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Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the Central Grassland region of the United States

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Abstract. A potentially important organizing principle in arid and semi-arid systems is the inverse-texture hypothesis which predicts that plant communities on coarse-textured soils should have higher above-ground net primary productivity (ANPP) than communities on fine-textured soils; the reverse is predicted to occur in humid regions. Our objectives were: (1) to test predictions from the inverse-texture hypothesis across a regional precipitation gradient, and (2) to evaluate changes in community composition and basal cover on coarse- and fine-textured soils across this gradient to determine how these structural parameters may affect ANPP. Sites were located along a precipitation gradient through the Central Grassland region of the United States: mean annual precipitation ranges from 311 mm/y to 711 mm/y, whereas mean annual temperature ranges from 9 °C to 11 °C.

For both coarse- and fine-textured sites in 1993 and 1994, August - July precipitation in the year of the study explained greater than 92% of the variability in ANPP. Soil texture did not explain a significant proportion of the variability in ANPP. However, soil texture did affect the proportion of ANPP contributed by different functional types. Forbs and shrubs made up a larger proportion of total ANPP on coarse- compared to fine-textured sites. Shrubs contributed more to ANPP at the drier end of the gradient. Basal cover of live vegetation was not significantly related to precipitation and was similar for both soil textures. Our results revealed that across a regional precipitation gradient, soil texture may play a larger role in determining community composition than in determining total ANPP.

Keywords: Functional type; Grasses; Inverse-texture hypothesis; Precipitation gradient; Regional analysis.

Nomenclature: Great Plains Flora Association (1986).

Abbreviations: ANPP = Above-ground net primary productivity; CO = Colorado; CPER = Central Plains Experimental Range; MAP = Mean annual precipitation; MAT = Mean annual temperature; NE = Nebraska; NMP = Northern mixed prairie; PPT = Precipitation; SGS = Shortgrass steppe; TGP = Tallgrass prairie; U.S. = United States of America; USDA = U.S. Department of Agriculture; WHC = Water-holding capacity.

Introduction

A potentially important organizing principle in arid and semi-arid systems is the inverse-texture hypothesis which predicts that plant communities on coarse-textured soils should have higher above-ground net primary productivity (ANPP) than communities on fine-textured soils; the reverse is predicted to occur in humid regions (Noy-Meir 1973; Sala et al. 1988). This hypothesis is based on the assumption that the availability of water for transpiration is a primary determinant of ANPP.

In arid and semi-arid regions, coarse-textured soils with high sand content may lose less water to bare-soil evaporation than fine-textured soils and thus may have higher water availability. Precipitation also percolates to a greater depth on coarse- compared to fine-textured soils (Tsoar 1990). The top layer of coarse-textured soils dries out quickly and forms a barrier to the conductance and evaporation of water from deeper soil layers (Alizai & Hulbert 1970; Jalota & Prihar 1986; Hide 1954; Lemon 1956). In humid regions, fine-textured soils may have higher water availability than coarse-textured soils, because fine-textured soils have a higher water-holding capacity and lose less water to deep drainage below the rooting zone. Losses of water to deep drainage increase with increasing precipitation, and in humid regions may become more significant than losses of water to bare-soil evaporation (Noy-Meir 1973; Lane 1995).

Predictions of the inverse-texture hypothesis were supported by a previous study which found a significant relationship between average estimates of ANPP and soil texture, when soil texture was converted to an estimate of water-holding capacity (Sala et al. 1988). Coarse-textured soils had higher ANPP than fine-textured soils below 370 mm of mean annual precipitation (MAP) whereas the reverse was found for higher amounts of precipitation. The study was based on a U.S. Department of Agriculture (USDA) Natural Resource Conservation Service database of average ANPP estimates for the potential native plant community of 9498 sites located across the Central Grassland region of the U.S. (Joyce et al. 1986). This analysis did not test the inverse-texture hypothesis with empirical field estimates of ANPP. Ideally, the inverse-texture hypothesis would be tested using long-term empirical field estimates, where ANPP was estimated at each site for identical years using consistent methods. Although logistical constraints limited our study to two years, it is the only regional synoptic data set that we know of containing entirely empirical estimates of ANPP for a range of sites with contrasting soil textures.

Changes in plant community composition across gradients of precipitation and soil texture may help explain changes in ANPP. Previous studies examined the effect of soil texture on plant community composition and on ANPP at individual sites, but did not look at the importance of community composition in explaining regional patterns of ANPP. In grasslands, the relative dominance of grasses and woody plants and the relative abundance of deep- versus shallow-rooted grass species was found to correlate with soil texture (Walker & Noy-Meir 1982; Barnes & Harrison 1982). In the shortgrass steppe, greater ANPP at coarse- compared to fine-textured sites was attributed to the presence of shrubs and half-shrubs at the coarse-textured sites (Liang et al. 1989). Thus, it is possible that the inverse-texture effect may result from changes in community composition, but may not be detectable for a single functional type such as grasses.

Our objectives were: (1) to test predictions from the inverse-texture hypothesis across a regional precipitation gradient, and (2) to evaluate changes in community composition and basal cover on coarse- and fine-textured soils across this gradient to determine how these structural parameters may affect ANPP. Our approach was to examine the relationship between soil texture and ANPP for the entire plant community and for different functional types, using two years of empirical field data for a range of sites located along a precipitation gradient through the Central Grassland region of the U.S. The Central Grassland region is well suited for this study because three different grassland types, with different functional type compositions, are found along a precipitation gradient (Coupland 1992). We chose to quantify the proportion of graminoid, forb, shrub, and cactus functional types across the precipitation gradient because these four types differ in life-history and resource use, and can be expected to respond in contrasting ways to different environmental conditions (Coffin & Lauenroth 1990; Liang et al. 1989; Soriano & Sala 1983; Sun et al. 1997).

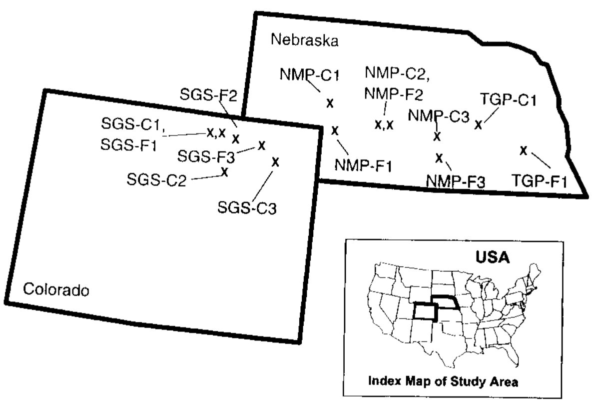

Fig. 1. Location of study sites in Colorado and Nebraska, USA. Sites labeled as in Table 1.

Methods

Site descriptions

The Central Grassland region of the U.S. is a large region (1.8×10^6 km^2; Sims 1991) extending 1100 km from the Rocky Mountains in the west to the deciduous forest border in the east, and 2100 km from Canada in the north to Mexico in the south (Borchert 1950; Sims 1991). Mean annual precipitation (MAP) increases from a low of 260 mm in the west to 1200 mm in the east; mean annual temperature (MAT) stays approximately constant for a given latitude, but increases from approximately 3 °C in the north to 22 °C in the south (Lauenroth & Burke 1995).

ANPP was estimated in 1993 and 1994 at 14 grassland sites along a west-east transect through the Central Grassland region, extending from eastern Colorado to eastern Nebraska at approximately 41°N latitude (Fig. 1; Table 1). Sites spanned three grassland types which differ substantially in physiognomy: shortgrass steppe (SGS), northern mixed prairie (NMP), and tallgrass prairie (TGP) (Coupland 1992). Half of the sites were on sandy soils ('coarse-textured') and half on loamy soils ('fine-textured') as determined by particle size analysis (see Sampling methods: soil texture). Based upon inspection of species composition and soils, and conversations with the current owners and managers of the sites, it appears that none of the areas used in the study have been plowed. However, we were not able to locate sites with identical management histories. Before 1993 when the study was initiated, five sites (SGS-C1, NMP-F1, NMP-C1, NMP-F3, TGP-F1) had not been grazed by cattle for 9, 24, 16, 3, and 33 years, respectively. The other nine sites were grazed up to the time of the study, but protected from cattle grazing during the study. One tallgrass site (TGP-F1) was burned in 1991; none of the other sites experienced controlled burns. These management differences likely introduced additional variability into the study. However, it is unlikely that these management differences introduced systematic biases that would affect the conclusions of the study; sites with long-term protection from grazing were distributed among coarse- and fine-textured soils, and across the precipitation gradient.

All sites experience a continental climate with cold, dry winters and warm, wet summers. Long-term mean annual precipitation and mean daily minimum, maximum, and average temperature were obtained from 25 years (1969-1993) of daily weather data from the weather station closest to each site (Table 2; Anon. 1988-). MAP increased from 333 mm at the western end of the transect to 759 mm at the eastern end (Table 1). Mean annual temperature ranged from 9 to 11 °C, with 12 out of the 14 sites having a mean annual temperature between 9 and 9.8 °C.

Monthly precipitation totals for the time of our study (August 1992 - July 1994) were obtained from the same weather stations described above. We used August 1992 - July 1993 and August 1993 - July 1994 precipitation totals, respectively, as an estimate of precipitation contributing to 1993 and 1994 ANPP. August to July precipitation was significantly related to MAP in both 1992-1993 ($r^2 = 0.92$, $p < 0.001$) and 1993-1994 ($r^2 = 0.84, p < 0.001$). However, inter-annual variability in August to July precipitation was not consistent across the gradient. In 1993, the six driest (shortgrass steppe) sites had below-average precipitation while the other eight sites had above-average precipitation. In 1994, all sites had above-average precipitation except for one (TGP-C1). At the four wettest sites, 1993 precipitation exceeded 1994 precipitation, while the reverse was true at all other sites. These precipitation patterns made general comparisons across the gradient difficult because the slope relating 1993 precipitation to long-term MAP for all sites was significantly steeper than the slope relating 1994 precipitation to MAP ($F = 26.5$, $df_1 = 3$, $df_2 = 24$, $p = 0.001$). Therefore, for most analyses, we analyzed each year separately.

At each of the nine sites currently grazed, 15 exclosures were constructed of a 15 cm^2 wire mesh to protect the plots from grazing by cattle. Because of the wide mesh spacing, we assumed that exclosures had minimal effects on light, rainfall, and temperature. To minimize edge effects, exclosures were designed to be at least three times larger than the area clipped for ANPP measurements.

Sampling methods: Soil texture

We sampled the top 30 cm of soils at each site to classify sites into a soil texture class (Anon. 1951) and to group sites into categories of coarse- or fine-textured (Table 3). Soil texture was determined by the hydrometer method (Gee & Bauder 1986) on a composite of five soil cores obtained within the area where ANPP plots were located (30 m × 20 m). Classification of each soil into a texture class (Anon. 1951) was based on the top 30 cm of soil because this layer contains the majority of root biomass in all three vegetation types (Liang et al. 1989; Coupland 1992; Weaver & Darland 1949). Sites classified as sands, loamy sands, or sandy loams with at least 80% sand were categorized as 'coarse-textured' sites. Sites classified as sandy clay loams, silty clay loams,

Table 1. Field site characteristics: location, climate, and vegetation type. All sites are located in Colorado or Nebraska, USA.

Field Site	State	Site code[1]	Elev. (m)	Lat. (N)	Long. (W)	MAT[2] (°C)	MAP[3] (mm)	Precipitation during study (mm) 08/92 -07/93	08/93 -07/94	Distance from Weather Station (km)
CPER[4] (Pasture 25SE)	CO	SGS-F1	1631	40°48'15"	104°43'12"	9.7	333	305	479	3.9
CPER (Owl Creek)	CO	SGS-C1	1650	40°50'56"	104°43'49"	9.7	333	305	479	3.3
Keota	CO	SGS-F2	1504	40°41'07"	104°04'15"	9.0	390	298	465	3.8
Keenesburg	CO	SGS-C2	1468	40°09'52"	104°27'42"	9.0	374	354	419	20.7
Stoneham	CO	SGS-F3	1408	40°37'38"	103°40'58"	9.1	365	313	466	14.1
Akron	CO	SGS-C3	1298	40°23'35"	103°11'58"	9.0	422	413	478	8.3
Ash Hollow	NE	NMP-F1	1097	41°15'16"	102°06'30"	9.1	483	536	564	38.4
Arapaho Prairie	NE	NMP-C1	1128	41°29'30"	101°51'06"	9.1	483	536	564	19.6
N. Platte Experiment Station	NE	NMP-F2	893	41°04'11"	100°45'39"	9.1	497	617	674	6.9
N. Platte Ranch	NE	NMP-C2	896	41°12'35"	100°38'14"	9.1	497	617	674	4.7
Kearney	NE	NMP-F3	695	40°42'20"	99°08'21"	9.8	636	968	750	10.3
Buffalo County Ranch	NE	NMP-C3	643	40°57'29"	99°01'53"	9.8	636	968	750	8.2
9-Mile Prairie	NE	TGP-F1	405	40°52'00"	96°48'59"	11.0	759	981	831	5.9
Central City Ranch	NE	TGP-C1	527	41°16'58"	98°00'23"	10.9	693	826	667	6.0

[1] SGS = Shortgrass steppe, NMP = Northern mixed prairie, TGP = Tallgrass prairie, C = Coarse-textured, F= Fine-textured;
[2] MAT = Mean annual temperature, calculated from average daily temperature values;
[3] MAP = Mean annual precipitation;
[4] CPER = Central Plains Experimental Range.

loams, silt loams, or sandy loams with less than 60% sand were categorized as 'fine-textured.'

Sampling methods for objective 1: Testing the inverse-texture hypothesis

At each site, ANPP was estimated during August of 1993 and 1994, which corresponded approximately to the time of peak biomass. At each site, three 30 m transects spaced 10 m apart were established on an upland area with minimal slope. Five plot locations were selected randomly along each transect. Using these same methods, three new transects and 15 new plots were established at each site in 1994, so that the plots sampled in 1993 were not resampled. A 0.25 m^2 ring was placed in the center of each plot, and all living and recent dead herbaceous biomass was clipped at ground level and separated by species. For shrubs, current year's growth (twigs and leaves) was clipped. No attempt was made to estimate increases in woody biomass. All samples were dried for eight days at 55 °C and weighed. For the cactus *Opuntia polyacantha* Haw., current year's cladodes were clipped and dried to constant weight. At Arapaho Prairie (NMP-C1), the succulent *Yucca glauca* Nutt. grew in some plots, but was excluded from the analysis because current year's growth could not be separated easily from prior year's biomass.

Harvesting current live plus recent dead biomass at the time of peak standing crop has been used to estimate ANPP for all three major vegetation types across the Central Grassland region (Lauenroth & Sala 1992; Barnes et al. 1983; Knapp 1984a). This method results in a close estimate to ANPP when production is dominated by species with similar phenologies (Lauenroth et al. 1986). We sampled in August to capture the peak standing crop for C_4 species because C_4 grasses typically dominate shortgrass steppe and tallgrass prairie (Lauenroth & Milchunas 1992; Kucera 1992). In northern mixed prairie, C_3 grasses (e.g. *Stipa*, *Agropyron*) are comparatively more important, although C_4 grasses are also present (Coupland 1992). Our sampling method underestimated current year's biomass that was detached or decomposed before the sampling periods; these losses were probably greater for C_3 than for C_4 species.

Statistical analyses

For each year, we took the mean of the 15 plots as a single estimate of ANPP ($g+m^{-2}+y^{-1}$) for that site, rather than treating the 15 plots sampled at each site as independent replicates. We indicated the variability in ANPP among the 15 plots at a site by calculating a coefficient of variation for these plots in 1993 and 1994.

We analyzed effects of precipitation and soil texture on ANPP using three approaches: analysis of covariance, linear regression, and multiple regression. The relationship between ANPP and soil texture, after adjusting for precipitation, was examined using an analysis of covariance (ANCOVA) (Ott 1993). This analysis formally tested the null hypothesis that the slope relating ANPP to precipitation is equal for fine- and coarse-textured sites. In ecological terms, ANCOVA was used to test the hypothesis that ANPP increases more rapidly for fine- than for coarse-textured sites with increased precipitation. Given equality of slopes, ANCOVA was then used to test whether there was a treatment effect of soil texture on ANPP. This analysis formally tested the null hypothesis that the intercept of the ANPP vs. precipitation line is equal for fine- and coarse-textured sites.

For each year, the analysis of covariance was conducted separately because of large inter-annual variabil-

Table 2. Weather station names, locations, and associated field sites. Field sites and site codes described in Table 1.

Weather Station	State	Associated field sites	Elevation (m)	Lat. (N)	Long. (W)
CPER	CO	SGS-F1, SGS-C1	1650	40°49'	104°46'
Briggsdale	CO	SGS-F2	1473	40°38'	104°19'
Greeley UNC	CO	SGS-C2	1437	40°25'	104°42'
New Raymer	CO	SGS-F3	1458	40°36'	103°51'
Akron 4E	CO	SGS-C3	1421	40°10'	103°13'
Kingsley Dam	NE	NMP-F1, NMP-C1	1011	41°13'	101°39'
North Platte Bird Field	NE	NMP-F2, NMP-C2	846	41°08'	100°41'
Kearney 4 NE	NE	NMP-F3, NMP-C3	649	40°44'	99°01'
Lincoln	NE	TGP-F1	372	40°48'	96°39'
Central City	NE	TGP-C1	517	41°07'	98°00'

Table 3. Soil texture (% sand, % silt, % clay), water-holding capacity, and texture class for the top 30 cm of soil at each site. Site codes as in Table 1.

Site code	Sand %	Silt %	Clay %	Water-holding capacity [1]	Texture class
Coarse-textured sites:					
SGS-C1	80	7	13	0.104	Sandy loam
SGS-C2	93	1	6	0.064	Sand
SGS-C3	89	5	6	0.072	Sand
NMP-C1	93	3	4	0.062	Sand
NMP-C2	92	3	6	0.068	Sand
NMP-C3	81	12	7	0.083	Loamy sand
TGP-C1	93	3	5	0.064	Sand
Fine-textured sites:					
SGS-F1	49	19	32	0.183	Sandy clay loam
SGS-F2	55	14	31	0.212	Sandy clay loam
SGS-F3	48	26	26	0.204	Sandy clay loam
NMP-F1	57	28	15	0.169	Sandy loam
NMP-F2	47	37	16	0.177	Loam
NMP-F3	10	65	25	0.279	Silt loam
TGP-F1	10	55	34	0.330	Silty clay loam

[1] Water holding capacity is expressed as a proportion of soil dry mass (g water/g soil).

ity in precipitation. ANPP was the dependent variable and soil texture (coarse or fine) was the categorical treatment variable. We repeated this analysis using two separate covariates: precipitation for the 12-month period preceding ANPP sampling (i.e., August 1992 - July 1993 precipitation or August 1993 - July 1994 precipitation) and MAP. August to July precipitation was used as a covariate because it estimated the precipitation potentially available to plants during the 1993 and 1994 growing seasons. MAP was used as a covariate because it can serve as a proxy for grassland type. We used the separate ANCOVAs to determine the relative importance of precipitation in the year of the study and vegetation structure (i.e., grassland type) to ANPP.

We examined the relationship between ANPP and soil water-holding capacity for sites grouped by precipitation. Soil water-holding capacity (g water/g soil) was used as an aggregate variable for soil texture (Burke et al. 1997). It was estimated by field capacity ($\psi = -0.033$ MPa) calculated using each site's soil texture and soil bulk density (J. Barrett unpubl. data), and regression equations of Cosby et al. (1984). Based on predictions from Sala et al. (1988), the low rainfall group included sites with MAP $\leq$ 370 mm and the high rainfall group included sites with MAP > 370 mm. Because the variance of the high rainfall sites was six times larger than the variance of the low rainfall sites, we were unable to use an ANCOVA to test the hypothesis that the relationship between ANPP and soil water-holding capacity differs for low and high rainfall sites. Instead, we used linear regression to test for a significant relationship between ANPP and water-holding capacity for each rainfall group in 1993 and in 1994.

Environmental controls on ANPP for 1993 and 1994 were evaluated with a stepwise multiple regression analysis (Anon. 1989). Candidate variables included in the analysis were: (1) precipitation in each year of the study (August - July precipitation) (mm); (2) water-holding capacity; (3) water-holding capacity * precipitation; and 4) a dummy variable representing the year of the study. An interaction term (water-holding capacity * precipitation) was included because there was a significant precipitation by water-holding capacity interaction term in the regression model described previously (Sala et al. 1988).

Methods for Objective 2: Evaluating changes in community composition

The percentage of total ANPP at each site contributed by graminoid, forb, shrub and cactus functional types was calculated based on the ANPP data described above. On average, the difference between 1993 and 1994 in the percent of total ANPP contributed by the different functional types was less than 10 %. Therefore, we presented the average for 1993 and 1994 of the percent contribution by functional type. We used ANCOVA to examine the relationship between the ANPP of graminoids, forbs, or shrubs and soil texture, after adjusting for August - July precipitation in the year of the study. These analyses followed the same methods as the ANCOVAs described for total ANPP in Objective 1.

Environmental controls on ANPP of graminoids and forbs for 1993 and 1994 were evaluated separately with stepwise multiple regression analysis (Anon. 1989). Shrubs were excluded from this analysis because there were no shrubs present at half of the sites. Candidate variables included in the analysis were identical to those described earlier for multiple regression analysis for total ANPP.

We measured plant basal cover along two 54 m transects at each site in 1994 to characterize the structure of the plant community. Basal cover was estimated using a 20 cm × 50 cm-quadrat located randomly in each 3m-segment of each transect (n = 36/site). Basal cover was determined for each species, bare ground, and litter (detached dead vegetation) using six cover classes adapted from Daubenmire (1959) (< 5, 5-14, 15-24, 25-39, 40-59, 60-100%). Species were then grouped into functional types. We tested whether the mean basal cover of graminoids, forbs, bare ground, or litter was significantly related to MAP across the precipitation gradient. Shrubs were excluded because of their low representation in the quadrats. We also tested whether the basal cover of live biomass was significantly related to MAP across the gradient.

Results

Objective 1: Testing the inverse-texture hypothesis

Across the precipitation gradient, ANPP ranged from 53 $g{+}m^{-2}{+}y^{-1}$ to 423 $g{+}m^{-2}{+}y^{-1}$ in 1993 and 28 $g{+}m^{-2}{+}y^{-1}$ to 406 $g{+}m^{-2}{+}y^{-1}$ in 1994 (Table 4). In both years, variability among the 15 sampling plots at a site was higher on coarse- compared to fine-textured sites, and in general was higher at the drier end of the precipitation gradient (Table 4).

In 1993 and 1994, ANPP increased significantly with increasing August to July precipitation and with increasing MAP for coarse- and fine-textured sites ($p < 0.001$ for August-July precipitation) (Fig. 2; MAP not shown). This increase with MAP was significant at the $p \leq 0.02$ level for fine-textured sites in both years and for coarse-textured sites in 1993, and was significant at the $p = 0.06$ level for coarse-textured sites in 1994. Thus, the relationship between ANPP and August to July precipitation was stronger than the relationship between ANPP and MAP. In both years, the slope of the relationship between ANPP and either August to July precipitation or MAP did not vary with soil texture (ANCOVA; $p \geq 0.20$). There was no significant difference between coarse- and fine-textured sites in the intercepts of the ANPP versus precipitation regression lines (ANCOVA; $p \geq 0.23$), indicating no effect of soil texture on ANPP across a gradient of either August to July precipitation or MAP.

In 1993, but not in 1994, ANPP decreased significantly ($p < 0.05$) with increasing soil water-holding capacity for the low rainfall sites (MAP ≤ 470 mm/y) (Fig. 3). There was no significant relationship between ANPP and soil water-holding capacity for the high rainfall sites (MAP > 470 mm/y) either in 1993 or in 1994.

The variability in total ANPP across the gradient in 1993 and 1994 was largely explained by precipitation in the year of the study (August to July precipitation) and by the dummy variable used for year (Fig. 2; Table 5). Precipitation explained 84% of the variability in ANPP while the variable for year explained 4% of the variability in ANPP. The addition of soil water-holding capacity or of a water-holding capacity by precipitation interaction term did not improve the multiple regression models.

Objective 2: Evaluating changes in vegetation structure

Graminoids made up the largest proportion of total ANPP at all sites, while forbs and shrubs made up a relatively larger proportion of total ANPP at coarse- compared to fine-textured sites (Fig. 4). For the fine-textured sites, the proportion of total ANPP attributed to forbs increased significantly with increasing August to July precipitation (1993: $r^2 = 0.60$, $p = 0.04$; 1994: $r^2 = 0.76$, $p = 0.01$). For the coarse-textured sites, the proportion of total ANPP attributed to forbs increased significantly with increasing August to July precipitation in 1993 only ($r^2 = 0.73, p = 0.015$). Shrubs contributed more to ANPP at the coarse-textured shortgrass steppe sites compared to the rest of the sites. Cactus contributed the most to ANPP at the fine-textured shortgrass steppe sites. At other sites, cactus contributed less than 5% to total ANPP.

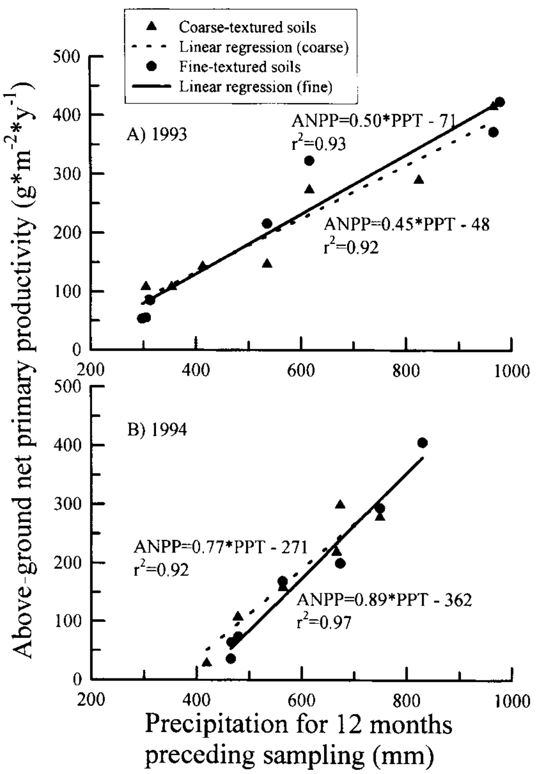

Fig. 2. Above-ground net primary productivity ($g+m^{-2}+y^{-1}$) in (A) 1993 and (B) 1994 as a function of total precipitation for the 12 months preceding sampling (i.e., August 1992 - July 1993 and August 1993 - July 1994, respectively). Regression lines and equations presented for significant linear regressions.

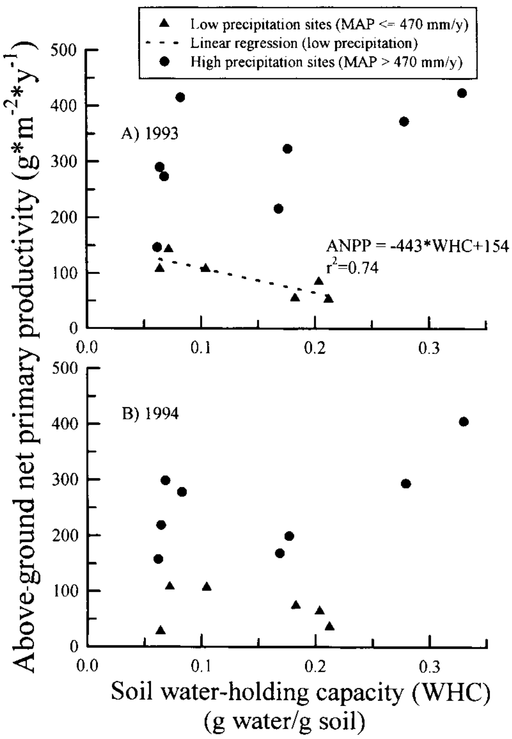

Fig. 3. Above-ground net primary productivity ($g+m^{-2}+y^{-1}$) in (A) 1993 and (B) 1994 as a function of soil water-holding capacity, with sites grouped by precipitation. Low precipitation sites have mean annual precipitation (MAP) less than or equal to 470 mm/y. High precipitation sites have MAP greater than 470 mm/y. Regression line and equation presented for the only significant linear regression.

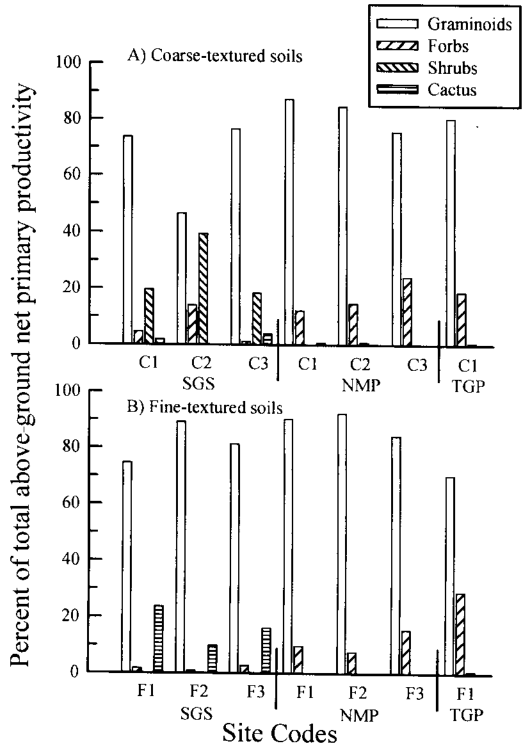

Fig. 4. Percent of total above-ground net primary productivity (ANPP) at each site attributable to graminoids, forbs, shrubs, and cactus for sites with (A) coarse-textured and (B) fine-textured soils. Values presented are the average for 1993 and 1994 of the percent contribution by functional types. Sites labeled as in Table 1.

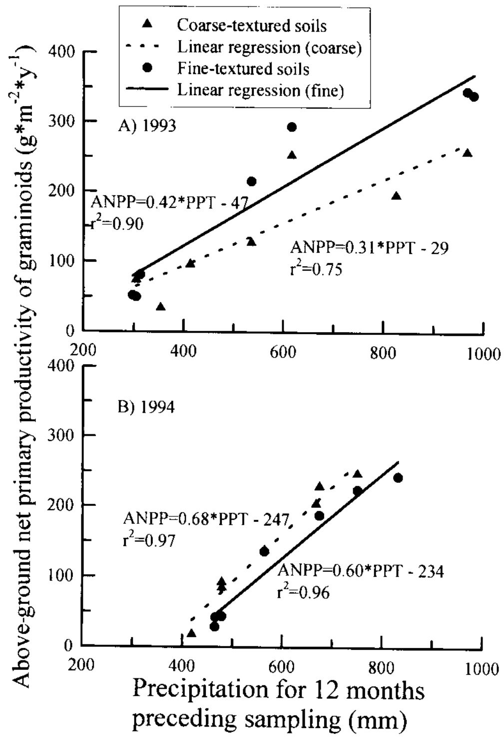

Fig. 5. Above-ground net primary productivity of graminoids ($g+m^{-2}+y^{-1}$) in (A) 1993 and (B) 1994 as a function of total precipitation for the 12 months preceding sampling (i.e. August 1992 - July 1993 and August 1993 - July 1994, respectively). Regression lines and equations presented for significant linear regressions.

For both years and both textures, ANPP of graminoids increased significantly with increasing August to July precipitation (Fig. 5) and with increasing MAP across the gradient (not shown) ($p < 0.05$). August to July precipitation explained a similar proportion of the variability in graminoid ANPP as total ANPP (> 90%) with the exception of coarse-textured sites in 1993 when precipitation explained only 75% of the variability in graminoid ANPP.

For both textures in 1993 and for fine-textured sites in 1994, ANPP of forbs increased significantly with increasing August to July precipitation (Fig. 6) and with increasing MAP (not shown) ($p < 0.05$). The proportion of variability in forb ANPP explained by August to July precipitation (< 90%) was lower than for graminoids or total vegetation. The low basal cover of forbs at the shortgrass steppe sites likely resulted in inadequate sampling of this group for ANPP estimates. In addition, low production estimates of C_3 forbs and graminoids was partly a consequence of sampling in August, approximately two months after the peak in C_3 production (Barnes & Harrison 1982).

Maximum ANPP of shrubs at any site, as well as the average shrub ANPP across all the sites, was more than four times higher in 1993 than in 1994 (1993: maximum shrub ANPP = 55 $g+m^{-2}+y^{-1}$; mean shrub ANPP = 10 $g+m^{-2}+y^{-1}$; 1994: maximum shrub ANPP = 12 $g+m^{-2}+y^{-1}$; mean shrub ANPP = 2.5 $g+m^{-2}+y^{-1}$). This large measured difference may not represent a decline in shrub ANPP between 1993 and 1994, but rather was due to patchy distribution of few shrubs. Despite random placement of quadrats, a total of 30 plots across all sites contained shrubs in 1993, while in 1994 only 15 plots contained shrubs.

Precipitation in the year of the study (August-July precipitation) explained 76% of the variability in ANPP of graminoids, while the variable for year explained 5% of the variability. Precipitation alone explained 55% of the variability in ANPP of forbs. Soil water-holding capacity did not improve significantly the multiple regression models explaining ANPP for forbs or for graminoids (Table 5).

Across the precipitation gradient, basal cover of live biomass ranged from 6% to 34%, but was not significantly related to MAP for either the fine- or coarse-textured sites (Table 6). For the fine-textured sites, the

Table 4. Mean above-ground net primary productivity (ANPP) with the associated coefficient of variation (CV) for 15 plots (0.25 m^2) sampled at sites along a precipitation gradient in 1993 and 1994. Site codes as in Table 1.

Site code	1993 ANPP ($g*m^{-2}*y^{-1}$)	1993 CV	1994 ANPP ($g*m^{-2}*y^{-1}$)	1994 CV
Coarse-textured sites:				
SGS-C1	108	118	107	43
SGS-C2	108	77	28	90
SGS-C3	143	82	108	40
NMP-C1	147	23	157	30
NMP-C2	273	33	299	26
NMP-C3	415	25	278	17
TGP-C1	289	22	219	19
Fine-textured sites:				
SGS-F1	55	31	74	63
SGS-F2	53	12	36	71
SGS-F3	85	32	64	65
NMP-F1	216	21	169	23
NMP-F2	323	33	200	30
NMP-F3	372	25	294	22
TGP-F1	423	16	406	32

Table 5. Multiple stepwise regression models of total, graminoid and forb above-ground net primary productivity (ANPP) against input variables. Input variables used as independent variables in the regression models were: precipitation in year of study (PPT) (mm), soil water-holding capacity (WHC) (g water/g soil), WHC * PPT, and a dummy variable representing the year of the study (1993 or 1994). Variables entered into the regression had to meet a 0.05 significance level requirement. WHC and WHC * PPT did not meet this requirement.

Variable	Estimate	Step	Partial r^2	Model r^2	P
Total ANPP:					
Intercept	– 103				
PPT	0.554	1	0.835	0.835	0.0001
YEAR	– 49.6	2	0.042	0.877	0.007
Graminoid ANPP:					
Intercept	– 72.3				
PPT	0.426	1	0.761	0.761	0.0001
YEAR	– 41.9	2	0.046	0.807	0.022
Forb ANPP:					
Intercept	– 58.0				
PPT	0.150	1	0.546	0.546	0.0001

basal cover of live biomass was higher at the shortgrass steppe sites than at the northern mixed prairie and tallgrass prairie sites, although canopy cover was highest at the tallgrass sites (Lane 1995). At all sites, graminoids contributed more than forbs to total vegetative basal cover (Table 6). Basal cover of graminoids was not significantly related to MAP for either texture. However, at the fine-textured sites, basal cover of forbs increased significantly with increasing MAP ($r^2 = 0.82$, $p = 0.005$). Percentage cover of bare ground decreased significantly (fine: $r^2 = 0.70$, $p = 0.02$; coarse: $r^2 = 0.63$, $p = 0.03$), and cover of litter increased significantly with increasing MAP for both soil textures (fine: $r^2 = 0.72$, $p = 0.02$; coarse: $r^2 = 0.61$, $p = 0.04$) (Table 6).

Discussion

Objective 1: Testing the inverse-texture hypothesis

In two years of field studies across a precipitation gradient through the Central Grassland region, ANPP was strongly related to August to July precipitation and to MAP but not to soil texture. ANPP was related significantly to soil water-holding capacity only in the case of shortgrass steppe sites in 1993. For these sites, ANPP was higher at sites with low water-holding capacity compared to sites with higher water-holding capacity because the sites with low water-holding capacity had high shrub productivity.

These results contrast with those of Sala et al. (1988) who found a significant effect of long-term average precipitation and soil water-holding capacity on estimated potential ANPP for 9498 unique range site-soil combinations. These results also contrast with those of Le Houérou (1984) who found higher productivity on coarse- compared to fine-textured soils where MAP was below 300 mm. Likely explanations for these contrasting results are: (1) the use of 14 sites in a 2-year study did not provide the statistical power necessary to detect a significant texture effect, (2) long-term or average estimates for ANPP of potential natural vegetation used in the Sala et al. (1988) study smoothed out the natural spatial and temporal variability in the ANPP of actual sites that can overwhelm the detection of a texture effect from a short-term study, and (3) high vegetative and litter cover at our sites resulted in high water infiltration across all soil textures — the inverse-texture effect may be stronger at degraded sites where fine-textured soils have low infiltration. Le Houérou (1984) reported that reductions in perennial plant cover and a sealing of the soil surface contributed to decreased productivity on fine-textured soils.

Another alternative, developed from the same database of potential natural vegetation used by Sala et al. (1988), is that the 'crossover' point of 370 mm MAP determined by Sala et al. (1988) is too low. The crossover point is the precipitation value below which coarse-textured sites are predicted to have greater productivity than fine-textured sites, and above which fine-textured sites are predicted to have greater productivity than coarse-textured sites. A new analysis found a crossover point for the inverse-texture effect between 800 and 850 mm MAP (Epstein et al. 1997). Under this hypothesis, we would expect to find that the coarse-textured sites had significantly higher ANPP than the fine-textured sites across the entire precipitation gradient in our study, where the maximum MAP was 759 mm. However, this was decidedly not the case. We did not find any consistently significant effect of soil texture on ANPP in our empirical field study.

The hypothesis of the inverse-texture effect is based on the assumption that soil texture controls water availability, a primary control on ANPP. However, soil texture may also exert a control on nutrient availability. Generally, fine-textured soils have higher levels of soil organic matter and greater nutrient availability than coarse-textured soils (Parton et al. 1993; Burke et al. 1989; Parton et al. 1987). In tallgrass prairie, productivity correlates with higher nitrogen and water availability (Schimel et al. 1991) and is likely to be maximized on fine-textured soils as a consequence of both greater nitrogen availability and higher soil water-holding capacity. However, in shortgrass steppe, nitrogen availability has not been shown to limit ANPP (Lauenroth et al. 1978). Considering nitrogen as a potential control on ANPP at the wetter end of the gradient would not change the predictions of the inverse-texture hypothesis. Our study design did not allow us to separate out effects of soil texture on water availability from effects of soil texture on nutrient availability. However, the fact that we did not detect any soil texture effect on ANPP across our gradient implies that the climatic control of precipitation overwhelms any effect of soil texture.

Soil nutrient availability may have co-varied with precipitation, as well as with soil texture. Across the Great Plains region of the United States, soil organic carbon and soil organic nitrogen increase with increasing precipitation (Burke et al. 1989). However, a separate investigation at the same sites used in this study did not find a significant relationship between precipitation and potential or field rates of nitrogen mineralization (J. Barrett unpubl. data). Thus, the positive correlation we observed between ANPP and precipitation is unlikely to have resulted from increased soil nutrient availability with increasing precipitation.

Previous studies indicate that texture effects may be detectable for ANPP data collected at single sites and averaged over several years. For example, at the driest shortgrass steppe site (CPER), average ANPP for 1990-

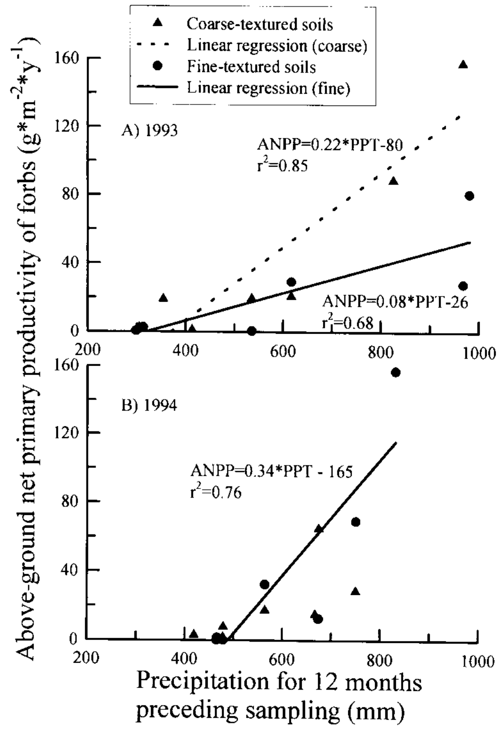

Fig. 6. Above-ground net primary productivity of forbs $(g + m^{-2} + y^{-1})$ in (A) 1993 and (B) 1994 as a function of total precipitation for the 12 months preceding sampling (i.e. August 1992 - July 1993 and August 1993 - July 1994, respectively). Regression lines and equations presented for all significant linear regressions.

Table 6. Basal cover (%) of live biomass, graminoids, forbs, bare ground, and litter at each site along a precipitation gradient. Site codes as in Table 1.

	Percent basal cover				
	Live biomass	Graminoids	Forbs*	Bare ground**	Litter ***
Coarse-textured sites:					
SGS-C1	25	21	3	63	18
SGS-C2	6	3	3	75	11
SGS-C3	18	17	1	46	46
NMP-C1	16	12	3	16	73
NMP-C2	24	19	4	21	64
NMP-C3	22	20	2	22	65
TGP-C1	22	19	3	18	69
Fine-textured sites:					
SGS-F1	34	32	1	77	< 1
SGS-F2	16	15	< 1	80	2
SGS-F3	17	13	1	80	< 1
NMP-F1	17	15	3	15	66
NMP-F2	15	15	1	3	74
NMP-F3	16	13	3	< 1	80
TGP-F1	18	12	7	1	80

* Basal cover of forbs increased significantly with increasing mean annual precipitation for fine-textured sites only ($p = 0.005$).
** Basal cover of bare ground decreased significantly with increasing mean annual precipitation for both soil textures (coarse: $p = 0.03$; fine: $p = 0.02$).
*** Basal cover of litter increased significantly with increasing mean annual precipitation for both soil textures (fine: $p = 0.02$; coarse: $p = 0.04$).

1994 was 126 $g{\cdot}m^{-2}{\cdot}y^{-1}$ on a sandy loam, compared to 72 $g{\cdot}m^{-2}{\cdot}y^{-1}$ on a clay loam (D. Milchunas & W. Lauenroth unpubl. data). At a mixed prairie site in Kansas (MAP = 570 mm; Tomanek & Hulett 1970), average productivity on a sandy soil was 197 $g{\cdot}m^{-2}{\cdot}y^{-1}$ compared to 182 $g{\cdot}m^{-2}{\cdot}y^{-1}$ on a loam and 135 $g{\cdot}m^{-2}{\cdot}y^{-1}$ on a silty clay loam (Tomanek 1964). Of the three textures, the silty clay loam would have the highest water-holding capacity and the sandy soil would have the lowest (Cosby et al. 1984). At a tallgrass prairie site in Kansas (MAP = 835 mm), an 18-year record showed that annually burned lowlands had significantly higher NPP than annually burned uplands (Briggs & Knapp 1995). The lowland soils have a higher water-holding capacity than the more shallow upland soils (Abrams et al. 1986; Knapp et al. 1993). Le Houérou (1984) found that olive production in Tunisia was higher on sandy than on silty soils when precipitation fell below 300 mm a year. In all of these cases, effects of soil texture or water-holding capacity were detectable over several years of study at single sites, where presumably other factors that could affect ANPP, such as management practices (Abrams et al. 1986), are more controlled than in a regional study such as this one.

Because both 1993 and 1994 were years of above-average precipitation at most of our sites, we cannot say whether the patterns we found would hold during drier conditions. August 1992 - July 1993 precipitation was between 110% and 152% of MAP at the eight mixed-grass and tallgrass prairie sites, and between 76% and 98% of MAP at the six shortgrass steppe sites. The following year, all sites had above-average precipitation except for one (TGP-C1). However, it seems likely that ANPP would be significantly related to precipitation in dry years, when water availability would presumably exert a stronger control over productivity than in wet years (e.g. Knapp 1984b). The finding of strong relationships between ANPP and precipitation in years with above-average precipitation lends strength to the possibility that our two years of field results may extrapolate into longer-term patterns. Ideally, the patterns that we found in this study would be tested with a long-term regional data set of empirically collected field ANPP estimates. However, to our knowledge, such a data set does not yet exist.

Across the gradient considered in this study, other factors co-varied with the increase in precipitation. Mean annual temperature (MAT) was higher at the tallgrass prairie sites (10.9 - 11 °C) compared to the other sites (9.0 - 9.8 °C). However, unlike precipitation, MAT did not increase consistently across the gradient. Across the Great Plains region of the United States, Epstein et al. (1997) found that MAT explained an average of 27% of the variation in ANPP when precipitation was held constant at intervals of 50 mm. This response to MAT took place over a range of MAT from 5 to 20 °C (Epstein et al. 1996). Given the large change in mean annual precipitation across our sites (333 to 759 mm/y) and the relatively small change in MAT ($\leq$ 2 °C), MAT is unlikely to explain a significant portion of the variability in ANPP. Thus, the correlation we observed between ANPP and precipitation is unlikely to be a result of temperature changes across the gradient.

Objective 2: Evaluating changes in community composition

Although soil texture did not have a significant effect on total ANPP, coarse- and fine-textured sites varied in community composition and in the proportion of ANPP made up by different functional types. Averaged over 1993 and 1994, shrubs accounted for 66% of the difference in total ANPP between coarse- and fine-textured shortgrass steppe sites. For these sites, the link between soil texture and ANPP is apparently mediated through the presence of shrubs. Soil texture also affected the contribution of forbs to ANPP. Our results are consistent with a previous study at one shortgrass steppe site (CPER: SGS-C1, SGS-F1) which found that differences in productivity between coarse- and fine-textured soils could be attributed to the presence of shrubs and half-shrubs on coarse-textured soils (Liang et al. 1989).

Across a precipitation gradient larger than the one we considered in our study, the increased importance of woody species with increasing precipitation could account for an inverse-texture effect that is mediated by community composition. At its wetter borders, tallgrass prairie can frequently intergrade into deciduous woodland along an ecotone dictated by both fire (Abrams et al. 1986) and soil texture. For example, on the Anoka Sand Plain in east-central Minnesota, USA, prairie vegetation is found on dune soils while oak woodland is found on glacial outwash soils with higher nutrient- and water-holding capacity (Ovington et al. 1963; Reiners 1972). Consequently, across a precipitation gradient reaching from the shortgrass steppe into woodlands, an inverse-texture effect could be accounted for by the greater importance of woody species on coarse-textured soils at the dry end of the gradient and on fine-textured soils at the wet end of the gradient. However, even with a better method for measuring shrub ANPP, we would have been unlikely to find such a woody species induced inverse-texture effect because the wettest point of our transect was regularly burned tallgrass prairie where shrubs generally do not account for a significant proportion of above-ground biomass (Kucera 1992; Abrams et al. 1986).

Across the precipitation gradient, there was no apparent link between vegetative basal cover and either ANPP or community composition. Basal cover of live vegetation was not significantly related to precipitation and on average was similar for coarse- and fine-textured sites. However, litter cover increased significantly with increasing precipitation, reflecting the higher productivity of the wetter sites. Litter cover increased with precipitation even at the coarse-textured sites, where 5 out of the 7 sites were grazed up until the years of sampling. At the wet end of the gradient, litter accumulation affects light availability (Lane 1995; Knapp 1984a) and plant water relations (Abrams et al. 1986; Knapp 1984a), and may influence ANPP (Knapp 1984a).

Conclusions

Our results from two years of empirical field data revealed that ANPP across a precipitation gradient through the Central Grassland Region of the U.S. was more strongly determined by August - July precipitation in the year of the study than by any other factor. Soil texture did not explain a significant proportion of variability in total ANPP across the entire precipitation gradient. However, soil texture did affect the proportion of ANPP contributed by different functional types. In the case of shortgrass steppe sites in 1993, ANPP decreased significantly with increasing soil water-holding capacity, because of high shrub productivity at the coarse-textured sites with low water-holding capacity. These results suggest that across this regional precipitation gradient, soil texture may play a larger role in determining community composition than in determining total ANPP.

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