

NON-DESTRUCTIVE ESTIMATION OF ABOVEGROUND PLANT BIOMASS IN SOUTH DAKOTA TALLGRASS PRAIRIE

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ABSTRACT

Understanding ecological processes in threatened tallgrass prairie ecosystems includes quantifying biomass production, yet destructive harvesting is not always possible. The purpose of this research was to quantify the relationship between aboveground plant biomass and plant abundance as determined by the point-intercept method (PIM) on a tallgrass prairie sampled in May, July, and September. We then compared these relationships from models based on different plants (58 species) and two morphological groupings to quantify how much this information changed the relationship between aboveground plant biomass and plant abundance compared to a model without this information. In all models, the mean slopes were similar, but there was a reduction in uncertainty of the slope (reduced 95% credible intervals) when species or morphological information was incorporated into the model. Estimates of the relationship between plant abundance and aboveground biomass were most precise in July and when species-level information was included in the model. The uncertainty of the estimates was reduced when plants were identified to growth form (graminoid and forb), and adding species-level information (the most labor-intensive) only minimally improved the model relative to growth form. Therefore, sampling with the PIM and identifying plant growth form would reduce the sampling time and would allow the sampling to be conducted by researchers with limited plant identification knowledge. The regression equations produced provide a non-destructive method to estimate aboveground biomass in tallgrass prairies.

Keywords

Bayesian statistics, grassland, point-intercept method, regression analysis, Spirit Mound Historic Prairie

INTRODUCTION

Grasslands are the largest ecosystem globally, and the North American grasslands include the tallgrass, mixed-grass, and shortgrass prairies (Jarchow et al. 2020). An important characteristic of prairies, and ecosystems in general, is the productivity of an ecosystem. Although prairie plants invest considerable amounts of resources belowground – more than 50% of a prairie plant's biomass may be belowground – aboveground biomass production is commonly measured to characterize the plant community and assess resources available to livestock and wildlife (Isbell and Wilsey 2011a).

Measuring aboveground biomass for grassland management and research can be time intensive and require destructive sampling, which is not permissible in all situations (Nagel 1967; Guo and Rundel 1997). The point-intercept method (PIM) is a commonly used, non-destructive alternative to harvesting aboveground biomass (Frank and McNaughton 1990; Press et al. 1998; Bråthen and Hagberg 2004; Brantley and Young 2007; Schuur et al. 2007; Montes et al. 2008; Wilsey et al. 2009; McLaren and Turkington 2010; Isbell and Wilsey 2011a, b; Jarchow and Liebman 2012). The PIM was used by Levy (1927) and then described by Levy and Madden (1933) and uses a frame with a “pin” (i.e., a thin metal rod) to quantify the number of “hits” (i.e., pin contacts with living plant material) within the sampling frame (Jonasson 1988). PIM is often less time consuming than biomass collection, and the same area can be sampled multiple times over the growing season with minimal disturbance to the plant community (Nagel 1967; Jonasson 1988).

Aboveground biomass is estimated with the PIM by determining the relationship between aboveground biomass and the number of hits using regression analysis. Developed regression equations can then be used to estimate aboveground biomass at sites where only the number of hits is known (Frank and McNaughton 1990; Bråthen and Hagberg 2004). Relationships between pin hits and biomass can vary widely among plants with different morphologies or at different times in the growing season (Bonham 2013). Accounting for this variation requires measuring pin hits and biomass for multiple morphological groups or species separately and at different times of the growing season. The purpose of this research was to develop regression equations to estimate aboveground biomass in tallgrass prairies. Specifically, we asked the question: Does the relationship between aboveground biomass and PIM differ over the growing season, among species, or among morphological groupings?

METHODS

Study Site—The study was conducted at Spirit Mound Historic Prairie (hereafter Spirit Mound), a 130 ha restored tallgrass prairie 8 km north of Vermillion, South Dakota (42.867608°N, 96.954431°W). The site was farmed for over 130 years before being returned to prairie beginning in 2001. In 2013, a vegetation survey at Spirit Mound found the plant community was 34% native forbs, 1%

native legumes, 4% native cool-season grasses, 52% native warm-season grasses, and 8% non-native forbs and grasses (total is 99% due to rounding; Millikin et al. 2016). The mean annual rainfall near Spirit Mound was ca. 75 cm in 2014, which was similar to the long-term average annual precipitation (National Weather Service 2021).

Sampling Design—We sampled Spirit Mound during the last two weeks of May, July, and September of 2014. We used a stratified random sampling design in which we divided Spirit Mound into six areas and established three - 100 m transects in each area with at least 200 m between the starting point of each transect. Every 20 m along the transect, starting at zero, we placed a square 1 m² point-intercept frame. The PVC frame was 1 m tall, and the top of the frame was an open square with a sliding bar that we moved across the frame. The sides of the open square had marks every 10 cm, and the sliding bar had holes drilled through it every 10 cm, which created 100 potential sampling points.

At each sampling location, we randomly selected 25 points to sample and dropped the pin (1.2 m tall, 9 mm diameter) vertically through a hole in the sliding bar to the ground. If the plant canopy was taller than 1.2 m, we would lift the pin to sample the plants. We used the all-contact method, where we recorded the identity and number of times any living plant part touched the pin from the top of the plant canopy to the soil surface. During the different sampling dates, each transect was moved 5 m to the east to account for the destructive harvest of biomass coinciding with the PIM.

Following the PIM sampling, we harvested all the living aboveground plant biomass within the 1 m² sampling area by manually cutting the plants to ground level with clippers. In the laboratory, we removed the dead biomass (litter and standing dead biomass) from the previous growing seasons and sorted current year growth to species. We dried the samples as separate species in paper bags at 60°C for at least 48 hours before weighing each sample to the nearest 0.1 g. We collected 108 biomass samples in July and September and 72 samples in May because a spring burn at the site removed all the biomass from six transects.

Data Analysis—Because our goal was to develop regression equations that can be used by others for estimating aboveground tallgrass prairie biomass at Spirit Mound and possibly other tallgrass prairies, we evaluated the precision of the biomass predictions when the plants were grouped in multiple ways. We used the *Manual of Vascular Plants of Northeastern United States and Adjacent Canada* (Gleason and Cronquist 1991) to obtain plant morphological information. We used Principal Components Analysis (PCA) to visualize how the plants clustered with different morphological characteristics including plant height, leaf shape, leaf (or leaflet) length, leaf length to width ratio, leaf arrangement, plant stature, and growth form (McCune and Mefford 2011).

To compare the relationships between biomass and hits, we developed seven linear mixed regression models with biomass as the response variable, pin hits as the predictor variable with combinations of species, morphology, form, area, and transect as either fixed predictor variables or random effects. Model structures are described Table 1. Four of the models were fit with datasets that contained either species-level information, information on one of two morphological groupings,

or neither species nor morphological information (Table 1). The three remaining models contained an interaction between hits and either plant species identity or one of two morphological groupings (Table 1). These three models were fit only with July data, since most tallgrass prairie species have their peak biomass in July (Bonham 2013). Fitting the models in these combinations allowed us to compare slopes among individual species or morphological groupings.

For each of the seven models described above, we estimated the posterior probability distribution of slopes using Bayesian analysis. In each model, priors for the intercept were assigned a normal distribution with a mean of 0 and standard deviation of 50, priors for the fixed effects were assigned a normal distribution with a mean of 0 and a standard deviation of 20, and priors for sigma were assigned a half-Cauchy distribution with a location of 0 and scale of 1, following McElreath (2015). Priors were chosen using prior predictive simulation (Wesner and Pomeranz 2021) to reflect prior knowledge about plant biomass measures (in grams) while allowing for a small number of extreme values (e.g., >10,000 grams). Models were fit using the *brms* package (Bürkner 2016) in R version 3.4.2 using Rstudio version 1.1.383 (RStudio Team 2016). The *brms* package generates posterior distributions using Hamiltonian Monte Carlo in *rstan* (Stan Development Team 2016). We estimated the joint posterior distribution using 2000 iterations of 4 chains, with the first 1000 iterations discarded as warmup. Convergence was checked with trace plots and by ensuring that \hat{r} was <1.1. To ensure that our models could reasonably represent the data-generation process, we generated 10 datasets from the fitted model and compared them to the original data using posterior predictive checks (Gelman et al. 2014). Data and R code are available at https://github.com/jswesner/jarchow_plants_git.

RESULTS AND DISCUSSION

The goal of the PCA was to identify ways to aggregate the species sampled into a smaller number of groups. We were able to identify mostly non-overlapping groupings in the PCA when we included information on growth form (graminoid versus forb), plant stature (decumbent or rosette versus erect), plant height for forbs, and leaf width for grasses, which resulted in five categories: decumbent or rosette forbs, short forbs (≤ 1.4 m tall), tall forbs (≥ 1.5 m tall), wide-leaved grasses (leaf length to width ratio <50), and narrow-leaved grasses (leaf length to width ratio ≥ 50) (hereafter morphological grouping) (Figure 1). We selected a second grouping that would be easier to use in the field: graminoids versus forbs (hereafter growth-form grouping).

Aggregating data at different levels (e.g., species level, morphological grouping) resulted in wide variation in the number of data points in each dataset, ranging from 284 data points in the dataset for Model 1 (no species or morphological group information collected in a plot) to 1701 data points when species-level information was collected at each plot (Table 1). This variation reflects the level of effort required to collect, sort, and weigh each sample (e.g., 284 samples versus 1701 samples).

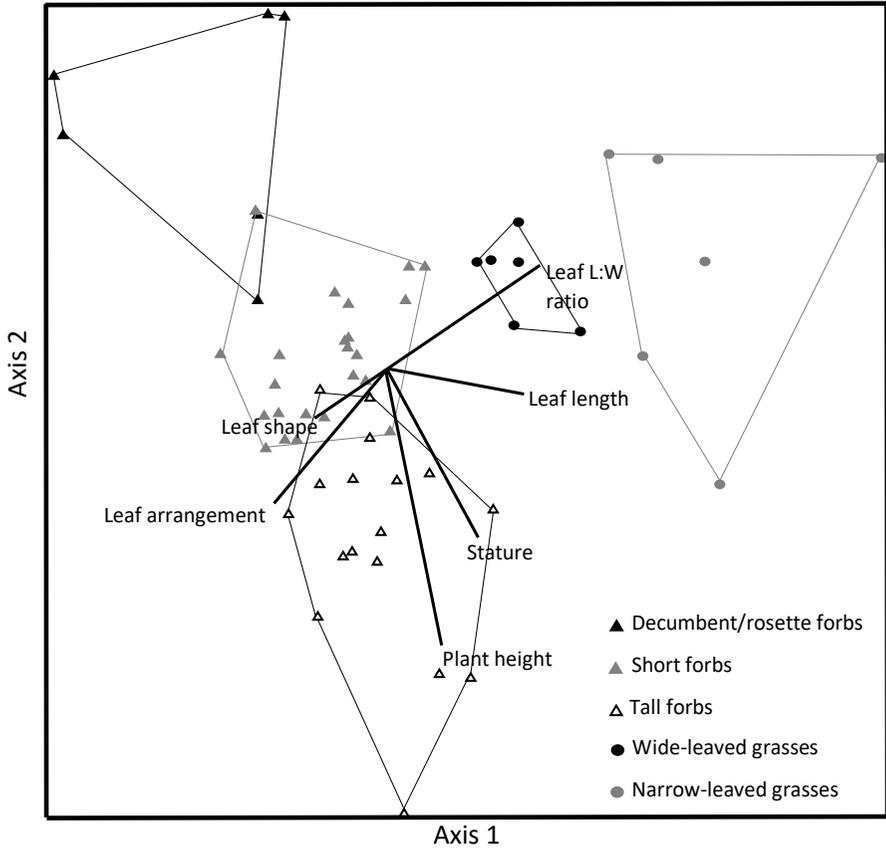


Figure 1. Principle Components Analysis bi-plot of the plant characteristics of the species found at Spirit Mound. Bi-plot lines indicate the magnitude of the contribution of each plant characteristic. Axes 1 and 2 explained 36% and 22% of the variability in the data, respectively.

Regardless of the level of data aggregation, there was a positive relationship between aboveground biomass and hits in all months (Figure 2), and mean r^2 values from each model ranged from 0.60-0.77. These r^2 values were generally lower than the r^2 values from studies in other grassland ecosystems: 0.83-0.96 for shortgrass prairie (Frank and McNaughton 1990; Byrne et al. 2011), 0.87-0.99 for Mediterranean grasslands (Barkaoui et al. 2013), and 0.90 for mixed-grass prairie (Byrne et al. 2011). One reason why our r^2 values may have been lower than those of other grassland studies is because of the greater quantity of biomass in tallgrass prairie than other grasslands.

For May and July, the average slopes were similar for all four models, ranging from 1.2 to 1.4 in May and 1.6 to 1.8 in July. However, the uncertainty in these mean slopes improved dramatically in models with species or morphological-group information compared to Model 1 with neither (Figure 3). For example, in May, there was a probability of 0.95 that the mean slope from Model 1 was 0.6 to

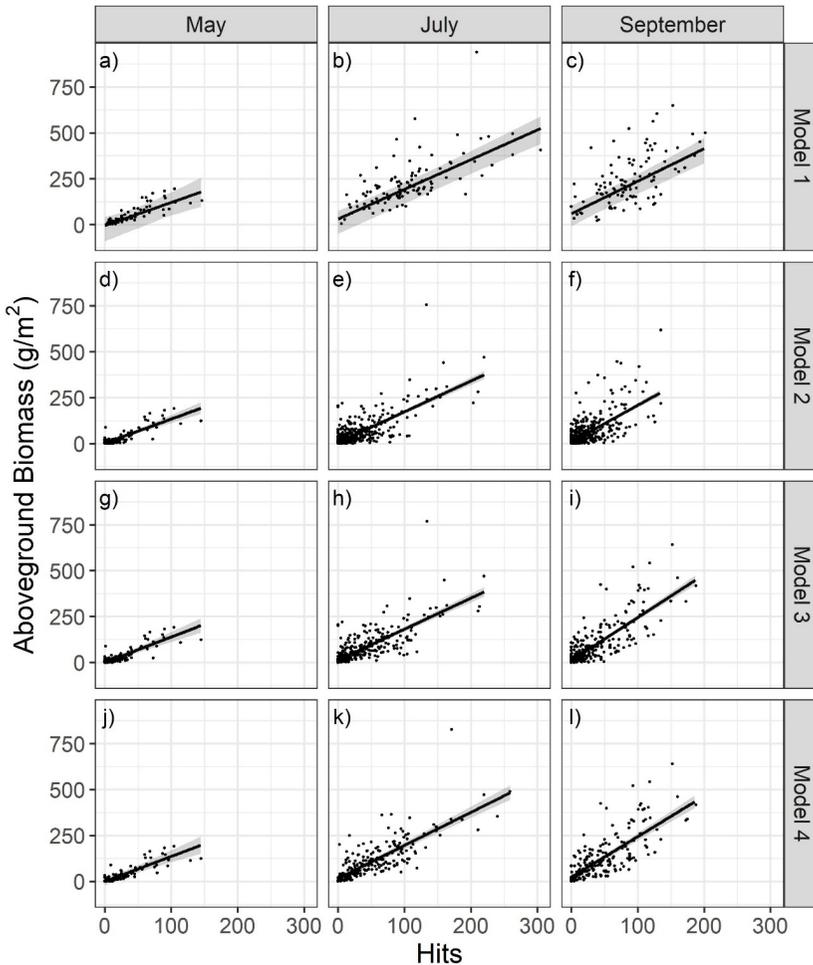


Figure 2. Relationship between hits and aboveground biomass for models representing four scenarios of data aggregation. In Model 1, no information on species or morphological grouping was included. In Model 2, hits and biomass were recorded for each species in a plot. In Model 3, hits and biomass were recorded for each of five morphological categories. In Model 4, hits and biomass were recorded for each of two growth-form categories. Dots indicate raw data, regression lines and shading represent the mean and 95% credible intervals for slopes.

1.8, representing a 3-fold gradient in uncertainty. In all other models, the gradient from the lower to upper 95% quantiles was between 1.5 and 1.7 fold (Table 2). Similar improvements in uncertainty occurred in each month (Table 2). Among the months, the 95% credible intervals were smallest in July compared to the other two months (Figure 3). In September, the estimates of the slopes differed among the models unlike the slope estimates for May and July (Figure 3). Part of the improvement in uncertainty is likely due to the increase in sample size as information on species or morphological groups is recorded. However,

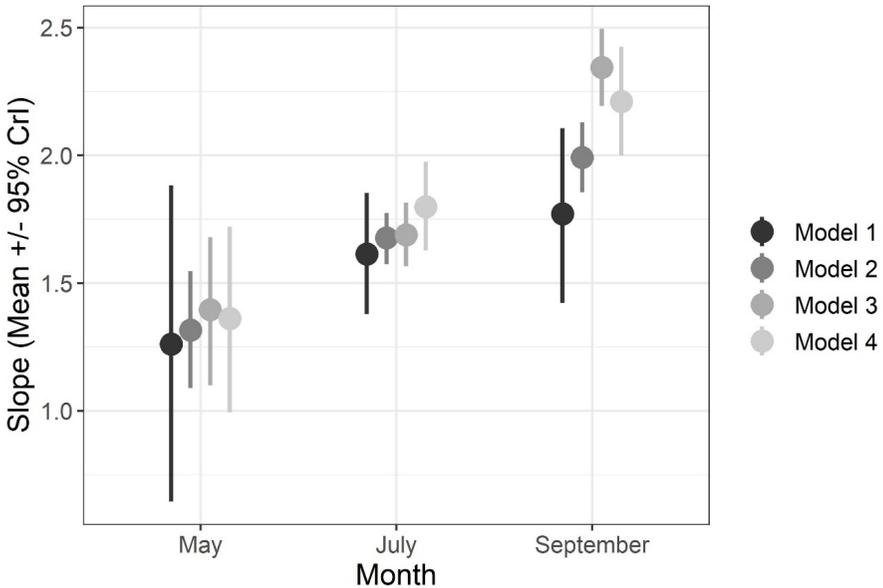


Figure 3. Mean and 95% credible intervals of the regression slope between hits and biomass across month for each model. In Model 1, no information on species or morphological group was included. In Model 2, hits and biomass were recorded for each species in a plot. In Model 3, hits and biomass were recorded for each of five morphological categories. In Model 4, hits and biomass were recorded for each of two growth-form categories.

sample size alone does not explain the improvement in fit. For example, adding information on two growth forms (Model 4) results in a substantial reduction in uncertainty (Figure 3) compared to the model with no information on species or morphological/growth forms (Model 1). The cost of this improvement is an increase in the number of samples by roughly 2-fold (e.g., 284 samples for Model 1 vs 554 samples for Model 4). However, while Models 2 and 3 contain higher sample sizes to deal with adding species-level or morphological-level information ($n = 978$ and 1701 , respectively), they show no additional reductions in uncertainty compared to the growth form model (Model 4). Thus, simply collecting information on two growth forms achieves a similar amount of improvement in model estimates as does collecting information on dozens of individual species (Figure 3).

The regression lines best fit the data when species-level information was included in the model from the July sampling period (Model 5) which resulted in an r^2 value of 0.76 with a narrow 95% confidence range of 0.74 to 0.77. Among the twelve most abundant species in July, there was a >95% probability that the slopes between hits and biomass were positive for all species, except field bindweed (*Convolvulus arvensis*), a decumbent forb, which had only a 40% probability of a positive slope (Tables 3 and 4). Of the remaining species, stiff goldenrod (*Oligoneuron rigidum*) and cup plant (*Silphium perfoliatum*) had the

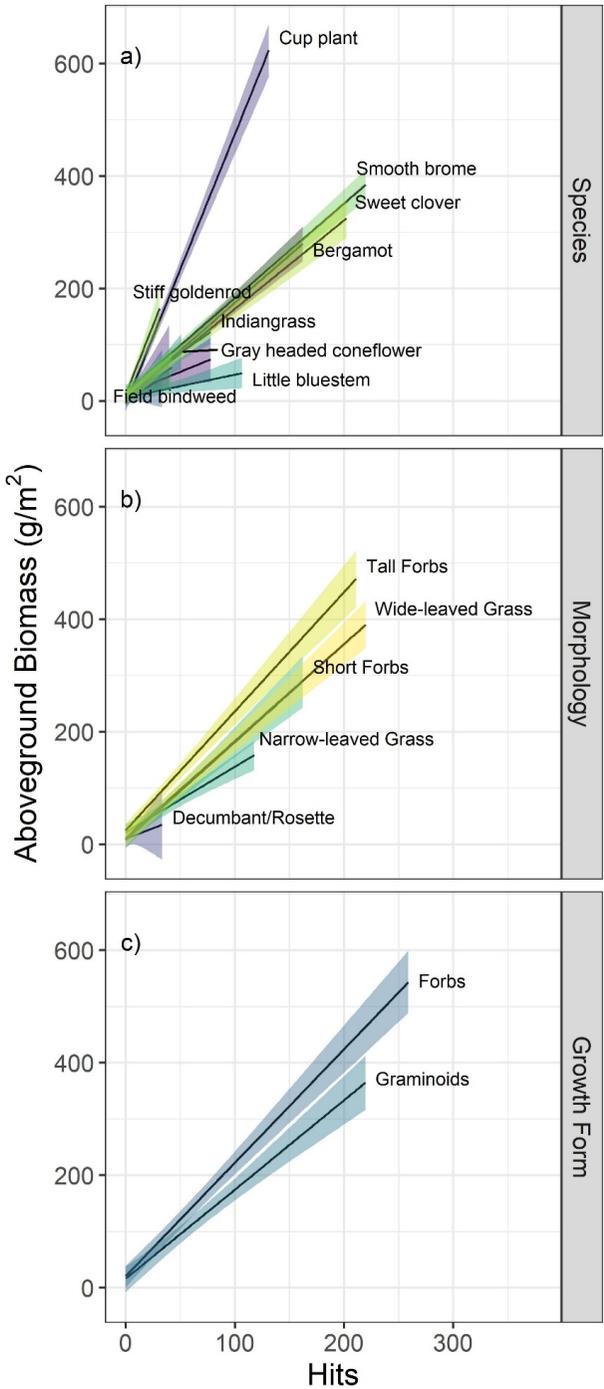


Figure 4. Relationship between hits and aboveground biomass in July for (a) the most abundant species, (b) the morphological grouping, and (c) the growth-form grouping. Regression lines and shading represent the mean and 95% credible intervals for slopes.

steepest slopes (averaging 4.8 and 4.9, respectively, Figure 4). Mean slopes for the remaining nine species were at or below 1.9 with little bluestem (*Schizachyrium scoparium*) having the lowest slope at 0.4 (Table 3, Figure 4). Beyond the twelve most abundant species, there was a large drop in the amount of data available for each species, which makes it difficult to determine if there are species-specific characteristics that are driving the observed relationship between hits and biomass.

Within the morphological grouping in July (Model 6), the r^2 value for the model was 0.66, and all five categories of plants had a >95% probability of being positive, except for the decumbent/rosette forbs (Table 5, Figure 4), which had a 78% probability of being positive. Mean slopes for the other categories ranged from 1.2 to 2.1 (Table 5). Within the growth-form grouping (Model 7), the r^2 value for the model was 0.65, and the slope for forbs averaged 2.0 and was higher than the slope for graminoids with 90% probability (Table 5, Figure 4).

CONCLUSIONS

There was variation in the relationship between hits and biomass over the growing season, and we found that the PIM was most accurate when the sampling occurred during peak plant growth. The estimations of aboveground biomass were improved by including plant characteristics – species identities and morphological-group information. Although estimating aboveground biomass was most accurate when regression equations were developed for each species, the species-level regression equations developed in this study are unlikely to cover all species found in other sites and collecting species-level information is the most time and knowledge intensive when sampling. The reductions in uncertainty of the estimation of aboveground biomass from the PIM was similar whether plants were grouped by a composite of morphological characteristics or growth form (graminoid versus forb). Sampling to the growth-form level would be much less time intensive and would allow the sampling to be conducted by people with limited plant identification knowledge.

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Table 1. Model specifications for each of the 7 models in this study. All models were fit with a Gaussian likelihood. See text for prior specifications.

Model	Response	Predictors	Random effects	Notes	n
1	biomass	hits+month+hits*month	area, transect	all data	284
2	biomass	hits+month+hits*month	area, transect, species	all data	1701
3	biomass	hits+month+hits*month	area, transect, morph	all data	978
4	biomass	hits+month+hits*month	area, transect, growth	all data	554
5	biomass	hits+species+hits*species	area, transect	July only	1701
6	biomass	hits+morph+hits*morph	area, transect	July only	978
7	biomass	hits+growth+hits*growth	area, transect	July only	554

Table 2. Posterior means and 95% credible intervals (CI) for regression parameters between hits and aboveground biomass. In Model 1, no information on species or morphological group was included. In Model 2, hits and biomass were recorded for each species in a plot. In Model 3, hits and biomass were recorded for each of five morphological categories. In Model 4, hits and biomass were recorded for each of two growth-form categories. r^2 represents the mean of the partial r^2 distribution using the bayes_R2() function in brms.

Model	Month	Mean	Intercept		Mean	Slope		r^2
			LowerCI	UpperCI		LowerCI	UpperCI	
1	May	-0.5	-69	42.6	1.2	0.6	1.8	0.44
	July	35.6	-32	76.7	1.6	1.4	1.8	0.49
	Sept	62.9	-2.7	106.4	1.8	1.4	2.1	0.48
2	May	2.4	-3.7	8.7	1.3	1.1	1.5	0.74
	July	5.7	0.2	11.3	1.7	1.6	1.8	0.62
	Sept	9.7	4.5	15	2	1.9	2.1	0.54
3	May	-0.5	-11.5	10.4	1.4	1.1	1.7	0.73
	July	12.8	2.6	23.2	1.7	1.6	1.8	0.63
	Sept	10.7	-0.1	21.2	2.3	2.2	2.5	0.67
4	May	0	-20.5	17.4	1.4	1.0	1.7	0.70
	July	16.5	-3.9	33.5	1.8	1.6	2.0	0.63
	Sept	22.5	3.1	39.3	2.2	2.0	2.4	0.60

Table 3. Posterior means and 95% credible intervals (CI) for intercept and slope in July of the twelve most abundant species. r^2 represents the mean of the partial r^2 distribution using the bayes_R2() function in brms.

Species ¹	Intercept			Slope			r ²
	Mean	LowerCI	UpperCI	Mean	LowerCI	UpperCI	
Bergamot	6.3	-0.4	13.2	1.7	1.5	1.9	0.70
Big bluestem	11.9	3.2	20.7	0.8	0.2	1.4	0.29
Canada wildrye	3.8	-6.1	13.1	1.9	0.4	3.3	0.66
Cup plant	-5.7	-18.2	6.7	4.8	4.4	5.2	0.88
Field bindweed	3.0	-11.1	17.5	1.1	-0.6	2.8	0.51
Gray headed coneflower	5.2	-3.6	14.3	1.6	0.9	2.3	0.45
Indiangrass	18.3	8.2	28.8	1.3	1.0	1.7	0.41
Little bluestem	6.4	-4.7	16.9	0.4	0.1	0.7	0.51
Sideoats grama	8.4	-1.7	18.7	1.2	0.2	2.1	0.43
Smooth brome	14.7	4.1	25.2	1.7	1.5	1.8	0.70
Stiff goldenrod	11.6	0.6	22.2	4.9	3.6	6.2	0.48
Sweet clover	6.3	-6.5	19.4	1.6	1.4	1.8	0.73

¹Bergamot (*Monarda fistulosa*), big bluestem (*Andropogon gerardii*), Canada wildrye (*Elymus canadensis*), cup plant (*Silphium perfoliatum*), field bindweed (*Convolvulus arvensis*), gray headed coneflower (*Ratibida pinnata*), Indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), smooth brome (*Bromus inermis*), stiff goldenrod (*Oligoneuron rigidum*), and sweet clover (*Melilotus officinalis*)

Table 4. Morphological characteristics and frequency of occurrence of the twelve most abundant species (Gleason and Cronquist 1991).

Species	Growth form	Plant stature	Plant height (cm)	Leaf length:width ratio	Frequency (% of hits, % of biomass)
Bergamot	forb	erect	120	2.9	13%, 11%
Big bluestem	graminoid	erect	300	56	4%, 5%
Canada wildrye	graminoid	erect	150	25	1%, 1%
Cup plant	forb	erect	200	1.5	3%, 6%
Field bindweed	forb	decumbent	NA	1.7	1%, <1%
Gray headed coneflower	forb	erect	120	2.5	4%, 3%
Indiangrass	graminoid	erect	200	50	18%, 24%
Little bluestem	graminoid	erect	95	75	12%, 6%
Sideoats grama	graminoid	erect	70	60	2%, 4%
Smooth brome	graminoid	erect	100	21	24%, 20%
Stiff goldenrod	forb	erect	160	1.5	3%, 8%
Sweet clover	forb	erect	200	4.5	11%, 8%

Table 5. Posterior means and 95% credible intervals (CI) for intercept and slope of linear regressions. r^2 represents the mean of the partial r^2 distribution using the bayes_R2() function in brms.

Model	Category	Mean	Intercept		Slope			r^2
			LowerCI	UpperCI	Mean	LowerCI	UpperCI	
Morphology	decumbent/rosette	10.3	-6.0	26.8	0.8	-1.4	2.7	0.36
	short forbs	8.1	-6.4	22.4	1.7	1.4	2.1	0.66
	tall forbs	24.7	10.8	38.5	2.1	1.8	2.4	0.57
	wide-leaved grass	11.2	-2.9	24.8	1.7	1.5	1.9	0.75
	narrow-leaved grass	21.5	5.3	36.8	1.2	0.9	1.5	0.57
Growth form	forbs	20.6	1.3	38.4	2.0	1.8	2.3	0.66
	graminoids	16.6	-6.4	37.9	1.6	1.3	1.9	0.64