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Floristic diversity of C_3 and C_4 graminoids in relation to the grazing / landscape location in short-grass steppe

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A study was conducted to determine the floristic diversity of C_3 and C_4 graminoids in relation to grazing intensity and topographic features at the Central Experiment Station within a short grass steppe in the United States. The species diversity of C_3 graminoids decreased as grazing intensity increased at all hill-slope positions: upper, mid-, lower. The variation of C_4 diversity, on the other hand, differed according to hill-slope position: an increase with intensified grazing level on the upperslopes; no significant change on the mid-slope; higher values with light or moderate grazing than with no or heavy grazing on the lowerslope. Species diversity, relating to all species or to forbs alone, showed the highest values with light grazing, supporting the "intermediate disturbance theory". However, the species diversity within the graminoid group did not show such a trend as a function of grazing intensity. As the grazing intensity increased, the total coverage of C_3 grarminoids decreased while that of C_4 graminoids increased on every part of the hill-slopes. The coverage response of individual species did not show uniform trends to grazing/landscape location within the C_4 group, but C_3 individual species in most cases showed higher values with no grazing than with heavy grazing intensity. The results indicate that the open spaces made by grazing may be occupied more swiftly by the C_4 components than C_3 components.

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Introduction

C_4 plants have been suggested to originate from dry or tropical climates in the extensive literature (e.g. Black 1971, Bjorkman 1973, Hasegawa 1979). Teeri and Stowe (1978) showed that the floristic diversity of C_4 grasses decreased with increased latitude in North America, which implies that they evolved in the tropical region. A climatological study on the distributional pattern of C_3 and C_4 plants was also undertaken in the humid climate of South Asia by Takeda and Hakoyama (1985) and similar patterns of C_3 and C_4 distribution were demonstrated. However, few studies have considered to what extent and how the C_4 plants invaded the C_3 territory and expanded their distribution.

One substantial factor that influence the distribution of C_4 plants, besides climatic conditions, may be human activity related to the clearing of forest, denudation, and pasturage. Because of the physiological advantage in C_4 plants in water limited and highly irradiated places (Cooper 1965, Downton & Tregunna 1968, Welkie & Caldwell 1970, Gifford 1974, Doliner & Jollife 1979), we suspect that C_4 plants invade such a place more swiftly than C_3 plants or that they can take over the C_3 plant habitat when the canopy cover is cleared and surface temperature and irradiance increase, while humidity decreases inside the plant community. Okuda (1986) suggested that herbivore grazing was one factor influencing the ecological distribution of C_4 plants, because herbivore grazing has the potential to alter these micro-environmental factors.

As a first step to demonstrate the expansion process of the C_4 distribution, it is important to know to what extent the grazing history over the rangeland ecosystem is effective in altering the abundance of C_3 and C_4 species. The primary objective of the present study is to clarify how such a displacement occurs in relation to long-term grazing history associated with landscape location. Although there are numerous studies of the response of plant coverage in short-grass steppe to grazing history (e.g. Klipple & Costello, 1960), few concern the changes in species diversity. A secondary objective is to establish which disturbance level optimizes species diversity and the extent to which optimization depends upon the life-form classification. For this purpose, we studied the changes in C_3 and C_4 dominance as well as those in graminoids and forbs at different grazing levels (grazing intensities) and different topographical locations in short-grass steppe.

Study area and Method

The study area was a short-grass steppe site on the United States Department of Agriculture - Agricultural Research Service Central Plains Experimental Range (CPER) about 13 km NE of Nunn, Colorado (40°49'N, 104°37'W) (Fig. 1). The topography of the area consisted of gently rolling hills (catenas) with broad summits separated by wide ephemeral stream courses with a mean elevation of 1650 m. Average annual precipitation is 310 mm, 70% of which falls during the growing season. Mean monthly temperatures range from below -5°C in December and January to 22°C in July. Soils at the CPER are mostly loams and range from clay loams to sandy loams. Catena summits were Ustic torriorthents formed in ancient coarse alluvium. Footslopes were typically Pachic argiustolls formed in recent fine textured alluvium (Schimel et al. 1985).

Since 1939 three pastures (each 130 ha) have been subjected to light, moderate and heavy summer grazing by cattle (Klipple & Costello 1960). Grazing pressure was regulated such that approximately 225 kg/ha, 365 kg/ha and 450 kg/ha remained at the end of each growing season on heavily, moderately and lightly grazed units, respectively. The double fenced areas between the different types of pasture and livestock exclosure (each 0.4 ha) have remained ungrazed and were regarded as non-grazing pasture. The biomass of non-grazing pasture was not measured, but is thought to be similar to that of light grazing.

Four catenas were sampled in each grazing treatment during late July and early August 1982, when most species were phenologically well developed (Dickinson & Dodd 1976). Catena backslopes were inclined 15° to 20° and were 200 to 300 m in length. Three plots, each consisting of ten quadrats (50 X 50 cm), were placed at each catena position: summit (upper slope), mid-way down backslope (mid-slope), footslope (lower slope). In total, 48 plots consisting of 480 quadrats were investigated and the canopy coverage (Daubenmire 1959) was estimated for each species observed in a quadrat.

C_3 and C_4 species were discriminated in accord with the study done by Waller and Lewis (1979). Since coverage of C_4 forbs (e.g. *Euphorbia fendleri*, *Kochia scoparia*, *Portulaca oleracea*) was too low to compare with that of C_3 forbs, the comparison of C_3 and C_4 distribution was made only for the graminoids. A species diversity index (Shannon & Weaver 1949) was calculated for each life form: forbs, graminoids (C_3 and C_4 graminoid) and all species based upon the coverage of each species, using the following equation:

$$H(S) = -\sum_{i=1}^{s}(Pi)(\log_2 Pi)$$

where *s* is the total number of species within each life form and *Pi* is the relative coverage of species *i* th.

Because we have no similar data on plant distribution and abundance prior to initiation of the grazing treatments in 1939, we must assume that differences observed at the time of sampling 43 years later largely reflect the differences between grazing treatments, not merely preexisting differences between areas.

ANOVA was used to examine the significance of the differences in mean values of *H(S)* among the different plots.

Results

1. Diversity and coverage of C_3 and C_4 species

The C_3 species diversity exhibited a descending trend with increase in grazing intensity. On the other hand, the variation of the C_4 species diversity was strictly dependent on the hill-slope position: on the upper slope, the variation was the opposite to that of C_3 species, while it showed little change on the mid-slope (Fig. 2). C_4 diversity declined sharply with heavy grazing on the lower slope and showed a variation curve with its optimum at light grazing. Only *Buchloë dactyloides* among the C_4 species group was abundant on the lower slopes of heavily grazed pasture. Although other C_4 species, such as *Bouteloua gracilis*, *Muhlenbergia torreyi*, and *Schedonnardus paniculatus* were found there, their coverage was usually less than 5%. *S. paniculatus* showed its highest value on the lower slopes of heavily grazed pasture among the sites where it occurred. Due to the high dominance of *B. ductyloides*, total coverage of C_4 species (cumulative value of C_4 species coverage) did not decline on the lower slopes of heavily grazed pastures as C_4 diversity did (Table 1). As a result, the total coverage of C_3 and C_4 species showed clear replacement as a function of grazing intensity; the former

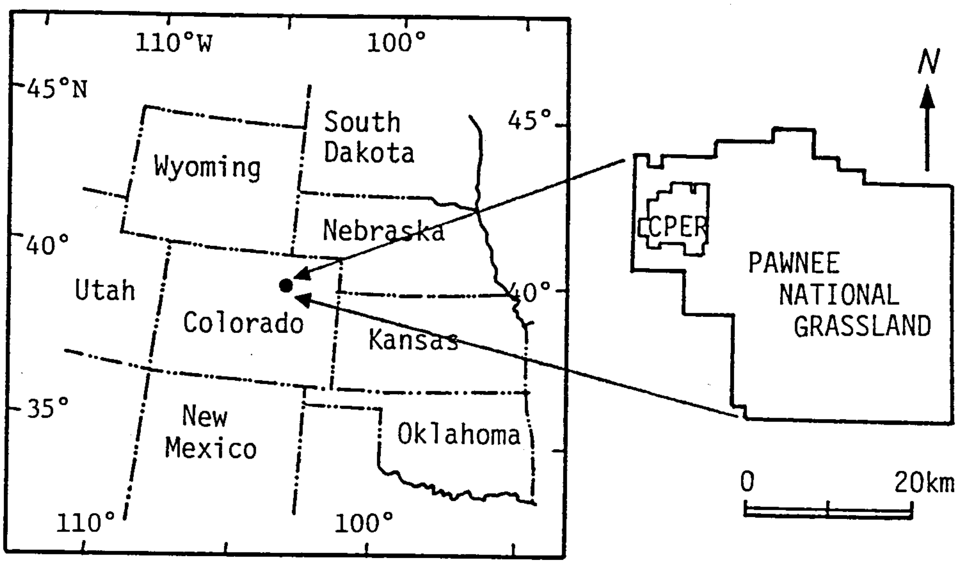

Fig. 1. The location of the study area, CPER (Central Plains Experimental Range) in Pawnee National Grassland.

decreased while the latter increased as the grazing level was intensified in every hillslope position. However, the coverage of individual C_3 and C_4 graminoids did not necessarily follow this trend.

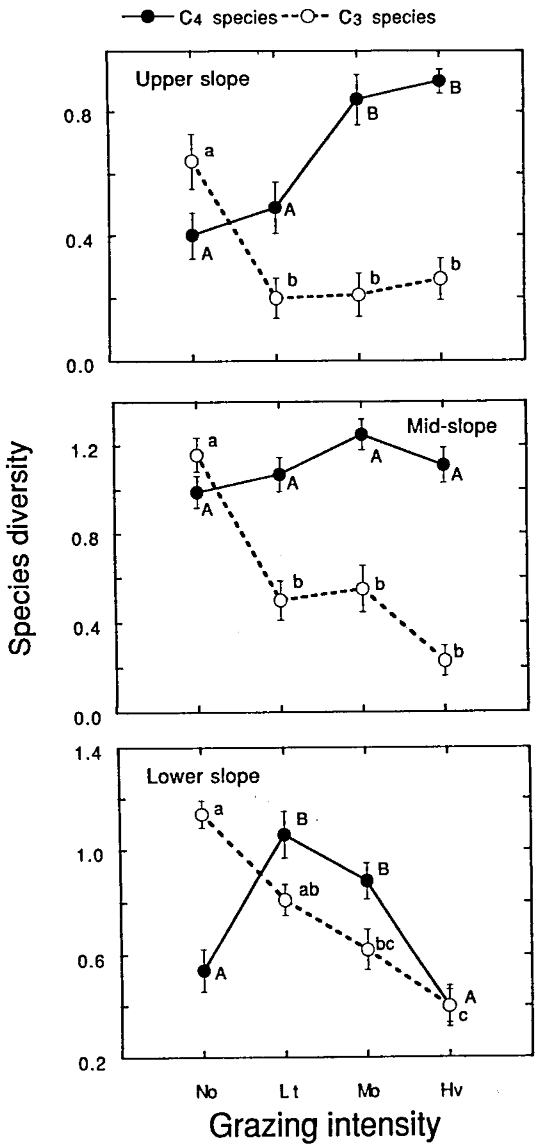

Fig. 2. The variation of C_3 and C_4 species diversity at four grazing intensities (No: Non, Lt: Light, Mo: Moderate and Hv: Heavy grazing) on three different hillslope positions. The vertical bars represent means ±1 SE. Different letters indicate differences between different grazing intensities in either of C_3 or C_4 diversity at $P<0.05$.

The species diversity of all graminoid species (C_3 + C_4 graminoids) did not show consistent changes along the grazing gradient among the three hillslope positions. Diversity based on all species showed a slightly higher value with light grazing than with no or heavy grazing. The trend was most distinct in the case of the lowerslopes; the value with light grazing was significantly higher ($P<0.05$) than with other grazing levels. The values in forbs follow this trend.

Species diversity for all three categorized groups (graminoids, forbs, all species) showed the lowest value on lowerslopes in heavily grazed pasture. In addifion to the low species richness of graminoids, only some forbs [*Chenopodium lepthophyllum* (C_3), *Euphorbia fendleri* (C_4), *Gaura coccinea* (C_3), *Sphaeralcea coccinea* (C_3), *Iva axillaris* (C_3), *Sophora sericea* (C_3)] were found with low coverage. During field observations on the heavily grazed pasture, we found that the cattle utilized intensively the lower slopes.

Discussion

Several authors (e.g. Grime 1973, Connell 1978, Huston 1979) have put forward the theory that a moderate level of disturbance optimizes species diversity. According to this theory, known as "intermediate disturbance hypothesis", the coexistence of species is allowed due to factors that interrupt competitive interactions. A higher diversity would be found in communities where competitive replacement is far from the equilibrium stage, and lower diversity in communities with a higher rate of competitive replacement. The intermediate stage (non-equilibrium stage), where disturbance factors prevent competitive replacement from reaching the equilibrium stage, allows the coexistence of species, and thus higher diversity can be maintained than in stages with higher or lower levels of disturbance. In the present study, the diversity values for all species or only forbs generally agreed with this trend. However, the

Table 1. Variation in mean coverage for individual C_3 and C_4 graminoids and sum of their coverage in each group in relation to grazing intensity; N: Non, L: Light, M: Moderate, H: Heavy.

	Upper slope				Mid-slope				Lower slope			
Species name	N	L	M	H	N	L	M	H	N	L	M	H
C_3 graminoid												
Agropyron smithii	8.8	3.0	1.0	0.3	9.8	13.0	2.5	–	22.0	23.0	11.5	6.3
Carex eleochalis	6.3	10.5	9.0	14.8	11.3	6.3	7.5	8.0	20.8	16.0	10.3	11.5
Carex filifolia	0.3	–	1.3	0.8	–	–	1.8	1.0	0.5	0.5	–	–
Festuca octoflora	–	–	–	–	0.5	–	–	0.3	–	–	–	–
Sitanion hystrix	4.0	2.5	0.3	2.3	6.0	1.0	2.5	2.5	2.0	–	0.8	2.0
Stipa comata	2.0	–	0.3	–	9.8	13.0	2.5	–	4.0	0.3	–	–
Coverage sum (C_3)	21.4	16.0	11.9	18.2	37.4	33.3	16.8	11.8	49.3	39.8	22.6	19.8
C_4 graminoid												
Aristida longiseta	1.0	2.3	3.8	0.3	17.0	7.3	12.8	12.3	–	1.3	1.0	–
Bouteloua curtipendula	–	0.5	–	–	–	–	–	–	–	–	–	–
Bouteloua gracilis	43.8	39.3	34.0	24.0	29.3	29.8	26.3	32.3	23.5	27.5	24.8	6.0
Buchloë dactyloides	3.8	8.3	16.0	33.3	7.3	15.3	18.0	13.0	7.3	14.3	31.8	54.0
Distichlis stricta	–	–	–	–	–	–	–	–	–	10.3	2.0	–
Muhlenbergia torreyi	0.5	0.8	1.5	0.8	–	2.8	2.0	1.0	–	1.3	1.0	0.3
Munroa squarrosa	–	–	–	–	–	–	–	–	0.5	–	–	–
Schedonnardus paniculatus	–	–	–	–	–	–	0.3	0.8	–	–	0.8	1.8
Sporobolus cryptandrus	–	–	–	–	0.5	1.5	2.8	3.8	4.0	1.0	0.3	0.3
Coverage sum (C_4)	49.1	51.2	55.3	58.4	54.1	56.7	62.2	63.2	35.3	55.7	61.7	62.4

value for the graminoids did not. Furthermore, when the graminoids were classified into C_3 and C_4 groups, the diversity values also did not follow the "intermediate disturbance hypothesis". This indicates that whether or not the hypothesis is applicable depends upon how the species composition of a community is categorized.

The variations of C_3 and C_4 diversity along the grazing gradient were not due to the uniform response of either C_3 or C_4 species to the grazing. In other words, the optimum growth range of a plant in the grazing gradient relates to species characteristics rather than to differences in photosynthefic pathways. However, it confers the difference in spatial utility that can be occupied by either C_3 or C_4 graminoids as grazing intensity is changed. The highest value of C_3 graminoid diversity in non-grazing for all hillslope positions suggests that more open space was available for C_3 graminoids in any kind of topographical situation as grazing intensity lessened. On the other hand, the lack of a clear relationship between C_4 diversity and grazing level suggests that for any particular grazing condition, there are C_4 candidates that can readily increase their dominance as soon as open space becomes available. These findings suggest that the C_3 aggregated range in the grazing gradient, where most of the C_3 species show optimum growth, was different from that of C_4 species. The former probably occurs with lighter grazing and the latter with heavier grazing.

Okuda (unpubl.) studied the variation in C_3 and C_4 diversity in relation to grazing intensity in secondary grassland of a humid and warm temperate region in Japan, and reported that C_3 species showed an indistinct response to the grazing gradient, but that C_4 species showed a distinct relationship; the latter increased as

Table 2. Variation in mean and standard error of species diversity (Shannon-Weaver Index) for graminoids, forbs and all species in relation to grazing intensity and to hill-slope position (n=40). Notation as in Table 1.

Group	Grazing intensity			
	N	L	M	H
Upper slope				
Graminoids	1.30±0.08	1.17±0.07	1.34±0.09	1.51±0.04
Forbs	0.83±0.11	1.37±0.12	0.69±0.11	0.47±0.11
All species	2.36±0.06	2.56±0.06	2.43±0.09	2.36±0.05
Mid-slope				
Graminoids	2.03±0.04	1.69±0.09	1.82±0.08	1.58±0.08
Forbs	1.31±0.13	1.56±0.11	1.16±0.11	1.38±0.12
All species	2.81±0.05	2.96±0.07	2.84±0.06	2.78±0.07
Lower slope				
Graminoids	1.81±0.06	1.93±0.05	1.60±0.07	1.13±0.08
Forbs	1.50±0.13	1.92±0.10	1.02±0.14	0.14±0.06
All species	2.67±0.08	3.00±0.06	2.36±0.09	1.49±0.10

grazing level intensified. The contrasts in the results can be attributed to the major climate differences i.e. the humid climate may create conditions more suited for C_3 species than C_4 species, while the arid or semi-arid climate allows the predominance of C_4 species.

The variation in C_3 and C_4 diversity relative to the grazing intensity may be attributed not only to the direct effects of grazing but also to its indirect effects. Van Haveren (1983) studied the soil bulk density as influenced by the grazing intensity at the CPER site. Soil compaction from grazing occurred primarily on fine texture soils. Since soil compaction apparently reduces the aerobic space in the soils (Orr 1975, Gifford et al. 1977), it subsequently influences the availability of water for the plant. The high dominance of some C_4 species in heavily grazed pasture may be due to the fact that they can use water very efficiently in highly compacted soil.

Besides the changes in soil properties, differences in mechanical tolerance between individual C_3 and C_4 graminoids or differences in herbivore selectivity for C_3 and C_4 species may be responsible for C_3 and C_4 replacement along the grazing gradient as were pointed out in previous literature (Caswell et al., 1973, Caswell & Reed 1975, 1976, Akin & Burdick 1977, Boutton et al. 1978). However, generalizations about grazing tolerance within the C_3 and C_4 group are difficult, as shown in the present study.

Schwarts and Nagy (1976) and Schwarts and Ellis (1981) studied dietary selectivity of cattle and pronghorn at the Pawnee site, where the present study was conducted, and reported that cattle mainly feed on grasses and that their dietary proportion of warm season grasses (C_4) was greater than that of cool season grasses (C_3) from March to July, with the situation being reversed from August to October. Pronghorn, a minor ungulate in the study area, ate 63–92% forbs when they were available, but relied mostly on cool season grasses (C_3) at other times. These discriminatory foraging patterns may cause higher values for C_4 grasses in heavily grazed pastures.

The variation of C_4 diversity along the grazing gradients depended on the position on the hill-slope. There are at least two interpretations for this: 1) differences in soil conditions; 2) discriminatory habitat utilization by herbivores (livestock animal). Schimel et al. (1985) described the soils along a hill-slope on the CPER site and found that soil physical properties, nutrient content and nitrogen mineralization rates changed significantly along the gradient. The moisture content of the soils was highest on the lower slope. Maximum available water was higher in the fine textured surface soils of the lower slope than in the coarse textured sands of the dune sites (upper slope).

Seasonal patterns of cattle grazing have also been described for this area (CPER) in the relationship to topographic features. Senft et al. (1983) compared the predicted and observed seasonal patterns of spatial use by cattle and found an excellent correlation with pasture characteristics. Cattle frequented the lower slopes during the growing season, while they used the upper slopes during the dormant season. We also found at CPER that the mid-slope was utilized less than the upper and lower slopes. The cattle appeared to utilize the mid-slope only when moving from lower to upper slopes.

It is likely that the response of C_4 species diversity to long-term grazing depends on several factors related to the hill-slope positions. Advantageous features of high water use efficiency in C_4 species may not be operative in the mesic site. This may have caused the lowest value for C_4 diversity to be on the lowerslopes with heavily grazed pasture. On the other hand, the negligible change in C_4 diversity due to grazing on the mid-slope might be due to lower utilization by cattle here. However, the present study failed to show that soil properties and habitat utilization by cattle were responsible for the individual response of C_4 species to grazing intensity.

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奥田敏統, S. Archer, J. K. Detling: ステップ草原における放牧圧と地形的要因が C_3, C_4 植物（穎花類）の種多様性にあたえる影響

C_4 植物の地理的分布をみるとその種類数は低緯度地，低海抜になるにほど上昇し，熱帯など暖かい地方がその起源であることがうかがえる．一方で C_4 植物は高日射，乾燥条件下で適応し，そのような環境が，森林伐採，放牧，開墾等によって部分的に作り出されたところで優占する．いいかえると，C_4 植物の分布の拡大と環境への撹乱作用の度合との間には密接な関連があるものと思われる．このことを明らかにする目的で，アメリカ中西部のステップ草原において C_3, C_4 植物の多様性（Shannon-Weaver Index）が牧牛を主体とする放牧圧の変化と牧野内の地形的要因（斜面の上部，中部，下部）によってどのような影響を受けるかを調べた．なお，C_4 植物はそのほとんどがイネ科，カヤツリグサ科（穎花類）によって占められるため，その比較のための C_3 植物も穎花類とし，広葉草本（forb）の多様性とは区別して解析した．その結果，C_3 植物の多様性は斜面の位置に関係なく，放牧圧が高くなるほど減少した．それに対して，C_4 植物の多様性は斜面の上部では放牧圧が高くなるほど上昇し，C_3 植物のそれと逆の傾向を示したが湿潤地である斜面の下部や放牧牛の利用頻度の低い斜面の中部では同様の傾向を示さなかった．放牧圧の変化に対する個々の C_3, C_4 植物の平均被度をみると C_3 植物の多くは放牧圧が高くなると減少したのに対して，C_4 植物ではそのような一定の傾向がみられなかった．斜面の上部のような乾燥しやすい環境下では高い放牧圧がかかると C_3植物の優占度が低下し，それらがもっていた占有空間をC_4 植物が埋めるように優占することが推察された．