

# Changes in grassland canopy structure across a precipitation gradient

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**Abstract.** In temperate grasslands, the relative importance of above-ground competition for light compared to below-ground competition for water and nutrients is hypothesized to increase with increasing precipitation. Thus, competition for light is likely to exert an increasing influence on canopy structure and species composition as precipitation increases. We quantified canopy structure, light availability and changes in species composition at seven sites across the central grassland region of the United States to determine how these properties change across a precipitation gradient. Across the region, there was a disproportionate increase in leaf area and canopy height with increasing precipitation, indicating that plants become taller and leafier across the gradient. Leaf area index increased by a factor of 12 across the gradient while above-ground net primary productivity increased by a factor of only 5.5. As precipitation increased, there was decreased light availability at the soil surface, increased seasonal variability in light transmission, increased biomass and leaf area at higher canopy layers and an increased proportion of tall-statured species. These observed changes in canopy structure support the prediction that competition for light increases in importance with increasing precipitation.

**Keywords:** Community structure; Functional type; Leaf area index; Light interception; Mixed-grass prairie; Net primary productivity; Short-grass steppe; Tallgrass prairie.

**Nomenclature:** Barkley (1986).

**Abbreviations:** ANPP = Above-ground net primary productivity; CO = Colorado; LAI = Leaf area index; MAP = Mean annual precipitation; NE = Nebraska; NMP = Northern mixed prairie; PAR = Photosynthetically active radiation; SGS = Short-grass steppe; TGP = Tallgrass prairie.

## Introduction

Temperate grasslands are systems structured primarily by below-ground competition for water or nutrients (Burke et al. 1998). Light availability, however, can be a co-limiting resource in subhumid grasslands (Knapp 1984). For example, low light availability at the soil surface can decrease tillering rates and seedling survival, and thus influence productivity and species composition (Eek & Zobel 1997; Jurik & Pleasants 1990; Deregibus et al. 1985).

We hypothesize that in temperate grasslands the relative importance of above-ground competition for light compared to below-ground competition for water and nutrients increases with increasing precipitation and productivity (Burke et al. 1998; Lauenroth & Coffin 1992; Tilman 1988; Wilson & Tilman 1991; Wilson & Tilman 1993). In sites with low precipitation and little above-ground biomass and leaf area, availability of below-ground resources is likely to control productivity and successional dynamics (Hyder et al. 1975; Lauenroth et al. 1978). New individuals will become established only when a 'below-ground gap' makes soil resources available (Coffin & Lauenroth 1990). As above-ground biomass and leaf area increase with increasing productivity, above-ground gaps that make light available are predicted to become increasingly important for seedling regeneration (Lauenroth & Coffin 1992; Jurik & Pleasants 1990). Thus, as precipitation increases, competition for light is likely to become an increasingly important factor in determining canopy structure and species composition.

Positive relationships between above-ground net primary productivity (ANPP) and precipitation in temperate grasslands such as the central grassland region of the United States (Sala et al. 1988; Lane et al. 1998) and Siberian grasslands (Titlyanova et al. 1999) do not tell us how canopy structure changes with precipitation or whether these changes are proportional to increases in precipitation. For example, the same increase in ANPP

could result from increased basal cover of vegetation with no change in height, or from increased height with no change in basal cover. As precipitation increases, we expect that competition for light will lead to disproportionate increases in leaf area and canopy height. Plants would tend to be 'short and sparse' with a small amount of leaf area concentrated near the ground if there were no competition for light, and increasingly 'tall and leafy' with leaf area distributed throughout the canopy if there were significant competition for light.

The reciprocal interactions between canopy structure and light availability mean that these properties cannot be studied in a simple cause-and-effect relationship. Canopy structure affects light availability through the distribution of biomass and leaf area in space. At the same time, light availability through the plant canopy will influence competitive relationships between individuals and will, therefore, affect canopy height, biomass distribution by height and changes in species composition. Because of these complex relationships, information about canopy structure and light availability must be considered together to infer the importance of above-ground competition.

Our overall objective was to examine the reciprocal interactions between light availability and canopy structure across a precipitation gradient through the central grassland region of the United States, as a means to infer the importance of above-ground competition across this gradient. We compared seasonal patterns of light transmission with vertical distributions of biomass and leaf area at seven natural grassland sites. We also determined changes in maximum canopy height and species composition along the precipitation gradient. Finally, we examined the strength of the relationship between ANPP and variables such as leaf area index (LAI), maximum canopy height, and the proportion of biomass in different vertical layers.

## Methods

### *Site descriptions*

Canopy structure was measured at seven natural grassland sites located along a 660 km precipitation and productivity gradient through the central grassland region of the USA in 1994. Sites were selected to represent three grassland types which differ substantially in physiognomy: short-grass steppe, northern mixed prairie and tallgrass prairie (Sims 1988). The productivity gradient ( $74$  to  $406 \text{ g m}^{-2} \text{ yr}^{-1}$ ) corresponds to a strong gradient of increasing mean annual precipitation (MAP) from west to east ( $333$  -  $759 \text{ mm}$ ) (Fig. 1). Across this

precipitation gradient, mean annual temperature remained approximately constant ( $9$  -  $11 \text{ }^\circ\text{C}$ ). All sites experience a temperate continental climate, with similar seasonal patterns of temperature and precipitation. All sites were on loamy soils (mean constituents: 39% sand, 35% silt, 26% clay) as determined by particle size analysis (Lane et al. 1998).

Our assessment – based on species composition, soil profiles and conversations with site owners and managers – is that none of the sites had been ploughed in the last 150 yr. We could not, however, locate sites with identical management histories. At the time of the study, three sites (NMP-1, NMP-3, TGP) had been protected from cattle grazing for 25, 4 and 34 yr, respectively. The other four sites (SGS-1, SGS-2, SGS-3, NMP-2) were grazed by cattle at the time of the study. At these four sites, individual wire exclosures were used to protect each plot from grazing during the growing season over the course of the study. The exclosures were 1 m in diameter and constructed of a  $15 \text{ cm}^2$  wire mesh to have minimal effects on light, rainfall and temperature. Measurements were taken at least 25 cm away from all edges of the exclosure. The tallgrass site (TGP) was burned in 1991; none of the other sites experienced controlled burns.

At each site, canopy measurements were taken throughout the growing season on a total of five  $0.1\text{-m}^2$  ( $20 \text{ cm} \times 50 \text{ cm}$ ) plots that were randomly distributed over two 15 m-transects. The transects were separated by 10 m and established on an upland area with minimal slope.

### *Objective 1: Light availability and canopy structure*

Vertical profiles of photosynthetically active radiation (PAR) transmission through the plant canopy were measured at each plot four times during the growing season. Measurements took place between May 23 - June 1, June 27 - June 30, July 25 - July 29 and August 15 - August 21, 1994. All measurements were taken between 8:30 a.m. and 1:30 p.m. local solar time under stable light conditions to minimize shadows and allow better comparisons across sites and sampling periods.

PAR, defined as radiation within the 400-700 nm wavelengths, was measured with a Sunfleck Ceptometer consisting of 80 light sensors at 1-cm intervals along a metal probe (Decagon Devices, Pullman, WA). To avoid the edges of exclosures, only 40 cm of the probe was used for measurements. Each measurement represented the mean of five readings taken in a 30 second period.

For each of the five plots at a site, the Ceptometer probe was inserted into the center of the plant canopy at 2, 5, 10, 15 and 20 cm above the soil, and then

every 10 cm until reaching the top of the canopy. PAR transmission to a certain height was calculated as the PAR reading at that height divided by the mean of two incoming PAR readings taken immediately before and after the canopy measurements.

Above-ground biomass on each canopy measurement plot was harvested in vertical layers at the approximate time of peak standing crop (August 15-21, 1994) to obtain vertical profiles of biomass and leaf area. Vegetation within a 0.1-m<sup>2</sup> quadrat was clipped in the following vertical layers, measured from the soil surface: 0-5 cm, 5-10 cm, 10-15 cm, 15-20 cm and then every 10 cm until the top of the canopy. All plant material within the boundaries of the 0.1-m<sup>2</sup> quadrat was clipped, even when leaves within the quadrat were attached to a plant rooted outside of the quadrat. Consequently, forb biomass was present in higher layers but not in lower layers at some sites.

Live and current year's standing dead vegetation were grouped together as live biomass and separated from litter (prior year's dead vegetation). Biomass of graminoids (grasses plus members of the *Cyperaceae* family) was measured separately from forbs. No shrubs were present in the plots. Cacti and other succulents were excluded from the analysis because of the difficulty of measuring leaf area for these species. Following leaf area measurements (see below), biomass was dried at 55 °C for 1 week and weighed. For each vertical layer at each site, the mean of the five plots was treated as a single estimate of biomass for that layer.

Projected area was measured using a LiCor Portable Area Meter, Model LI-3000 (Lincoln, NE). Although all vegetative parts were included in the area measurements, we refer to the measurements as 'leaf area' for simplicity. Because leaves would sometimes overlap slightly during measurements, we measured the same material three times and used the median reading as the estimate of leaf area for the sample. All leaves were flattened before measurement. Non-flat leaves and stems were generally confined to the bottom 10 cm of the canopy. Consequently, leaf area for these layers may be underestimates of true leaf area since a correction for leaf shape or stem diameter was not applied.

Leaf area of the entire sample was measured for all forbs and for samples containing a small amount of graminoid biomass (ca. 2 g dry weight or less). For large graminoid samples, leaf area was measured on five subsamples (ca. 0.2 to 0.6 g dry weight each) selected randomly. We calculated specific leaf area (cm<sup>2</sup> area /g biomass) for graminoids in each canopy layer by dividing the leaf area and biomass measurements for each subsample and calculating mean values.

We estimated total leaf area for the large graminoid samples from a regression equation relating leaf area to biomass for a given layer in a given plot, forced through the origin.

LAI was calculated for each layer by dividing the total leaf area estimate for that layer by the area of the quadrat (0.1 m<sup>2</sup>). All above-ground plant parts were included in the calculation of LAI. This type of LAI has also been termed 'Foliage area index' (Warren Wilson 1959, 1965).

#### *Objective 2: Canopy height and species composition*

The maximum canopy height of each plot was recorded during the same four time periods that PAR measurements were taken. Maximum canopy height was defined as the highest point above-ground of any part of the vegetation within the plot, including flowering stalks.

Species composition at each site was determined from the list of identified species sampled in at least one of 15 plots (0.25 m<sup>2</sup>) clipped for ANPP measurements in 1994 (Lane et al. 1998). Unidentified plants accounted for less than 5% of total ANPP. For each species, we determined a standard mean height by calculating means of the minimum and maximum heights for the species listed in a standard regional flora (Barkley 1986). When a plant sample was identified to genus only, we calculated means from the smallest minimum height and the largest maximum height from the pool of species in that genus potentially present at the site according to species range maps (Anon. 1977). Mean height was used to classify species into three height classes: less than 30 cm, 30 - 70 cm and greater than 70 cm.

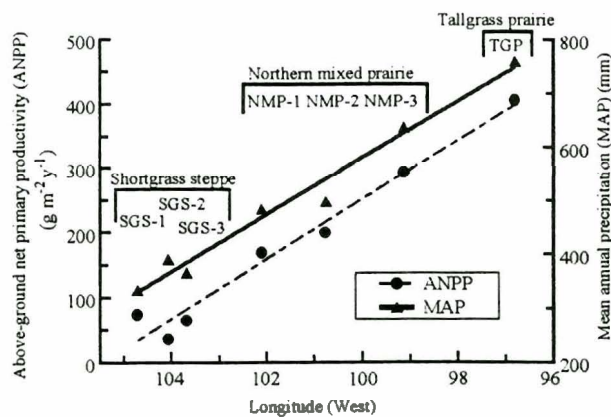
#### *Objective 3: ANPP and canopy structure*

ANPP at each site was measured at the time of peak standing crop in 1994 (Lane et al. 1998). The 15 plots clipped for ANPP estimates at each site were nearby but separate from the canopy measurement plots.

## **Results**

#### *Objective 1: Light availability and canopy structure*

At the three short-grass steppe sites, PAR transmission decreased slightly from the top to the bottom of the canopy but never fell below 92% of incoming PAR (Fig. 2a-c). For each layer at each site, PAR transmission differed by less than 5% across the growing season.

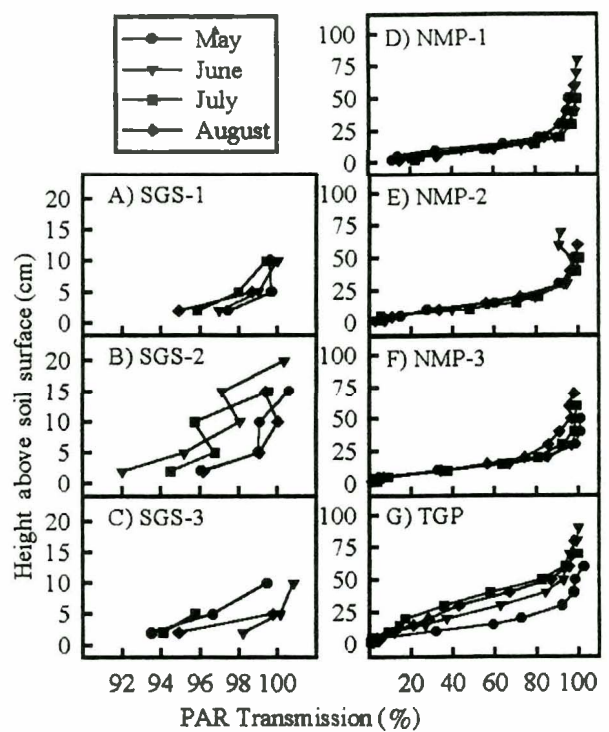


**Fig. 1.** Above-ground net primary productivity (ANPP) ( $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ ) for 1994 and mean annual precipitation (mm) for 1969–1993 of seven study sites, arranged along a longitudinal gradient. Site codes abbreviate vegetation types: SGS = Shortgrass steppe; NMP = Northern mixed prairie; TGP = Tallgrass prairie. Within a vegetation type, sites are numbered from west to east. All sites were located within  $1^\circ$  of  $41^\circ\text{N}$  latitude, in either Colorado or Nebraska, USA. Mean annual precipitation was calculated using data from the weather station closest to each field site (Anon. 1988-). ANPP was determined in a separate study by harvesting above-ground biomass at the time of peak standing crop (Lane et al. 1998).

PAR transmission at the northern mixed prairie sites differed substantially from PAR transmission at the short-grass steppe sites (Fig. 2d-f). At the northern mixed prairie sites, PAR transmission at 2 cm above the soil surface was between 0 and 22%. Transmission generally increased between 5 and 30 cm, and then levelled off above 30 cm where transmission remained above 90%. Although there were greater differences in transmission across the growing season at the northern mixed prairie sites compared to the short-grass steppe sites, seasonal patterns were not consistent across sites.

At the tallgrass prairie site, PAR transmission at 2 cm above the soil surface was between 0 and 5% (Fig. 2g). Transmission increased between 10 cm and 40–60 cm and then levelled off. Seasonal changes in transmission were most important at the tallgrass prairie site. For the layers between 10 cm and 40 cm, transmission in July was only 20%–60% of the transmission in May. Seasonal changes in transmission were minor for the lowest layers (2–5 cm), which remained covered by litter and for the highest layers (70–90 cm) which never fell below 94%.

At all sites, the greatest proportion of live above-ground biomass (graminoids plus forbs) was found in the lowest canopy layers (Fig. 3a-g). The 0–5 cm layer accounted for greater than 80% of total biomass at the short-grass steppe sites (Fig. 3a-c), but only 19%



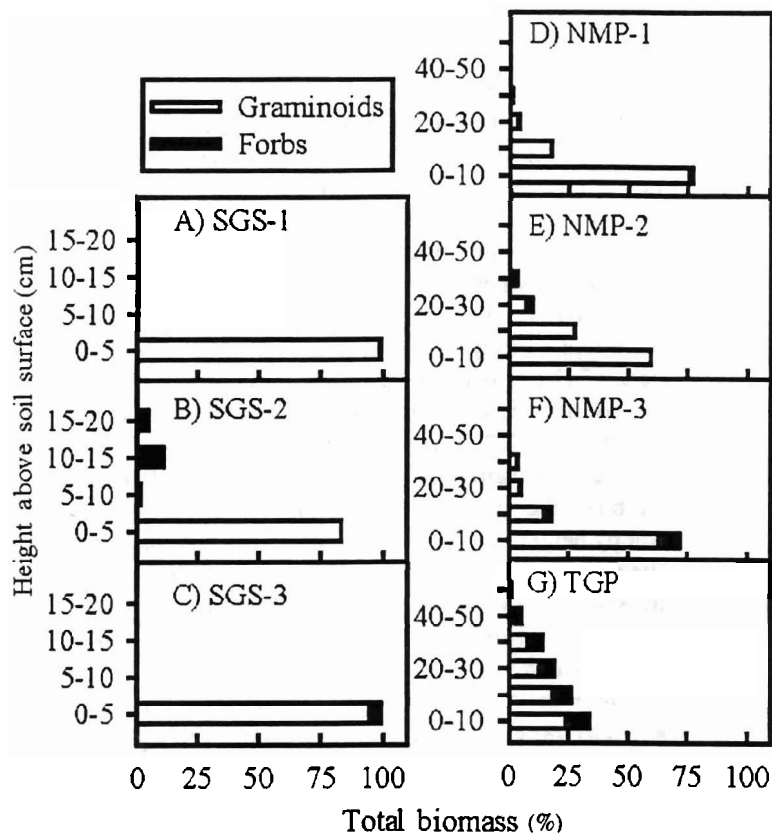
**Fig. 2.** Vertical profiles of the percent transmission of incoming photosynthetically active radiation (PAR) to different heights in the plant canopy. Each panel presents four sets of measurements taken during the 1994 growing season at each site. Note the difference in vertical scale between the shortgrass steppe (SGS) sites (a-c) and the northern mixed prairie (NMP) and tallgrass prairie (TGP) sites (d-g). Sites are labelled as in Fig. 1.

to 52% of total biomass at the northern mixed prairie and tallgrass sites (not shown). Similarly, the 0–10 cm layer accounted for 59% to 77% of total biomass at the northern mixed prairie sites, but only 34% of total biomass at the tallgrass prairie site (Fig. 3d-g).

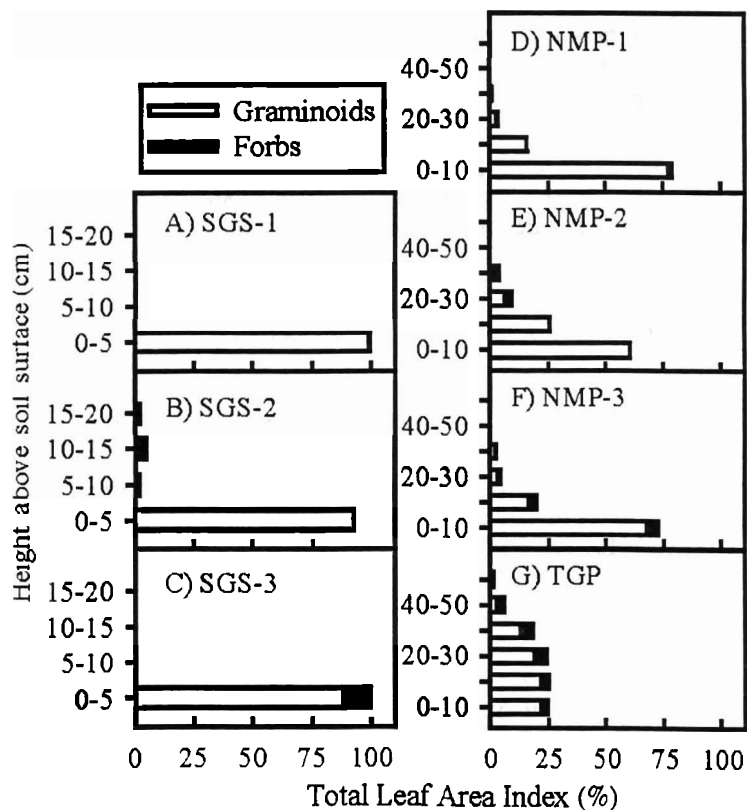
Profiles of graminoid biomass had the same concave shape as profiles of total biomass due to the large contribution of graminoids to total biomass (Fig. 3a-g). Profiles of forb biomass had a concave shape at the two wettest sites (NMP-3, TGP), but were highly variable at the other sites.

At all sites, except the tallgrass prairie site, the greatest proportion of total leaf area was found in the lowest canopy layer (Fig. 4a-g). The 0–5 cm layer contained 88% to 99% of total leaf area at the short-grass steppe sites (Fig. 4a-c), but only 12% to 56% of total leaf area at the northern mixed prairie and tallgrass sites (not shown). The tallgrass prairie site had the greatest amount of leaf area in the 10–20 cm layer (Fig. 4g) and had a more even distribution of leaf area across layers compared to the other sites.

**Fig. 3.** Vertical profiles of the percent of total above-ground biomass in layers of fixed height. Values for graminoids and forbs are presented separately. Each panel presents results for one site. Note the difference in vertical scale between the short-grass steppe (SGS) sites (a-c) and the northern mixed prairie (NMP) and tallgrass prairie (TGP) sites (d-g). Sites are labelled as in Fig. 1.



**Fig. 4.** Vertical profiles of the percent of total leaf area index in layers of fixed height. Values for graminoids and forbs are presented separately. Each panel presents results for one site. Note the difference in vertical scale between the short-grass steppe (SGS) sites (a-c) and the northern mixed prairie (NMP) and tallgrass prairie (TGP) sites (d-g). Sites are labelled as in Fig. 1.



### Objective 2: Canopy height and species composition

The largest changes in canopy height occurred between vegetation types (Fig. 5). Between the wettest short-grass steppe site (SGS-3) and the driest northern mixed prairie site (NMP-1), maximum canopy height increased from a seasonal mean of 6 cm to a seasonal mean of 51 cm. This eight-fold increase in height corresponded to a doubling of ANPP and a 32% increase in MAP. Between the wettest northern mixed prairie site (NMP-3) and the tallgrass prairie site (TGP), maximum canopy height increased from a seasonal mean of 47 cm to a seasonal mean of 70 cm. This 49% increase in height corresponded to a 40% increase in ANPP and a 20% increase in MAP.

The three wettest sites (NMP-2, NMP-3, and TGP) exhibited the greatest absolute change in maximum canopy height from May to August (> 10 cm) (Fig. 5). The relative change in canopy height during the growing season was greater at sites NMP-2 and NMP-3 (43% and 78%, respectively) than at the tallgrass prairie site, which exhibited a relative change of only 30%. The three short-grass sites did not differ in maximum height by more than 3 cm at any one date. At sites SGS-1 and SGS-3, this small absolute change in height (< 3 cm) corresponded to a 30% increase in height between the minimum and maximum measurements.

Across the productivity gradient, species composition shifted from predominantly short species to predominantly tall species (Table 1). Ten out of 14 species at the short-grass steppe sites were classified as short-statured (< 30 cm), compared to one of 18 species at the tallgrass prairie site. In contrast, eight of 18 species at the tallgrass prairie site were classified as tall-statured (> 70 cm), compared to two of 14 species at the short-grass steppe sites. Species of intermediate stature (30 - 70 cm) made up 16 of 26 species at the northern mixed prairie sites.

### Objective 3: ANPP and canopy structure

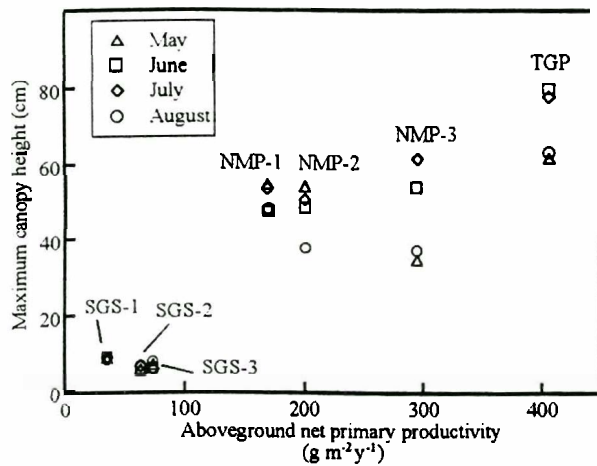
ANPP was significantly related to a range of canopy structure variables. Maximum canopy height was positively correlated with ANPP across the transect throughout the growing season (Spearman's rank order correlation coefficient  $\geq 0.75$  for all four sampling dates) (Fig. 5). In contrast, ANPP was negatively correlated with both the proportion of biomass in the 0-5 cm layer (Spearman's rank order correlation coefficient = -0.82) and with the proportion of leaf area in the 0-5 cm layer (Spearman's rank order correlation coefficient = -0.85). Specific leaf area of graminoids showed a strong positive correlation with ANPP for the 10-20 cm layer (Spearman's rank order correlation coefficient = 0.83),

**Table 1.** Species composition of each site (clip plots harvested in 1994) arranged by height classes. Mean height calculated from minimum and maximum heights listed in a regional flora (see Text). Functional groups: C = cactus, F = forb, G = graminoid.

		Short-grass steppe			Northern mixed prairie			Tall-grass prairie
		1	2	3	1	2	3	1
<b>Mean height &lt; 30 cm</b>								
<i>Opuntia polyacantha</i>	C	.	.	.				
<i>Gaura coccinea</i>	F				.	.		
<i>Lepidium densiflorum</i>	F	.	.					
<i>Plantago patagonica</i>	F	.	.	.				
<i>Sphaeralcea coccinea</i>	F	.	.	.	.			
<i>Bouteloua hirsuta</i>	G		.		.	.	.	
<i>Bouteloua gracilis</i>	G	.	.	.	.	.	.	
<i>Buchloe dactyloides</i>	G	.	.	.				
<i>Carex filifolia</i>	G				.			
<i>Carex heliophila</i>	G	.	.	.				
<i>Festuca octoflora</i>	G	.	.	.				
<i>Muhlenbergia torreyi</i>	G		.					
<b>Mean height 30 - 70 cm</b>								
<i>Amaranthus albus</i>	F							.
<i>Ambrosia psilostachya</i>	F							.
<i>Amorpha canescens</i>	F							.
<i>Chenopodium leptophyllum</i>	F							.
<i>Dalea purpurea</i>	F							.
<i>Eriogonum annuum</i>	F							.
<i>Helianthus spp.</i>	F							.
<i>Psoralea argophylla</i>	F							.
<i>Psoralea tenuiflora</i>	F					.	.	.
<i>Ratibida columnifera</i>	F					.		.
<i>Andropogon scoparius</i>	G					.	.	.
<i>Aristida purpurea</i>	G	.				.	.	.
<i>Bouteloua curtipendula</i>	G					.	.	.
<i>Bromus tectorum</i>	G					.	.	.
<i>Dichanthelium oligosanthes</i>	G					.	.	.
<i>Koeleria pyramidata</i>	G					.	.	.
<i>Poa pratensis</i>	G					.	.	.
<i>Sporobolus cryptandrus</i>	G	.				.	.	.
<i>Stipa comata</i>	G					.	.	.
<b>Mean height &gt; 70 cm</b>								
<i>Aster ericoides</i>	F							.
<i>Coreopsis tinctoria</i>	F							.
<i>Helianthus annuus</i>	F							.
<i>Salsola iberica</i>	F							.
<i>Solidago rigida</i>	F							.
<i>Solidago spp.</i>	F							.
<i>Agropyron smithii</i>	G					.	.	.
<i>Andropogon gerardii</i>	G					.	.	.
<i>Bromus inermis</i>	G							.
<i>Panicum virgatum</i>	G							.
<i>Sorghastrum nutans</i>	G							.
<i>Sporobolus asper</i>	G							.

but not for the other canopy layers (Spearman's rank order correlation coefficient < 0.4).

LAI increased significantly with increasing ANPP across the entire precipitation gradient (Fig. 6a). Consequently, leaf area efficiency, defined here as ANPP ( $\text{g m}^{-2} \text{yr}^{-1}$ ) per  $\text{cm}^2$  of leaf area, decreased significantly across the precipitation gradient (Fig. 6b). ANPP



**Fig. 5.** Maximum canopy height as a function of above-ground net primary productivity (ANPP) at seven sites across a productivity gradient. At each site, height was measured during four sampling periods spaced throughout the 1994 growing season. Sites are labelled as in Fig. 1.

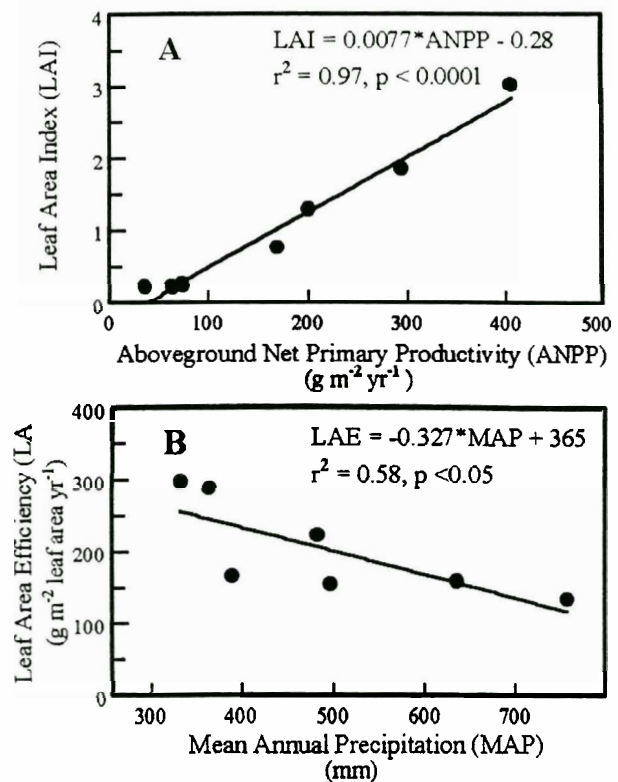
increased only by a factor of 5.5 across the gradient while LAI increased by a factor of 12.

## Discussion

### Comparisons with previous studies

The conclusions of this study are limited by the restriction of data collection to one year and seven sites. Across the gradient, precipitation during the 12 months leading up to the study (August 1993 - July 1994) was between 9% and 44% higher than mean annual precipitation (1969-1993) (Lane et al. 1998). Although our results are likely to apply to wet years more than to drought years, general features of canopy structure may remain relatively constant from year to year because all sites are dominated by perennial species. Relative comparisons between vegetation types, however, may be more representative of long-term patterns than absolute differences in properties such as canopy height.

Our values for LAI and PAR transmission compare closely with previous studies of canopy structure in the central grassland region. At the Central Plains Experimental Range (site SGS-1), LAI in August was estimated as 0.25 in 1970 (Knight 1973) and 0.2 in 1988 (Hazlett 1992) using the inclined point-quadrat technique, compared to our estimate of 0.22. At an ungrazed tallgrass prairie in Oklahoma, LAI in August was



**Fig. 6. a.** Leaf area index (LAI) as a function of above-ground net primary productivity (ANPP); **b.** Leaf area efficiency (LAE) as a function of mean annual precipitation (MAP). LAE was defined as ANPP per m<sup>2</sup> of leaf area. Equations are presented for the linear regression.

estimated as 2.9 in 1971 using the inclined point-quadrat technique (Conant & Risser 1974), compared to our estimate of 3.0 for our site TGP in Nebraska. These LAI values of approximately 3 correspond better with July LAI estimates of 2.3 for tallgrass prairie at the Konza research site in Kansas than for August estimates of 1.0 (Schimel et al. 1991). The values of PAR transmission we observed at site TGP on July 29 1994 agree closely with values measured on August 3 1982 in unburned tallgrass prairie at the Konza site (Knapp 1984).

### Light availability and canopy structure across the precipitation gradient

The short-grass steppe sites were characterized by high light availability at the soil surface across the growing season, resulting from a small amount of leaf surface area available for light interception. Above-ground competition for light is likely to be relatively unimportant at these sites, compared to the more humid grassland types. A concentration of biomass near the soil surface is

characteristic of low productivity grasslands (Fliervoet & Werger 1984; Werger et al. 1986).

Compared to the short-grass steppe sites, the northern mixed prairie sites were characterized by sharply reduced light availability at and near the soil surface, resulting from a greater leaf surface area available for light interception. Reduced light availability at and near the soil surface of these sites is likely to affect processes such as seedling growth (Jurik & Pleasants 1990) and tillering rates (Deregibus et al. 1985). The concave profiles of biomass and leaf area at these sites indicate that competition for light is not severe enough to result in either (1) a reallocation of leaf area away from the lowest canopy layer or (2) a shift in species composition to species which display foliage in higher canopy layers. Thus, although above-ground processes may affect some aspects of community dynamics in northern mixed prairie, below-ground processes are likely to be more frequently important for structuring the community.

Compared to short-grass steppe and northern mixed prairie sites, the tallgrass prairie site was characterized by sharply reduced light availability within 20 cm of the soil surface, resulting from the highest amount of leaf surface area. The tallgrass prairie site also had the most even distribution of biomass and leaf area. The change from strongly concave leaf area profiles at the short-grass steppe sites to a slightly convex profile at the tallgrass prairie site is similar to the change in leaf area profiles between Dutch grasslands with common drought conditions and those with constant moisture conditions (Werger et al. 1986). The steep reduction in light in canopy layers below 50 cm suggests that canopy structure may be having important effects on ecological processes. For example, the amount of available light within the canopy may affect nitrogen allocation patterns (Hirose & Werger 1987) and photosynthetic rates (Schimel et al. 1991). Seasonal variability in light availability and leaf area has been found in several studies of tallgrass prairie (Knapp 1984; Schimel et al. 1991; Conant & Risser 1974), and may be characteristic of grasslands with higher productivity.

#### *Canopy height, leaf area, and species composition*

Increases in canopy height and leaf area across the precipitation gradient indicate that plants became disproportionately taller and leafier as precipitation increased. Across the gradient, canopy height increased by a factor of 10, leaf area increased by a factor of 12 but precipitation increased by a factor of only 2.5. Basal cover of vegetation does not increase across this gradient (Lane et al. 1998). Thus, as plants grow larger

across the precipitation gradient, vegetation becomes disproportionately taller, with biomass and leaf area displayed at higher canopy layers, and an overall decrease in the density of leaf area with height. These disproportionate increases in canopy height and leaf area with increasing precipitation again suggest that competition for light becomes increasingly important across this gradient.

Changes in canopy structure across the gradient resulted primarily from changes in the proportion of species of different stature (e.g. Mitchley & Willems 1995) and not from shifts in the biomass allocation of individual species (e.g. Olff 1992). These shifts in species composition provide further indirect evidence that competition for a resource other than water may be structuring these communities. If water was the sole limiting resource across this gradient, the short-grass steppe species which are most competitive for water would be expected to thrive across the gradient. Instead, the short-grass steppe species are progressively replaced by species of taller stature that compete more successfully for light. In addition to light competition, increasing competition for nitrogen across the gradient could account for shifts in species composition. Competition for nitrogen, however, would not explain the disproportionate increases in canopy height that accompany the shifts in species composition.

#### *Relationship between LAI and ANPP*

The significant relationships between LAI, ANPP and precipitation across the grassland precipitation gradient in this study correspond to similar relationships found for forest ecosystems across elevation and precipitation gradients (Grier & Running 1977; Gholz 1982). Because ANPP in grasslands is dominated by foliage biomass, LAI and ANPP are expected to be correlated. The ratio of ANPP to LAI did not remain constant across the precipitation gradient, however. Instead, leaf area efficiency (defined here as ANPP per cm<sup>2</sup> leaf area) decreased significantly with increasing precipitation. Across the gradient, an increase in the specific leaf area of graminoid leaves at the 10 - 20 cm canopy height may account for some of this decrease in leaf area efficiency, although the relationship is complicated by variation in specific leaf area at different canopy heights. Changes in the proportion of foliage biomass to total biomass (which was not measured here) would also influence leaf area efficiency.



## Conclusions

The changes in canopy structure that we documented support the prediction that competition for light increases in importance with increasing precipitation (Lauenroth & Coffin 1992). These changes in canopy structure are likely to affect resource availability and successional dynamics across a precipitation gradient. We also found that changes in the proportion of species of different stature collectively resulted in changes in community canopy structure. Because of the close relationships between species composition, canopy structure and ecosystem function, further studies of grassland canopy structure may be fruitful for studying specific feedback mechanisms between plant community composition and ecosystem processes (Chapin et al. 1998).

**Acknowledgements.** This project was supported by the National Science Foundation (BSR #9013881). Additional support was provided by NSF (BSR #9106183) and by the Shortgrass Steppe Long-Term Ecological Research Program (BSR #9011659). This material is based upon work supported under a National Science Foundation Graduate Research Fellowship to D. Lane. We thank Ingrid Burke, F.W. Smith, and three anonymous reviewers for comments on an earlier version of this manuscript and Phil Chapman for assistance with statistical analyses. We thank F.W. Smith, Daniel Smith, and Joe Trlica at Colorado State University for loaning us equipment for the PAR and leaf area measurements. We thank the following individuals and organizations for access to property they own or manage: Roger Brandes, Dave Colburn, Rex Davis, Robert Kaul, Dusty Rodiek, Dennis Shimmin, John Wurdeman, USDA Central Plains Experimental Range, USDA Forest Service, Pawnee National Grassland, Ash Hollow State Park, University of Nebraska's West Central Research and Extension Center, Cottonmill Park, Kearney, Nine-mile Prairie, Lincoln.

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Received 10 May 1999;

Revision received 15 October 1999;

Accepted 15 October 1999.

Coordinating Editor: J.B. Wilson.