FORAGE & GRAZING LANDS

Productivity and Stability Relationships in Mowed Pasture Communities of Varying Species Composition

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ABSTRACT

Plant species composition of most managed pasture lands tends to be dominated by one or two species, usually a perennial grass and a legume. Recent ecological research suggests that increasing this forage diversity could increase pasture productivity and stability. We conducted a 4-yr field experiment to determine whether increasing the diversity of pasture mixtures would increase yields and improve interannual yield stability. Mixtures of cool-season pasture plants ranging from one to 15 species were planted into 2.25-m^2 plots in May 1998. Interannual yield variation and yield responses to mowing frequency (2- vs. 4-wk frequency) were used to evaluate stability. Forage yields averaged <400 g m^{-2} yr^{-1} in mixtures having one or two species, while mixtures with three or more species averaged >1000 g m^{-2} yr^{-1}. Increasing the diversity of mixtures beyond three sown species did not consistently improve yields. Interannual yield variation was lowest in the one- and two-species mixtures, and showed no consistent relationship with increasing species diversity. The number of species planted in each mixture declined by approximately 30% from 1999 to 2001, with the mixtures becoming dominated by perennial grasses. Although limitations in our experimental design prevent us from making strong conclusions about relationships between forage diversity and pasture productivity, our findings suggest that increased forage yield and stability may be best achieved by planting two or three forage species that are well matched to specific environmental conditions rather than planting a random assemblage of forage species in a complex mixture.

RECENT RESEARCH SUGGESTS that positive relationships between plant diversity and aboveground productivity may be common in grasslands (Bullock et al., 2001; Hector et al., 1999; Naeem et al., 1994; Tilman et al., 2001). The positive relationship between plant diversity and production in grasslands may involve resource use complementarity among plants where different species complement each other by having different rooting depths, leaf architecture, and growth rates. If species complement each other in resource use, then the community as a whole may use local resources more efficiently and rates of primary productivity may increase as a result (Hector et al., 1999; Naeem et al., 1994; Tilman et al., 1996). The same explanation can be invoked to explain why more diverse plant communities often show improved soil nutrient retention (Hooper and Vitousek, 1997, 1998; Tilman et al., 1996).

Stability is another important component of sustainable agroecosystems, and some evidence suggests that greater plant diversity in grasslands may improve aboveground biomass stability in the face of disturbance (Frank and McNaughton, 1991; McNaughton, 1977; Mellinger and McNaughton, 1975; Tilman and Downing, 1994). This result reflects the probability that a large species pool should, by chance, possess one or two stress-tolerant species that are able to resist disturbance (e.g., drought). Stress-tolerant species should compensate for the loss of other species during the disturbance and help stabilize biomass across time.

Pastures in the northeastern USA are typically species rich, but this richness is dominated by transient weedy plants that contribute little forage value to livestock (Tracy and Sanderson, 2000b). The species richness of forage plants that dominate the biomass of pastures is low, usually consisting of one perennial grass and one legume species. Pasture productivity and stability might be improved if the species composition of pasture communities could be shifted from dominance of one or two species to more complex, multispecies-dominated communities. In 1998, we began a field experiment to address questions about the relationship between forage species composition and yield in pasture communities common to the northeastern USA. We planted cool-season pasture forages into 2.25-m^2 plots and varied the species composition of the plots by manipulating species richness (no. of species per mixture). Although such an approach limits some of the conclusions we can make about the relationship between species diversity and pasture productivity (see Materials and Methods), it still provides valuable insights into how different pasture mixtures may perform across time. Our objectives specifically addressed three questions: (i) Do forage yields increase if we increase the diversity of plant species composition in pasture mixes? (ii) Is the interannual variation of forage yield more stable in more diverse pasture communities? (iii) How does species composition change across time in mixtures of differing diversity?

MATERIALS AND METHODS

The experiment was conducted at the Russell E. Larson Agricultural Research Center at Rock Springs, PA (40°43′24″N, 77°55′90″W). Climate at the site is Midwestern, continental with annual temperature averaging 9.4°C and annual precipitation averaging 880 mm (Pennsylvania State University Weather Station, State College, PA). Soils at the site are mostly Alfisols, classified as Typic Hapludalfs in the Hagerstown series (Braker, 1981). Five randomly located soil cores (2.5-cm diam., 10-cm

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Table 1. List of individual species divided into plant functional groups and the eight randomly chosen species combinations that were planted in the field experiment.

Perennial grasses	Legumes	Perennial forbs	Annual forbs
A—Orchardgrass, *Dactylis glomerata* L.	**H—Birdsfoot trefoil, *Lotus corniculatus* L.**	**L—Chicory, *Cichorium intybus* L.**	**N—Turnip, *Brassica rapa* subsp. *rapa***
B—Tall fescue, *Festuca arundinacea* Schreb.	**I—Alfalfa, *Medicago sativa* L.**	**M—Plantain, *Plantago lanceolata* L.**	**O—Rape, *Brassica napus* (L.)**
C—Reed canarygrass, *Phalaris arundinacea* L.	**J—White clover, *Trifolium repens* L.**		
D—Timothy, *Phleum pratense* L.	**K—Red clover, *Trifolium pratense* L.**		
E—Smooth bromegrass, *Bromus inermis* Leyss.			
F—Bluegrass, *Poa pratensis* L.			
G—Perennial ryegrass, *Lolium perenne* L.			

Species mixes

1—A
2—C, G
3—B, H, J
4—B, D, F, K
6—B, E, F, G, K, O
8—D, F, G, H, I, J, L, N
10—B, E, F, G, H, I, K, L, M, N
15—A through O

depth) were taken from the site before planting and analyzed at the Pennsylvania State University Agricultural Analytical Laboratory. Soil tests indicated a mean pH of 6.3, extractable P of 78 kg ha^{-1}, and K, Mg, and Ca levels averaging 0.60, 1.44, and 7.28 cmol$_c$ Kg^{-1} soil, respectively. Soil organic matter averaged 3.46% and soils were classified as silty clay.

Plots were established in April 1998. Existing vegetation was treated with glyphosate isopropylamine salt herbicide, plowed under, and then the site was disced, harrowed, and packed. Seed mixes were manually broadcast into small plots (2.25 m^2) in May 1998. Each plot received 120 g of seed divided equally among the respective species. Eight pasture mixes of 1, 2, 3, 4, 6, 8, 10, and 15 species were chosen by random selection from the same pool of 15 species (Table 1). Plots were arranged in a randomized complete block design with 12 blocks and eight species mixes for a total of 96 plots. Plots were separated by 1.5-m alleys. Plots were not irrigated or fertilized during 1998. In 1999, 2000, and 2001, all plots were fertilized once in April with ammonium nitrate at an equivalent of 4.4 gN m^{-2}. Annual forbs were seeded back into their respective plots in May 1999 and 2000, but did not establish. All species were cool-season, C_3 forage plants that are commonly planted in pastures and haylands of the northeast USA and many other humid, temperate regions of the world (Moser and Hoveland, 1996; Taylor, 1985). Warm-season grasses (C_4 photosynthetic pathway) are difficult to establish in mixture with these competitive cool-season forage species, so we did not include them in the experimental mixtures. Since the composition of the species mixtures remained the same within each diversity treatment, the design technically replicates only species composition. Our conclusions regarding relationships between diversity and pasture production are therefore confined to limitations imposed by the experimental design.

In 1998, forages were allowed to establish for 2 mo after planting and then mowed to a stubble height of 8 cm. Plots were mowed to an 8-cm stubble height thereafter every 4 wk until October to mimic a 4-wk rest interval in a rotationally stocked pasture. In subsequent years, plots were also mowed to an 8-cm stubble height every 4 wk starting in mid-April and ending in mid-October. Detailed measurements and data collection started in May 1999 and continued through the 2001 growing season. Forage yields were estimated before each 4-wk mowing interval by clipping one 10- by 100-cm quadrat per plot to a 2.5-cm height. Forage clippings were dried for 48 h at 55°C and then weighed. Total seasonal yield for each plot was calculated by summing the dry weights from each respective harvest. The May and July harvests from each year were sorted to species before drying to evaluate changes in species composition. Since the number of seeds sown to each plot (i.e., seed weight of individual species) could have affected the relative abundance of forage species in the aboveground vegetation, we also compared the relative abundance of each species present in May 1999 to the number of seeds that were sown in that respective plot.

During the 2000 and 2001 growing seasons, one-half of the blocks ($n = 6$) were randomly chosen to receive more frequent mowing. Plots ($n = 48$) in these six blocks were mowed every 2 wk rather than the regular 4-wk interval. The increased mowing frequency was imposed to determine how the yield stability would respond to an additional mowing disturbance. Throughout the experiment, plots were regularly weeded to maintain the planted species composition.

Percentage soil moisture was measured daily under a nearby experimental plot (<100-m distance) that was planted with perennial grasses and legumes (Table 2). Soil moisture was monitored with a ThetaProbe soil moisture sensor (Dynamax, Inc., Houston) installed to a depth of 10 cm. No extended drought periods occurred during the experiment, but precipitation in May 1999, May 2001, and September 2000 was unusually low (Table 2).

Differences in forage yield among the pasture mixes was analyzed using one-way ANOVA with species mixture as a main effect (df = 7). In 1999, before the additional mowing treatment was introduced into the experiment, all plots were used in the ANOVA (df = 7, 88). Forage yield from plots mowed every 2 or 4 wk were analyzed separately (df = 7, 40) in subsequent years. Stability was assessed by calculating the yield CV from 1999 to 2001 in each plot. Total forage yield (g m^{-2} yr^{-1}) in each plot was averaged from 1999 to 2001 and then divided by the standard deviation to calculate the CV. Yield CVs for 2- and 4-wk mowed plots were analyzed separately. Differences among the mixture CVs were evaluated using one-way AVOVA as described above. We used an α set at 0.05 to determine significance.

RESULTS

Forage species composition affected yields in all years of the experiment ($P < 0.001$). This significant effect

Table 2. Air temperature, rainfall, and soil moisture at Rock Springs, PA, during the growing seasons of 1998, 1999, 2000, and 2001.

	Avg. monthly air temperature					Rainfall					Soil moisture			
Month	1998	1999	2000	2001	30-yr avg.	1998	1999	2000	2001	30-yr avg.	1998	1999	2000	2001
	°C					mm					m^3 m^{-3}			
April	10.0	9.0	8.6	9.4	8.7	172.0	94.0	74.0	62.0	74.0	–	0.34	0.34	0.34
May	17.0	15.1	15.9	14.4	14.8	116.0	37.0	62.0	35.0	92.0	–	0.21	0.24	0.18
June	18.5	19.2	19.7	19.3	19.5	131.0	104.0	97.0	138.0	102.0	0.34	0.18	0.29	0.25
July	20.7	22.9	18.9	19.5	21.8	89.0	61.0	53.0	59.0	92.0	0.31	0.18	0.25	0.26
August	20.9	19.4	19.1	21.3	20.9	71.0	146.0	74.0	91.0	81.0	0.26	0.23	0.28	0.22
September	18.6	16.9	15.1	15.1	16.8	44.0	133.0	48.0	80.0	82.0	0.19	0.30	0.23	0.24
Mean	17.6	17.1	17.7	16.5	17.1	103.8	95.8	68.0	77.5	87.2	0.27	0.24	0.27	0.25

primarily resulted from low yields in the one- and two-species mixtures (Fig. 1). Yields among plots having more than two species were generally similar. Most notably, plots sown with three and eight species tended to yield more than other mixtures in the 2000 and 2001 growing seasons (Fig. 1). Compared with 4-wk clip plots, the higher mowing frequency, imposed every 2 wk, significantly reduced yields (mean g m^{-2} yr^{-1} ± 1 SE) by about 25% in 2000 (1111 ± 66 vs. 828 ± 44, $n = 48$) and 2001 (552 ± 33 vs. 413 ± 24, $n = 48$) (paired *t* tests, $P < 0.001$). Yield differences among the mixtures showed the same pattern whether they were mowed every 2 or 4 wk. Yields were lowest in 2001 possibly because of low rainfall in April, May, and July (Table 2).

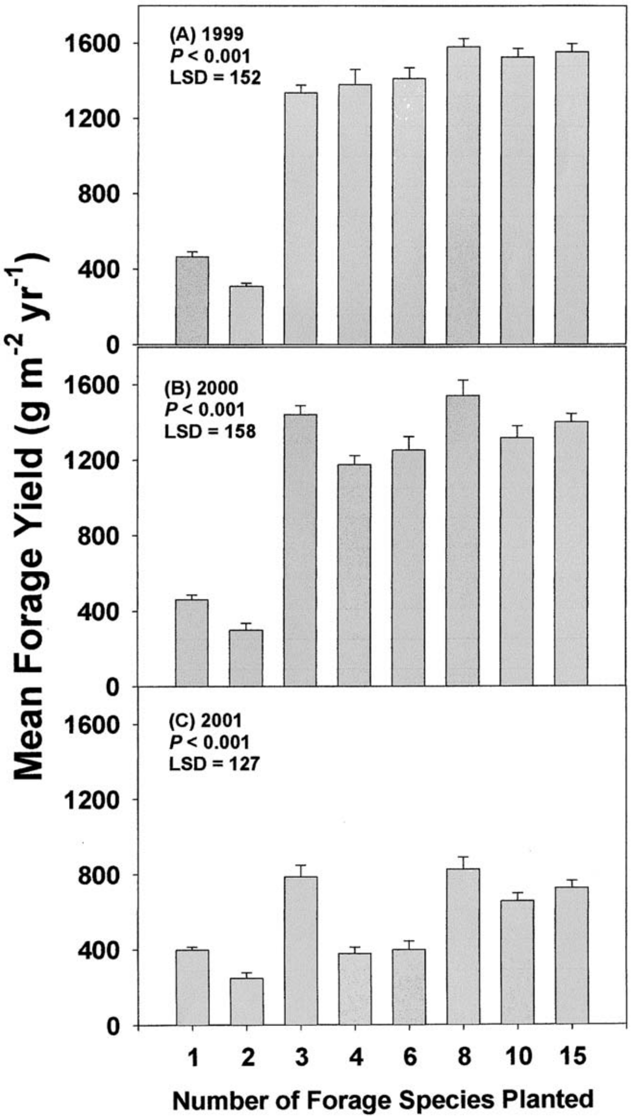

Fig. 1. Mean cumulative yield (dry wt.) in the eight pasture mixtures in (A) 1999, (B) 2000, and (C) 2001. Data are for plots mowed every 4 wk only. Bars are means with ±1 SE.

We calculated CVs from each plot to access the interannual stability of yield among the different forage mixtures. Yield variation from 1999 to 2001 was lowest in the one- and two-species mixtures, while plots sown with four or six species were the most variable (Fig. 2). The higher mowing frequency (2 wk) increased the overall interannual yield variation compared with the 4-wk clip plots. Among the different mixtures, yield variation exhibited a similar pattern in plots mowed every 2 wk to those mowed every 4wk (Fig. 2).

We measured species composition each year by sorting and identifying species from the May and July harvests. Using data from the May harvests, we found significant changes in species composition during the experiment. The number of forage species present in most plots declined from 1999 to 2001 (paired *t* test, $P = 0.003$, df = 5). Excluding plots with one and two sown species, the remaining plots had an average of 6 ± 0.38 species in 1999, 4 ± 0.24 species in 2000, and 4 ± 0.26 species by May 2001. Of the nine perennial grasses originally planted, only three contributed significantly to yield in 2001. Tall fescue (*Festuca arundinacea* Schreb.), orchardgrass (*Dactylis glomerata* L.), and bluegrass (*Poa pratensis* L.) increased in abundance from 1999 to 2001 (Table 3). In contrast, both red clover (*Trifolium pra-*

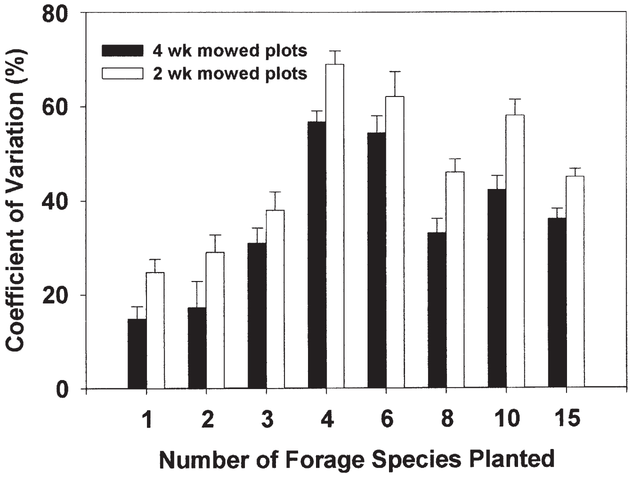

Fig. 2. Interannual yield CV from 1999 to 2001 in plots mowed every 2 and 4 wk. Bars are means with ±1 SE.

Table 3. Proportional change in relative abundance of the forage species from May 1999 to May 2001. Relative abundance was indexed by the change in aboveground biomass of the respective species. Values are means of plots mowed every 4 wk ($n = 6$).

	Number of species planted in each mixture							
	1	2	3	4	6	8	10	15
Orchardgrass	NC†	–	–	–	–	–	–	+0.32
Tall fescue	–	–	+0.53	+0.28	+0.12	–	+0.12	+0.08
Reed canarygrass	–	−0.02	–	–	–	–	–	NP‡
Timothy	–	–	–	+0.01	–	NP	–	NP
Smooth bromegrass	–	–	–	–	−0.02	–	NC	NP
Bluegrass	–	–	–	+0.40	+0.43	+0.51	+0.39	+0.29
Perennial ryegrass	–	+0.02	–	–	−0.03	−0.04	+0.02	+0.02
Birdsfoot trefoil	–	–	−0.02	–	–	NP	NP	NP
Alfalfa	–	–	–	–	–	−0.14	+0.04	+0.01
White clover	–	–	−0.51	–	–	−0.36	–	−0.08
Red clover	–	–	–	−0.69	−0.50	–	−0.66	−0.64
Chicory	–	–	–	–	–	+0.03	+0.10	+0.01
Plantain	–	–	–	–	–	–	−0.01	−0.01
Turnip	–	–	–	–	–	NP	NP	NP
Rape	–	–	–	–	NP	–	–	NP

† NC refers to species that were present but exhibited no change in relative abundance.

‡ NP indicates species that were not present in the plots.

tense L.) and white clover (*Trifolium repens* L.) abundance decreased from 1999 to 2001, while alfalfa (*Medicago sativa* L.) and chicory (*Cichorium intybus* L.) remained at a low, but constant relative abundance (Table 3). Birdsfoot trefoil (*Lotus corniculatus* L.), timothy (*Phleum pretense* L.), reed canarygrass (*Phalaris arundinacea* L.), narrowleaf plantain (*Plantago lanceolata* L.), and Brassicas were largely absent from the mixtures by 2001. The number of seeds sown to each plot was not consistently related to the relative abundance of species present in the aboveground vegetation (Table 4). Two species with comparatively heavy seeds, red clover, and perennial ryegrass (*Lolium perenne* L.), were abundant in mixtures. Other species that had seeds of similar size to red clover and perennial ryegrass [e.g., alfalfa, smooth bromegrass (*Bromus inermis* Leyss.), tall fescue] were not as consistently abundant in mixtures (Table 4). Except for white clover, small-seeded species (e.g., bluegrass, timothy) were not abundant in the aboveground biomass in 1999.

DISCUSSION

Because of limitations of our experimental design, we cannot make strong conclusions about the role of plant diversity per se, and its effect on pasture production and stability. Since the composition of the species mixtures remained the same within each diversity treatment, the design technically replicates only species composition. Given that caveat, our results showed that relatively simple communities can be just as productive and stable as more complex communities if they contain both productive and stress-tolerant species. These findings differ from some recent field experiments that found higher aboveground plant production as plant diversity was increased in grassland communities (Hector et al., 1999; Naeem et al., 1994; Symstad et al., 1998; Tilman et al., 1996, 1997). Several studies have also found increased yields with greater species diversity in agricultural grasslands. Bullock et al. (2001) showed that British haylands sown with 25 to 41 species yielded more than communities sown with six to 17 species. Studies from New Zealand found that pastures sown with 10 to 25 species

Table 4. Relationship between species relative abundance (RA) in May 1999 and number of seeds sown per plot in the different mixtures. Relative abundance is the proportion of aboveground biomass accounted for by that particular species. Annuals turnip and rape were not present in plots by 1999 so were excluded from the table.

	No. of species													
	15		10		8		6		4		3		2	
	RA	Seeds sown × 1000	RA	Seeds sown × 1000	RA	Seeds sown × 1000	RA	Seeds sown × 1000	RA	Seeds sown × 1000	RA	Seeds sown × 1000	RA	Seeds sown × 1000
	%		%		%		%		%		%		%	
Orchardgrass	1.80	8.8	–	–	–	–	–	–	–	–	–	–	–	–
Tall fescue	0.00	3.4	0.15	5.2	–	–	0.57	8.6	20.8	12.9	32.8	17.2	–	–
Reed canary	0.00	9.7	–	–	–	–	–	–	–	–	–	–	0.49	72.8
Timothy	0.03	25.2	–	–	0.11	47.3	–	–	1.9	94.6	–	–	–	–
Smooth bromegrass	0.72	2.6	1.10	3.9	–	–	2.20	6.6	–	–	–	–	–	–
Bluegrass	0.23	35.3	0.15	52.9	0.43	66.1	0.70	88.2	3.8	132.3	–	–	–	–
Perennial ryegrass	16.60	4.4	19.8	6.6	40.70	8.3	36.40	11.0	–	–	–	–	99.50	33.1
Birdsfoot trefoil	0.07	6.6	0.18	9.9	0.25	12.4	–	–	–	–	1.4	33.1	–	–
Alfalfa	3.60	3.9	5.40	5.8	18.70	7.3	–	–	–	–	–	–	–	–
White clover	9.70	15.2	–	–	36.80	28.4	–	–	–	–	65.8	75.8	–	–
Red clover	65.50	3.9	70.20	5.8	–	–	60.10	9.7	73.6	14.6	–	–	–	–
Chicory	0.64	7.5	1.20	11.2	3.10	14.0	–	–	–	–	–	–	–	–
Plantain	1.20	7.1	1.90	10.6	–	–	–	–	–	–	–	–	–	–

outyielded perennial ryegrass and white clover mixtures, particularly in the spring and summer months (Daly et al., 1996; Ruz-Jerez et al., 1991). In our study, the most complex pasture mixtures, sown with 10 and 15 species, yielded similarly to most of the simpler mixtures. The low yields of the one- and two-species mixtures reflected the fact that they included only perennial grasses that were minimally fertilized. Mixtures with three or more species contained legumes that contributed biomass to mixtures and possibly N to soils through N fixation. The additional legume biomass and possible improvements to soil fertility may have helped to increase yields over the one- and two-species mixtures. Interestingly, one of our simplest mixtures containing three species often yielded more than complex mixtures. The three-species mixture was dominated by a productive, stress-tolerant grass, tall fescue, and a stoloniferous legume, white clover. The production responses in this relatively simple community suggest that optimal production in some pasture communities could be achieved with only two species. In this location, the combination of tall fescue and white clover appeared to be the most favorable.

Many studies have also shown that plant diversity can improve aspects of community stability in grasslands (Frank and McNaughton, 1991; McNaughton, 1977; Mellinger and McNaughton, 1975; Naeem and Li, 1997; Tilman and Downing, 1994). Unlike simple plant communities, diverse plant communities usually contain subdominant species that have the potential to increase in abundance if dominant plants decline (McNaughton, 1977). This compensatory response maintains a stable community biomass across time. Compensation, however, may not always be required for community stability. Some studies suggest that community stability depends more on the presence of stress-tolerant species rather than diversity (Leps et al., 1982; MacGillivray et al., 1995). In tropical grasslands, Sankaran and McNaughton (1999) found that community stability was not dependant on species diversity but was a function of plant community characteristics and their adaptations to local site variables and disturbance history.

We found little evidence that increasing mixture diversity lead to greater interannual yield stability. The simplest mixtures sown with one and two species showed the lowest variation in yield during this experiment. This yield stability mainly reflects the absence of legumes in these mixtures. Legumes present in other mixtures declined in abundance from 1999 to 2001, while perennial grasses generally increased. Since the one- and two-species mixes contained only perennial grasses and no legumes, their yields remained relatively stable. In other plots, most of the interannual yield variation resulted from changes in red clover abundance. For example, mixtures sown with four or six species varied the most because red clover declined across time and was replaced mostly by bluegrass (Table 3). Bluegrass is smaller and less productive than red clover, so its biomass could not compensate for the yield lost due to red clover decline. Although the 10- and 15-species mixtures also lost red clover biomass, it was replaced by more robust species, like orchardgrass, tall fescue, and chicory. Therefore, these mixtures did not exhibit such drastic yield declines. In contrast, mixtures sown with three and eight species contained legumes but still exhibited high stability. The three- and eight-species plots contained prostrate-growing white clover, instead of the larger, more erect-growing red clover. So even though white clover abundance declined in these plots, it did not severely affect yield variation because the perennial grasses compensated the biomass reduction. Overall, legume abundance appears to strongly control stability in mixtures. Loss of large, erect-growing legumes like red clover are difficult to overcome unless mixtures have similarly sized plants that can compensate for the loss.

During the 2000 and 2001 growing seasons, one-half of the plots received more frequent mowing, every 2 wk instead of 4 wk, to determine how the yield stability would respond to an additional mowing disturbance. Plots mowed every 2 wk showed higher interannual yield variation compared with plots mowed every 4 wk (Fig. 2). The higher yield variation occurred because the 2-wk mowing treatments started in 2000 and this reduced yields about 25% compared with 1999. Although the 2-wk mowing frequency reduced yields and presumably stressed mixtures, yield variation among the different mixtures was similar in both 2-wk and 4-wk mowed plots. Although this finding suggests that grazing intensity may not strongly influence interannual yield stability of pasture mixtures, selective grazing by cattle under more realistic pasture conditions might produce different results.

The species composition of the mixtures changed significantly from 1999 to 2001. The number of species planted in each mix declined by 30%, on average, across all plots. Plantain did not persist and disappeared from mixtures by 2001. Sanderson et al. (2003) similarly found that plantain cultivars did not persist after two winters in Pennsylvania and concluded that they were not well adapted to the northeastern USA. Birdsfoot trefoil, timothy, and reed canarygrass were slow to establish, absent, or remained at low abundance in mixtures. These species may not do well in mixtures under these particular environmental conditions. By the end of the 2001 growing season, most mixtures became dominated by perennial grasses while legumes declined in abundance. Daly et al. (1996) noted a similar trend in their New Zealand pastures that were planted with 10 or more species. These findings differ from the results of Tilman et al. (2001), who showed only small reductions in species richness after 7 yr in plots ranging from one to 16 species. The loss of species in our experiment may have resulted from the regular mowing intervals, which may have reduced additional seed input into our plots by prevention of reproductive development. Mowing for hay production has a strong effect on the diversity and dispersal of species in agricultural grasslands (Coulson et al., 2001; Kirkham and Tallowin, 1995; Smith et al., 1996). The repression of seed rain from frequent mowing in our study may have severely limited germination opportunities for many of the forage species. This should reflect most grazing systems, however, since good management should prevent most forage species from reaching reproductive stages. Losses of species that depend upon seed production for persistence should be expected in most intensively grazed or hayed systems.

Our plots also lacked the patchiness common to most grazed pastures. Such patches caused by uneven grazing, trampling, and waste deposition may provide sites for forage plant germination, which may help increase species diversity across time (Sternberg et al., 2000; Tracy and Sanderson, 2000a). The lack of patchiness in our small plots may have prevented some of the slowly establishing species (e.g., reed canarygrass) from becoming more abundant in the plots. Moreover, the highly competitive nature of many of these cool season forage species and the relative high fertility of the soils in our study may not allow for maintenance of high species diversity across time since there will be a natural tendency for one or two productive species to outcompete others (Grime, 1973).

Lastly, it is noteworthy that we did not attempt to equalize the number of seeds per species that were sown into the plots. As a result, species with smaller seeds were overrepresented in the mixtures relative to larger-seeded species, and this could have affected their relative abundance of species in the aboveground vegetation (Gross and Werner, 1982; McConnaughay and Bazzaz, 1987). To evaluate this possibility, we also compared the relative abundance of each species present in May 1999 to the number of seeds that were sown in that respective plot. Overall, we found that the number of seeds sown to each plot was not a good predictor of abundance in the aboveground biomass. Although some larger-seeded species were highly abundant in the aboveground biomass (e.g., red clover and perennial ryegrass), other species with similar-sized seeds were not as consistently abundant across mixtures (e.g., alfalfa, tall fescue, smooth bromegrass). Most small-seeded species, except for white clover, were not abundant in the aboveground biomass in 1999. Although bluegrass accounted for only a small proportion of biomass in 1999, it increased in abundance in subsequent years (Table 3). The high number of bluegrass seeds sown to plots probably influenced its raise in abundance during the 3 yr of this study. Unlike most perennial grasses, bluegrass tends to form a persistent seedbank (Chippindale and Milton, 1934; Jalloq, 1975; Tracy and Sanderson, 2000a). Bluegrass recruitment from this relatively large and persistent seedbank may have helped it increase in abundance during the 3 yr of this study.

CONCLUSIONS

Overall, our results suggest that the best strategy to increase pasture productivity and stability might be to plant two or three species that are well matched to specific environmental conditions rather than a complex mixture of plants. Because of limitations in our experimental design, however, we cannot be sure that such simple mixtures will always perform similarly to more complex mixtures. As many recent studies suggest, there may be conditions where complex mixtures might improve pasture production and stability more than simple mixtures. Moreover, whether our findings would apply at larger spatial scales with grazing animals remains unknown. At larger scales (>1 ha), the multiple species in a complex mix may tend to sort out along topoedaphic gradients. This selection process should result in different species dominating in sites where they are best adapted. Compared with simple mixtures whose sorting potential is less, complex mixtures should result in greater overall pasture yields and stability, particularly in pastures with significant environmental heterogeneity. The patchiness created by cattle grazing, trampling, wallowing, and waste deposition may provide sites that favor the recruitment and coexistence of multiple species. Larger-scale pasture studies that simultaneously evaluate forage production and grazing animal performance are in progress to answer these questions.

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