The Distribution of Photosynthetic Pathway Types on a Mixed-grass Prairie Hillside

STEVE ARCHER[1]

Range Science Department and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins 80523

ABSTRACT: Plant distributions were examined on a N-facing, mixed-grass prairie hillside near Fort Collins, Colorado. Three plant communities were recognized along the hillside. An *Agropyron smithii*-dominated community was found at the hilltop, while a *Poa-Hordeum*-dominated community was located at the base of the slope. Midslope areas supported a *Bouteloua-Agropyron*-dominated community. Each topographic location had different soil moistures and textures. Grasses with the C_4 photosynthetic pathway had highest importance values on well-drained sites where soil moisture was lowest and soils were coarsest. C_3 graminoids predominated on the relatively moist upper and lower portions of the hillside.

INTRODUCTION

The distribution of plant species with different photosynthetic pathways has been directly and indirectly related to a wide range of regional and continental environmental gradients (Teeri and Stowe, 1976; Syvertson *et al.*, 1976; Eickmeier, 1978; Vogel and Ellis, 1978; Tieszen *et al.*, 1979; Boutton *et al.*, 1980). Less information exists with regard to local distributions of C_3 and C_4 plants, however. The array of interactions between photosynthetic physiology and environment implies a host of important hypotheses concerning local variations in the distribution of C_3 and C_4 species.

Photosynthetic pathways can be a major means by which niche overlap among plants is reduced in both time (Williams and Markely, 1973; Ode *et al.*, 1980) and space. Interspecific competition may be substantially reduced if plants are differentially distributed along local environmental gradients as a result of differences in photosynthetic physiology. The object of this study was to quantify the spatial distribution and abundance of plants, using different photosynthetic pathways, with regard to microtopographic features of the landscape. It was hypothesized that graminoids with the C_3 pathway would dominate moister portions of the slope while C_4 graminoids would dominate more xeric portions of the gradient.

SITE DESCRIPTION

A remnant mixed-grass prairie hillside 9 km S of Fort Collins, Colorado, at an elevation of approximately 1500 m was selected. The area is on the western fringe of what Dix (1974) classified as the Great Plains Province. The overall climate of this area has been classified as semiarid, with warm summers and cold winters. Approximately 75% of the 30-cm average annual precipitation occurs during the growing season between May and September, primarily as irregularly spaced convectional thunderstorms (Smith, 1972). Hot dry winds in the summer and warm chinook winds in the winter significantly reduce effective precipitation. The mean annual temperature is 8.0 C, with an average annual maximum of 19.8 C in July and August and an average minimum of 3.2 C in January. The typical growing season is approximately 130 days, beginning about 5 May and ending about 30 September. Soils were mollisols with a sandy to silty loam surface texture derived from a highly calcareous parent material of alluvial-colluvial origin (Hanson and Smith, 1928). The 32-ha prairie was privately owned and has never been cultivated. Domestic livestock have not been on the area for at least 10 years.

[1] Present address: Range Science Department, Texas A&M University, College Station, TX 77843

METHODS

Nine stands were selected for study, three each from the top, middle and bottom of the hillside. The hillside had a 15° slope and was approximately 400 m long. Summit and bottom positions were relatively flat and uniform topographically, with an average inclination of less than 5°. All slope positions were dominated by grasses. Stands at each slope position were separate from one another and were selected on the basis of maturity, uniformity and lack of recent disturbance. Each stand was large enough to include all species of regular occurrence. A 100-m transect was positioned along the contour in each stand. Twenty 0.1 m^2 (20x50 cm) quadrats were placed along each transect at 5-m intervals. Canopy cover was estimated for each species in early October 1981 using Daubenmire's (1959) method. The reliability of similar ocular estimation techniques has been documented by Winkworth *et al.* (1962). Species presence was used to determine frequency. Relative cover and frequency were summed to give an importance value. Stand diversity was computed using Simpson's Index of Diversity (Krebs, 1978). Species photosynthetic pathways were determined from Vories *et al.* (1977) and Waller and Lewis (1979). Plant nomenclature followed Harrington (1954).

For each quadrat the following parameters were estimated: (1) percent bare soil; (2) effective height of vegetation, and (3) rockiness of the soil. Effective height of vegetation was estimated by averaging the height of a random subsample of all species encountered. Rockiness of soil was estimated using a scaler ranging from 0-4 (Table 1). Three cores of the top 20 cm of soil were randomly collected in each stand and used to estimate the soil moisture content gravimetrically. There had been no precipitation on the site for at least 2 weeks prior to the soil moisture determinations.

RESULTS

Midslope stands had the most (18) species (Table 2). Stands on the relatively flat upper portion of the hillside were dominated by a dense growth of western wheat grass (*Agropyron smithii*) interspersed with needle and thread (*Stipa comata*) and green needle grass (*Stipa viridula*) (Table 2). Stands on the steep, N-facing portion of the hillside comprised a blue grama (*Bouteloua gracilis*)-western wheat grass-sideoats grama (*Bouteloua curtipendula*) complex. Soils of the midslope stands were well-drained, coarse-textured and rocky. Kentucky bluegrass (*Poa pratensis*) dominated stands at the bottom of the hill where soils were poorly drained and fine-textured. Cheat grass (*Bromus tectorum*), foxtail barley (*Hordeum jubatum*) and witch grass (*Panicum capillare*) were common, but subordinate constituents of these stands. Species with the C_3 pathway had highest importance values on top- and bottomslope positions, while species possessing the C_4 pathway had the highest importance values at midslope positions (Table 2). A total of 88, 90 and 83% of the total flora encountered were of the C_3 pathway at the bottom-, top- and midslope positions, respectively (Table 3). All forbs encountered had the C_3 pathway. Of the graminoid lifeforms encountered, 80, 83 and 63% were of the C_3 pathway at the bottom-, top- and midslope positions, respectively.

Stands at the bottom of the slope had the highest percent soil moisture and midslope stands the lowest (Table 3). Vegetation height, an indicator of standing crop, was greatest at the slope base, followed by top- and midslope positions, respectively. Total number of species, percent bare soil and rockiness were lowest in the bottom stands and

TABLE 1. — Scaler values used to estimate rockiness of soils on a N-facing, mixed-grass prairie hillside

Scaler value	Rock size
0	No pebbles or rocks present
1	Small pebbles (< 0.5 cm diameter)
2	Large pebbles (0.5-2.0 cm diameter)
3	Stones (2-15 cm diameter)
4	Rocks or boulders (> 15 cm diameter)

highest in midslope stands. Diversity was greatest in midslope stands and lowest in topslope stands.

DISCUSSION

Hanson and Smith (1928), Hanson (1955) and Hanson and Dahl (1957) studied grassland vegetation along the Front Range of northern Colorado. They described associations corresponding closely to the communities on this N-facing hillside. A more recent study by Moir (1969) also confirmed the widespread distribution of these associations with respect to topographical features, noting that *Agropyron smithii* (C_3) communities occurred on relatively flat, poorly drained areas or in slight depressions on upland terraces, whereas *Bouteloua* (C_4) communities occurred mostly on well-drained soils on gentle slopes.

It was hypothesized that C_3 graminoids would occupy more mesic portions of the slope gradient while C_4 graminoids would occupy the more xeric. To a large extent this was the case. Grasses with the C_4 pathway had highest importance values on the well-

TABLE 2.—Species list and importance values for stands located at the top, middle and bottom of a N-facing prairie catena. Importance values represent the sum of the relative cover and relative frequency for each species in each stand. Three stands at each slope position were averaged

Species	Mean importance value			Photosynthetic pathway
	Top	Middle	Bottom	
Graminoids				
Agropyron smithii	117.4	38.3		C_3
Stipa comata	16.5	24.0		C_3
S. viridula	20.0	12.4		C_3
Bromus tectorum	10.8		46.2	C_3
Koeleria cristata	6.7	8.5		C_3
Oryzopsis hymenoides		1.2		C_3
Poa pratensis			69.3	C_3
Hordeum jubatum			29.6	C_3
Juncus spp.			7.9	C_3
Panicum capillare	3.6		26.1	C_4
Bouteloua gracilis		58.3		C_4
B. curtipendula		34.9		C_4
Andropogon scoparius		1.1		C_4
Forbs				
Liatrus punctata	1.8	3.2		C_3
Helianthus spp.	9.5	1.1	7.9	C_3
Haplopappus spinulosus	1.8			C_3
Eriogonum effusum	1.8	2.1	5.1	C_3
Circium spp.				C_3
Polygonum spp.			10.3	C_3
Zanthocephalum sarothrae		3.2		C_3
Opuntia polyacantha		2.3		CAM
Aster spp.		2.5		C_3
Astragalus spp.		1.1		C_3
Artemisia ludoviciana		3.2		C_3
Rosa spp.		1.2		C_3
Penstemon spp.		1.1		C_3
Total number of species	10	18	8	

drained hillside where relative soil moisture was lowest and soils were coarsest. C_3 graminoids dominated the level upland site and the very wet lowland site. These observations agree with those made by Boutton *et al.* (1980), who qualitatively observed that for any given site over a wide elevational gradient, low-lying areas typically supported more C_3 grass and forb biomass and less C_4 biomass than surrounding upland areas at the same site. Teeri (1979) qualitatively discussed the distribution of photosynthetic pathways with regard to microclimatic variables and noted that both C_3 and C_4 species were broadly distributed among habitats ranging from shaded to nonshaded and moist to dry, with the relative proportion of C_4 grasses being greater in the open and drier habitats.

Data presented in this study agree with observations made by Barnes and Tieszen (1978), Tieszen *et al.* (1979), Boutton *et al.* (1980) and Barnes and Harrison (1982), which suggest that on a local basis water availability may be of primary importance in governing the distribution of C_3 and C_4 graminoids despite regional temperature regimes. Thus, while the C_4 pathway is an important adaptive mechanism in hot regional environments where irradiance levels are high it does not necessarily provide a significant advantage on local sites where moisture is sufficiently available to C_3 plants. However, physical and chemical differences in soils along toposequences (Kleiss, 1970; Malo *et al.*, 1974; Jenny, 1980), coupled with variations in water movement, storage and overall slope energy budgets, undoubtedly interact and play a key role in governing plant distributions and resource partitioning strategies on a local level.

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TABLE 3.—Summary of vegetation-slope characteristics of a N-facing, mixed-grass prairie hillside near Fort Collins, Colorado. Numerical values are means computed for each group of three stands. Row means followed by the same letter are not significantly different at $P < .05$

Parameter	Slope position		
	Top	Middle	Bottom
Dominant species	Agsm[1]	Bogr-Agsm-Bocu[2]	Popr-Hoju-Paca[3]
% Soil moisture	18b	11c	73a
Rockiness	0.2b	1.8a	0.0b
% C_3 (graminoids only)	83a	63b	80a
% C_3 (total flora)	90a	83b	88a
Vegetation height (cm)	40b	18c	90a
% Bare soil	11b	21a	4c
Total number species[4]	10b	18a	8b
Stand diversity[5]	0.62b	0.88a	0.68b

[1] *Agropyron smithii*
[2] *Bouteloua gracilis-Agropyron smithii-Bouteloua curtipendula*
[3] *Poa pratensis-Hordeum jubatum-Panicum capillare*
[4] Refers to total number of species encountered in sampling regime averaged for each group of three stands
[5] Simpson's Diversity Index (Krebs, 1978)

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