relationship between the percent cover and AGB, which was improved after square root transformation of both cover and AGB, and after incorporating the number of days after peak NDVI that the biomass and cover were measured. These results show that AGB of cheatgrass can be reliably estimated from cover. It is likely that allometric equations based on cover will be effective for other grass species, but care must be taken to account for phenology (e.g., peak NDVI) in the estimation.

1. Introduction

The aboveground biomass (AGB) of plants is an important ecological property and a key indicator of how terrestrial ecosystem function responds to global change. Invasions of non-native grasses have altered the abundance and spatial distribution of plant AGB in many areas across the United States (Fusco et al., 2019) and other parts of the world (Miller et al., 2010; Milton, 2004; Setterfield et al., 2010). This can lead to the modification of fire activity, often leading to loss of human life and property, substantial financial costs, and loss of ecosystem functions (Brooks et al., 2004; D'Antonio and Vitousek, 1992). One of the most well-documented examples of a fire-prone, non-native grass is cheatgrass (*Bromus tectorum* L.). Cheatgrass has colonized most of the western United States, and is particularly dominant in the Great Basin. There, cheatgrass increases the connectivity of fine fuels such that fire spreads through colonized landscapes more readily than through native, perennial-dominated landscapes (Davies and Nafus, 2013). As a result, in areas dominated by cheatgrass, fires are twice as likely to occur and tend to become much larger than in native vegetation from which cheatgrass is absent (Balch et al., 2013; Bradley et al., 2018). The ongoing expansion of cheatgrass has disrupted ecosystem functioning (Turnbull et al., 2012; Wilcox et al., 2012) and led to a loss of plant biodiversity (Mahood and Balch 2019).

Allometric equations are a useful tool for using proxy measures to estimate biomass or carbon stocks. Many of the measurements used in allometric equations require on-the-ground measurements that are labor intensive. Equations for woody plants typically require field measurements of diameter at breast height or basal area, canopy diameter, and

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canopy height (Bayen et al., 2020; Dimobe et al., 2018). Biomass of perennial grass species has been estimated using canopy diameter, tillers m^{-2}, basal area or diameter, height, and number of seedheads (Andariese and Covington, 1986; Assaeed, 1997; Rojo et al., 2017). Often these equations are site-specific, accounting for overstory tree type, fire history, livestock grazing, and site identity (Andariese and Covington, 1986; Nafus et al., 2009). This can limit the feasibility of scaling site-specific measurements to regional models of abundance.

In herbaceous communities, allometric equations are sometimes created for aggregated functional groups. But it appears that single-species models are more accurate than multispecies models (Chieppa et al., 2020; Nafus et al., 2009; Pottier and Jabot, 2017). In addition, single-species models might be more generalizable from site to site (Pottier and Jabot, 2017), and perhaps from year to year. This could be because herbaceous plants are more sensitive to water availability than woody plants. In different years and at different sites, the relative abundances of herbaceous plants varies in response to water availability. These ecological responses could explain why interannual variability in precipitation has been documented to cause interannual variability in the relationship between cover and biomass (Ónodi et al., 2017).

Cover is one proxy for biomass that can be estimated rapidly and does not require destructive sampling. Annual estimates of cheatgrass cover at regional extents have been derived from remotely sensed images (Boyte et al., 2019; Boyte and Wylie, 2016; Bradley et al., 2018; Bradley and Mustard, 2006; Jones et al., 2018; Peterson, 2005). The accuracy and spatial and temporal resolution of these estimates are increasing over time. For example, Boyte et al. (2019) modeled cheatgrass cover across the Great Basin at 250 m resolution with a mean absolute error of 12.6%. These approaches suggest that regional estimates of cheatgrass cover can be derived from remotely sensed data in near real time (Boyte et al., 2019; Boyte and Wylie, 2016; Bradley et al., 2018; Bradley and Mustard, 2006; Peterson, 2005). However, AGB is a more directly informative ecological property than cover, a more accurate proxy of carbon storage and net primary productivity than cover, and is necessary for modeling fire occurrence (Hantson et al., 2016; Pilliod et al., 2017) and emissions (Kennedy et al., 2020). Nevertheless, the relationship between cover and AGB of cheatgrass remains largely unexplored. If the estimates of cheatgrass cover from regional cover models could be reliably converted to AGB with an allometric equation, fire risk assessment could be improved through a more accurate estimation of fine fuel load. In addition, the outputs of regional cover models could be more easily transferred to models of net primary productivity and carbon storage, and perhaps be integrated into global dynamic vegetation models.

Another unresolved question about the relationship between AGB and cover is whether it is strictly linear. For many species of herbaceous plants, when cover is low, the relationship appears to be linear (Axmanová et al., 2012; Chieppa et al., 2020; Flombaum and Sala, 2007; Muukkonen et al., 2006; Pottier and Jabot, 2017). At higher levels of cover, there is more uncertainty in the functional form of the relationship (Boyte et al., 2019). As the density of stems increases, overlapping canopies and increased vegetation height may cause AGB to increase exponentially, while the relationship between stem density and cover reaches saturation as cover approaches 100% (Axmanová et al., 2012; Marushia and Allen, 2011; Pottier and Jabot, 2017). However, as stem density increases, AGB could also reach saturation at some theoretical maximum as well, due to intraspecific competition or resource limitation (Fig. 1). This phenomenon is more likely when plant height varies considerably, creating a complex canopy with many layers. A complex canopy is more likely to develop when the community includes many species, especially perennial plants of different ages and species. Annual plants may be more likely to grow to similar heights and have a simple canopy. In our case, cheatgrass often occurs in a near monoculture, with a single canopy layer. Therefore, the relationship between AGB and cover may remain linear even as cover approaches 100%.

One possible confounding factor in the relationship between cover and AGB is the response of annual plants to interannual climatic variations. Annual plants in the Great Basin, especially cheatgrass, are highly responsive to precipitation, aridity, and temperature (Larson et al., 2017; Mangla et al., 2011). Not only are the abundance and phenology of cheatgrass responsive to interannual variation, but the specific leaf area, or leaf area per unit biomass, can vary as a function of moisture availability (Butterfield et al., 2017; Fernández and Reynolds, 2000; Poulin et al., 2007; Sandel and Low, 2019; Tardella et al., 2017). If the relationship between cover and AGB is highly variable among years, then predicting AGB as a function of cover may require accounting for functional trait response to interannual climate variability.

Here, we sampled cover and AGB of cheatgrass, and modeled their relationship, at 380 locations across the Great Basin from 2016 to 2019. Our primary research goal was to develop an allometric equation that could estimate biomass using cover as the only field-based measurement. Such an equation could be applied to models of cover at regional extents to (Boyte et al., 2019; Jones et al., 2018) to estimate AGB. We hypothesized that at low cover values, the relationship between cover and biomass is linear, but could become non-linear at high-cover values.

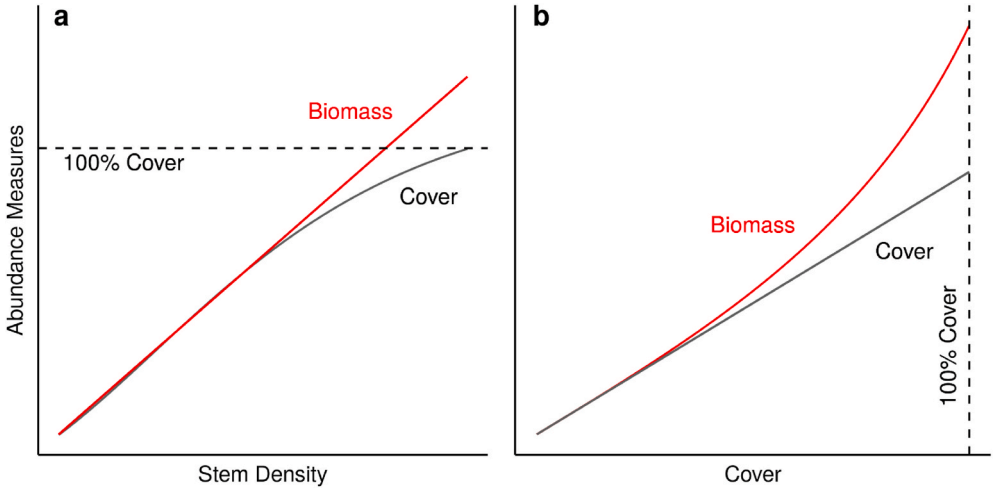

Fig. 1. The saturation effect, where aboveground biomass increases linearly with stem density, but cover reaches saturation as it approaches 100 percent (panel a), and the expected form of the cover to biomass relationship as cover increases (panel b). This relationship would lead to greater inherent sampling error at higher values of cover.

We also examined the effect of sample size and aggregation on estimates of AGB. At 60 locations, we aggregated samples from 0.1 m^2 quadrats to represent cover at the level of 30–50 m transects. At 320 locations, we collected and processed samples at the level of the individual 1 m^2 quadrat to represent the full range of cover values observed at that scale.

2. Methods

2.1. Study area

The study area encompassed 312,750 km^2 across the states of Nevada, Utah, California, and Idaho in the Great Basin of the western United States. The region has hot, dry summers and cold, wet winters. Annual precipitation (±standard deviation) averages 266 ± 46 mm, falling mostly from November to May. Average mean annual temperatures are 9.4 ± 0.5 °C, with seasonal extremes of 22 ± 0.5 °C in July and −1±0.5 °C in December. The region consists of mountain ranges that run approximately north-south, and the sagebrush ecosystems that are the most likely to be invaded by or replaced by cheatgrass generally lie on the lower slopes of the mountains or in the intervening valleys. Our sites ranged from 1273 to 1604 m in elevation with an average of 1396 m. Mean precipitation for the water year preceding sampling (±standard deviation) at our study locations was 360 ± 50 mm in 2016, 344 ± 66 mm in 2017, and 274 ± 49 mm in 2018.

2.2. Field sampling

We used two sampling methods to measure cover and AGB of cheatgrass. The first method (hereafter, transect-level) was intended to capture the variation in cover and AGB at approximately the resolution of a Landsat pixel. We measured cover with ocular estimates and clipped all standing cheatgrass biomass in multiple 0.1 m^2 quadrats along 30 or 50 m transects. We then averaged cover and summed biomass. The second method (hereafter, quadrat-level) was intended to encompass the full range of possible cover values. For these samples, we measured cover using ocular estimates in individual 1 m^2 quadrats along a range of cover values from 0 to 100%. We then clipped a one 0.1 m^2 subset from each quadrat that appeared to be representative of the 1 m^2 quadrat. We dried all biomass samples at 60 °C and weighed them when the mass stabilized.

2.3. Transect-level sampling design 1

We used two different designs for sampling along transects. In June 2016, we sampled cheatgrass at its peak AGB at 20 locations in the north-central Great Basin (Fig. 2). We selected locations after reviewing fire and soil maps from the US Bureau of Land Management (BLM) and consulting with land managers from the BLM's Winnemucca Field Office. The slopes (0–5%) and elevations (1297–1607 m) of the locations were similar, and locations were separated by at least 1.5 km. Eleven locations were dominated by sagebrush (*Artemisia tridentata*). Cheatgrass cover in the understory of six of these sites was <5%. Native shrubs were not present in nine sites, which instead were dominated by cheatgrass (>5% cover) and annual forbs (<5% cover). Permitted levels of livestock grazing in summer and autumn were similar among locations.

At each location, we established three pairs of parallel, 50-m transects, each separated by 20 m. We sampled 0.1 m^2 quadrats every 5 m along each transect. For each of the 60 transects, we averaged measurements of cover and summed measurements of biomass among the 22 quadrats.

2.4. Transect-level sampling design 2

In the first week of July in 2017 and 2018, and in September 2019, we sampled 40 locations in the north-central Great Basin (Fig. 2). Sampling in 2017 and 2018 coincided with peak AGB of cheatgrass. Sampling in 2019 followed senescence and seed dispersal. Half of the sites were dominated by sagebrush and half were dominated by cheatgrass and annual forbs. Elevations ranged from 1200 to 1700 m, and all locations had a history of livestock grazing. At each location, we established one 30-m transect with five 0.1 m^2 quadrats randomly located along the transect. In 2017–2018, we averaged cover and aggregated biomass across the five quadrats to calculate transect-level cover and biomass. For locations sampled in 2019, we recorded cover and AGB from each quadrat separately. This allowed us to evaluate whether aggregation affected the relationship between AGB and cover.

2.5. Quadrat-level sampling design

We sampled quadrats at 90 locations in the northern Great Basin (Owyhee County, Idaho; 30 in late June and early July 2016, 20 in late

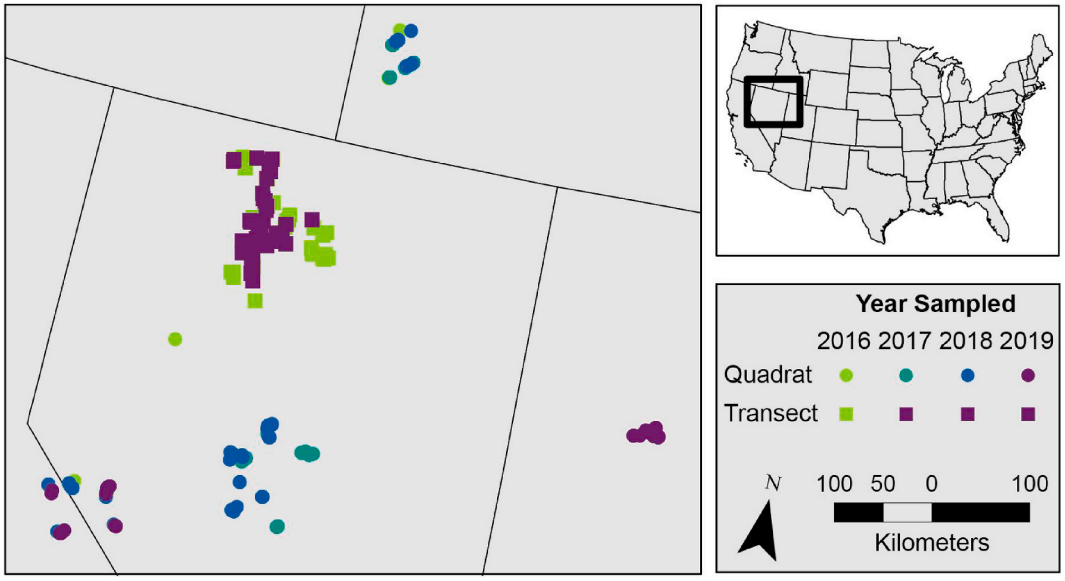

Fig. 2. Study area and sampling sites. Circles represent the locations of 1 m^2 quadrat-level samples, which were collected from 2016 to 2019. Squares represent the locations of transect-level samples collected from 2016 to 2019. Note that the same transect-level sites were resampled from 2017 to 2019.

June and early-mid July 2017, and 40 in June 2018), 33 locations in the eastern Great Basin (Tooele County, Utah) in June 2017, 90 locations in the central Great Basin (Lander, Nye, and Eureka Counties, Nevada; 40 in June and early July 2018 and 50 in June and early July 2019), and 124 locations in the western Great Basin (Mono and Alpine Counties, California and Mineral, Lyon, and Douglas Counties, Nevada; 50 in June–August 2016, 34 in June 2017, and 40 in June–July 2018; Fig. 2). Many locations were tens of km apart (e.g., some locations in the central Great Basin were 90 km apart).

2.6. Ancillary data

We used satellite remote sensing data extracted at each sampling location to explore the potential confounding effects of elevation, precipitation, and the time since peak greenness that the cover and biomass were sampled (hereafter, t_{PG}). For elevation we used 30-m digital elevation models (Rabus et al., 2003). For precipitation, we used estimates of monthly precipitation at 800-m resolution from PRISM (PRISM Climate Group, 2016) and calculated the cumulative precipitation from May of the year preceding sampling through June of the sampling year for each sampling location. For t_{PG}, we used Google Earth Engine (Gorelick et al., 2017) to extract the daily time series of the Normalized Differenced Vegetation Index (NDVI) from the Moderate Resolution Imaging Spectroradiometer on both the Terra and Aqua satellites (MOD09) (Vermote et al., 2015) for each sampling location. We then calculated the date with the highest NDVI for each year at each location and subtracted the date of peak NDVI from the date of sampling for each location to estimate t_{PG}.

2.7. Statistical modeling

We used linear models to estimate the relationship between percent cover and AGB from the transect-level samples collected at peak AGB (June 2016, July 2017, and July 2018). First, we created a set of ordinary least squares (OLS) models, each with data from one year, and another OLS model with the data from all three years. Cover was the predictor and AGB was the response variable. Next, we created linear mixed models with the data from all three years (Bates et al., 2015; Pinheiro et al., 2021). We explored including the year of sampling as a random effect, adding a random slope, and fixing the intercept at zero. We also explored incorporating nonlinear effects by square root- and log-transforming both AGB and cover (as in Guevara et al., 2002). Finally, we explored adding precipitation, elevation, and t_{PG} as covariates. To determine which model was the best fit to the data, we inspected diagnostic plots, used Akaike's Information Criterion (AIC; Burnham and Anderson, 2002a,b) to compare the models with the same transformation type, and used the R^2 values of the observed versus predicted values (OvP R^2; Piñeiro et al., 2008) to compare models with different transformation types.

To evaluate whether aggregating the AGB collected in individual quadrats affected the relationship between percent cover and AGB, we aggregated the data collected in September 2019 by location, and created separate OLS models with the aggregated and unaggregated data. Because the two OLS models were not nested, we compared them by examining R^2 and standard errors of the coefficients.

We also created linear models from the samples collected at the quadrat level, but the coefficients appeared to be unrealistically low, and many models did not pass diagnostic tests, even when restricted to low cover values (Figure S1). Exponential and non-linear models had similar problems. There are at least three possible reasons for this. First, samples were not consistently collected at peak biomass. Second, estimating cover at 1 m^2 while collecting AGB in a 0.1 m^2 subset of that square meter led to high levels of sampling error due to heterogeneity within the 1-m^2 quadrat. Third, there was strong among-observer variation in cover estimates (Table S1). Therefore, we were concerned that these data were not reliable, and excluded them from the final estimation of the relationship between biomass and cover.

All statistical analysis was done in R (R Core Team, 2020). Data and code to reproduce the analysis are at www.github.com/admahood/cg_biomass.

3. Results

We found strong, linear relationships between percent cover and AGB of cheatgrass. For transect-level samples collected from 2016 to 2019, coefficients ranged from 3.3 to 7.8 g m^{-2} for a 1% increase in cover (Fig. 3). However, because the 2019 sample was collected in September, cheatgrass seeds had already shed, and so it does not represent the relationship at peak AGB. Accordingly, we used our transect-level measurements from 2016 to 2018 to estimate the allometric equation for calculating AGB from cover at peak biomass.

The best model was an OLS model with both cover and AGB square root-transformed, and t_{PG} as a covariate (Table 1). This model was among the top performing models according to AIC and OvP R^2, and also had the best diagnostics (Figure S3). Most of the variation explained by the random effects in our mixed models was likely due to variation in t_{PG}. Once we added t_{PG}, the amount of variation explained by the random effects was essentially zero, as indicated by the similarity of the marginal and conditional R^2 values (Table 1). Both elevation and precipitation had little effect on the AGB cover relationship (Table S2). The allometric equation we estimated is:

$$\text{AGB (g m}^{-2})^{0.5} = 2.67\ (\pm 0.8) * \text{Cover (\%)}^{0.5} + 1.53\ (\pm 0.49)$$

The linear model we used to estimate this relationship had an R^2 value of 0.89 (coefficients are in Table 2).

In our comparison of aggregated versus unaggregated samples, the coefficients were the same, but the variance explained was somewhat greater when samples were aggregated by transects ($R^2 = 0.89$, $p < 0.05$) than when samples were not aggregated ($R^2 = 0.84$, $p < 0.05$; Figure S2).

4. Discussion

The relationship between AGB and cover of cheatgrass was strong (Figs. 3 and 4). Both the response and the predictor variables in our final model were square root-transformed, which suggests that the relationship may be nonlinear at higher values (Table 1). Our final allometric equation, as well as the coefficients from our models of individual years (Fig. 3a–c), were similar (after back-transformation) to the equations estimated by Chieppa et al. (2020) for short-lived grasses (6.06) and long-lived grasses (6.54), in which no variables were transformed.

We found suggestive evidence from our quadrat-level data that the relationship between cover and AGB may become nonlinear as cover approaches 100% (e.g., Figure S1g). However, our inferences from those data are tentative for the reasons outlined above (see Methods). We include those data here only to highlight the importance of careful study design and data collection. We still found evidence of a nonlinear relationship in our transect-level data, and this saturation effect may lead to higher sampling error at higher cover values (as in Boyte et al., 2019). However, because cheatgrass cover rarely exceeds 50% at the resolution of a 30-m Landsat pixel, even where it grows in dense monocultures (Boyte et al., 2019), increased error at high values is unlikely to affect regional models of AGB.

Despite high variability in cheatgrass cover among years (Bradley and Mustard, 2006), the relationship between cover and AGB at the time of peak biomass appears to be relatively stable. We anticipated that intraspecific variation in plant functional traits could be a confounding factor in making the allometric equation transferable to other sites, or for scaling up to regional models. We did not find that to be the case here, but intraspecific trait variation may affect the relationship in other species. These traits may vary spatially along topographic and moisture

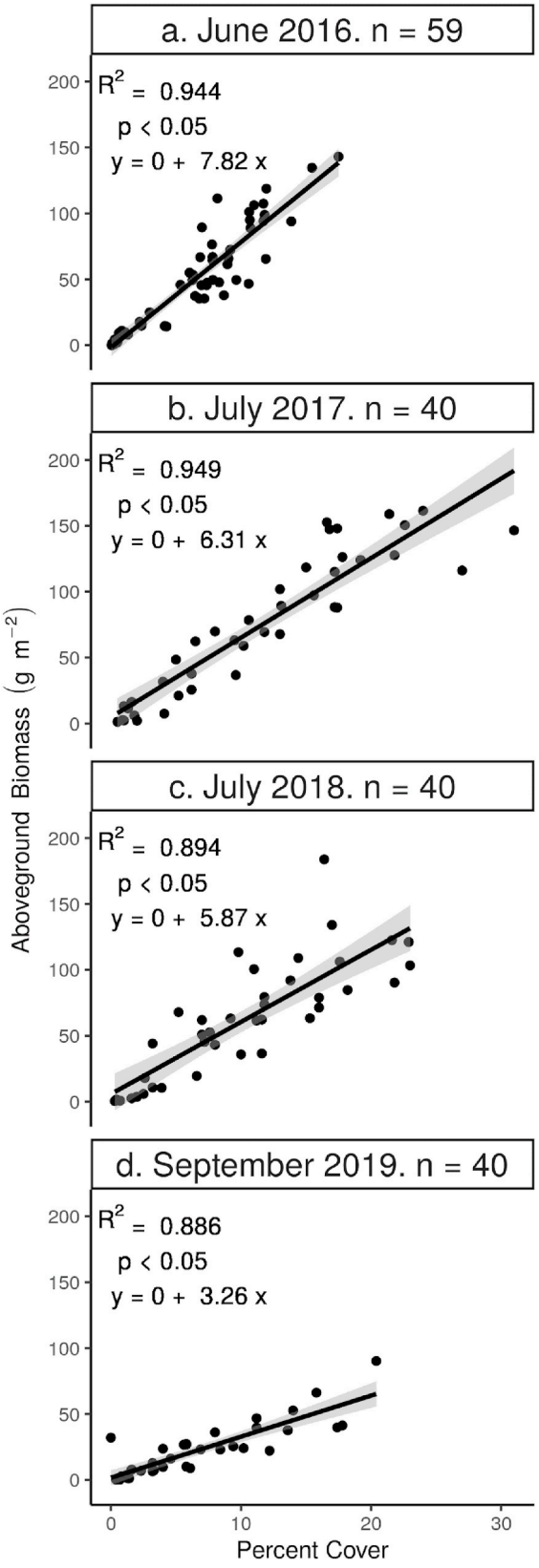

Fig. 3. Percent cover and aboveground biomass of cheatgrass from the four transect-level sampling efforts. Lines are estimates from ordinary least squares regression models. The shaded area is the 95% confidence interval. Data in 2016–2018 were collected near peak aboveground biomass (AGB). Data in 2019 were collected in September, which was at the end of the growing season and well past peak AGB.

Table 1
Performance of all candidate models. The final model is in bold. AIC = Akaike's Information Criterion, R^2_C = conditional R^2, R^2_M = marginal R^2, OvP R^2 = observed versus predicted R^2. AGB, aboveground biomass.

Model Formula	AIC	R^2_C	R^2_M	R^2	OvP R^2
AGB ~ 0 + cover	1237.5	–	–	0.921	0.795
AGB ~ cover	1236.1	–	–	0.795	0.795
AGB ~ 0 + cover + (cover | study)	1231.9	0.857	0.807	–	0.821
AGB ~ cover + (cover | study)	1233	0.837	0.804	–	0.821
log (AGB) ~ 0 + log (cover)	423.8	–	–	0.913	0.638
log (AGB) ~ 0 + log (cover) + (cover | study)	217.8	0.932	0.932	–	0.599
log (AGB) ~ log (cover) + (cover | study)	208.6	0.933	0.875	–	0.619
log (AGB) ~ log (cover) + (1 | study)	207.5	0.917	0.907	–	0.638
$AGB^{0.5} \sim cover^{0.5}$	457.2	–	–	0.875	0.799
$AGB^{0.5} \sim cover^{0.5} + t_{PG}$	**445.6**	**-**	**-**	**0.886**	**0.801**
$AGB^{0.5} \sim cover^{0.5} + t_{PG}$ + (1 | study)	447.6	0.887	0.887	–	0.801
$AGB^{0.5} \sim cover^{0.5}$ + elevation + (1 | study)	455.2	0.89	0.881	–	0.807
$AGB^{0.5} \sim cover^{0.5}$ + ppt + (1 | study)	455.3	0.89	0.882	–	0.807
$AGB^{0.5} \sim cover^{0.5}$ + (1 | study)	453.3	0.89	0.881	–	0.806

Table 2
Model coefficients for the final model. t_{PG} = days after peak NDVI that the data was collected.

Variable	Estimate	Standard Error	T-value	p-value
Intercept	1.53	0.49	3.1	<0.01
Cover $(\%)^{0.5}$	2.67	0.084	31.7	<0.01
t_{PG}	−0.034	0.0091	−3.7	<0.01

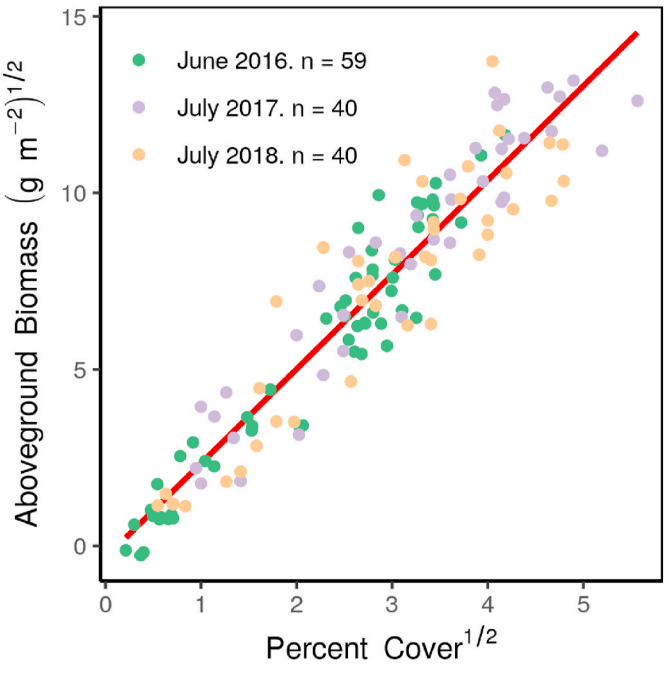

Fig. 4. Partial effects of cover on aboveground biomass, after accounting for days since peak NDVI, for the linear model of the three years of transect-level data collected around peak biomass. Note that the axes are square root-transformed.

gradients (measured as soil moisture, supplemental watering, climatic water deficit, topographic position, and precipitation, respectively; Butterfield et al., 2017; Fernández and Reynolds, 2000; Poulin et al., 2007; Sandel and Low, 2019; Tardella et al., 2017), and temporally throughout the growing season (Svejcar, 1990). If one considers percent cover to be a function of leaf area, then the relationship between AGB and percent cover would be a function of specific leaf area (SLA; leaf area divided by leaf dry mass). SLA and leaf area can vary among individuals of the same species, and within and among communities. If SLA is higher, a given cover value would predict a lower AGB value, so the cover to AGB coefficient would be lower.

Cheatgrass SLA has been documented to be higher at lower elevations (Ziska et al., 2005), and SLA within individual cheatgrass plants reaches a maximum at peak biomass and then declines as the growing season progresses (Svejcar 1990). We found that inclusion of elevation did not improve our models. But we did find a within-season effect, in that the coefficient of the cover to biomass relationship was lower in samples collected later in the growing season than at peak biomass (Fig. 3, Table 2). This is the opposite of what one would expect if SLA was the principal driver of changes in the cover-biomass relationship as the growing season progresses. Rather, the variation in coefficients is likely to be more strongly influenced by seed shedding.

The SLAs of grass species in general have also been observed to be sensitive to interannual variation in precipitation. As precipitation increases, SLA tends to increase (Butterfield et al., 2017; Fernández and Reynolds, 2000; Poulin et al., 2007; Sandel and Low, 2019; Tardella et al., 2017). Therefore, one would expect a higher slope of the cover to AGB relationship in dry years. However, adding precipitation as a covariate did not improve our models. The discrepancy between the documented variation in SLA in other studies and our results might be due to differences among species in strategies for surviving drought. Cheatgrass mitigates the effects of seasonal drought by germinating in early spring as soon as moisture is available and completing its life cycle before soil moisture decreases, and atmospheric vapor pressure deficit increases, during summer (Mack and Pyke, 1983). Perennial grasses like *Elymus elymoides* and *Poa secunda*, in contrast, must allocate fewer resources to aboveground growth during the period when moisture availability is high, and more to underground carbon storage to survive the summer drought (Blumenthal et al., 2021; Johnson et al., 2015). These differences in resource allocation strategies may explain why the SLA of cheatgrass, unlike the SLA of other grasses, does not appear to be as sensitive to precipitation.

Height may be another confounding factor, especially at high values of cover. Estimating AGB as cover approaches 100% is challenging because plant height still can increase after canopy cover reaches a maximum. One could incorporate vegetation height into a model of AGB, but several of the largest existing sets of training data, which include tens of thousands of data points, do not include measurements of height (see Boyte et al., 2019). Models of canopy height derived from remote sensing typically focus on tree or shrub cover (Alonzo et al., 2018; Narine et al., 2019). Annual grass height is much more difficult to model with satellite remote sensing. Therefore, there are trade-offs between increases in model accuracy and the prompt availability of data. It may be possible to model cheatgrass height on the basis of topography and current year climate, and incorporate those values into models of AGB. These concerns may be moot, however, given that Chieppa et al. (2020) found no improvement in model accuracy when they added height to models of AGB predicted by cover for grass species.

Many annual grass species have become dominant in other areas of the western United States. These include various species of *Bromus* and *Avena* throughout California, red brome (*Bromus rubens* L.) in the Mojave Desert, and Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) in the northern Great Basin. Like cheatgrass, these species generally form a simple, single-layer canopy. It is very likely that AGB of these species can also be estimated from allometric equations that are based on cover. Differences among species in, for example, SLA, height, and seed mass may prevent application of the identical equation. Furthermore, one must account for the effect of interannual climate variability on phenology of any annual species. However, we believe that allometric equations converting cover to biomass are likely to be consistently applicable for single species, and that it may be possible to apply allometric equations within functional groups more generally.

CRediT authorship contribution statement

Adam L. Mahood: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Erica Fleishman:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Jennifer K. Balch:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision. **Frank Fogarty:** Investigation, Writing – review & editing. **Ned Horning:** Investigation, Writing – review & editing. **Matthias Leu:** Investigation, Writing – review & editing. **Martha Zillig:** Investigation, Writing – review & editing. **Bethany A. Bradley:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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