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Species Diversity and Functional Composition of Pastures that Vary in Landscape Position and Grazing Management

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ABSTRACT

The productivity of grasslands depends in part on their diversity of species and functional composition. Our objective was to examine the effects of three landscape positions (summit, backslope, and toeslope) and three stocking systems (continuous, rotational, and nongrazed) on species diversity and percentage of cover of grass, legume, and weed species functional types in southeastern Iowa pastures. Data were collected in 0.2-m^2 plots randomly distributed throughout each of four replicate pastures in spring and summer 2000 and 2001. Backslope landscape positions within pastures managed with either continuous or rotational stocking contained the greatest overall diversity of species. Across years, overall species richness under grazing averaged 4.8 on backslopes, 3.5 on summits, and 2.9 on toeslopes. Legume cover was greatest within the rotational stocking system, averaging 21% on backslopes, 10% on summits, and 3% on toeslopes across years. Cool-season grasses dominated summits and toeslopes, consisting of 88 to 94% of the cover. Weed species diversity and cover were greatest on backslopes within the continuous stocking system. Our results showed that rotational stocking had more desirable effects through greater legume cover and less weed cover on backslopes than continuous stocking. This research suggested that spatial components of pastures should be considered to optimize the production and quality of forage for grazing livestock.

The productivity and stability of aboveground biomass in grassland ecosystems depends in part on the functional composition and diversity of plant species. Recent experiments showed that species-rich grasslands have greater productivity (Hector et al., 1999; Tilman et al., 2001) and reduced year-to-year variability of aboveground biomass (Tilman, 1996). These experiments have been controversial in that the effects of species diversity were not evaluated independently from the effects of key species (Aarrsen, 1997; Huston, 1997). Some scientists have suggested that the productivity and stability of ecosystems do not depend on the number of species but rather the presence of key species and functional types (Grime, 1997; Huston, 1997).

Plant species are commonly classified into either response or effect plant functional types (Diaz et al., 2002). Response plant functional types are groups of plant species that respond similarly to the abiotic and biotic environment. Classification of plants as increasers, decreasers, and invaders in response to grazing (Dyksterhuis, 1949) is an example of grouping plants by their response to the biotic environment. Plants that show resistance to grazing may be further classified into those that exhibit avoidance or tolerance mechanisms (Briske, 1996). Effect plant functional types are groups of plant species that affect ecosystem processes such as productivity, nutrient cycling, and trophic transfer similarly (Diaz et al., 2002). In experiments examining the effects of diversity on productivity of grasslands, functional types included C_3 grasses, C_4 grasses, legumes, non-N-fixing forbs, and woody plants (Hooper and Vitousek, 1997; Tilman et al., 1997). Effect and response plant functional types may further be classified by life history (annuals, biennials, and perennials) and growth form. Perennial grasses may be bunch- or sod-forming (Briske, 1996), and legumes may be clone- or crown-forming (Beuselinck et al., 1994).

Patterns of plant species diversity and functional composition of pastures have been evaluated in the northeastern USA. These pastures generally received little improvements and grazing management for several decades and were dominated by white clover, Kentucky bluegrass, and dandelion (Tracy and Sanderson, 2000b; see Table 1 for taxonomy). Annual and perennial non-N-fixing forbs consisted of ≈90% of the species pool (Tracy and Sanderson, 2000b). Annual and perennial forbs also dominated the seedbanks of these pastures, and it was concluded that a manager, seeking to establish a diverse, mixed-species pasture consisting of productive grasses and legumes, must reseed the desired species (Tracy and Sanderson, 2000a).

Landscape position and grazing management have been shown to affect legume species diversity and abundance in southeastern Iowa pastures. Legume biomass and legume species diversity were greater on backslope positions than on summit or toeslope positions, and pastures managed with continuous and rotational stocking produced greater legume biomass than nongrazed pastures (Harmoney et al., 2001). Spatial patterns of species richness also existed and varied by grazing treatment (Barker et al., 2002). Continuously stocked pastures had a complex structure consisting of species-rich and species-poor patches with secondary patches occurring within primary patches (Barker et al., 2002). How landscape position and grazing management affected overall species diversity and functional composition of these pastures was not determined. This information is important to improving the management of pastures for grazing livestock in spatially heterogeneous environments.

Thus, the objectives of our experiment were to: (i) determine the effects of three landscape positions (summit, backslope, and toeslope) and three stocking systems (continuous, rotational, and nongrazed) on overall species, forage grass, forage legume, and weed species di-

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Abbreviations: AUM, animal unit months.

Table 1. Plant species occurring in experimental pastures at Rhodes, IA. Each pasture consisted of three landscape positions (summit, backslope, and toeslope) and three stocking systems (rotational, continuous, and nongrazed). Values represent the mean aerial cover of each species across all pastures. Pastures were sampled during May and July 2000 and 2001.

Functional group	Common name	Scientific name	Growth form	Cover
				%
Forage grasses	smooth brome	*Bromus inermis* Leyss.	grass	40
	reed canarygrass	*Phalaris arundinacea* L.	grass	33
	Kentucky bluegrass	*Poa pratensis* L.	grass	8
	orchardgrass	*Dactylis glomerata* L.	grass	4
	timothy	*Phleum pratense* L.	grass	1
	tall fescue	*Festuca arundinacea* Schreb.	grass	<1
Forage legumes	birdsfoot trefoil	*Lotus corniculatus* L.	legume	6
	red clover	*Trifolium pratense* L.	legume	1
	white clover	*Trifolium repens* L.	legume	1
	alfalfa	*Medicago sativa* L.	legume	<1
	sweetclovers	*Melilotus* spp.	legume	<1
	cicer milk-vetch	*Astragalus cicer* L.	legume	<1
	kura clover	*Trifolium ambiguum* M. Bieb.	legume	<1
Weed species	quackgrass	*Elytrigia repens* (L.) Desv. ex Nevski	grass	<1
	sedges	*Carex and Cyperus* spp.	grass	<1
	foxtail species	*Setaria* spp.	grass	<1
	redtop bent	*Agrostis stolonifera* L.	grass	<1
	barnyardgrass	*Echinochloa crus-galli* (L.) P. Beauv.	grass	<1
	dandelion	*Taraxacum officinale* F.H. Wigg. aggr.	forb	7
	pale dock	*Rumex altissimus* Alph. Wood	forb	<1
	curly dock	*Rumex crispus* L.	forb	<1
	common yarrow	*Achillea millefolium* L.	forb	<1
	bull thistle	*Cirsium vulgare* (Savi) Ten.	forb	<1
	musk thistle	*Carduus nutans* L.	forb	<1
	Canada thistle	*Cirsium arvense* (L.) Scop.	forb	<1
	tall thistle	*Cirsium altissimum* (L.) Spreng.	forb	<1
	daisy fleabane	*Erigeron strigosus* Muhl. ex Willd.	forb	<1
	hoary vervain	*Verbena stricta* Vent.	forb	<1
	sulfur cinquefoil	*Potentilla recta* L.	forb	<1
	Canada goldenrod	*Solidago canadensis* L.	forb	<1
	common ragweed	*Ambrosia artemisiifolia* L.	forb	<1
	yellow rocket	*Barbarea vulgaris* R. Br.	forb	<1
	field pennycress	*Thlaspi arvense* L.	forb	<1
	hoary alyssum	*Berteroa incana* (L.) DC.	forb	<1
	shepherd's-purse	*Capsella bursa-pastoris* (L.) Medik.	forb	<1
	yellow woodsorrel	*Oxalis stricta* L.	forb	<1
	horseweed	*Conyza canadensis* (L.) Cronquist	forb	<1
	henbit	*Lamium amplexicaule* L.	forb	<1
	blackseed plantain	*Plantago rugelii* Decne.	forb	<1
	common lambs-quarters	*Chenopodium album* L.	forb	<1
	motherwort	*Leonurus cardiaca* L.	forb	<1
	horse-nettle	*Solanum carolinense* L.	forb	<1
	redroot pigweed	*Amaranthus retroflexus* L.	forb	<1
	stinging nettle	*Urtica dioica* L.	forb	<1

versity, and (ii) examine how these factors affect the cover of these functional groups and individual species within pastures. We chose these functional types because grasses provide most of the biomass (Harmoney et al., 2001) and competitively displace legumes (Guretzky et al., 2004) in these pastures. Legumes have high forage quality (Van Soest, 1982), fix atmospheric N_2 through a symbiotic relationship with *Rhizobium* bacteria (Heichel et al., 1985), and usually improve productivity of pasture mixtures (Sleugh et al., 2000). Weed species contribute to biomass, but their forage quality is usually less than that of grasses and legumes, especially as they mature (Marten and Andersen, 1975; Marten et al., 1987). Discussion of the life history and growth habit of the dominant species within the functional types in response to landscape position and grazing management was provided.

MATERIALS AND METHODS

We conducted the experiment at the Iowa State University Rhodes Research Farm (41°52′ N, 93°10′ W) in pastures described by Harmoney et al. (2001). In 1995, a mixture of legumes was frost-seeded into four established cool-season grass pastures. The legumes used were alfalfa, biennial yellow sweetclover [*Melilotus officinalis* (L.) Lam.], biennial white sweetclover (*M. albus* Medik.), birdsfoot trefoil, white clover, red clover, kura clover, cicer milk-vetch, berseem clover (*Trifolium alexandrinum* L.), striate lespedeza [*Kummerowia striata* (Thunb.) Schindler], and annual white sweetclover (*M. albus* Medik.). Because of poor establishment in the first seeding, the legumes were resown in the grass sod in 1996.

Each pasture replicate contained three landscape positions: summit, backslope, and toeslope, and was subdivided into paddocks that used three different stocking systems: continuous, rotational, and nongrazed. The paddocks of each pasture were 0.4 ha. Summit and backslope positions consisted of Downs (fine-silty, mixed, superactive, mesic Mollic Hapludalf) soils, and toeslope positions consisted of Colo (fine-silty, mixed, superactive, mesic Cumulic Endoaquoll) and Ackmore (fine-silty, mixed, superactive, nonacid, mesic Mollic Fluvaquent) soils (Oelmann, 1981). Slopes ranged from 0 to 5% on summit and toeslope positions and 10 to 24% on backslope positions. Previous research showed that aspect did not affect legume diversity or composition of these pastures (Harmoney et al., 2001). Thus, effects of aspect were not examined.

Grazing treatments were initiated in 1996. From 1996 to 1998, grazing began at the end of May and continued until early to mid-August within the continuously stocked plots. Each of the rotationally stocked plots was grazed for 4 d in mid-May, early July, and late October. Stocking rates were similar among the rotational and continuous stocking treatments: 9.4 animal unit months (AUM) ha^{-1} within the rotational system and 10.1 AUM ha^{-1} within the continuous system. An AUM was equivalent to the amount of dry forage that a 454-kg cow, dry or with a calf less than 6 mo old, who eats about 12 kg of dry matter per day, would consume in 1 mo (Iowa State University Extension, 1998). Nongrazed plots were not grazed, but dead vegetation was mowed in mid-November (Harmoney et al., 2001).

From 1999 to 2001, pastures managed with continuous stocking were grazed by two mature, nonlactating beef cows for 28 d in May and June, 21 d in July, and 14 d in October. Pastures managed with rotational stocking were grazed with eight to nine cows for 4 d in May, seven to eight cows for 4 d in July, and six to seven cows for 4 d in October. Initiation of grazing within the continuous and rotational stocking treatments occurred on the same date. Cows were removed from the continuous stocking system when residue height for the majority of the herbage was <13 cm. Cows were removed from the rotational stocking system after the 4-d period of each grazing event. Stocking density within the rotational stocking system was intended to be heavy enough to reduce selective grazing, remove the majority of forage within a 4-d span, and increase the period of rest between grazing events relative to the continuous stocking system.

We used a percentage cover method (Daubenmire, 1968) to visually estimate aerial cover of each plant species throughout the stocking systems and landscape positions. Approximately 100 0.2-m^2 sample plots were randomly distributed and sampled each spring (May) and summer (July) of 2000 and 2001 within each stocking system of each pasture. The landscape position of each sample was noted. An unequal number of plots were sampled throughout the landscape positions of each pasture replicate because the positions of each pasture differed in area.

The relative percentage of cover for each species on a 0 to 100% scale was calculated for each sample plot because the total percentage of aerial cover for all species within a plot could sum to > or <100% due to overlapping of species or gaps between species. Plant species occurring within the pastures were classified into three functional types: forage grasses, forage legumes, and weed species (Table 1). The forage grasses group consisted of perennial cool-season grasses that were desirable within pastures. The forage legumes group consisted of any of the legume species that persisted following initial establishment in 1995 and 1996. All remaining plant species found within the pastures were classified as weed species.

Species diversity was determined for each 0.2-m^2 sample using two measures: richness and the Shannon-Wiener index of diversity (H′). Species richness was calculated by summing the number of different species for the forage grass, forage legume, and weed species functional types found within each sample. The Shannon-Wiener index of diversity was calculated with the formula: $H' = -\Sigma\, p_i \ln p_i$, where p_i was the proportion of sample cover by each species. A correlation analysis also was conducted across years, pastures, landscape positions, stocking systems, and season ($n = 144$) to examine how overall species diversity (richness and H′) and diversity within functional types related to the percentage cover of each functional type. Means were not presented for H′ because of the strong correlations with species richness.

The experiment was a randomized complete block design. Landscape position and stocking system treatments were arranged as a split block within each of the four pasture replicates. Because unequal numbers of 0.2-m^2 samples occurred within each treatment combination, the experiment was analyzed as a randomized complete block design with unequal subclass numbers (Piepho, 1997) using Proc Mixed within the Statistical Analysis System software (SAS Institute, Inc., Cary, NC). The Mixed Procedure, however, could not support the combined analysis of the 4484 plots sampled across both years. Thus, landscape position and stocking system effects were analyzed and presented separately for 2000 and 2001. Pairwise comparisons were made using the DIFF option in Proc Mixed. Significant season effects and interactions of season with landscape position and stocking system occurred ($P < 0.05$) and are mentioned. However, because these effects generally were minor, means are presented and discussed as averaged across spring and summer samples. Landscape position, stocking system, and season were considered fixed and pasture replicates random.

RESULTS

Species Diversity

Overall species richness was greatest on backslope landscape positions within pastures managed with continuous or rotational stocking. Overall species richness averaged 4.1 on backslopes, 3.1 on summits, and 2.5 on toeslopes in 2000 (Table 2). In 2001, a landscape position, stocking system, and season interaction occurred

Table 2. Species richness of pastures at Rhodes, IA, as affected by landscape position, stocking system, and year. Means for overall species richness and richness of forage grass, forage legume, and weed species functional groups were determined among 0.2-m^2 subsamples randomly distributed throughout four replicate pastures in 2000 and 2001. Pairwise comparisons were made only for significant interactions or main effects. Means without a similar letter within a year differ ($P < 0.05$).

		Landscape position							
		2000				2001			
Functional group	Stocking system	Summit	Backslope	Toeslope	Mean	Summit	Backslope	Toeslope	Mean
Overall	continuous	3.5	4.9	2.8	3.7a	3.7c	5.4a	3.2cde	4.1
	rotational	3.3	4.2	2.8	3.4a	3.3cd	4.8b	2.7def	3.6
	nongrazed	2.5	3.1	2.0	2.5b	2.7ef	3.4c	2.1f	2.7
	mean	3.1b	4.1a	2.5b		3.2	4.5	2.6	
Forage grasses	continuous	2.2	2.7	2.1	2.3a	2.3	2.6	2.1	2.4a
	rotational	2.3	2.5	2.1	2.3a	2.1	2.5	2.0	2.2a
	nongrazed	2.0	2.2	1.7	2.0b	2.1	2.2	1.6	1.9b
	mean	2.2ab	2.4a	2.0b		2.2ab	2.4a	1.9b	
Forage legumes	continuous	0.5	0.9	0.1	0.5a	0.5bc	1.1a	0.2d	0.6
	rotational	0.5	1.0	0.2	0.6a	0.5bc	1.2a	0.1d	0.6
	nongrazed	0.3	0.5	0.0	0.3b	0.3cd	0.6b	0.1d	0.4
	mean	0.4b	0.8a	0.1c		0.4	1.0	0.1	
Weed species	continuous	0.8b	1.3a	0.6bcd	0.9	0.8	1.6	0.8	1.1a
	rotational	0.5bcd	0.7bc	0.5bcd	0.6	0.7	1.1	0.5	0.8ab
	nongrazed	0.2d	0.4bcd	0.3cd	0.3	0.3	0.6	0.4	0.4b
	mean	0.5	0.8	0.4		0.6b	1.1a	0.6b	

Table 3. ANOVA table for species richness and percent cover of forage grasses, forage legumes, weed species, and overall species richness in pastures at Rhodes, IA. Sources of variation included four pastures (P), three stocking systems (G), three landscape positions (L), and two seasons (S). The *P* values for main effects and interactions are presented by year.

			Forage grass				Forage legume				Weed species				Overall species richness	
			Richness		Cover		Richness		Cover		Richness		Cover			
Source	*F* test	df	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001
P		3														
G	MS (G)/MS (P × G)	2	*	*	*	***	*	***	ns	**	ns	**	ns	**	***	***
P × G		6														
L	MS (L)/MS (P × L)	2	*	*	***	***	**	***	**	**	**	***	*	**	**	***
P × L		6														
G × L	MS (G × L)/MS (P × G × L)	4	ns	ns	ns	**	ns	**	ns	*	**	ns	*	**	ns	*
P × G × L		12														
S	MS (S)/MS (P × G × L × S)	1	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns
G × S	MS (G × S)/MS (P × G × L × S)	2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
L × S	MS (L × S)/MS (P × G × L × S)	2	ns	ns	ns	ns	*	ns	ns	ns	ns	***	ns	ns	ns	**
G × L × S	MS (G × L × S)/MS (P × G × L × S)	4	ns	ns	ns	ns	ns	***	ns	ns	ns	*	ns	ns	ns	*
P × G × L × S		12														

* Denotes significance at the 0.05 probability level.
** Denotes significance at the 0.01 probability level.
*** Denotes significance at the 0.001 probability level.
ns, not significant

(Table 3). Differences among landscape positions were greater within the continuous and rotational stocking systems than within the nongrazed pastures and when sampled during summer than during spring (data not shown). Overall, species richness was similar among rotational and continuous stocking systems regardless of landscape position or year (Table 2).

Backslope landscape positions consisted of a greater diversity of forage grass and legume species. In 2000 and 2001, an average of 2.4 grass species occurred among plots on backslopes, compared with 2.2 and 2.0 grass species on summits and toeslopes, respectively (Table 2). Landscape position effects on legume species richness depended on season in 2000 and stocking system and season in 2001 (Table 3). In 2000, legume species richness averaged 0.7 in spring and 1.0 in summer among plots on backslopes but was not affected by season on summits and toeslopes, averaging 0.4 and 0.1 on these positions, respectively (data not shown). In 2001, legume species richness was affected in a similar pattern as overall species richness in that backslopes within the continuous and rotational stocking system had the greatest legume species richness and differences were greater when sampling occurred during summer than during spring (Table 2).

Continuous and rotational stocking had similar forage grass and legume species diversity. On average, across landscape positions and years, 2.3 grass species and 0.6 legume species were found among plots in continuous and rotational stocking systems compared with 2.0 grass species and 0.4 legume species among plots in the nongrazed pastures (Table 2). Weed species diversity was greatest on summits and backslopes within the continuous stocking system. Across years, weed species richness on summits and backslopes ranged from 0.8 to 1.6 within the continuous stocking system, 0.5 to 1.1 within the rotational stocking system, and 0.2 to 0.6 within the nongrazed system. Weed species richness was similar among stocking systems on toeslopes in 2000 and 2001 (Table 2).

Landscape position and stocking system effects on overall species diversity and diversity within each functional type were similar whether measured by richness or H′ (data not shown). Within each functional type, correlations of species richness and H′ were $r = 0.87$ for legumes, $r = 0.59$ for grasses, and $r = 0.72$ for weeds (Table 4). The diversity measures also showed strong correlations within functional types to the percentage of ground cover consisting of each functional type (Table 4). These correlations were positive for legumes and weeds and negative for grasses. Overall species richness and H′ were positively correlated with legume and weed species cover and negatively correlated with grass species cover (Table 4).

Functional Composition

Forage grasses, as a percentage of cover, were greatest on summit and toeslope positions within the nongrazed pastures. In 2000, they consisted of 86, 76, and 95% of the cover on summits, backslopes, and toeslopes, respectively, and their cover was 8 to 11% greater within the nongrazed system than within the rotational and continuous stocking systems (Table 5). In 2001, a landscape position and stocking system interaction occurred (Table 3). Forage grass cover was similar among grazed and nongrazed pastures on summits and toeslopes, but on backslopes was 16 to 23% less within the rotational and continuous stocking systems, respectively, than within the nongrazed pastures (Table 5).

Reed canarygrass consisted of 18, 11, and 69% of the cover on summit, backslope, and toeslope positions, respectively, across years ($P < 0.001$). On these same positions, Kentucky bluegrass consisted of 10, 11, and 4% of the cover across years ($P < 0.05$). Stocking system did not affect either species. Interactions of landscape position and stocking system affected the percentage cover of smooth brome in 2000 and 2001 ($P < 0.05$ and < 0.05). Compared with nongrazed pastures, rotational and continuous stocking reduced the cover of smooth brome on backslopes by 20 to 30% across years (Table 6). Smooth brome cover remained similar among the stocking systems on summit and toeslope positions.

Table 4. Correlations between the percentage cover, species richness, and Shannon's diversity index (H′), of forage grasses, forage legumes, and weed species functional groups of pastures at Rhodes, IA. Pearson correlation coefficients (*r*) were computed across four pastures, three landscape positions, three stocking methods, 2 yr, and two seasons ($P < 0.05$; $n = 144$).

		Forage grasses			Forage legumes			Weed species			Overall	
Functional group	Index	% Cover	Richness	H′	% Cover	Richness	H′	% Cover	Richness	H′	Richness	H′
Forage grasses	% Cover	1.00	−0.51	−0.38	−0.85	−0.87	−0.79	−0.69	−0.73	−0.54	−0.86	−0.60
	richness		1.00	0.59	0.54	0.65	0.58	0.22	0.36	0.20	0.80	0.56
	H′			1.00	0.27	0.36	0.59	0.34	0.36	0.59	0.53	0.94
Forage legumes	% cover				1.00	0.89	0.83	0.19	0.35	ns	0.71	0.41
	richness					1.00	0.87	0.39	0.55	0.27	0.88	0.52
	H′						1.00	0.33	0.48	0.41	0.77	0.74
Weed species	% cover							1.00	0.86	0.81	0.62	0.54
	richness								1.00	0.72	0.79	0.57
	H′									1.00	0.50	0.78
Overall	richness										1.00	0.67
	H′											1.00

ns, not significant

Landscape position and stocking system did not affect the percentage of cover consisting of orchardgrass, timothy, and tall fescue (Table 1).

Across years, legumes, as a percentage of cover, tended to be greatest on backslope positions within pastures managed with rotational stocking. In 2000, legumes were not affected by stocking system and consisted of 9, 17, and 1% of the cover on summits, backslopes, and toeslopes, respectively (Table 5). In 2001, a landscape position and stocking system interaction occurred (Table 3). Legumes consisted of 21, 16, and 10% cover on backslopes within rotationally stocked, continuously stocked, and nongrazed pastures, respectively (Table 5). Legume cover was similar among stocking systems on summits and toeslopes.

Red clover consisted of 5% cover on backslopes within the rotational stocking system, but <1% across the other positions and stocking systems in 2000 and 2001 (Table 6; $P < 0.05$ and < 0.05). White clover provided 3 to 4% cover on backslopes within the continuous stocking system but <1% across the other positions and stocking systems in 2000 and 2001 (Table 6; $P < 0.05$ and < 0.09). Landscape position and stocking system had negligible effects on the percentage cover of birdsfoot trefoil, alfalfa, sweetclover, kura clover, and cicer milk-vetch (Table 1).

Landscape position and stocking system interactions affected the percentage of weed species cover both years (Table 3). Weed species cover was greatest on backslope positions within the continuous stocking system (Table 5). Dandelion, the dominant weed species of these pastures, consisted of 8 to 14% of the cover on backslopes within the continuous stocking system (Table 6). Weed species cover was similar among landscape positions within the rotational and nongrazed pastures both years. All other weed species comprised <1% cover throughout the pastures and generally were not affected by landscape position or stocking system (Table 1).

DISCUSSION

Backslope landscape positions consisted of an overall greater diversity of species than summit or toeslope positions. Species diversity was probably inhibited by competition from grasses, accumulation of litter, and low penetration of light through the canopy. It has been shown that as aboveground productivity increases in grasslands a lower diversity of seedlings germinate and survive (Tilman, 1993). Competition from grasses inhibited legume survival on summits (Guretzky et al., 2004), and would likely on toeslopes, because aboveground biomass of grasses decreases from backslopes to summits to toeslopes (Harmoney et al., 2001).

A diversity of species likely contributes to maintenance and stability of aboveground biomass both spatially and temporally in pastures. Experimental manipulations of plant species richness have shown that increased plant diversity causes increased aboveground biomass (Hec-

Table 5. Percentage of cover consisting of forage grasses, forage legumes, and weed species in pastures at Rhodes, IA. Values for each functional group represent main effects of landscape position and stocking system and their interactions by sampling year. Pairwise comparisons were made only for significant interactions or main effects. Means without a similar letter within a year differ ($P < 0.05$).

		Landscape position							
		2000				2001			
Functional group	Stocking system	Summit	Backslope	Toeslope	Mean	Summit	Backslope	Toeslope	Mean
		%							
Forage grasses	continuous	81	68	94	81b	87ab	63d	93ab	81
	rotational	84	74	92	84b	87ab	70c	92ab	83
	nongrazed	92	85	98	92a	93ab	86b	94a	91
	mean	86b	76c	95a		89	73	93	
Forage legumes	continuous	9	17	2	9	6cd	16b	2d	8
	rotational	11	21	3	11	8cd	21a	3d	11
	nongrazed	7	12	0	6	5cd	10c	2d	6
	mean	9b	17a	1c		6	16	2	
Weed species	continuous	10b	15a	5c	10	7bc	21a	6bc	11
	rotational	5bc	5c	5bc	5	5bc	9b	5bc	6
	nongrazed	1c	3c	2c	2	2c	4bc	3bc	3
	mean	5	7	4		5	11	5	

Table 6. Percentage of cover consisting of smooth brome, red clover, white clover, and dandelion in pastures at Rhodes, IA. Values for each species represent means as affected by landscape position and grazing management interactions. Means without a similar letter within a year differ ($P < 0.05$).

		Landscape position							
		2000				2001			
Species	Stocking system	Summit	Backslope	Toeslope	Mean	Summit	Backslope	Toeslope	Mean
		%							
Smooth brome	continuous	50ab	36bcd	13e	33	51bc	30d	13d	31
	rotational	54ab	44bc	26cde	41	54abc	42c	20d	39
	nongrazed	65a	65a	21de	50	61a	61a	23d	49
	mean	56	48	20		55	44	19	
Red clover	continuous	0b	2b	0c	1	0c	3b	1bc	1
	rotational	2b	5a	0c	2	1bc	5a	0c	2
	nongrazed	0b	0c	0c	0	0c	1c	0c	0
	mean	1	2	0		0	3	0	
White clover	continuous	2b	4a	0c	2	1b	3a	0b	1
	rotational	1bc	0bc	0c	0	1b	0b	0b	1
	nongrazed	0c	0c	0c	0	0b	1b	0b	0
	mean	1	1	0		1	1	0	
Dandelion	continuous	3b	8a	1b	4	3b	14a	3b	7
	rotational	1b	1b	0b	1	1b	3b	1b	1
	nongrazed	0b	1b	0b	0	1b	2b	1b	1
	mean	1	3	1		2	6	1	

tor et al., 1999; Tilman et al., 2001) and reduces year-to-year variability of biomass (Tilman, 1996) in grasslands. Niche complementation is a proposed mechanism that allows species-rich mixtures to capture and use resources more completely and have greater productivity than less diverse versions or monocultures of any individual species (Hector et al., 1999; Tilman et al., 2001). The importance of diversity, however, depends on soil fertility (Huston, 1997) and moisture (Mulder et al., 2001), and diversity effects on productivity are likely to be greater when and where these factors are limited (Huston, 1994).

A greater overall diversity of species may be necessary to capture and convert available light to biomass on backslopes because these positions likely have less fertility and/or moisture than summits and toeslopes. We did not determine the relationship of landscape positions with soil properties in these pastures because previous attempts have been largely unsuccessful; summit, backslope, and toeslope positions were similar for several properties, including soil P, K, pH, organic matter, and texture (Harmoney, 1999). Summits and toeslopes, however, produced 0.5 and 2.4 Mg ha^{-1}, respectively, more grass biomass than backslopes (Harmoney et al., 2001). Along rolling landscapes, soil organic matter and A-horizon thickness tends to be proportional to slope, and soils on steep slopes tend to be thin and have low organic matter in the A-horizon (Birkeland, 1999). Toeslopes also have been shown to have greater soil moisture and exhibit poorer drainage than other landscape positions (Hanna et al., 1982; Knapp et al., 1993).

Grazing increased overall species diversity in these pastures. We found that pastures managed with either continuous or rotational stocking had greater overall species diversity than nongrazed pastures, particularly on backslope landscape positions. Competitive interactions have been shown to decrease species richness of grasslands when disturbances such as grazing are absent (Collins et al., 1998). In remnant prairies in Wisconsin, lack of disturbance led to reductions of plant diversity, species small in stature and seed size, and N_2 fixing plants (Leach and Givnish, 1996). Large grazing animals create heterogeneity in plant communities through patch-selective defoliation, trampling, and excretion of manure and urine (Steinauer and Collins, 1995).

The diet selection process of cattle consists of a hierarchy from the landscape scale down to the individual plant (Stuth, 1991). At the landscape level, distance to water and steepness of slopes can impede cattle grazing of certain plant communities (Stuth, 1991). In our pastures, slope gradients did not exceed 24%, and paddocks were small, 0.4 ha, and did not restrict cattle from grazing away from the water source. We also did not observe cattle preferring to graze one landscape position before another. Previous studies showed that at a landscape scale, cattle preference for plant communities (Walker et al., 1989a) and the quality and botanical composition of their diets (Walker et al., 1989b) were similar among rotational and continuous stocking systems.

Within plant communities, selection occurs primarily at the patch scale (Hodgson et al., 1994). Cattle generally show preference for patches with a high abundance of leaves before stems, live before dead components, and legumes before grasses, and generally, avoid patches with toxic plants, mature seed heads, and plant materials with high structural strength (Hodgson et al., 1994). In our pastures, stocking rates were similar among the rotational and continuous stocking systems. Continuous stocking, however, allowed less time for plant recovery between defoliations and created patches that varied in degree of utilization. Sward heights were ≈2 to 5 cm within heavily-utilized patches and 20 to 30 cm within under-utilized patches. By midsummer, underutilized patches appeared to be dominated by mature grasses. Within the rotational stocking system, cattle were stocked at a high density for a short period to minimize patch-selective grazing. Sward heights, following each rotation, were ≈10 to 20 cm on summits and backslopes and 20 to 30 cm on toeslopes. Despite differences in selection and time of recovery, overall species diversity was similar among the rotational and continuous stocking systems. Our results contrasted with Barker et al. (2002), who found that patches varied more in species richness under continuous stocking than under rotational stocking. The differences may have been due to different sampling techniques as we characterized the vegetation at a courser scale using plots as opposed to a fine-scale using transects.

Species diversity within functional types (Tilman et al., 1997) and the presence of key species or functional groups (Grime, 1997; Huston, 1997) is also known to affect the productivity and stability of grasslands. Perennial cool-season grasses dominated summit and toeslope positions, particularly in the nongrazed pastures. These grasses were primarily sod-forming, and averaged across years and stocking systems, they accounted for 88% of cover on summits and 94% of cover on toeslopes (Table 5). Reed canarygrass dominated the toeslopes and smooth brome dominated the summits and backslopes. Kentucky bluegrass was a subordinate grass species having greater cover on summits and backslopes than toeslopes.

As with overall species diversity, we found that grazing effects on species composition and diversity within functional types were strongest on backslope positions. Forage grass species richness and H′ were correlated negatively with the percentage of cover consisting of grasses (Table 4). Grazing reduced cover of smooth brome by 20 to 30% within the rotational and continuous stocking systems relative to the nongrazed pastures (Table 6). Smooth brome, a grass with high forage quality, is susceptible to energy depletion when grazing occurs during jointing and if recovery periods following defoliation are inadequate (Brummer and Moore, 2000). As grazing reduced cover of smooth brome, the occurrence of minor grass species like Kentucky bluegrass, orchardgrass, and timothy increased in these pastures (Guretzky et al., 2002), thus increasing grass species diversity.

Legumes provided a greater percentage of cover on backslope positions, especially within pastures managed with rotational stocking. Continuous stocking increased cover of white clover and weed species, particularly dandelion, on backslopes, while rotational stocking increased cover of red clover. Taller grazing heights, which occurred throughout the rotationally stocked system, favor upright-growing legumes like red clover (Carlassarre and Karsten, 2002). Shorter heights, which occurred within the heavily utilized patches of the continuous stocking system, favor less productive, prostrate-growing species like white clover and dandelion (Carlassarre and Karsten, 2002). Birdsfoot trefoil, an intermediate-growing species, was the dominant legume but was not favored by any method of stocking. The accumulation of tannins within birdsfoot trefoil may have enhanced its success throughout these pastures, as grazing animals often avoid legumes that produce secondary compounds (Hodgson et al., 1994).

Seeding a diverse assemblage of legume species improves forage production and quality on backslopes and may improve its fertility (Harmoney, 1999; Harmoney et al., 2001). Legumes fix atmospheric N_2 through a symbiotic relationship with *Rhizobium* bacteria, and as their roots, nodules, and leaf residues decompose, soil N may increase (Heichel et al., 1985). Legumes may improve the nutritional value of forage mixtures because of their high crude protein and digestibility (Van Soest, 1982). Our results concurred with Harmoney et al. (2001), who found an average of 2.2 legume species on backslopes, 1.3 on summits, and 0.9 on toeslopes among these pastures. Across landscape positions, stocking systems, and pastures, legumes, as a percentage of dry matter, were correlated positively with legume species richness and species dry matter diversity (Harmoney et al., 2001). We found similar positive correlations between the percentage of pasture cover consisting of legumes and legume species richness and H′ (Table 5).

Weed species diversity was greatest on backslope positions within the continuous stocking system (Table 2). The weed species functional type consisted of annual grasses, sedges, rushes, and annual, biennial, and perennial forbs (Table 1). These species, especially annual and perennial forbs, have high seed rain and comprise most of the species in seed banks of pastures (Tracy and Sanderson, 2000a). Selective grazing and trampling by cattle probably favors their recruitment (Tracy and Sanderson, 2000b). Weed species, as a percentage of pasture cover, were positively correlated with overall species richness (Table 5) contrasting with the hypothesis that as species richness increases in grasslands, weed invasion should decrease (Tilman, 1997). This may have occurred because our study was conducted in temperate pastures where approximately one-third of the species within a sample plot were weed species as opposed to ungrazed, native grasslands as in Tilman (1997). Tracy and Sanderson (2000b) found that 90% of the species pool in northeastern U.S. pastures was comprised of weed species.

In conclusion, our experiment indicated that landscape positions differ in the diversity and composition of grass, legume, and weed species, and that grazing was important to the maintenance of species diversity in pastures. In pastures that vary in landscape positions or grazing conditions, a diversity of grass and legume species may be necessary to exploit heterogeneity in resource conditions (Tilman, 1996) and maintain yield and quality of forage both spatially and temporally (Harmoney et al., 2001; Sleugh et al., 2000). By producing greater legume cover and less weed cover on backslope positions, rotational stocking had more desirable effects on the diversity and functional composition of these pastures than continuous stocking. Our research suggested that forage managers consider spatial components of pastures to optimize forage productivity and quality for grazing livestock.

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