Plant Species Diversity and Management of Temperate Forage and Grazing Land Ecosystems

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ABSTRACT

More than a century since Charles Darwin stated that diverse grasslands produce more herbage than monocultures, scientists still debate the relationship between species diversity and ecosystem function. Postulated benefits of diversity in experimental grasslands include greater and more stable primary production along with more efficient nutrient use. These benefits have been extrapolated to forage and grazing land systems with little supporting objective data. Most information on the potential benefits of increased plant diversity comes from studies of synthesized grasslands that have not included domestic grazing animals. We explore this debate relative to the management of temperate forage and grazing lands. Plant species diversity refers to the number of species (richness) and their relative abundance (evenness) within a defined area. Plant relations influence biodiversity responses through positive (e.g., facilitation, N_2 fixation, hydraulic lift) and negative interactions (e.g., competitive exclusion, allelopathy). Early 20th century research on complex mixtures of forage species (limited to grasses and legumes) for pasture indicated equivocal results regarding benefits of species-rich mixtures and typically recommended using the best adapted species in simple grass–legume mixtures. Recent research indicates potential herbage yield benefits from species-rich mixtures for pastures. Limited animal productivity research on species-rich mixtures indicates variable responses and much more research is needed. Grazing land productivity is a primary focus for biodiversity benefits because of the direct economic relevance to producers. However, taking a broader view of the multifunctionality of grazing lands to include environmental and aesthetic benefits to humans reveals a great scope for using biodiversity in grazing land management.

CHARLES DARWIN (1872) boldly stated that "It has been experimentally proved, that if a plot of ground be sown with one species of grass, and a similar plot sown with several distinct genera of grasses, a greater number and greater weight of dry herbage can be raised in the latter than in the former case." Unfortunately, Darwin omitted details of the soils, climate, grazing pressure, and spatial scale that give the context for his statement on grassland species diversity. This omis-

sion illustrates the difficulty that current researchers face in obtaining consensus from this generality.

Species diversity is a hot topic in grassland ecology research because the reported benefits of biodiversity appear to contradict the high productivity obtained from relatively few species (through high inputs of fertilizers and chemicals) and from an increasingly narrow genetic diversity seen in current agriculture. Some research results indicate that increased plant species diversity increases primary production in grasslands and benefits other ecosystem functions such as nutrient retention and resistance to weed invasions.

These results and concepts have spilled over into other areas (Brummer, 1998), such as forage and grazing land research, and are beginning to influence management recommendations. For example, Tilman et al. (1999) suggested exploring the concept of high diversity grazing lands for livestock production. Similarly, Minns et al. (2001) extrapolated results from the large BIODEPTH (BIODiversity and Ecosystem Processes in Terrestrial Herbaceous Ecosystems) experiment in Europe to agricultural management. It is not clear, however, how these results and concepts relate to managed forage and grazing lands. Most grassland studies reporting the effects of plant species diversity on ecosystem functioning have used cutting, fire, or in some cases no form of herbage removal, rather than grazing. Results under grazing could be very different because of the capacity of grazers to affect plant community diversity and structure (Bullock and Marriott, 2000; Rook and Tallowin, 2003).

Early research on pasture management seemed to advocate relatively complex mixtures of grasses and legumes (Foster, 1988). During the 1950s, however, the emphasis shifted to monocultures of grasses maintained by N fertilizers or simple mixtures of grasses and legumes (e.g., one of each) and management of those mixtures to maintain the legume component (Blaser et al., 1952; Donald, 1963). Blaser et al. (1952) stated that complex mixtures of grasses and legumes were destined to fail because of seedling competition. Thus, forage and pasture management research since that time focused on monocultures or simple forage mixtures.

Grazing lands are an important component of global land use. Roughly 50% of the earth's terrestrial surface is grazed by large herbivores (Frank et al., 1998). Forage and grazing lands form the backbone of profitable forage–livestock systems and contribute substantially to the agricultural economy. Interest in the management of pastures in temperate regions is moving beyond traditional concerns, such as management to optimize the quality and quantity of herbage for animal production, to encompass a new set of issues. These issues cross traditional boundaries between farming, agronomy, conservation, ecology, and landscape management to include

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sustainability, reduced inputs of fertilizers and pesticides, soil protection, C sequestration, animal biodiversity, resistance to invasion by alien plants and insects, and the aesthetic value of the landscape (Spellerberg et al., 1991; Watkinson and Ormerod, 2001; Krueger et al., 2002). It is within this context that increased biodiversity may play an important role.

In this paper we review recent concepts of plant diversity and their applicability to the management of pastureland. We first discuss the measurement of species diversity and its interrelationship with scale and then explore the relative diversity of plant species in pastures. Then we briefly summarize the ecological research on the relationship between plant diversity and ecosystem function in grasslands. Finally, we consider the available evidence relating plant diversity to ecosystem function in forage and grazing lands and discuss the potential application of biodiversity concepts to pasture management.

Diversity: Measurement, Scale, and Interpretation

Plant species diversity refers to the number of species and their relative abundance in a defined area. Diversity measurements incorporate both species richness (S, the number of plant species in a community) and species evenness (J, an estimate of species distribution within a community). A community is perfectly "even" if all the species in the community have an equal number of individuals and are all the same size. Various indices combine these two factors to measure diversity in plant communities. Commonly used diversity indices include the Shannon-Wiener index (H′) and Simpson's diversity index. Peet (1974) and Magurran (1988) present comprehensive reviews of various diversity indices.

Species richness, the most commonly reported diversity measurement, is relatively easy to interpret. For example, Pasture A with 20 plant species per unit area would be considered more diverse than a Pasture B that has 10 species. Richness, however, does not take into account the distribution of the plant species within the pasture. Although Pasture A has more species, those species may not be evenly distributed across the pasture compared with Pasture B. For example, 50% of the species richness in Pasture A could be associated with a previously disturbed area that accounts for less than 1% of the pasture area. Taking species evenness into account and calculating the Shannon-Wiener index, we would probably see that Pastures A and B have similar levels of diversity even though their species richness differs significantly. This example may be extreme, but illustrates a problem with using only species richness as an index of pasture diversity. More important, the evenness at which plant species are distributed should be closely linked to how that diversity affects ecosystem function (e.g., productivity, nutrient cycling). Recent papers have demonstrated the importance of species evenness in explaining productivity and pest invasion in grasslands (Wilsey and Potvin, 2000; Stirling and Wilsey, 2001; Wilsey and Polley, 2002).

Spatial scale strongly influences biodiversity (Crawley

and Harral, 2001; Symstad et al., 2003). Two important principles are that (i) species richness increases with the area sampled and (ii) that small-scale (α) diversity varies independently from large-scale (β) diversity.

At the smallest scale (<1 cm^2), species diversity is low because of the physical limitation of the space occupied by a single individual. As the scale or area measured increases, species richness increases, but at a declining rate. Although this positive relationship results partly from the greater variability encountered with larger sampling areas, it also occurs within uniform environments. Because species richness (and biodiversity) is related to the size of area measured, all studies on plant species diversity must report the scale at which observations are made.

Alpha diversity refers to diversity within a close spatial scale or within plant communities. Beta diversity refers to variation in species composition at large spatial scales or between plant communities. Typically in agriculture there is both low α diversity resulting from fields of relatively few plant species, and also low β diversity from those same species being used in adjacent fields, counties and states. At large (farm and region) scales we have the practical option of using small-scale (α) diversity within fields, and also larger-scale (β) diversity of using forage seed mixtures customized for the environmental, topographic and management conditions of each field or region. Such specificity might include both the number and identity of species used.

Thus, measuring and evaluating species diversity on grazing lands is more than simply counting or listing the number of species encountered. Evaluating species richness without taking into account evenness and spatial scale effects could underestimate the importance of diversity in shaping the function of pasture ecosystems.

Extent of Plant Diversity in Pastureland

To a casual observer, sown grazing lands present a largely uniform surface with the appearance of a homogeneous mixture of species. Closer examination reveals a complex structure of temporal and spatial distribution of both species (e.g., of white clover, *Trifolium repens* L., Edwards et al., 1996; Nie et al., 1996) and species richness (Barker et al., 2002; Parsons and Dumont, 2003) in pastures. The significance of spatial patterns on plant and livestock production (and other ecosystem functions) is of particular interest and currently is a deficiency in our knowledge.

In the early 20th century, there were several surveys of the botanical composition of grazing lands in the northeastern USA (e.g., Sprague and Reuszer, 1928; Johnstone-Wallace, 1933; Pierre et al., 1937). Although these surveys did not address plant species diversity per se, they are instructive in comparing trends. The predominant species found in earlier surveys included *Poa*, *Agrostis*, and white clover and the weedy grasses sweet vernalgrass (*Anthoxanthum odoratum* L.) and poverty grass (*Danthonia spicata* L.). Frequently occurring weedy forbs included yarrow (*Achillea milleflorum* L.), hawkweed (*Hieracium canadense* L.), and buttercup (*Ranun-*

culus acris L.). Most of the weedy grasses and forbs were typical of low soil fertility conditions (Cooper et al., 1929). A recent survey also showed dominance by *Poa* and white clover in northeastern grazing lands (Tracy and Sanderson, 2000); however, the dominant weedy species included quackgrass [*Elytrigia repens* (L.) Desv. Ex Nevski], broadleaf plantain (*Plantago major* L.), and dandelion (*Taraxacum officinale* Webber in Wiggers). The weedy species in the recent survey are more typical of higher soil fertility conditions. The data indicated that changes in grazing land management including new forage species and cultivars along with improvements in soil fertility management likely contributed to the changes in botanical composition during the 20th century (Sanderson et al., 2001). Even in cases where management has not changed, the species composition and diversity of grazing lands in northern Europe and Great Britain have changed in the last few decades because of chronic nitrogen loading from air pollution (Bobbink, 1991; Smith et al., 1999) For example, regional atmospheric N deposition rates in the Netherlands have exceeded 50 kg N ha^{-1} since the 1980s. Rates of N deposition in the North American Midwest and Northeast, although not as high as those seen in Europe, may have similarly affected the species composition and diversity of managed and natural grasslands (Wedin and Tilman, 1996).

In one of the few recent studies available on the degree of plant diversity in pastures, total plant species richness of northeastern grazing lands ranged from 16 to 49 species 1000 m^{-2} with an average of 32 species 1000 m^{-2} (Tracy and Sanderson, 2000; Sanderson et al., 2002). The Shannon-Weiner index of northeastern grazing lands ranged from 0 to 3.0 with an average of 1.6 (based on 1-m^2 quadrats) and evenness (J) ranged from 0.13 to 1.00 with an average of 0.75. Perennial and annual forbs, along with perennial grasses, dominated the above ground species pool, whereas bluegrass (*Poa pratensis* L.) and white clover dominated the soil seed bank (Tracy and Sanderson, 1999). In comparison, Stohlgren et al. (1999) reported a range of nine to 50 native plant species and one to eight exotic plant species 1000 m^{-2} at several sites in Rocky Mountain grasslands. Species evenness in that study tended to be greater than reported for managed pastures in the northeastern USA. Species richness in traditionally managed grasslands (i.e., species-rich ancient grazing lands such as chalk grassland and heathland) in northwest Europe ranged from 50 to 60 species 100 m^{-2}, whereas more intensively managed grasslands contained 10 to 20 species 100 m^{-2} (Peeters and Janssens, 1998).

In North America, managed grazing lands are often assumed to be less diverse than natural grassland ecosystems. The European experience with traditional grazing lands calls this generalization into question, however. Rangeland research also emphasizes the role of grazers, domestic or native, in maintaining grassland diversity (Collins et al., 1998; Milchunas et al., 1998). Information is lacking, however, on the level of plant diversity that actually occurs on farms. Producers frequently manage several different forage species in pastures whether grown in complex mixtures or spatially distributed among different pastures.

Plant Diversity and Ecosystem Function

Greater plant diversity in grassland plant communities has been linked to increased primary production (Naeem et al., 1994; Tilman et al., 1996; Hector et al., 1999), greater stability in response to disturbance (McNaughton, 1977; Frank and McNaughton, 1991; Tilman and Downing, 1994), reduced invasion by exotic species through more complete use of available resources (Naeem et al., 2000; Tilman, 1997; Tracy and Sanderson, 2004; but see Stohlgren et al. (2003) and Renne and Tracy, 2003), and better nutrient retention (Tilman et al., 1996; Reich et al., 2001). These studies suggest that managing for increased plant species diversity on pasturelands could increase forage yield, improve yield stability, and reduce soil nutrient losses.

The proposed mechanisms behind the observed responses to plant diversity in grasslands include (i) the "sampling effect," resulting from the greater chance of including more productive species in highly diverse plant communities (Huston, 1997; Wardle, 1999); (ii) facilitation, whereby the presence of one species increases the growth or survival of another species (Callaway and Walker, 1997; Brooker and Callaghan, 1998; Callaway, 1998); (iii) niche differentiation–niche separation, or greater coverage of habitat caused by a wider range of species traits in a more diverse community; and (iv) the "insurance effect," where a highly diverse plant community is buffered from environmental extremes by having some species that are tolerant of different stresses and thereby stabilize productivity (McNaughton, 1977; Ives et al., 2000; Yachi and Loreau, 2001). Physiological and phenological diversity in complex plant communities may allow for complementarity among species and result in more efficient use of soil, water, air, and light resources compared with simple plant communities (Hector, 1998).

The ecological literature, although reporting on relatively recently planted experimental grassland plots, has emphasized long-term benefits of diversity, perhaps in an attempt to relate the results to permanent, natural ecosystems. An obvious and common example of species diversity in grassland establishment would be the use of cover or nurse species, such as annual grains, to facilitate slow growing perennial grasses and legumes. This phenomenon is at the center of some of the controversy in the ecological literature regarding the interpretation of results from diversity experiments. Huston (1997) argued that the increased productivity of high diversity experimental plots reported by Tilman et al. (1996) was simply a consequence of those plots having fast growing, weedy species, particularly yarrow and black-eyed susan (*Rudbeckia hirta* L.). Thus, the mechanism responsible for the diversity effect was the sampling effect, and the effect would be short-lived. Later analyses by Tilman et al. (2001) indicated that the diversity effect observed initially in their experiment was largely a sampling effect with niche differentiation be-

coming more important when the plantings were several years old. Thus, it is likely that the observed effect of diversity on productivity and the mechanism responsible will change with time, especially for relatively young or newly planted grasslands. Even if the positive effects of diversity turn out to be short-lived in managed grasslands, the "nurse crop" effect may be important considering the effort and expense involved with grassland establishment.

Although there is a general consensus that diversity benefits ecosystem function, there are reports that indicate no general benefit of increased plant diversity (e.g., see Huston et al., 2000; Wardle et al., 2000). Frequently, highly productive agricultural systems rely on low plant species diversity [e.g., row-crop production; alfalfa (*Medicago sativa* L.) hay, etc., Huston, (1994)]. Others, however, have argued that the benefits of plant species diversity depend on the environment and the spatial scale considered (Fridley, 2001).

Trenbath (1974) reviewed several studies involving species mixtures in agricultural systems and suggested that a true benefit from increased diversity occurred only when mixtures yielded more than the most productive species in monoculture. This stricter standard is appropriate for agriculture where the best performing species or mixtures are selected and managed for maximum productivity. Total yield, however, is not the only criterion for evaluating the potential benefits of increased biodiversity in grazing lands. Seasonal distribution of yield, amount and costs of inputs needed to achieve maximum yield (Ruz-Jerez et al., 1991; Kanneganti et al., 1998), as well as nonagronomic benefits (e.g., improved wildlife habitat) from increased biodiversity must also be considered (Table 1).

The basic ecosystem functions include not only primary productivity, nutrient cycling, and decomposition, but also many anthropocentric functions of value to humans (Table 1). It is of relevance to most farmers that strategies to maximize anthropocentric function (e.g., high use of external inputs to maximize yield) often have a negative effect on the environment. Although we might be focused primarily on productive output, grazing lands are almost universally fulfilling multiple functions simultaneously (Table 1). Sustainable use of pasturelands is likely to result from maximizing the number of functions they provide.

Yield and Diversity—A Question of Cause or Effect?

Much of the ecological literature has focused on the relationship between diversity and yield, with yield the independent variable and diversity the dependent variable (Tilman and Pacala, 1993; Schmid, 2002). In the debate on the relationship between diversity and ecosystem function, the discussion currently focuses on productivity and its response to diversity (i.e., yield is the dependent variable and diversity the independent variable; e.g., Tilman et al., 1996; Hector et al., 1999). We focus on the yield vs. diversity relationship, with diversity the independent variable and yield the dependent variable. This relationship has a mechanistic interpreta-tion because the species present in the vegetation are the actual components of the resultant yield. Where positive species interactions occur (such as with nitrogen fixation, species sheltering other species, or synergistic benefits of water uplift or rooting depth), we might see positive responses of diversity and yield. Where simple replacement occurs, we might see no response of yield to diversity. Where competition occurs (e.g., competitive suppression, allelochemical effects), we might see negative effects of diversity on yield.

On occasions where there is a positive response between diversity and yield, the debate between diversity vs. yield or yield vs. diversity might be one of semantics, because the essential relationship is identical. However, where nonlinear responses (e.g., the unimodal response proposed by Waide et al., 1999) are proposed, the debate between diversity vs. yield or yield vs. diversity is significant because these responses and the causative biology are not the same.

Evidence for Diversity Effects in Pastureland

In this section, we review several studies relative to species diversity effects on pastureland. Some of the most frequently cited studies on diversity effects in grasslands were done in small plots with no ungulate grazers and with nonagronomic species. It would not be surprising if results from these types of experiments cannot be extrapolated to pastures. For example, species richness is frequently correlated with low soil fertility; however, maintaining high species richness by not correcting soil nutrient deficiencies will be counter-productive to agricultural performance. As another example, weeds (forbs) are positive components of vegetation diversity (in ecological terms), but frequently are associated with negative effects on livestock (e.g., they can be invasive, have undesirable production patterns, and can contain antiquality chemical constituents). Traditional pasture management focuses on species with desirable characteristics for domestic livestock production and excludes many weed species.

Morphological and Physiological Interactions in Diverse Forage Plant Communities

Diversity theory suggests that greater plant diversity buffers plant communities from environmental extremes. For example, the productivity of grazing lands during summer drought could be improved by sowing a percentage of pastures to warm-season grasses (Skinner et al., 2002) or by planting multispecies mixtures that include some of the more drought resistant cool-season grasses and forbs (Lucero et al., 1999). Interactions among species within complex mixtures may also improve the ability of normally drought-sensitive species to maintain production under stressful conditions.

Some evidence suggests that growing drought sensitive species in complex mixtures rather than as monocultures might improve their productivity during dry years (Lucero et al., 1999; Trenbath, 1974). Many deep-rooted rangeland species can transfer water from relatively moist, deep soil layers to dry layers near the soil surface

Table 1. Fifteen functional characteristics of temperate pasture and natural grassland systems and their effect on anthropocentric value (factors having immediate economic implications for producers and consumers) and environmental benefit (factors not having immediate economic effect).

Functional characteristic	Temperate pasture		Natural grassland†
	Anthropocentric impact	Environmental impact	
Total production‡	production is positively related to food supply and economic return (but poorly related to profit)	high production has a negative impact from increased nutrient leakage, increased agri-chemical use, and greater methane and CO_2 losses to the atmosphere	high production has a small positive benefit since energy from primary producers ultimately supports more organisms
Distribution of production‡	uniform production has a high positive human impact since, a) it ensures uniformity of food supply (although livestock demands are not uniform), b) minimizes requirements for supplemented forages, c) higher production efficiency in temperate than seasonal climates	uniform production has a moderate negative impact since inputs (e.g., N and water) are required to 'minimize' environmental variability	uniform production has a small positive impact resulting from a year-round supply of nutrition to wildlife (although wildlife demands are not uniform). Unseasonal disruption of food supply is rare, but devastating.
Forage quality‡	high forage quality has a high positive benefit resulting from high production efficiency and products with high value	high forage quality has a small negative impact resulting from the associated use of inputs (e.g. agri-chemicals, N, P)	forage quality has little relevance, livestock can select higher quality components as they require
Stand persistence	persistent stands have moderate positive value since establishment costs are spread over more years	persistent stands have a small positive benefit from soil stability, improved soil structure and less mechanical intervention	persistence is a vital process in natural grasslands since it is the basis of their survival
Resistance to weed invasion	weed resistance has only a small but positive impact, since a) most 'weeds' are controlled by grazing, b) weeds rarely prevent forage production, and c) herbicides control is relatively inexpensive	weed resistance has a moderate positive benefit since there is less intervention (e.g. replanting or herbicides), unintended species are an environmental contaminant	weed resistance has a high positive benefit since weed (non-native) species are highly undesirable and sometimes invasive. It depends what is considered to be a weed?
Pest and disease resistance	pest and disease resistance has a high positive value, since there are few economic pasture pests, and pesticide control is rarely economic (a notable exception is insect control in alfalfa)	pest and disease resistance has a moderate positive benefit resulting from less intervention from replanting and pesticide use.	pest and disease resistance is vital in natural grasslands, fungal and insect populations will be in equilibrium.
Drought recovery and resistance	drought resistance has low value (in the rare cases that pastures are lost to drought they are readily replanted)	drought resistance has low environmental benefit since pastures are rarely lost to drought	drought resistance is vital in natural grasslands, stands lost to drought can only be re-vegetated from buried seed
Winter survival/cold tolerance	cold tolerance has low to moderate value (occasional losses such as frost heaved alfalfa are replanted)	cold tolerance has low environmental benefit since pastures are rarely lost to cold	cold tolerance is vital in natural grasslands, stands lost to freezing can only be re-vegetated from buried seed
Nutrient cycling‡	nutrient cycling has low value because of the influence from applied fertilizer	nutrient cycling has moderate positive benefit in reducing dependence on fertilizer application	nutrient cycling has high value in natural systems since there are no other sources of nutrients
Biodiversity	biodiversity has both moderate, positive and negative value, a) much of this function is substituted by germplasm libraries, and variation in cultivars used, b) positive effects on production and livestock production, but c) is negatively correlated with other factors e.g. low production and high biodiversity at low fertility	biodiversity has moderate positive benefits, such as providing a stable vegetation cover, and habitat for wildlife.	biodiversity has high positive benefits resulting from a) species richness, b) rare species, and c) reducing the potential for weed ingress (Q. Do weeds add-to or detract-from biodiversity?)
Social values (aesthetics)	forages have moderate positive value, since a well managed pasture "looks good"	aesthetics have little environmental contribution	natural grasslands have high aesthetic value, e.g. national parks, restored prairie
Water harvesting-amount	water yield has a high positive value–compared to other vegetation, grasslands have high water yield	high water yield has a negative environmental value, since it can contribute to uneven stream flow (a high water yield results in low transpiration and storage)	high water yield has small negative value in natural systems (a high water yield results in low transpiration and storage)

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(Caldwell et al., 1998) by a process known as hydraulic lift (Richards and Caldwell, 1987). Neighbors near species that lift water hydraulically can use a significant proportion of that water resource, effectively ameliorat-ing the adverse effects of drought (Dawson, 1993). Through niche separation (Tilman, 1999), deep-rooted species might also preferentially use water from lower soil levels, leaving more surface water available for shal-

Table 1. Continued.

Functional characteristic	Temperate pasture		Natural grassland†
	Anthropocentric impact	Environmental impact	
Water harvesting–quality‡	high water quality has high value-grasslands have low sediment, but can contribute NO_3 and coliforms to runoff	generally high water quality from grasslands has high environmental value. Grasslands typically have low N and P 'leakage', and vegetation cover minimizes soil erosion, however, lack of shading can result in warmer streams.	high water quality has low value in natural grasslands–low sediment losses contribute to unsilted streams.
Sustain wildlife‡	wildlife have a low negative value–with the exception of commercial deer and wildlife farms	wildlife make a small positive contribution in managed grasslands	wildlife are a vital component of natural grasslands
Carbon sequestration	carbon sequestration has a moderate negative value, since a) there is no carbon tax system in place, b) stored carbon = 'lost' production	carbon sequestration has a moderate positive benefit from increased soil organic matter (drainage, soil structure)	carbon sequestration has low impact in natural systems since these are in carbon equilibrium

† Natural grasslands include those grasslands maintained in close to their natural state (most are under some degree of management that might include regulation of wildlife populations, fire control, and weed control). The benefits in natural grasslands are predominantly environmental since anthropocentric value is assumed to be relatively low.

‡ Variations in these functional characteristics occur when timeliness of the response is included, such as a specific requirement for forage supply to livestock (or wildlife) to achieve specific production targets (perhaps related to out-of-season production).

low-rooted species. Similarly, Berendse (1982) suggested that the association of deep- and shallow-rooted grassland species in mixture could cause greater nutrient extraction from deeper soil layers by the deep-rooted species than would normally be observed in monoculture. Nutrients taken up by deep-rooted species can also be deposited on the soil surface via litter fall and thus made available to shallow-rooted species (Callaway, 1995).

Neighboring plants can also favorably alter other environmental conditions. For example, shading by larger plants can lower soil temperature, reducing heat stress effects while also reducing evapotranspiration leading to improved leaf water relations of smaller neighboring species (Wilson, 1996; Shumway, 2000; Carrillo-Garcia et al., 2000). In a New Zealand study, deferred grazing of perennial ryegrass (*Lolium perenne* L.)–white clover pastures during the summer resulted in increased herbage accumulation which, in turn, led to lower soil temperatures, increased soil moisture, and improved white clover survival compared with conventionally grazed pastures (Harris et al., 1999). Sheltered plants can also benefit in cold environments where shade from neighbors provides protection from the direct effects of low temperature due to radiation frost as well as protection from photoinhibition resulting from the combined effects of low temperature and high irradiation (Egerton et al., 2000). Shading by salt marsh plants that limits surface evaporation can also reduce the accumulation of soil salts (Bertness and Hacker, 1994). In addition, oxygenation of submerged soils by aerenchymous plants can enhance nutrient availability and increase survival of nonaerenchymous neighbors (Callaway, 1995).

Most examples of facilitative interactions in the literature are from extreme environments such as desert and alpine ecosystems. However, as Harris et al. (1999) observed, amelioration of less extreme environments can also occur. Additional research is needed to determine the importance of positive plant-plant interactions in temperate pasture systems.

Diversity and Nutrient Cycling in Forage Plant Communities

Aboveground plant composition can strongly affect nutrient cycling rates in pastures. Probably the best example is the well documented effects of legume addition to grass mixtures and subsequent increases in soil nitrogen availability because of N fixation (Haynes and Williams, 1993). Beyond this simple fertilization effect, aboveground plant diversity may also influence nutrient cycling through microbial decomposition of plant litter.

Most studies on decomposition of plant litter have evaluated decomposition dynamics using single species assays (e.g., Cornelissen, 1996; Kalburtji et al., 1998; Koukoura, 1998). But in multispecies plant communities, like pasture, litters of different plant species usually decompose mixed together. In such a situation, litters that differ in quality (e.g., N concentration) may interact antagonistically or synergistically to produce decomposition dynamics that differ from those predicted from species decomposing alone. Plant diversity may also modify the microenvironment for decomposition (Hector et al., 2000). Contrasting results concerning plant diversity effects on litter decomposition in experimental systems [e.g., positive effects (Bardgett and Shine, 1999); no effects (Wardle et al., 1997), or mixed results (Hector et al., 2000; Knops et al., 2001)] demonstrate that much more remains to be done to clarify how aboveground plant diversity affects belowground processes in grazing land (Wardle, 2002).

Increasing the diversity of grassland plant communities may increase nutrient retention. Soil nitrate levels, both within and below the rooting zone, were reduced as the number of plant species increased in growth chamber studies and in tallgrass prairie communities (Naeem et al., 1994; Tilman et al., 1996). On serpentine grasslands, diverse mixtures of plants used total resources more completely compared with simpler plant communities (Hooper and Vitousek, 1998). Whether reductions in soil nitrate

were caused by true complementarity among different species (i.e., a diversity effect), reduced soil N mineralization (Reich et al., 2001), or by one deep rooted, species with high N uptake rates is not clear. In pastureland, deep rooted species like alfalfa have been shown to lower water tables and reduce nitrate losses when seeded into grass mixtures (Cransberg and MacFarlane, 1994; Owens et al., 1994), so it is possible that one species could have a dominant effect on nitrate uptake in some communities. For example, increasing the diversity of nonleguminous species grown with legumes in grassland mixtures could help reduce nitrate leaching species while still benefiting production through N fertilization (Scherer-Lorenzen et al., 2003). Given the potential for environmental problems associated with nitrate losses in pasture-based systems, more tests of this concept are needed under realistic grazing conditions and backed up with experiments that evaluate nitrate losses from mixtures and monoculture treatments (Hooper and Vitousek, 1998).

Forage Productivity Trials with Diverse Mixtures

Much of the early applied research on complex forage mixtures was done in clipping studies to screen various combinations of forages. For example, early research in Connecticut compared 50 different single and multiple species combinations of grasses and legumes (1, 2, 3, 4, or 7 species) for yield under clipping (Brown and Munsell, 1936). The range in herbage yield was large for the single species and two species plots, but there was no significant trend in yield with increasing seeded species richness (Fig. 1). The yields of the complex mixtures were

mid range of the two-species mixtures. The highest yielding two-species mixture included a large-leaved (Ladino type) white clover cultivar, which is more adapted to infrequent cutting. In most of the mixtures, the legume component had nearly disappeared by the third year probably as a result of the relatively lax cutting interval.

In another large screening study, 93 combinations of grasses and legumes containing 1 to 7 species were evaluated for herbage yield in clipped and grazed plots under irrigation (Bateman and Keller, 1956). Combining data from all experiments indicated a positive relationship between herbage yield and seeded species richness (Fig. 2). Generally, when higher-yielding species were included, yields increased (an example of the "sampling effect"). Bateman and Keller (1956) selected a subsample of treatments that were mixtures of the seven highest yielding grass and legume species to illustrate the point that increased mixture complexity improved herbage yields (Fig. 3). Their conclusion was that there was "a clear trend of higher yields with increasing numbers of productive species."

Research in Ontario, Canada, indicated that pastures planted to a complex mixture of six cool-season grasses and three legumes maintained this complexity and increased in productivity after several years of intensive grazing management (Clark, 2001). The primary conclusion was that mixture complexity per se was not as important as the use of strategically selected and appropriately managed complexity. In New Zealand, pastures seeded with a mixture of 10 to 23 species of cool-season grasses and pasture herbs yielded more herbage under sheep grazing than did simple perennial ryegrass–white clover mixtures (Ruz-Jerez et al., 1991; Daly et al., 1996). The "herbal ley" mixture of Ruz-Jerez et al. (1991) produced 90% of the yield of perennial ryegrass fertilized with 400 kg N ha^{-1} (Fig. 4). The increased produc-
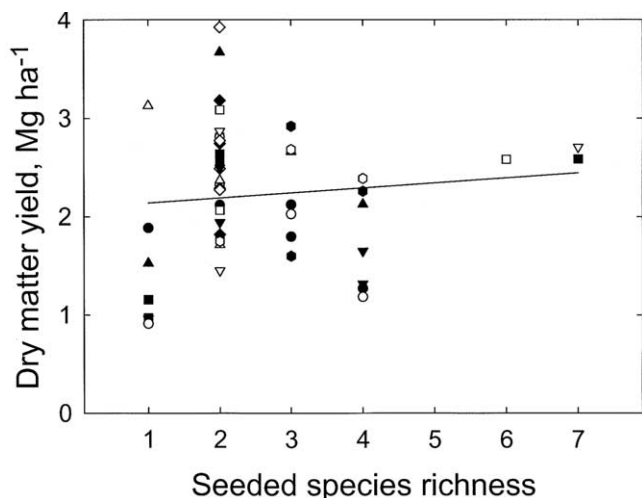

Fig. 1. Dry matter yields of 50 different grass–legume mixtures planted in 2.7- by 15.3-m plots near Storrs, CT, in 1932. The soil was a Charlton fine sandy loam (coarse-loamy, mixed, active, mesic Typic Dystrudepts) with pH 5.8. Plots were harvested three times per year during 1933, 1934, and 1935. Data points are 3-yr averages for each mixture. Adapted from Table 5 of Brown and Munsell (1936). Legumes included red clover, white clover (small leaf and large leaf type), alfalfa, and alsike clover (*Trifolium hybridum* L.). Grasses included orchardgrass, perennial ryegrass, timothy, smooth bromegrass, tall oatgrass [*Arrhenatherum elatius* (L.) Beauv. ex J. & K. Pres], meadow fescue (*Festuca pratensis* Huds.), redtop (*Agrostis alba* L.), reed canarygrass, bentgrass (*Agrostis tenuis* L.), Kentucky bluegrass, Canada bluegrass (*Poa compressa* L.), and sweet vernal grass.
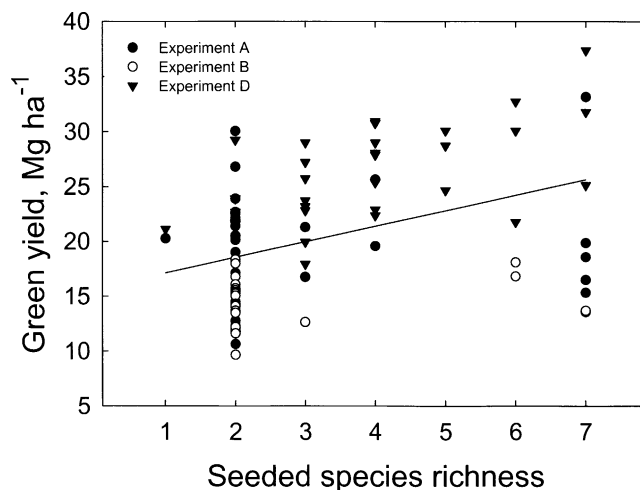

Fig. 2. Yield of fresh green forage from 93 grass–legume mixtures grown in three different experiments under irrigation at Logan, UT, during 1944 to 1951. The soil type was a Millville silt loam (Coarse-silty, carbonatic, mesic Typic Haploxerolls). Manure and P fertilizer had been applied to maintain high soil fertility. Plots were grazed three or four times per year with milking cows and yields measured before grazing. Data points are averages of 6 yr in Experiment A, 4 yr in Experiment B, and 5 yr in Experiment D. Adapted from Tables 5, 8, and 11 from Bateman and Keller (1956).

tion of complex mixtures resulted from greater forage growth during the summer contributed mainly by the legume and forb components. Species-rich (25 to 41 species of grasses, forbs, and a legume) grassland managed for hay produced more forage than species-poor (6 to 17 species) field plots at six sites during 4 yr in southern England (Bullock et al., 2001).

Other field-plot studies have shown no benefit to forage production from highly complex forage mixtures (e.g., Zannone et al., 1983; Tracy and Sanderson, 2001). Several studies in the New Zealand hill country reported inconsistent evidence of production responses to forage species richness (Nicholas et al., 1997; Dodd et al., 2003, White et al., 2003). Nicholas et al. (1997) reported a positive response of species number (up to 12 species) on herbage yield at one hill site, but a weak response ($R^2 = 0.1$) at a second hill site. Of interest in her study was a high coefficient of variation (CV) for low numbers of species and a decreasing CV as species number increased, evidence of reduced risk from species-rich grasslands. Another study at the same location found a strong negative relationship between sward functional characteristics (such as crude protein, digestibility, fiber, and growth rate) and species richness (White et al., 2003). These sites were also correlated with a negative relationship between fertility and species richness. To overcome potential problems of bias that can result from fertility differences from sites selected to have differences in species richness (and thus yield), Dodd et al. (2003) sowed mixtures of up to 11 species from eight functional groups into hill soil. The dominant influences on herbage accumulation were en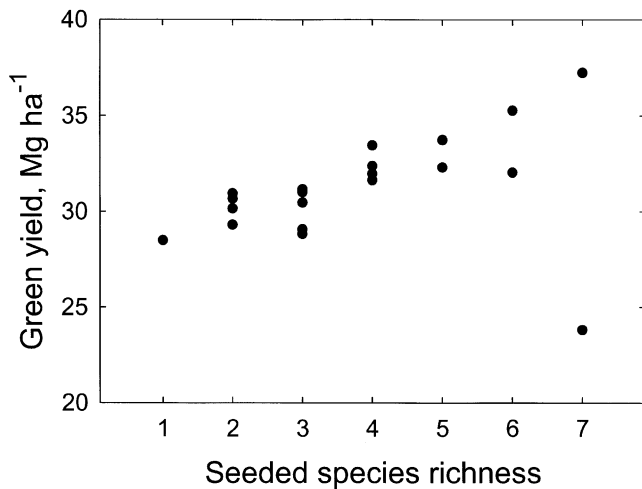vironmental (site, fertility, and slope) rather than species diversity, and were related to the presence of particular species rather than the number of species. The number of species sown negatively affected the contribution of unsown species to yield, showing advantages to sowing diverse mixtures in terms of resistance to weed invasion (Tracy and Sanderson, 2004).

Simple and complex mixtures (1 to 12 species) of grasses, legumes, and a forb were compared for herbage yield under grazing in a multilocation trial in Ohio and Pennsylvania (Barker et al., 2003). In all seasons and at all sites, there was a positive relationship between the number of species sown and forage production (Fig. 5). In Ohio, where summer–fall production was more severely affected than in Pennsylvania, this relationship was less pronounced than in other instances. The highest yielding treatment in most seasons and sites had only one or two sown species; however, in most instances, this was not significantly different from the nine-species treatment. The identity of the highest yielding treatments varied among sites and seasons. It was concluded that although maximum forage yield might occur for monocultures or two-species mixtures of the best adapted species, the difficulty in predicting which species to use, and variation in the best species between spring and summer, suggests forage production might be most consistently maximized from planting complex mixtures.

Contrasting results from studies conducted with different forage species, environments, and conditions preclude clear-cut, unifying conclusions. Clearly there are instances where forage yield on pasture is maximized at low diversity and other instances where yield is maximized at high diversity. One difficulty with some published research on diversity effects on pasture is that the species used were not randomly selected, but were biased by knowledge of species performance. In many studies, the low diversity treatments included species with a history of good performance in the environment in question, and high diversity treatments included species that might be less well adapted. For simple functional expectations (e.g., high yield) from stable environments with
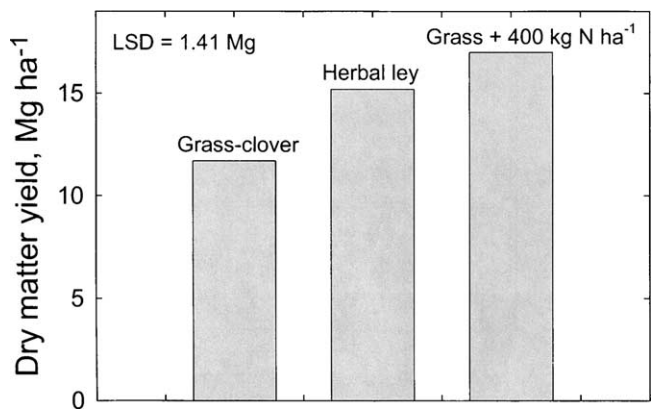

Fig. 3. Yield of fresh green forage from selected grass–legume mixtures grown under irrigation at Logan, UT, during 1947 to 1951. The selected mixtures were of the seven highest yielding legumes and grasses (Ladino white clover, alfalfa, red clover, smooth bromegrass, orchardgrass, tall oatgrass, and reed canarygrass) from Experiment D in Fig. 2. The low-yielding seven-species mixture consisted of a (then) recommended mixture of smooth bromegrass, orchardgrass, alsike clover, Kentucky bluegrass, meadow fescue, perennial ryegrass, and a small-leafed white clover. This mixture became dominated by grasses during the experiment. Plots were grazed three or four times per year with milking cows and yields measured before grazing. Data points are averages of 5 yr. Adapted from Table 9 from Bateman and Keller (1956).

Fig. 4. Dry matter yields of a perennial ryegrass–white clover mixture and a herbal ley mixture (23 species of grasses, legumes, and forbs) compared with perennial ryegrass fertilized with 400 kg N ha^{-1} under sheep grazing in New Zealand. The herbal ley and grass monoculture did not differ in yield, whereas both treatments yielded more than the grass–clover mixture. Data are from Ruz-Jerez et al. (1991). LSD = least significant difference.
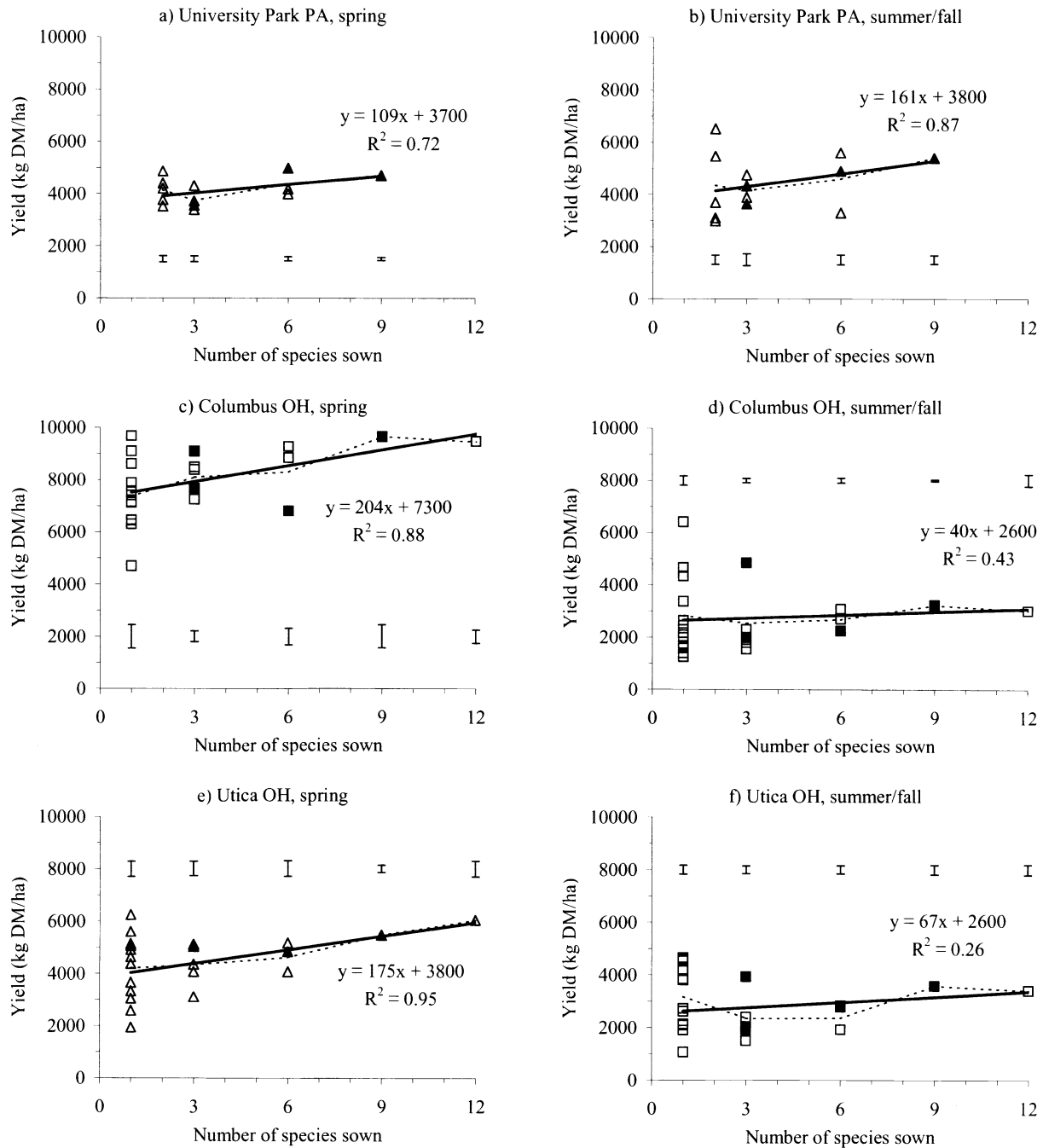
Fig. 5. Spring (April to May) and summer–fall (June–October) yield vs. species number sown for one site in Pennsylvania and two sites in Ohio. Open symbols are treatments unique to that site and closed symbols are treatments common to all three sites, dotted lines connect the mean for each number of species and solid lines are the regression for those means, vertical bars show mean standard error for each species treatment, symbols are means of three or four replicates. Data are revised from Barker et al. (2003).

few limitations to production, it is a reasonable hypothesis that yields might be maximized from a low diversity stand comprised of species well adapted to that environment. As functional expectations increase (i.e., more items from the list in Table 1), pastureland sustainability might be maximized from more complex mixtures.

Animal Productivity Trials with Diverse Mixtures

Grazing animals have a key role in affecting plant species diversity in grazing lands (Rook and Tallowin,

2003); however, there are few data on how biodiversity affects animal performance. The paucity of studies probably reflects the large spatial scale and inputs required to conduct replicated field experiments where animal performance is measured from pastures sown to different diversity. Animal productivity in a grazing system is a function of the output per animal (e.g., milk per cow, gain per head; a measure of forage quality) and the number of animals that a unit of grazing land will support (Mott and Moore, 1985). Voluntary dry matter intake

Table 2. Milk production of dairy cows grazing N-fertilized grass or two grass–legume mixtures in Minnesota (adapted from Wedin et al., 1965).

Treatment	Carrying capacity	Milk production	
	Animal days ha^{-1}	kg cow^{-1} d^{-1}	kg ha^{-1}
Grass+N†	325	17.1	4733
Simple mixture‡	300	16.8	4233
Complex mixture§	301	15.8	3789

† Smooth bromegrass and orchardgrass received 450 kg N ha^{-1} yr^{-1} in three applications during year 1 and 235 kg ha^{-1} yr^{-1} in two applications during year 2.
‡ Alfalfa, white clover, smooth bromegrass, and orchardgrass.
§ Alfalfa, red clover, alsike clover, white clover, smooth bromegrass, orchardgrass, timothy, meadow fescue, and reed canarygrass.

and stocking rate are key determinants of animal performance on pasture. The botanical composition and population of grazing land along with the morphology and structure of the sward affect the amount of herbage grown and consumed (Hodgson, 1990).

Research on New Zealand high-country grazing lands showed that species richness and evenness were weakly associated with sheep carrying capacity or stability of production (coefficient of variation in annual carrying capacity; Scott, 2001). Grazing research with lactating dairy cows indicated that there was no benefit to planting a complex mixture of grasses and legumes for grazing (Wedin et al., 1965). Dairy cows grazed on replicated pastures of N-fertilized grass, a simple (four species) grass–legume mixture, and a complex (eight species) grass–legume mixture. Nitrogen-fertilized grass was the most productive (greatest carrying capacity), whereas individual cow milk production was similar among treatments (Table 2). Both the simple and complex mixtures were primarily dominated by alfalfa-smooth bromegrass (*Bromus inermis* Leyss.), with less than 10% of the other seeded species present.

Recent dairy grazing research indicated that individual animal performance was similar among simple (orchardgrass-white clover) and complex swards (three to nine species of grasses, legumes, and chicory; Soder et al., 2003) Forage production per hectare (and by extrapolation, animal production per hectare) was greater on complex forage mixtures (7400 kg dry matter ha^{-1}) compared with the simple grass–legume mixture (4800 kg ha^{-1}). Lactating dairy cattle grazed replicated ha^{-1} pastures of 2, 3, 6, or 9 species at equal levels of herbage on offer and milk yield, dry matter intake, and herbage yield were measured. Milk production averaged 35.6 kg cow^{-1} d^{-1} and dry matter (grazed forage) intake averaged 13.7 kg cow^{-1} d^{-1}. The greater herbage yield on the complex mixtures likely resulted in a greater carrying capacity.

More animal production studies are needed to ascertain the effects of species diversity on per head and per hectare production along with effects on the composition of animal food products (e.g., Carpino et al., 2003). Such studies must be long term to consider whether the effects of species diversity on the seasonal supply of herbage (Daly et al., 1996) contribute to improved animal performance. They must also be long term to consider the dynamic interaction between grazing and plant species diversity (Provenza et al., 2003), in particular

how changes in species diversity under grazing (e.g., abundance of preferred/non preferred herbage) affects animal performance.

CONCLUSIONS

As found with several ecological studies on natural and experimental grasslands, the evidence for diversity effects is equivocal for pasturelands. Where positive effects of plant species diversity have been reported in forage and grazing land experiments, the benefits have been attributed to the sampling effect (inclusion of a highly productive forb or legume), facilitation (hydraulic lift in grass-forb-legume mixtures), and niche separation or complementarity (N fixation resulting from the inclusion of a legume functional group).

Despite the limited research, we believe that enough evidence exists to support some general recommendations. First, diversity is not simply a numbers game. The proportional abundance of species, their unique attributes, and their spatial distribution across the landscape are critical features in pasturelands. Thus, a highly diverse system may not be appropriate for a highly productive, stable environment where the objective is simply maximum forage production. Most temperate grazing lands, however, are highly heterogeneous in soil resources, climate, and landscape and often fulfill multiple functions for producers (e.g., animal production, resource protection, and wildlife enhancement). It is in these situations where greater plant diversity may be most beneficial.

Second, research on plant diversity in temperate pastures must move beyond small-scale experiments dealing mainly with α diversity and primary production. More data are needed from grazing trials that measure animal productivity, behavior, and selection on a range of species mixtures at relevant scales so that practical recommendations can be made for grazing management. In particular, we must determine how changes in diversity associated with grazing may affect the benefits of planting species-rich mixtures. Vegetation has pronounced spatial patterns; however, we do not fully understand the significance and practical benefits of this variability. Systems research is needed on using diversity at the farm scale where combinations of simple forage mixtures or monocultures are used in several pastures to complement work on complex intimate mixtures of forages in single fields. Finally, embracing a multifunctional view of grazing lands to include environmental benefits as well as productivity opens the door for greater use of biodiversity in sustainable grazing land management.

REFERENCES

Bardgett, R.D., and A. Shine. 1999. Linkages between plant diversity, soil microbial biomass, and ecosystem function in temperate grasslands. Soil Biol. Biochem. 31:317–321.

Barker, D.J., K.J. Moore, and J.A. Guretzky. 2002. Spatial variation in species richness under contrasting topographies and grazing regimes. p. 222–225. *In* T. Terrill (ed.) Proc. Am. Forage Grassl. Conf., Bloomington, MN. 14–17 July 2002. Am. Forage and Grassl. Council, Georgetown, TX.

Barker, D.J., R.M. Sulc, A. Deak, M.H. Hall, M.A. Sanderson, and

T.L. Bultemeir. 2003. Performance of pastures with high and low species richness in northeast USA. p. 172–176. *In* T. Terrill (ed.) Proc. Am. Forage Grassl. Conf., Lafayette, LA. 26–30 April 2003. Am. Forage and Grassl. Council, Georgetown, TX.

Bateman, G.O., and W. Keller. 1956. Grass-legume mixtures for irrigated pastures for dairy cattle. Bull. 382. Utah Agric. Exp. Sta. Logan, UT.

Berendse, F. 1982. Competition between plant populations with differing rooting depths. III. field experiments. Oecologia (Berlin) 53:50–55.

Bertness, M.D., and S.D. Hacker. 1994. Physical stress and positive associations among marsh plants. Am. Nat. 144:363–372.

Blaser, R.E., W.H. Skrdla, and T.H. Taylor. 1952. Ecological and physiological factors in compounding seed mixtures. Adv. Agron. 4:179–218.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. J. Appl. Ecol. 28:28–41.

Brooker, R.W., and T.V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: A model. Oikos 81:196–207.

Brown, B.R., and R.I. Munsell. 1936. Species and varieties of grasses and legumes for pastures. Bull. 208. Storrs Agric. Expt. Sta. Storrs, CT.

Brummer, E.C. 1998. Diversity, stability, and sustainable American agriculture. Agron. J. 90:1–2.

Bullock, J.M., and C.A. Marriott. 2000. Plant responses to grazing, and opportunities for manipulation. p. 17–26. *In* A.J. Rook and P.D. Penning (ed.) Grazing management. Occasional Symp. No. 34. British Grassl. Soc., Reading, U.K.

Bullock, J.M., R.F. Pywell, M.J.W. Burke, and K.J. Walker. 2001. Restoration of biodiversity enhances agricultural production. Ecol. Lett. 4:185–189.

Caldwell, M.M., T.E. Dawson, and J.H. Richards. 1998. Hydraulic lift: Consequences of water efflux from the roots of plants. Oecologia (Berlin) 113:151–161.

Callaway, R.M. 1995. Positive interactions among plants. Bot. Rev. 61:306–349.

Callaway, R.M. 1998. Are positive interactions species-specific? Oikos 82:202–207.

Callaway, R.M., and L.R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78:1958–1965.

Carpino, S., G. Licitra, and P.J. Van Soest. 2003. Selection of forage species by dairy cattle on complex Sicilian pastures. Anim. Feed Sci. Technol. 105:205–214.

Carrillo-Garcia, A., Y. Bashan, and G.J. Bethlenfalvay. 2000. Resource-island soils and the survival of the giant cactus, cardon, of Baja California Sur. Plant Soil 218:207–214.

Clark, E.A. 2001. Diversity and stability in humid temperate pastures. p. 103–118. *In* P.G. Tow and A. Lazenby (ed.) Competition and succession in pastures. CAB Intl. Publ., New York.

Collins, S.L., A.K. Knapp, J.M. Briggs, J.M. Blair, and E.M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science (Washington, DC.) 280:745–747.

Cornelissen, J.H.C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J. Ecol. 84:573–582.

Cooper, H.P., J.K. Wilson, and J.H. Baron. 1929. Ecological factors determining the pasture flora in the northeastern United States. J. Am. Soc. Agron. 607–627.

Cransberg, L., and D.J. MacFarlane. 1994. Can perennial pastures provide the basis for a sustainable farming system in southern Australia? N. Z. J. Agric. Res. 37:287–294.

Crawley, M.J., and J.E. Harral. 2001. Scale dependence in plant biodiversity. Science (Washington, DC.) 291:864–868.

Daly, M.J., R.M. Hunter, G.N. Green, and L. Hunt. 1996. A comparison of multi-species pasture with ryegrass-white clover pastures under dryland conditions. Proc. N. Z. Grassl. Assoc. 58:53–58.

Darwin, C. 1872. The origin of species. Reprinted 1978 by Macmillan Publ. Co., New York.

Dawson, T.E. 1993. Hydraulic lift and water use by plants: Implications for water balance, performance, and plant-plant interactions. Oecologia (Berlin) 95:565–574.

Dodd, M.B., D.J. Barker, and M.E. Wedderburn. 2003. Practical bene-
fits of pasture diversity in hill country. Proc. N. Z. Grassl. Assoc. 65:127–132.

Donald, C.M. 1963. Competition among crop and pasture plants. Adv. Agron. 15:1–114.

Edwards, G.R., J.A. Newman, A.J. Parsons, and I.A. Wright. 1996. The spatial pattern of vegetation in cut and grazed white clover pastures. Grass Forage Sci. 51:219–231.

Egerton, J.J.G., J.C.G. Banks, A. Gibson, R.B. Cunningham, and M.C. Ball. 2000. Facilitation of seedling establishment: Reduction in irradiance enhances winter growth of *Eucalyptus pauciflora*. Ecology 81:1437–1449.

Foster, L. 1988. Herbs in pastures. Development and research in Britain, 1850–1984. Biol. Agric. Hort. 5:97–133.

Frank, D.A., and S.J. McNaughton. 1991. Stability increases with diversity in plant communities: Empirical evidence from the 1988 Yellowstone drought. Oikos 62:360–362.

Frank, D.A., S.J. McNaughton, and B.F. Tracy. 1998. The ecology of the earth's grazing ecosystems. Bioscience 48:513–521.

Fridley, J.D. 2001. The influence of species diversity on ecosystem productivity: How, where, why? Oikos 93:514–526.

Harris, S.L., C.D. Waugh, R.J. McCabe, and V.T. van Vught. 1999. Effect of deferred grazing during summer on white clover content of Waikato dairy pastures, New Zealand. N. Z. J. Agric. Res. 42:1–7.

Haynes, R.J., and P.H. Williams. 1993. Nutrient cycling and soil fertility in the grazed pasture ecosystem. Adv. Agron. 49:119–199.

Hector, A. 1998. The effect of diversity on productivity: Detecting the role of species complementarity. Oikos 82:597–599.

Hector, A. (and 33 coauthors). 1999. Plant diversity and productivity experiments in European grasslands. Science (Washington, DC.) 286:1123–1127.

Hector, A., A.J. Beale, A. Minns, S.J. Otway, and J.H. Lawton. 2000. Consequences of the reduction of plant diversity for litter decomposition: Effects through litter quality and microenvironment. Oikos 90:357–371.

Hodgson, J. 1990. Grazing management: Science into practice. John Wiley and Sons, Inc., New York.

Hooper, D.U., and P.M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. Ecol. Monogr. 68:121–149.

Huston, M.A. 1994. Biological diversity. Cambridge Univ. Press, UK.

Huston, M.A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. Oecologia (Berlin) 110:449–460.

Huston, M.A., L.W. Aarssen, and M.P. Austin. 2000. No consistent effect of plant diversity on productivity. Science (Washington, DC.) 289:1255.

Ives, A.R., J.L. King, and K. Gross. 2000. Stability and species richness in complex communities. Ecol. Lett. 3:399–411.

Johnstone-Wallace, D.B. 1933. The soils and crop production in Genesee County, New York. Part II. Pastures. Cornell Univ. Agric. Exp. Stn. Bull. 567.

Kanneganti, V.R., R.P. Walgenbach, and L.J. Massingill. 1998. Daily and seasonal forage availability under rotational grazing of a mixed-species temperate pasture. J. Sust. Agric. 12:49–66.

Kalburtji, K.L., A.P. Mamolos, and S.K. Kostopoulou. 1998. Litter dynamics of *Dactylis glomerata* and *Vicia villosa* with respect to climate and soil characteristics. Grass Forage Sci. 53:225–232.

Knops, J.M.H., D. Wedin, and D. Tilman. 2001. Biodiversity and decomposition in experimental grassland systems. Oecologia (Berlin) 126:429–433.

Koukoura, A. 1998. Decomposition and nutrient release from C_3 and C_4 plant litters in a natural grassland. Acta Oecologia 19:115–123.

Krueger, W.C., M.A. Sanderson, J.B. Cropper, M. Miller-Goodman, C.E. Kelley, R.D. Pieper, P.L. Shaver, and M.J. Trlica. 2002. Environmental impacts of livestock on U.S. grazing lands. Council for Agricultural Science and Technology issue paper No. 22. CAST, Ames, IA.

Lucero, D.W., P. Grieu, and A. Guckert. 1999. Effects of water deficits and plant interaction on morphological growth parameters and yield of white clover (*Trifolium repens* L.) mixtures. Eur. J. Agron. 11:167–177.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton Univ. Press, Princeton, NJ.

McNaughton, S.J. 1977. Diversity and stability of ecological communi-

ties: A comment on the role of empiricism in ecology. Am. Nat. 111:512–515.

Milchunas, D.G., O.E. Sala, and W.K. Lauenroth. 1998. A generalized model of the effects of grazing by large herbivores on grassland community structure. Am. Nat. 132:87–106.

Minns, A., J. Finn, A. Hector, M. Caldeira, J. Joshi, C. Palmborg, B. Schmid, M. Scherer-Lorenzen, E. Spehn, and A. Troubis. 2001. The functioning of European grassland ecosystems: Potential benefits of biodiversity to agriculture. Outlook Agric. 30:179–185.

Mott, G.O., and J.E. Moore. 1985. Evaluating forage production. p. 422–429. In M.E. Heath et al. (ed.) Forages: The science of grassland agriculture. 4th ed. Iowa State Univ. Press, Ames.

Naeem, S., L.J. Thompson, S.P. Lawler, J.H. Lawton, and R.M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature (London) 368:734–737.

Naeem, S., J.M.H. Knops, D. Tilman, K.M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108.

Nicholas, P.K., P.D. Kemp, D.J. Barker, J.L. Brock, and D.A. Grant. 1997. Production, stability and biodiversity of North Island New Zealand hill pastures. p. 21–9 to 21–10. In J.G Buchanan-Smith et al. (ed.) Proc. Intl. Grassl. Congr., 18th, Winnipeg, MB, Canada. 8–17 June 1997. Association Management Centre, Calgary, AB, Canada.

Nie, Z.N., I. Valentine, A.D. Mackay, D.J. Barker, and J. Hodgson. 1996. Long-term effects of pastoral fallowing on white clover (Trifolium repens L.) and grass growth in a hill pasture. p. 75–78. In D.R. Woodfield (ed.) White clover: New Zealand's competitive edge. Agron. Soc. of New Zealand Spec. Publ. No. 11, New Zealand Grassl. Assoc. Research and Practice Series No. 6, Lincoln University, New Zealand.

Owens, L.B., W.M. Edwards, and R.W. Van Keuren. 1994. Groundwater nitrate levels under fertilized grass and grass-legume pastures. J. Environ. Qual. 23:752–758.

Parsons, A.J., and B. Dumont. 2003. Spatial heterogeneity and grazing processes. Anim. Res. 52:161–179.

Peet, R.K. 1974. The measurement of species diversity. Annu. Rev. Ecol. Syst. 5:285–307.

Peeters, A., and F. Janssens. 1998. Species-rich grasslands: Diagnostics, restoration, and use in intensive livestock production systems. p. 375–393. In G. Nagy and K. Peto (ed.) Grassl. Sci. Eur. 3:375–393.

Pierre, W.H., T.H. Longwell, R.R. Robinson, G.M. Browning, I. McKeever, and R.F. Copple. 1937. West Virginia pastures: Vegetation, carrying capacity, and soil properties. West Virginia Agric. Exp. Stn. Bull. 280.

Provenza, F.D., J.J. Villalba, L.E. Dziba, S.B. Atwood, and R.E. Banner. 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. Small Ruminant Res. 49:257–274.

Reich, P.B., J. Knops, D. Tilman, J. Craine, D. Ellsworth, M. Tjoelker, T. Lee, S. Naeem, D. Wedin, D. Bahauddin, G. Hendrey, S. Jose, K. Wrage, J. Goth, and W. Bengston. 2001. Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. Nature (London) 410:809–812.

Renne, I., and B.F. Tracy. 2003. The rich get richer. Response. Front. Ecol. Environ. 1:122.

Richards, J.H., and M.M. Caldwell. 1987. Hydraulic lift: Substantial nocturnal water transport between soil layers by Artemisia tridentata roots. Oecologia (Berlin) 73:486–489.

Rook, A.J., and J.R.B. Tallowin. 2003. Grazing and pasture management for biodiversity management. Anim. Res. 52:181–189.

Ruz-Jerez, B.E., P.R. Ball, R.E. White, and P.E.H. Gregg. 1991. Comparison of a herbal ley with a ryegrass-white clover pasture and pure ryegrass sward receiving fertilizer nitrogen. Proc. N. Z. Grassl. Assoc. 53:225–230.

Sanderson, M.A., B.F. Tracy, R.H. Skinner, D. Gustine, and R. Byers. 2001. Changes in the plant species composition of northeastern grazing lands during the 20th century. p. 365–373. In Proc. 1st Natl. Conf. on Grazing Lands, Las Vegas, NV. 5–8 Dec. 2000. Natl. Assoc. Conserv. Districts, Washington, DC.

Sanderson, M.A., F. Taube, B.F. Tracy, and M. Wachendorf. 2002. Plant species diversity in grasslands of the northeastern USA and northern Germany. Grassl. Sci. Eur. 7:399–401.

Scherer-Lorenzen, M., C. Palmborg, A. Prinz, and E.D. Shulze. 2003.

The role of plant diversity and composition for nitrate leaching in grasslands. Ecology 84:1539–1552.

Schmid, B. 2002. The species richness-productivity controversy. Trend. Ecol. Evol. 17:113–114.

Scott, D. 2001. Sustainability of New Zealand high-country pastures under contrasting development inputs. 7. Environmental gradients, plant species selection, and diversity. N. Z. J. Agric. Res. 44:59–90.

Shumway, S.W. 2000. Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. Oecologia (Berlin) 124: 138–148.

Skinner, R.H., J.D. Hanson, G.L. Hutchinson, and G.E. Schuman. 2002. Response of C_3 and C_4 grasses to supplemental summer precipitation. J. Range Manage. 55:517–522.

Smith, V.H., G.D. Tilman, and J.C. Nekola. 1999. Eutrophication: Impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environ. Poll. 100:179–196.

Soder, K.J., M.A. Sanderson, and L.D. Muller. 2003. Effects of forage diversity on intake and productivity of grazing lactating dairy cows. Am. Assoc. Dairy Sci. Abstr. p. 93.

Spellerberg, I.F., F.B. Goldsmith, and M.G. Morris. 1991 The scientific management of temperate communities for conservation. Blackwell Scientific Publications, Oxford, UK.

Sprague, H.B., and H.W. Reuszer. 1928. A study of permanent dairy pastures in New Jersey. New Jersey Agric. Exp. Stn. Circ. 141.

Stirling, G., and B. Wilsey. 2001. Empirical relationships between species richness, evenness, and proportional diversity. Am. Nat. 158:286–299.

Stohlgren, T.J., L.D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecol. Appl. 9:45–64.

Stohlgren, T.J., D.T. Barnett, and J.T. Kartesz. 2003. The rich get richer: Patterns of plant invasions in the United States. Front. Ecol. Environ. 1:11–14.

Symstad, A.J., F.S. Chapin, III, D.H. Wall, K.L. Gross, L.F. Huenneke, G.G. Mittelbach, D.P.C. Peters, and D. Tilman. 2003. Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. Bioscience 53:89–98.

Tilman, G.D. 1997. Community invasibility, recruitment limitation and grassland biodiversity. Ecology 78:81–92.

Tilman, G.D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80:1455–1474.

Tilman, G.D., and S. Pacala. 1993. The maintenance of species richness in plant communities. p. 13–25. In R. E. Ricklefs and D. Schluter (ed.) Species diversity in ecological communities. Univ. Chicago Press, Chicago.

Tilman, G.D., and J.A. Downing. 1994. Biodiversity and stability in grasslands. Nature (London) 367:363–365.

Tilman, G.D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature (London) 379:718–720.

Tilman, G.D., D.N. Duvick, S.B. Brush, R.J. Cook, G.C. Daily, G.M. Heal, S. Naeem, and D.R. Notter. 1999. Benefits of biodiversity. Task force report 133. Council for Agricultural Science and Technology, Ames, IA.

Tilman, G.D., P.B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. Science (Washington, DC.) 294:843–845.

Tracy, B.F., and M.A. Sanderson. 1999. Seedbank diversity in grazing lands of the Northeast United States. J. Range Manage. 53:114–118.

Tracy, B.F., and M.A. Sanderson. 2000. Patterns of plant species richness in pasture lands of the Northeast United States. Plant Ecol. 149:169–180.

Tracy, B.F., and M.A. Sanderson. 2001. Productivity and stability relationships in clipped pasture communities of varying diversity. p. 96. In Ecol. Soc. Am. Abstr. Ecol. Soc. Am., Washington, DC.

Tracy, B.F., and M.A. Sanderson. 2004. Relationships between forage plant diversity and weed invasion in pasture communities. Agric. Ecosyt. Environ. 102:175–183.

Trenbath, B.R. 1974. Biomass productivity of mixtures. Adv. Agron. 26:177–210.

Waide, R.B., M.R. Willig, C.F. Steiner, G. Mittelbach, L. Gough, S.I. Dodson, G.P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. Annu. Rev. Ecol. Syst. 30:257–300.

Wardle, D.A. 1999. Is "sampling effect" a problem for experiments investigating biodiversity–ecosystem function relationships? Oikos 87:403–407.

Wardle, D.A. 2002. Communities and ecosystems: Linking the aboveground and belowground components. Princeton Univ. Press, Princeton, NJ.

Wardle, D.A., K.I. Bonner, and K.S. Nicholson. 1997. Biodiversity and plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79:247–258.

Wardle, D.A., M.A. Huston, and J.P. Grime. 2000. Biodiversity and ecosystem function: An issue in ecology. Bull. Ecol. Soc. Am. 81: 235–239.

Watkinson, A.R., and S.J. Ormerod. 2001. Grasslands, grazing and biodiversity: Editors' introduction. J. Appl. Ecol. 38:233–237.

Wedin, D.A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. Science (Washington, DC.) 274:1720–1723.

Wedin, W.F., J.D. Donker, and G.C. Marten. 1965. An evaluation of nitrogen fertilization in legume-grass and all-grass pasture. Agron. J. 58:185–188.

White, T.A., D.J. Barker, and K.J. Moore. 2003 Vegetation diversity, growth, quality and decomposition in managed grasslands. Agric. Ecosyst. Environ. 101:73–84.

Wilsey, B.J., and C. Potvin. 2000. Biodiversity and ecosystem functioning: Importance of species evenness in an old field. Ecology 81: 887–892.

Wilsey, B.J., and H.W. Polley. 2002. Reductions in grassland species evenness increase dicot seeding invasion and spittle bug infestation. Ecol. Lett. 5:676–684.

Wilson, J.R. 1996. Shade-stimulated growth and nitrogen uptake by pasture grasses in a subtropical environment. Aust. J. Agric. Res. 47:1075–1093.

Yachi, S., and M. Loreau. 2001. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc. Natl. Acad. Sci. USA 96:1463–1468.

Zannone, L., L. Assemat, P. Rotili, and P. Jacquard. 1983. An experimental study of intraspecfic competition within several forage crops. Agronomie 3:451–459.