

Linking plant growth responses across topographic gradients in tallgrass prairie

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Abstract Aboveground biomass in grasslands varies according to landscape gradients in resource availability and seasonal patterns of growth. Using a transect spanning a topographic gradient in annually burned ungrazed tallgrass prairie, we measured changes in the height of four abundant C₄ grass species, LAI, biomass, and cumulative carbon flux using two closely located eddy flux towers. We hypothesized that seasonal patterns of plant growth would be similar across the gradient, but the magnitude of growth and biomass accumulation would vary by topographic position, reflecting spatial differences in microclimate,

slope, elevation, and soil depth. Thus, identifying and measuring local growth responses according to topographic variability should significantly improve landscape predictions of aboveground biomass. For most of the growth variables measured, classifying topography into four positions best captured the inherent spatial variability. Biomass produced, seasonal LAI and species height increased from the upland and break positions to the slope and lowland. Similarly, cumulative carbon flux in 2008 was greater in lowland versus upland tower locations (difference of 64 g m⁻² by DOY 272). Differences in growth by topographic position reflected increased production of flowering culms by *Andropogon gerardii* and *Sorghastrum nutans* in lowland. Varying growth responses by these species may be a significant driver of biomass and carbon flux differences by topographic position, at least for wet years. Using a digital elevation model to classify the watershed into topographic positions, we performed a geographically weighted regression to predict landscape biomass. The minimum and maximum predictions of aboveground biomass for this watershed had a large range (86–393 t per 40.4 ha), illustrating the drastic spatial variability in growth within this annually-burned grassland.

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Introduction

During the mid-nineteenth century, the grassland region of central North America was termed “the Great Plains” to reflect the expansive skylines and flat valley bottoms common across the landscape (Lewis 1966). This

perception of structural and biological simplicity may be suitable from a continental perspective in comparison with the eastern deciduous forests, and the Rocky Mountains to the west. However, local and regional differences in ecosystem structure and function within the sub-Great Plains geographic regions are large, and vary broadly according to climate gradients (Burke et al. 1991; Epstein et al. 1997; Knapp et al. 2008; Heisler-White et al. 2009), landscape heterogeneity (Rossum and Lavin 2000), and ecological complexity (Risser et al. 1981; Risser 1990; Briggs and Knapp 1995; Paruelo and Lauenroth 1996). Despite the characterization of a simple landscape across the Great Plains, it remains unclear how local terrain-related variability impacts local processes such as growth and carbon flux.

Within the Flint Hills of eastern Kansas, complex geomorphic terrain creates spatial variability in above- and belowground environmental conditions in tallgrass prairie (Schimel et al. 1991; Knapp et al. 1993). This landscape is comprised of drainage basins with varying strata of Permian chert-bearing shale and limestone. The effect of long-term weathering and erosion has created a non-uniform topography, with relief of 20–50 m within watershed basins, consisting of flat, upland ridges with shallow soils, steep intermediate hillsides, and lowland with deep soils (Oviatt 1998). This landscape variability has a strong influence on surface soil moisture (Knapp et al. 1993; Briggs and Knapp 1995) and nutrient availability (Schimel et al. 1991; Turner et al. 1997), with ecological impacts on species niche-partitioning and water-use (Turner et al. 1995; Nippert and Knapp 2007), plant species richness and diversity (Gibson and Hulbert 1987; Turner et al. 1995; Hartnett et al. 1996), primary productivity (Abrams et al. 1986; Knapp et al. 1993; Briggs and Knapp 1995), watershed evapotranspiration (Brunsell et al. 2008), and the ecosystem carbon balance (Shonkwiler Arnold 2010).

Topographic gradients have indistinct breaks across the landscape, rendering classification of topographic positions rather subjective. In mesic grasslands, the simplest classification of topographic positions (upland/lowland) has been commonly used because land surface physiognomy is easily assessed and regions of uncertainty (e.g., hillsides, seeps, breaks) are avoided (Abrams et al. 1986; Turner et al. 1995; Turner et al. 1997). An alternate approach uses segmented transects spanning topographic gradients with measured edaphic characteristics along the transect (Schimel et al. 1991; Knapp et al. 1993). Transect approaches provide detailed information of land surface variability, but responses at a specific transect location are difficult to generalize to other transects or to other sites. Thus, the usefulness of simple physiognomic–topographic classification may be appropriate for plant growth parameters with minimal landscape variability, but it is unclear how much

detail of physical land-surface heterogeneity in grasslands is required to compare growth responses across broad scales spanning the individual plant to the landscape.

The goal for this research was to identify the sources of variability in aboveground plant growth and carbon flux in a tallgrass prairie as a function of landscape topography. Using a transect spanning a topographic gradient (from upland to lowland) between two eddy flux towers, we predicted that (1) the magnitude of growth and flux responses will vary significantly from lowland to upland sites, with the highest productivity in the lowlands, (2) the patterns of seasonal growth and carbon flux will be similar across topographic gradients, and (3) including topographic position classifications into model predictions of landscape biomass will capture the range of variability present and constrain landscape estimates of aboveground biomass.

Materials and methods

Site description

This research was conducted in 2008 and 2009 at the Konza Prairie Biological Station (KPBS), a 3,487-ha native tallgrass prairie located in northeastern Kansas, USA (39°05'N, 96°35'W). This region of the central Great Plains is characterized by a mid-continental climate consisting of cool, dry winters and warm, wet summers with high climatic variability in both temperature and precipitation within and between years (Borchert 1950; Hayden 1998). Long-term (30 years) average annual precipitation at KPBS is 844 mm, 75% of which occurs during the growing season (April–September). Total precipitation in 2008 and 2009 was above-average (891 and 949 mm, respectively). The long-term mean daily air temperature is 13°C with mean January and July temperatures ranging between –9 to 3°C and 20 to 33°C, respectively. The mean daily air temperature in 2008 and 2009 was 11.7 and 11.9°C, respectively. Aboveground productivity on KPBS is dominated by a few species of C₄ grasses, while a diverse assemblage of C₃ herbaceous species (>500 species) co-occurs within this matrix (Freeman and Hulbert 1985; Towne 2002).

This research was performed on a 40.4-ha watershed, which has not been grazed for >40 years and has been burned annually in April since 1981. The long-term mean aboveground net primary productivity for this watershed (1984–2008) varies between upland and lowland locations (upland: $\bar{x} = 337 \text{ g m}^{-2}$, SE = 21; lowland: $\bar{x} = 514 \text{ g m}^{-2}$, SE = 33). Soil depth varies by location with thin, rocky upland soils characteristic of the surficial Florence limestone bedrock (<0.5 m), while lowland soils are silty-clay loams (Tully soils) and can be relatively deep (>2 m) (Schimel et al. 1991; Ransom et al. 1998).

Flux and sensor measurements

Two eddy covariance towers were in operation on this watershed in 2008, positioned in upland and lowland locations, 340 m apart. The upland tower has operated continuously at this location since 1996 as part of an ongoing Long-Term Ecological Research project, while the lowland tower was deployed at this site from 2006 to 08. In 2009, only the upland tower was present. Net carbon exchange and water vapor flux were measured by eddy covariance using a triaxial sonic anemometer (CSAT-3; Campbell scientific, Logan, UT, USA) and an open-path gas analyzer (LI-7500; Li-Cor, Lincoln, NE, USA). The eddy flux equipment is positioned 3 m above the surface and sampled using a Campbell CR1000 datalogger. Velocities, gas concentrations, and virtual temperatures were sampled at 20 Hz. Access to streamwise data allows spectral correction using low pass filtering or analytical methods (Massman and Lee 2002), including corrections for sensor separation and volume averaging. Coordinate rotations were performed using the planer fit method (Paw U et al. 2000). Other corrections, such as the adjustment for simultaneous fluxes of heat and water vapor (Webb et al. 1980), were performed following the approach described by Ham and Heilman (2003). Data from the tower sites were processed using the EdiRe software package (version 1.4.3.1167; R. Clement, University of Edinburgh, UK). Missing data (due to equipment problems or inclement weather) were gap-filled when necessary using a moving diurnal mean (Falge et al. 2001).

A 457-m transect with 10 2×2 -m plots spaced at approximately 50-m intervals was established across the topographic gradient in May 2008. Plot 1 was in an upland position 48 m south of the upland eddy covariance tower, while the lowland tower was located between plots 6 and 7. Vertical relief along the transect was 22 m, but most of this change occurred between plots 4–7 (10 m) and 8–9 (5 m). In general, the aspect at each plot was approximately 240° , except plot 4 (157°). Soil depth varied along the transect, and plot 5 was located in a hillside seep (Table 1). The microclimate of each plot was characterized during the growing season (April–October) by measuring soil moisture at 10 cm (Hydraprobe II; Stevens Water Monitoring Systems, Portland, OR, USA), wind speed (3-cup anemometer; Gill Instruments, Lymington, UK), air temperature (100 K thermistor; Betatherm, Hampton, VA, USA) and relative humidity (HM1500; Humirel, Hampton, VA, USA) enclosed in a radiation shield (41003; RM Young, Traverse City, MI, USA). Measured relative humidity and air temperature were used to calculate the vapor pressure deficit (VPD) for each plot. All sensors were sampled every 10 s using CR10X dataloggers at each plot (Campbell Scientific, Logan, UT, USA) and 30-in averages were recorded.

Table 1 Five candidate models classifying the 10-plot transect into subjective topographic positions

Plot	Soil depth (m)	Classifications of topographic position				
		Model 1	Model 2	Model 3	Model 4	Model 5
1	0.8	Upland	Upland	Upland	Upland	Upland
2	0.8	Upland	Upland	Upland	Upland	Upland
3	0.2	Upland	Upland	Break	Break	Break
4	0.1	Upland	Upland	Break	Break	Break
5	>1	Lowland	Slope	Slope	Slope	Seep
6	0.4	Lowland	Slope	Slope	Break	Break
7	>1	Lowland	Slope	Slope	Slope	Slope
8	>1	Lowland	Slope	Slope	Slope	Slope
9	>1	Lowland	Lowland	Lowland	Lowland	Lowland
10	>1	Lowland	Lowland	Lowland	Lowland	Lowland

Plant growth measurements

We identified a total of 29 herbaceous species in plots along the entire transect, but most were patchily distributed. Four perennial C_4 grass species were present at each plot: *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*. Because this watershed is burned every spring, no litter from prior growing seasons or woody plants was present. To assess temporal dynamics and spatial patterns of plant growth at multiple scales over the growing season, we measured changes in maximum height of the four most common C_4 grass species, canopy development, and end-of-season aboveground biomass. In 2008, we recorded changes in the maximum height of the 4 main C_4 grasses by plot to the nearest centimeter every 2 weeks from June to October. In 2009, we identified 3 replicate plants/plot for each of the 4 grass species and measured the height of these individuals in bi-weekly intervals over the growing season. Canopy development was measured by calculating the leaf area index (LAI) at each plot (LAI-2000; Li-COR). LAI was estimated every 2 weeks using 5 below-canopy readings taken at fixed locations (1/plot quadrant and the plot center). In early October, above-ground biomass from the entire plot (4 m^2) was clipped at ground level and sorted by C_4 grass-vegetative, C_4 grass-flowering culm and C_3 forbs. Biomass was dried for 72 h at 60°C and weighed to the nearest 0.1 g.

Topographic position classification

To aggregate plots with similar responses along the transect, we created five candidate classification models based on measured physiognomic and edaphic conditions (Table 1). Classification models varied by the number of topographic position descriptions included. Model 1 was

the simplest, with plots grouped according to the inherent physiognomic break (upland/lowland). Model 2 organized plots according to changes in vertical relief. Models 3 and 4 classified plots according to changes in vertical relief and soil depth. Model 5 is the same as model 4, except plot 5 is recognized as a seep.

We used an information theoretic approach (Burnham and Anderson 2002) to identify the most parsimonious topographic classification model for each plant growth and biomass variable measured (Table 2). To assess differences in species height, canopy LAI, and end-of-season biomass by topographic position, data were analyzed using a mixed-effects model where topographic position, year, and sample date were fixed effects, and plot number and the model intercept were random effects. The height data in 2009 was treated as a repeated measure, so sample date was included as a random effect. All analyses were done using R (<http://www.r-project.org/>).

Geographically-weighted regression

To estimate landscape-level vegetation characteristics and biomass accumulation in this watershed, we classified the

Table 2 Model ΔAIC_c scores from partitioning the 10-plot transect into descriptive topographic positions identified by geomorphic complexity (Table 1)

Response variables	Number of topographic positions in model				
	Model 1	Model 2	Model 3	Model 4	Model 5
Biomass					
Grass-vegetative	0*	1.8*	4.5*	5.5*	6.3
Grass-culm	27.2*	25.1*	0*	8.3*	3.3*
Forb	0.5	2.5	0	2.6	2.6
Total biomass	16.7*	11.8*	0*	3.6*	5.6*
Culm/veg. ratio	23.2*	19.7*	0*	0.1*	0.4*
Mean culm wt.	21.3*	17.1*	0*	13.5*	15.5*
No. flowering culms	0*	2.9	2.9	2.3	4.6
Canopy density					
LAI	3.8*	2.1*	7.6*	0*	10.3
Mean species height					
<i>A. gerardii</i>	14.5	13	0*	6.6*	9.5*
<i>S. nutans</i>	4.3*	6.3*	2*	0*	3.3*
<i>S. scoparium</i>	0*	3.7	12.3	6.7	10.4
<i>P. virgatum</i>	6.3*	0*	2*	0.9*	4.4*
Mean growth rate					
<i>A. gerardii</i>	2*	0*	6.9*	3.7*	1.4*
<i>S. nutans</i>	0*	3.7	5.7	7.8	8.5
<i>S. scoparium</i>	0*	3.1	3.3	5.5	7.3
<i>P. virgatum</i>	3.9*	5.7*	0.1*	0*	3.8*

The most parsimonious topographic model for each response variable has a score of 0. ΔAIC_c scores of 1–2 also have considerable support

* Indicate a significant position effect ($p < 0.05$) when analyzed using mixed-effects ANOVA

landscape of the watershed into four topographic positions (upland, break, slope, lowland) or two topographic positions (upland, lowland) using a digital elevation model (DEM) to identify maximum differences in slope, aspect, and elevation. We used a geographically weighted regression (GWR) to extrapolate biomass values measured in the transect plots to the entire watershed areas using the GWR tool in ArcGIS 10.0 (ESRI). Using this relationship, we generated 250 randomly positioned points across the watershed, which were then used as the predictive locations in the GWR. We first calculated predicted biomass values for each of these locations based on our topographically-explicit model, and then used an inverse distance weighted (IDW) interpolation to create a raster surface of predicted biomass across the entire watershed. IDW interpolation has been previously shown to be an appropriate technique at similar scales (Chuanyan et al. 2005). Zonal statistics were used to quantify the end values by watershed location and slope position. Using the GWR, predicted biomass for the 10-plot transect was correlated to measured biomass from the transect averaged for 2008 and 2009 ($r = 0.75$). Thus, the final form of the GWR applied used a single explanatory variable (slope) to predict landscape biomass as a function of landscape location, which was defined by differences in soil depth, aspect and elevation using a DEM of this watershed. For further information on GWR theory and application, we refer the reader to Mennis (2006).

Results

Topographic position classification

The best topographic classification model (ΔAIC_c score = 0) for grouping similar transect plot responses into topographic positions varied by dependant variable (Table 2). Subsequently, the best topographic classification model for each dependant variable was used to present data (Figs. 1, 2, 3, 4 and 5). For example, grass-vegetative biomass was best described by the simplest 2-position model (upland/lowland), while the responses of total, grass-culm and forb biomass were best described by the 4-position model (Fig. 1). In general, the 4-position models (models 3 and 4) or the simplest 2-position model (model 1) were the most parsimonious for the majority of growth variables measured (Table 2).

Growth responses

End-of-season plant biomass was not significantly different between years ($p > 0.05$) but did vary significantly by topographic position (Fig. 1). Total aboveground biomass varied by position ($p = 0.0001$), with the most biomass in

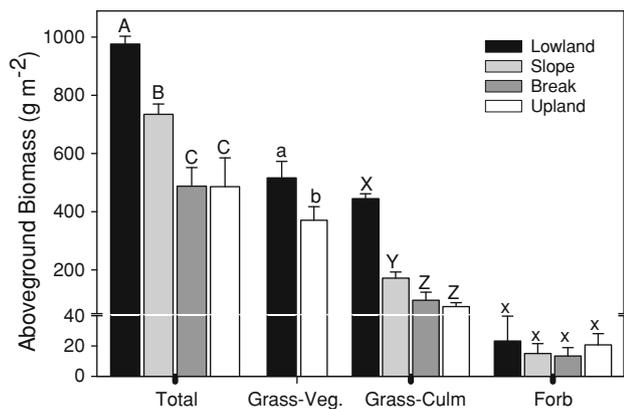


Fig. 1 Mean aboveground biomass across transect positions for 2008 and 2009. Biomass did not vary by year ($p > 0.05$). Each bar represents the mean response (± 1 SE) by transect position. Significant biomass differences among topographic positions are signified by varying letters using Tukey's HSD ($p < 0.05$). Varying topographic positions for each response variable reflects the best classification model identified in Table 2

the lowland position and the least in the upland and break positions (Fig. 1). Total biomass largely reflected grass biomass (vegetative and flowering culms) with minor contributions from forbs, which did not vary by topographic position ($p = 0.68$) (Fig. 1). The 2-position topographic model was the most parsimonious for vegetative grass biomass, which was significantly higher in the lowland than the upland ($p = 0.01$) (Table 2). Flowering-culm biomass varied significantly across the topographic gradient ($p = 0.0001$) with the highest mean biomass in the lowland (± 1 SE) ($444 \pm 40 \text{ g m}^{-2}$), intermediate biomass at slope positions ($171 \pm 27 \text{ g m}^{-2}$), and lowest biomass at the break/upland positions ($85 \pm 16 \text{ g m}^{-2}$), which were not different from one another (Fig. 1).

The production of flowering culms did not vary between years ($p > 0.05$), but did vary significantly by topographic position ($p < 0.01$) (Fig. 2). The density and mean weight of individual culms was highest in the lowland (Fig. 2).

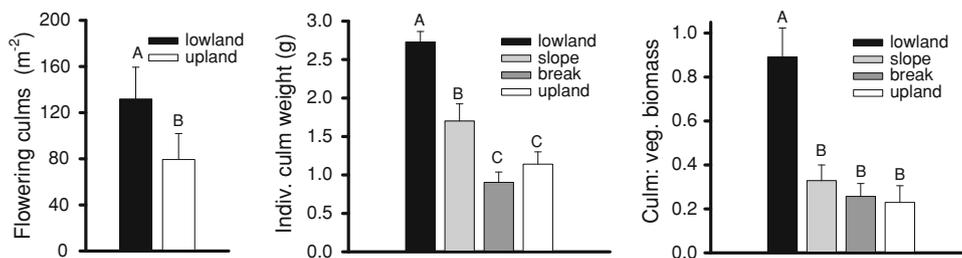


Fig. 2 Production of flowering culms by the C₄ grass species. The left panel shows the mean number of culms (± 1 SE) by transect position. The center panel shows the mean weight per culm (± 1 SE) by transect position. The right panel is the ratio of total biomass allocated to culm versus vegetative biomass by transect position. Data

are from 2008 and 2009. Significant differences among transect positions are indicated by varying letters using Tukey's HSD ($p < 0.05$). Varying topographic positions for each response variable reflects the best model identified in Table 2

Similarly, the amount of total plant production allocated to grass culms was nearly equal to grass vegetative biomass in the lowland (culm:grass biomass ratio of 89%), whereas culm biomass was only 35% of total production for the other three positions (Fig. 2). LAI did not vary significantly by year ($p = 0.08$), but did vary by day of year (DOY, $p < 0.0001$) and topographic position ($p < 0.0001$) (Fig. 3). The DOY \times topographic position interaction was not significant ($p = 0.48$), suggesting that, while the magnitude of canopy development varied across the topographic transect, temporal changes in LAI by position were generally consistent across transect positions. Results from both years revealed similar patterns by topographic position, with greater canopy development early in the growing season for lowland/slope plots relative to break/upland plots (Fig. 3). During 2008, LAI increased until late July, for the lowland/slope locations, while LAI in the break/upland locations continued to increase until late September. During 2009, all positions had similar increases in LAI until mid-August when values began to decrease as some leaves senesced. Despite the varying trajectories of canopy development during both years, the final LAI values recorded in late September were similar at all positions (Fig. 3).

The maximum height of individual C₄ grass species in 2008 varied by day of year (DOY \times species, $p < 0.0001$) and topographic position (DOY \times topographic position, $p = 0.009$) (Fig. 4). For each grass species, maximum plant height did not vary by topographic position until flowering culms were produced, the timing of which varied by species (Fig. 4). For example, the maximum height of *A. gerardii* doubled between mid- and late July as culms were produced (Fig. 4). Following culm production, maximum height varied predictably along the transect with the greatest heights in the lowland and lowest in the upland/break positions. Spatial patterns of *S. nutans* height were similar to *A. gerardii*, except that flowering occurred a month later (mid-August) and maximum heights at each

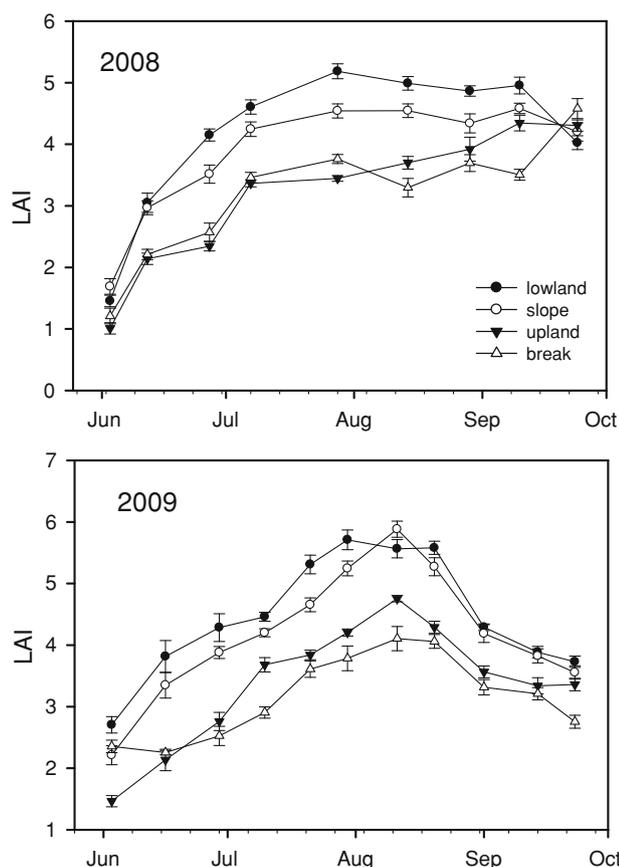


Fig. 3 Mean leaf area index (LAI) (± 1 SE) from June to October 2008 and 2009

transect position continued to increase until late September (Fig. 4). The heights of *S. scoparium* continued to increase until late September and maximum heights did not vary by transect position before or after the production of culms (mid-August) (Fig. 4). *P. virgatum* had similar heights at each transect position until early July when flowering was initiated, after which heights sorted by transect positions similar to responses noted for *A. gerardii* and *S. nutans* (Fig. 4).

In 2009, the heights of the same three individual tillers of each species in each plot were recorded bi-weekly across the growing season to quantify height growth rates (change in height between measurement intervals). The height growth rate of individual species varied by topographic position, and there were significant DOY \times species ($p < 0.0001$) and DOY \times topographic position interactions ($p = 0.0002$) (Fig. 5). For *A. gerardii*, there was little effect of topographic position for most of the growing season with a relatively consistent height growth rate (~ 0.5 cm day $^{-1}$). *P. virgatum* had the greatest height growth rates in late June for all positions, with declining rates across the rest of the growing season (Fig. 5). *S. scoparium* in the lowland had the greatest height growth

rates until late July, when upland plots had higher rates until mid-September. Rates of height growth for *S. nutans* were constant across the growing season, and were consistently higher in lowland relative to upland plots (Fig. 5). None of marked individuals we measured in 2009 produced flowering culms, despite flowering by other individuals of these species in other regions of the 4 m $^{-2}$ plots.

Flux and sensor measurements

The rate of cumulative carbon flux during the growing season (April–September) was comparable between upland and lowland positions, but the lowland tower had greater cumulative carbon gain by DOY 272 in 2008 (465 g m $^{-2}$) compared to the upland tower (401 g m $^{-2}$) (Fig. 6). Temporal patterns of carbon flux at the upland tower were similar for both years, but 2009 had greater cumulative respiration (95 g m $^{-2}$) in the non-growing season (DOY 127) and greater cumulative carbon assimilation during the growing season (451 g m $^{-2}$ by DOY 272) (Fig. 6).

The environmental sensor data along the transect varied over the course of the growing season in 2009, with the largest differences among topographic position recorded for volumetric water content at 10 cm depth (Figs. S1 and S2). For T_{air} , VPD, and wind speed, differences between topographic positions were more subtle than water content, but in general, the upland and break positions had higher values than either slope or lowland positions (Figs. S1 and S2).

Spatial predictions of landscape biomass

Pairing a digital elevation model with geographically-weighted regression (GWR), landscape biomass was estimated for the entire watershed, using a 2-position topographic classification (upland/lowland; Fig. 7a) and a 4-position topographic classification (Fig. 7b). Both GWR models (Fig. 7a, b) explained a considerable amount of the variance in landscape biomass ($r^2 = 0.83$ for the 2-position classification and $r^2 = 0.73$ for the 4-position classification), but the 4-position topographic classification of this landscape provided the best fit to the observed data when the models were compared ($AIC_c = 132.8$ vs. 197.9 for the 4-position classification vs. 2-position classification, respectively). Estimates of mean aboveground biomass varied by $\sim 5\%$ between the 2-position and 4-position models (698.48 ± 156.98 vs. 652.81 g m $^{-2} \pm 195.73$). However, the range of predicted biomass was constrained for the 2-position model, as the minimum versus maximum predicted values had complete overlap for upland and lowlands positions (Table 3). In comparison, the absolute range of predicted values using the 4-position model was highly variable (212–971 g m $^{-2}$; Table 3), but similar to

Fig. 4 Changes in mean maximum height (± 1 SE) from June to October 2008 for the most abundant perennial C₄ grass species. Organization of species \times topographic position reflects the best model identified in Table 2. Arrows indicate the date when flowering culms were first identified

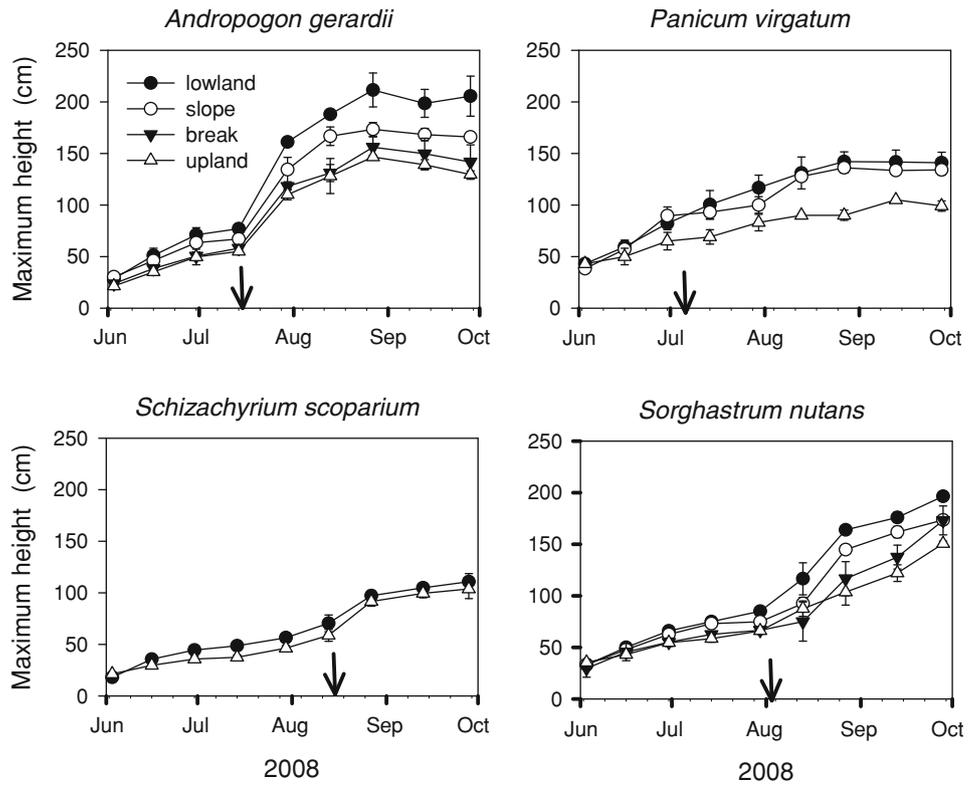
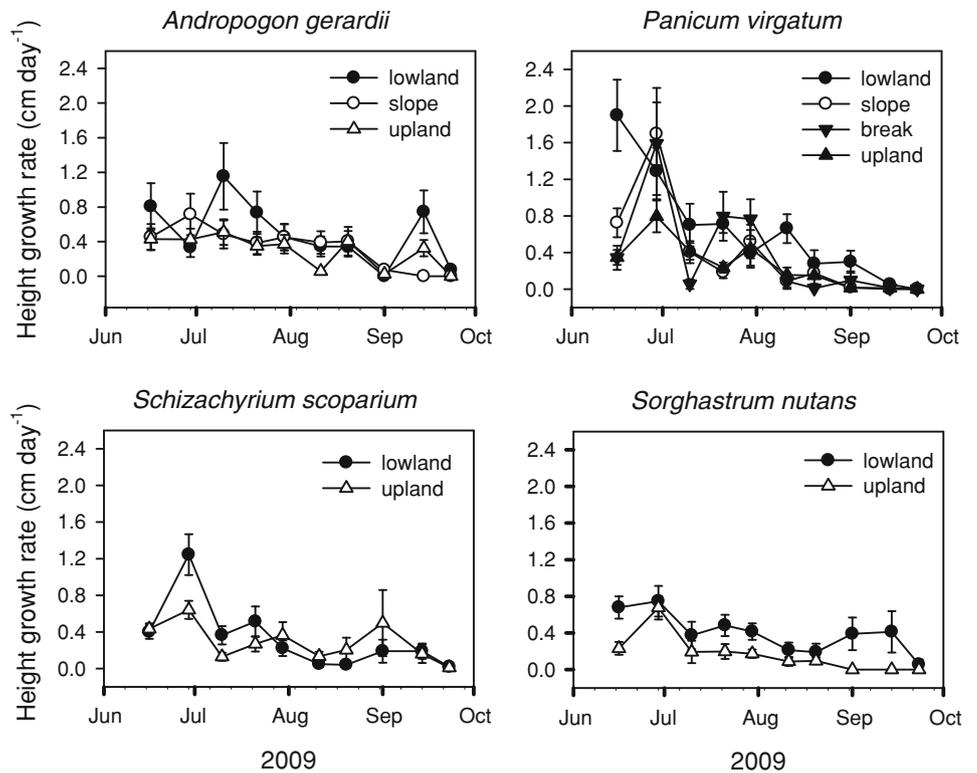


Fig. 5 Changes in the mean height growth rate (± 1 SE) from June to October 2009 for four perennial C₄ grass species. Growth rates reflect changes in height since previous measurement on the same individual ($n = 3$ per species per plot). Organization of species \times topographic position reflects the best model identified in Table 2



the range of measured biomass values during 2008–2009 (242–1,027 g m⁻²). Using the 4-position model, the total watershed area classified within each topographic position

(upland, break, slope, lowland) was similar (7.5–11.5 ha) (Table 3), yet predicted biomass for the combined upland and slope positions accounted for only 33.4% of the total

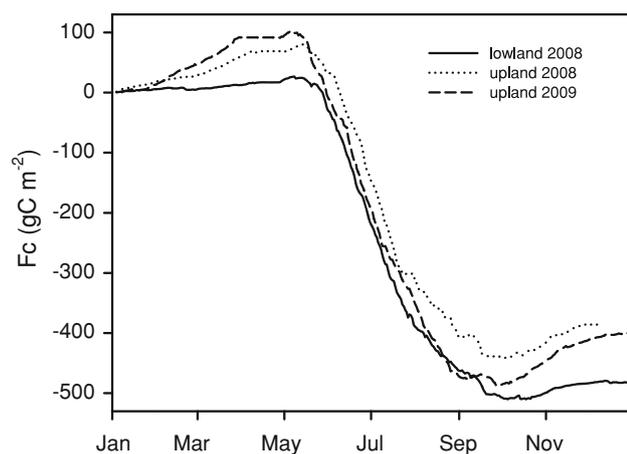


Fig. 6 Cumulative net carbon exchange measured at the upland eddy flux tower (2008 and 2009) and the lowland tower (2008 only). The data shown do not consider carbon losses to fire, which occur in early April and constitute a large portion of the annual net carbon exchange

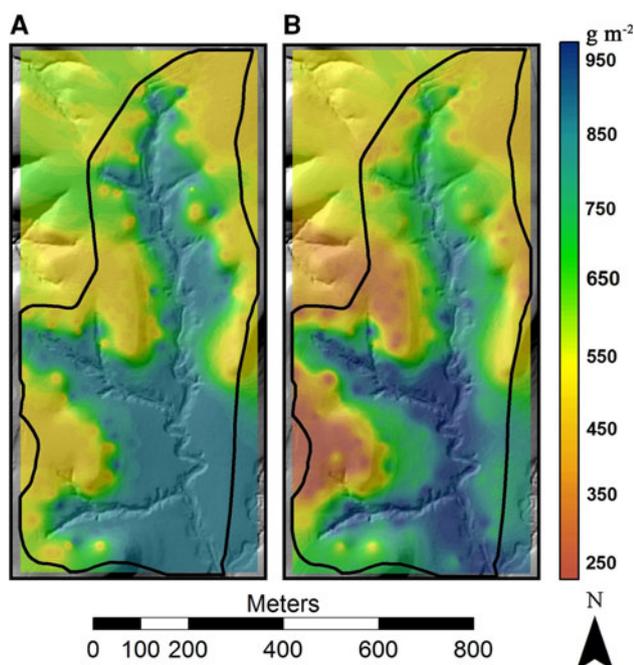


Fig. 7 Predicted landscape biomass (g m^{-2}) using a digital elevation model parameterized with measured biomass from the transect during 2008 and 2009. **a** Predictions using a 2-position topographic model, and **b** predictions using a 4-position topographic model

watershed biomass (Table 3; Fig. 7). Thus, our model estimates indicate that nearly two-thirds of the total accumulated biomass on this watershed is produced in the slope and lowland topographic positions. If total biomass for this 40.4-ha watershed was estimated using only the minimum or the maximum predictions (Table 3), then significant under- (86 t) or over-estimation (393 t) would occur compared to the estimate of total biomass for the watershed using the 4-position topographically-based model (264 t).

Discussion

Nearly 20 years has passed since the First ISLSCP Field Experiments (FIFE) data were reported, linking empirically-measured fluxes to remotely-sensed imagery in mesic grassland (Schimel et al. 1991; Verma et al. 1992; Knapp et al. 1993; Sellers et al. 1995). FIFE provided the impetus to link leaf-level to canopy CO_2 and water flux across a wide range of spatial scales, including the leaf (Knapp 1985; Polley et al. 1992; Turner et al. 1995; Nippert et al. 2007), landscape (100+ m: Ham and Knapp 1998; Shonkwiler Arnold 2010; Bremer and Ham 2010), ecosystem (1,000+ m: Brunsell et al. 2008), and regional model simulations (Seastedt et al. 1994). However, a detailed assessment of variability in carbon flux at sub-watershed scales (20–50 m) remains incomplete (Bartha et al. 1995). The results of this study address questions focused on scaling estimates of plant growth and biomass, including at which scales can we extrapolate growth (from individual to landscape) in mesic grasslands and how should we classify topographic gradients and quantify the inherent variability across these gradients to best reflect the local growth responses and fluxes that underlie large-scale patterns?

Total biomass measured at the end of the growing season varied by topographic position, with the most production in the lowland and the least in the break/upland positions (Fig. 1). Biomass responses by topographic position were consistent with other growth responses including LAI (Fig. 3), maximum height (Fig. 4), and cumulative net carbon exchange (Fig. 6). However, the primary constituents of total biomass (grass-vegetative, grass-culm) varied by topography. Vegetative grass biomass was greater in lowland compared to upland, consistent with long-term data on aboveground net primary productivity (ANPP) reported for upland/lowland positions at this site (Briggs and Knapp 1995). Mean flowering culm biomass for 2008–2009 was over 5 times greater in lowland than break/upland and 2.5 times greater than plots in the topographic slope. These differences in lowland flowering represented a significant fraction of the total biomass produced ($\sim 50\%$; Fig. 2). Greater total biomass of flowering culms in lowland reflects both greater stem density and weight per stem (Fig. 2) which may be driven by differences in species abundance by topographic position. Previously, Craine et al. (2010) used long-term KPBS data and showed that *S. nutans* (1984–2008) and *A. gerardii* (1999–2008) had higher culm biomass in lowlands versus uplands, but *S. scoparium* culm biomass did not vary by topography. Thus, differential flowering responses by species \times topographic position may be a significant driver of spatial patterns in aboveground productivity and flowering-culm biomass constitutes a significant portion of total productivity in this ecosystem.

Table 3 Predicted above-ground biomass for watershed 1D using a 2-position model (upland/lowland) or a 4-position topographic classification (upland/break/slope/lowland)

	Total area (ha)	Predicted biomass (g m^{-2})					Total biomass (T) per position
		Min	Max	Range	Mean	SD	
2-Position model							
Upland	18.27	469.88	869.68	399.50	543.43	84.02	99.28
Lowland	22.13	469.88	869.45	399.57	810.17	83.51	179.29
Whole watershed	40.40	469.88	869.45	399.57	689.48	156.98	278.55
4-Position model							
Upland	10.77	212.48	735.10	522.63	450.73	116.18	48.54
Break	7.50	222.32	950.95	728.62	527.31	98.85	39.54
Slope	10.59	285.93	965.63	679.70	719.31	103.09	76.15
Lowland	11.54	402.48	971.45	568.97	862.06	95.89	99.52
Whole watershed	40.40	212.48	971.44	758.97	652.81	195.73	264.10

Data correspond with Fig. 7

When the growth responses of the four dominant C_4 grass species were compared, the patterns, timing, and magnitude of growth varied (Figs. 4 and 5), despite the perceived similarity of these species as ‘functional equivalents’ (Nippert et al. 2009). Inter- and intra-specific differences in maximum height exhibited minimal variability by topographic position, until flowering culms were produced (arrows in Fig. 4), after which persistent trends in height with topographic position (tallest in the lowland, shortest in the break/upland) were evident. Minimal differences in cumulative grass height by species or topographic position measured in 2008 were supported by the height growth rate data from 2009 (Fig. 5). The individuals selected in May 2009 did not flower, and thus changes in height growth rate reflect changes in grass-vegetative responses only. These responses were largely driven by 2 species, as the largest differences in maximum height between lowland and break/upland occur for *A. gerardii* and *S. nutans*. This height data reinforced varying grass-vegetative and grass-culm biomass results (Fig. 1), suggesting grass-vegetative responses are relatively similar on the landscape, at least during years with above-average precipitation. Rather, differences in flowering culm production along topographic gradients are the likely drivers of differences in measured biomass and carbon flux in this annually-burned tallgrass prairie.

Despite the differences in measured growth responses by topographic position, these results have limited utility if landscape-level biomass accumulation (or C flux) can be reliably estimated using a static estimate of landscape biomass without incorporating landscape heterogeneity into predictions. As an example, soil respiration was previously shown to vary significantly in forests according to topographic variability and microclimate (temperature, soil

moisture) (Webster et al. 2008; Martin and Bolstad 2009). Thus, inference of modeled soil respiration was reduced if model resolution failed to incorporate the inherent land surface heterogeneity (Li et al. 2008). Our results in this tallgrass prairie also illustrate the utility of quantifying the effect of topographic variability for estimates of landscape biomass (Fig. 7). A simple 2-position landscape model (upland or lowland) had similar predictions of mean biomass compared to the 4-position model, but predictions from the 2-position model were dichotomous (approximately 500 g m^{-2} in upland regions or 850 g m^{-2} in lowland regions) and did not reflect the inherent spatial gradients. Thus, greater classification of topography provided greater resolution in predictions of landscape biomass. If landscape heterogeneity was ignored, estimates of landscape biomass had sizeable errors. For example, had biomass been estimated using a minimum upland position value (212 g m^{-2}) or the maximum lowland value (971 g m^{-2}), variability in predictions of landscape biomass would exceed 300 t for this 40.4 ha watershed (Table 3; Fig. 7).

The two co-located eddy covariance towers (340 m) in 2008 provided a rare opportunity to compare our plot-based measurements of plant growth to whole-ecosystem estimates of net C exchange and assess the impact of microclimatic spatial variability over short distances within a single watershed or management unit. To our knowledge, few studies exist where multiple towers are used in close proximity within the same ecosystem to identify the impacts of within landscape heterogeneity as drivers of variability in flux measurements (but see Hollinger et al. 2004; Richardson and Hollinger 2005). Previously, the annual net carbon exchange for annually-burned tallgrass prairie has been reported as zero (Suyker and Verma 2001),

but daily NEE is highly variable ($\pm 25 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$) depending on season, preceding environmental conditions, and land management (Bremer and Ham 2010). In this study, the significant spatial variation of carbon fluxes between upland and lowland towers in 2008 confirms that the processes underlying carbon exchange in the footprints (source areas) of these towers vary, even at this short distance (Brunsell et al. 2010). This spatial variation in carbon flux is most likely due to a combination of thermal and hydrologic differences that impact plant growth and physiology along the topographic gradient, rather than differences in plant species assemblages. Upland soils with more direct exposure are generally warmer than lowland soils, and lowland soils are generally wetter than upland soils following spring burning in April/May (Fig. S1). This spatial variation illustrates the importance of tower location for monitoring annual carbon flux, e.g., the so-called 'location bias' (Schmid and Lloyd 1999) as well as the care that needs to be taken when upscaling tower data to larger spatial scales (Li et al. 2008).

Differences in the measured flux tower data (upland vs. lowland) were similar to model predictions of landscape biomass by topographic position (Fig. 7b). For example, lowland cumulative carbon gain in 2008 was 465 g m^{-2} (Fig. 6). Scaling this value to the total area identified as lowland and slope topographic positions (22.13 ha; Table 3) yields an estimated net CO_2 gain of 102.9 t for the slope and lowland positions during the growing season. This value is comparable to predicted biomass for these topographic positions (175 t, 4-position model; Table 3), considering that dry plant biomass in this grassland is approximately 41–43% carbon (Bremer and Ham 2010) and these estimates of biomass do not consider carbon allocated for root turnover belowground. Using predicted biomass for the upland and break positions (18.3 ha), cumulative net carbon exchange in 2008 ($401 \text{ g m}^{-2}/73.3 \text{ t}$) was also comparable to predicted biomass for these topographic positions (88.1 t). The difference in aboveground growth per net CO_2 gain is less for the upland and break positions compared to the lowland and slope positions, which may reflect proportionally greater allocation belowground than aboveground in uplands compared to lowland (Nippert et al., unpublished data).

These results quantify the error associated with static predictions of landscape biomass, but it remains to be determined how interannual differences in annual precipitation impact growth across the landscape and if growth responses by topographic position have differential sensitivity to high and low rainfall years. Previously, variability in soil moisture was identified as the most likely driver of differences in carbon flux/biomass along topographic gradients at KPBS (Knapp et al. 1993; Briggs and Knapp 1995). Indeed, the sensor data associated with this transect showed

the greatest differences in surface soil moisture, but air temperature, VPD, and wind speed also varied as a function of landscape position (Figs. S1 and S2). Distinct soil moisture–growth responses by topographic position are typically greatest during periods of water limitation. Yet these data show topographic differences in the magnitude of growth/C flux during 2 years when surface soil water was available at all topographic positions during the growing season (Fig. S1a). What besides water may be contributing to these responses? Soil N mineralization can vary by topographic position, with greater availability in upland than lowland (Turner et al. 1997). These differences were previously related to soil texture differences and amounts of potentially mineralizable N by topographic position (Turner et al. 1997). Foliar N is correlated with biomass at this site (Schimel et al. 1991); thereby increased N availability during a wet year may have had a greater impact on CO_2 uptake and growth in lowland versus upland locations. Additionally, it is possible that intra-specific genotype differences along topographic gradients impact growth/C flux independent of productivity limitations set by water and N availability alone.

These results highlight the importance of measuring growth associated with small-scale landscape variability. Grasslands are commonly viewed as a physically homogeneous landscape, yet these results suggest point measurements or limited spatial sampling would inadequately describe within-landscape growth dynamics. The source of topographic differences in biomass and LAI were largely species-specific responses (Figs. 4 and 5), highlighting the role of dominant species and flowering stem growth as key components of ecosystem production. When growth responses were grouped by multiple topographic positions, accounting for integrated topographic complexity (slope, elevation, soil characteristics), estimates of landscape biomass more closely resembled measured biomass, underscoring the utility to incorporate watershed complexity on scales of 20–50 m into landscape predictions of growth in mesic grasslands.

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