Weed Technology. 2004. Volume :000-000

Name /wete/2004s\_55

GALLET 202

CYNTHIA S. BROWN<sup>2</sup>

**Abstract:** Categorizing species according to their functional traits, such as spatial and temporal patterns of resource use, effects on ecosystems, and responses to environmental perturbations, can facilitate successful restoration of plant communities. Functional guilds condense species lists by grouping species according to similarities in characteristics we believe to be important in a particular context. These groupings can allow us to (1) ensure community and ecosystem structural and functional attributes, (2) increase competitiveness of the community to deter the establishment of undesirable species, (3) simplify and test models of community assembly including resistance to invasion, succession, and species coexistence, and (4) facilitate cross-site comparisons. As useful as functional guilds can be, we must not overlook the potentially important roles of individual species. In restoration, including multiple species that represent each functional type within a target community may provide a buffer against environmental change. Functional guilds provide realistic conceptual units to ensure that restored plant communities include species that confer the ecological functions of most importance the majority of the time.

**Abbreviations:** CCNHA, Cedar Creek Natural History Area; CO<sub>2</sub>, carbon dioxide; N, nitrogen; NO<sub>3</sub>, nitrate.

Additional index words: Community assembly, competition, functional traits, invasion, resource use, stability.

### INTRODUCTION

10/07/2004 02:21PM Plate # 0-Composite

Classification of species has been practiced for ages and myriad schemes to group species have been invoked, each focusing on the traits deemed most important for the purpose of the classifier (see Smith et al. 1997). Groups of species may be defined a priori by life history, life form, taxonomy or physiology of the species, or some combination of these traits among others (Box 1981; Dukes 2001, 2002; Fargione et al. 2003; Grime 1988; Hooper 1998; Hooper and Vitousek 1997, 1998; Knops et al. 1999; Naeem et al. 2000; Prentice et al. 1992; Raunkiaer 1934; Symstad 2000; Tilman 1997). Some authors have applied analytical techniques to create groups of species (Craine et al. 2002; Kindscher and Wells 1995). Recent classification schemes have focused on functional attributes of species or grouping organisms according to their responses to environmental factors to improve the ability to project vegetation dynamics and geographical distributions under future global change (Schulze and Mooney 1994; Smith et al. 1997). Although the terms have different meanings in some contexts (Gitay and Noble 1997), I will use functional guild, functional group, and functional type interchangeably.

Despite the great diversity of approaches (reviewed by Smith et al. 1997), there is a "need for functional type classifications as a means of reducing taxonomic species diversity to manageable levels of understanding" (Woodward et al. 1997, p. 355). For a functional-type classification to be useful, the goals, temporal and spatial scales, and environmental contexts for which it was created must be clear. Which attributes are relevant will vary with the purpose of the classification, and as a result, different groupings will emerge (Westoby and Leishman 1997). Classification of plants according to how they affect and are affected by their environments (Shugart 1997) can be valuable for restoration of plant communities that have characteristics we seek, such as stability, productivity, and resistance to subsequent invasion by undesirable species.

Conclusions from research investigating the use of functional types have been mixed. Traditional functional-group classification schemes based on morphological, taxonomic, and life-history traits were somewhat useful in predicting responses to elevated carbon dioxide ( $CO_2$ ) and available nitrogen (N) in a low-N, mid-

<sup>&</sup>lt;sup>1</sup> Received for publication April 7, 2004, and in revised form September 2, 2004.

<sup>&</sup>lt;sup>2</sup> Assistant Professor, Department of Bioagricultural Sciences and Pest Management, 1177 Campus Delivery, Colorado State University, Fort Collins, CO 80523-1177. Corresponding author's E-mail: csbrown@lamar.colostate.edu.

GALLET 203

WEED TECHNOLOGY

western prairie community (Reich et al. 2003a, 2003b). Although functional groups responded differently to CO<sub>2</sub> and N, there was a great deal of variation among species within functional groups, which made drawing generalizations difficult (Reich 2003a, 2003b). Craine et al. (2003) found little difference among the traditional functional types, C3 and C4 grasses, and between grasses and forbs in fine and coarse belowground biomass. In contrast, Craine et al. (2002) examined a wide range of traits and found that principal components analysis divided species into categories that were consistent with the traditional classification scheme (C3 grasses, C4 grasses, forbs, legumes, and woody species) and also identified two strategies (N fixation and low-N suite of traits), which extended organ-level traits to ecosystem-level processes.

Functional types have been used successfully to test ecological theory by a number of authors. For example, Dukes (2002) examined the effect of functionalgroup diversity on plant invasions. Using early-season annual forbs, late-season annual forbs, N-fixers, and perennial bunchgrasses, he found that greater functional-group richness but not species richness was associated with reduced success of a noxious weed in a microcosm experiment. Nevertheless, the more species-rich treatments were not as negatively affected by the invader as less-diverse treatments. In addition, monocultures of a resident species that was of the same functional group as the invader suppressed growth of the invader as much as the most functionally rich resident community.

Hooper (1998) and Hooper and Vitousek (1997, 1998) examined the roles played by the same functional types invoked by Dukes (2002) and found that relative resource use differed among functional types. They further examined the role of functional-type richness and determined that the identities of the functional types present more strongly determined the ecosystem processes measured than the number of functional types present. These results indicate that both functional and species richness may have important effects on ecosystem characteristics and processes such as invasibility and that the traits of particular species may play a dominant role at the community level.

In this study, I provide some additional evidence that functional guilds can be useful for plant community assembly. I will describe how this type of classification system can reflect ecosystem-level functional attributes and some benefits that functional guilds can provide for restoration ecology.

## MATERIALS AND METHODS

**Experimental Setup.** The biodiversity experiment established in 1994 at Cedar Creek Natural History Area (CCNHA), Minnesota, and named E123 is described in Tilman et al. (1996). Each of 147 plots  $(3 \times 3 \text{ m})$  was planted to 1, 2, 4, 6, 8, 12, or 24 species in a complete randomized design, with species for each plot randomly drawn from a pool of 24 tallgrass prairie perennials (Table 1). The pool included four herbaceous functional types: C4 grasses, C3 grasses, legumes, and other forbs. These four functional types have been studied previously at CCNHA (e.g., Davis and Pelsor 2001; Kennedy et al. 2002; Knops et al. 1999; Naeem et al. 2000; Symstad 2000; Tilman et al. 1997). This simple classification system can readily be applied to any species based on phylogenetic criteria. Extractable soil nitrate (NO<sub>3</sub>), soil water content, and light transmittance were measured in each 9-m<sup>2</sup> plot in areas where no introduced species were added in mid-July of each year.

In the seed addition component of the experiment (described in Fargione et al. 2003), viable seeds of 27 species were introduced into 0.5-m<sup>2</sup> subplots within the existing species diversity plots in their fourth growing season (1997) (Table 1). The introduced species represented the four herbaceous functional guilds described above but had not been previously planted in the biodiversity experiment. Data collection methods are described in Fargione et al. (2003). Percent cover of each species was visually estimated in late July-early August in each 0.5m<sup>2</sup> subplot each year. Bare ground in 1997 (initial bare ground) is used as a measure of the availability of open space for germination. Treatment effects became stronger through time as the introduced plants matured; thus, I report only results from 1999. Statistical analyses and diagnostics for multicollinearity of dependent variables in multiple linear regressions and equality of variances were conducted with JMP 3.2.2.<sup>3</sup>

# **RESULTS AND DISCUSSION**

**Type Classification Can Reflect Functional Attributes.** Traditional functional-guild classification has resulted in meaningful groupings in some cases. Fargione et al. (2003) and other studies conducted at CCNHA (see Knops et al. 1999; Naeem et al. 2000; Symstad 2000; Tilman 1997) divided the herbaceous species in their experiments into C3 (cool-season) grasses, C4 (warm-season) grasses, legumes, and non–N-fixing forbs, groups based on taxonomy, life history, and physiological char-

<sup>&</sup>lt;sup>3</sup> SAS Institute, Inc., SAS Circle, Box 8000, Cary, NC.

Name /wete/2004s\_55

10/07/2004 02:21PM

### GALLEY 264

BROWN: FUNCTIONAL GROUPS AND RESTORATION

Table 1. Resident species in and species introduced into the diversity experimental plots and their classification by functional guild.

Plate # 0-Composite

Established communities		Introduced species			
Species	Functional guild	Species	Functional guild		
Pascopyrum smithii (Rydb.) A. Löve <sup>a</sup>	C3 grass	Agrostis gigantea Roth <sup>a</sup>	C3 grass		
Elymus canadensis L. <sup>b</sup>	C3 grass	Festuca ovina L. <sup>b</sup>	C3 grass		
Koeleria macrantha (Ledeb.) J.A. Shultes <sup>a</sup>	C3 grass	Festuca rubra L. <sup>b</sup>	C3 grass		
Poa pratensis L. <sup>a</sup>	C3 grass	Phleum pratense L. <sup>a</sup>	C3 grass		
Andropogon gerardii Vitman <sup>b</sup>	C4 grass	Calamovilfa longifolia (Hook.) Scribn.b	C4 grass		
Bouteloua gracilis (Kunth) Griffiths <sup>a</sup>	C4 grass	Eragrostis trichodes (Nutt.) A. Wood. <sup>b</sup>	C4 grass		
Buchloe dactyloides (Nutt.) Engelm <sup>b</sup>	C4 grass	Setaria viridis (L.) P. Beauv. <sup>a</sup>	C4 grass		
Panicum virgatum L. <sup>b</sup>	C4 grass	Setaria glauca L. <sup>b</sup>	C4 grass		
Schizachyrium scoparium (Michaux) Nasha	C4 grass	Ambrosia artemisiifolia L. <sup>b</sup>	Forb		
Sorghastrum nutans (L.) Nash <sup>b</sup>	C4 grass	Artemisia ludoviciana Nutt. <sup>b</sup>	Forb		
Sporobolus cryptandrus (Torrey) A. Graya	C4 grass	Asclepias syriaca L. <sup>b</sup>	Forb		
Achillea millefolium L. <sup>a</sup>	Forb	Chenopodium album L. <sup>a</sup>	Forb		
Anemone cylindrica A. Gray <sup>b</sup>	Forb	Gnaphalium obtusifolium L. <sup>b</sup>	Forb		
Asclepias tuberosa L <sup>b</sup>	Forb	Helianthus $\times$ laetiflorus Pers. <sup>b</sup>	Forb		
Aster oolentangiensis Riddell <sup>b</sup>	Forb	Oenothera biennis L. <sup>a</sup>	Forb		
Coreopsis palmata Nutt. <sup>b</sup>	Forb	Penstemon grandiflorus Nutt. <sup>b</sup>	Forb		
Euphorbia corollata L. <sup>b</sup>	Forb	Polygonum convolvulus L. <sup>a</sup>	Forb		
Liatris aspera Michx. <sup>b</sup>	Forb	Potentilla arguta Pursh. <sup>b</sup>	Forb		
Rudbeckia hirta var. pulcherrima Farw. <sup>b</sup>	Forb	Rumex acetosella L. <sup>a</sup>	Forb		
Solidago nemoralis Aiton. <sup>b</sup>	Forb	Tragopogon dubius Scop. <sup>b</sup>	Forb		
Astragalus canadensis L. <sup>a</sup>	Legume	Chamaecrista fasciculata (Michx.) Greeneb	Legume		
Lespedeza capitata Michx. <sup>b</sup>	Legume	Desmodium canadense (L.) DC. <sup>b</sup>	Legume		
Dalea purpurea Vent. <sup>b</sup>	Legume	Medicago lupulina L. <sup>a</sup>	Legume		
Vicia villosa Roth <sup>b</sup>	Legume	Melilotus alba Medikus <sup>a</sup>	Legume		
		Melilotus officinalis (L.) Pall. <sup>a</sup>	Legume		
		Trifolium pratense L. <sup>b</sup>	Legume		
		Trifolium repens L. <sup>b</sup>	Legume		
Summary					
Total number of C3 grasses	4		4		
Total number of C4 grasses	7		4		
Total number of forbs	9		12		
Total number of legumes	4		7		
e					

<sup>a</sup> Nomenclature according to Hickman (1993).

<sup>b</sup> Nomenclature according to Gleason and Cronquist (1998).

acteristics. In the experiment described in Fargione et al. (2003), community-level characteristics were influenced by the identity of the functional guilds (sensu Root 1967) present. In particular, resource levels in the established communities were related to the abundance of different functional guilds (Table 2). Resident C4 grasses were the functional guild most strongly associated with all resources measured. As C4 grass cover increased, soil NO<sub>3</sub>, light, and initial bare ground decreased, whereas soil moisture increased. Increased resident C3 grass, forb, and legume cover were associated with decreased soil moisture, and increased resident legume cover was correlated with decreased light. These results suggest that the presence and abundance of different functional guilds resulted in varying levels of different resources and had important implications for invasibility of the plant communities (Fargione et al. 2003).

**Classifying Species into Functional Guilds Can Benefit Restoration.** Functional guilds defined a priori can reflect important features that influence the interactions among their composite species, other organisms, and the environment. These attributes can make functional guilds very useful for restoration. As discussed above, functional guilds allow us to simplify long lists of species into fewer, more manageable units. This simplification can assist us in restoring the structural and functional characteristics of communities and ecosystems. For instance, some invasions cause dramatic changes in physical structure. Dominant herbaceous species may be replaced by woody species as in the invasion of Chinese tallowtree [Sapium sebiferum (L) Roxb.] into native prairies of the southeastern United States (Bruce et al. 1995, 1997). Alternatively, dominant-woody species may be replaced by a herbaceous plant community (D'Antonio and Vitousek 1992). One well-known example of this is the invasion of cheatgrass or downy brome (Bromus tectorum L.) into western North America. Cheatgrass has been implicated in increasing fire frequencies and intensities (Klemmedson and Smith 1964; Knick and Rotenberry 1997; Stewart and Hull 1949; Whisenant 1990),

### WEED TECHNOLOGY

Table 2.	Parameter	estimates f	for four	multiple	regressions of	of resident	functional	guild	cover aga	inst resource	levels.	3
----------	-----------	-------------	----------	----------	----------------	-------------	------------	-------	-----------	---------------	---------	---

Source of variation	df	Log resident forb cover	Log resident C3 grass cover	Log resident C4 grass cover	Log resident legume cover
Soil nitrate	1	-1.971	-1.417	-6.428***	-0.636
Initial bare ground	1	-0.008	0.0004	-0.014**	-0.003
Light	1	0.299	-0.335	-3.018***	-1.878***
Soil water	1	$-0.582^{***}$	-0.34*	0.696***	$-0.872^{***}$
Overall R <sup>2</sup>		0.14	0.06	0.42	0.30
Overall P		0.0003	0.066	< 0.0001	< 0.0001

<sup>a</sup> Bare ground was measured in 1997, the year that seeds were added to the established communities. The other variables were measured in 1999. Variance inflation factors for response variables are <1.5, indicating that they are not appreciably collinear.

\* P < 0.05; \*\* P < 0.01; and \*\*\* P < 0.001.

which has led to its replacement of shrubs and perennial grasses (DiTomaso 2000). Cheatgrass also is known to have negative effects on native species through competition, reducing establishment and growth of native perennial grasses and shrubs (Harris 1967; Rafferty and Young 2002; Svejcar 1990). We can use our knowledge of the structure of the desired plant community to assist us in recreating it. When guilds of species that provide the vertical structure of the historical plant community are missing from or are underrepresented in the disturbed system, they must be replaced during the restoration process to regain critical features of the healthy ecosystem.

Functional features of plant communities and ecosystems, such as energy balance and nutrient cycling, also may be restored using functional guilds as tools. As mentioned above, the invasion of exotic grasses into systems dominated by woody species can result in increased fire frequency and intensity (D'Antonio and Vitousek 1992). Reduction of the functional guilds that contribute to the alteration of the fire cycle (e.g., exotic grasses) and reestablishment of guilds that have been replaced (i.e., native trees and shrubs) may be an effective approach to reinstating more traditional fire cycles. When nutrient cycles have been affected by the introduction of species with novel characteristics, such as the invasion of the actinorrhizal N-fixer Myrica faya Ait. into Hawaii (D'Antonio and Vitousek 1992; Vitousek 1990), functional guilds may be applied to help us understand the invasion process and recover ecosystem function. Myrica has invaded N-deficient soils of recent volcanic deposition, increasing N inputs by four times, in contrast to the natural primary successional sere that does not include symbiotic N-fixers (Vitousek 1990). Control efforts for Myrica have been abandoned (Vitousek 1990), but restoration of communities will be necessary to conserve native flora. This will require removal of the Myrica to stop N additions and reduction of N availability through immobilization (e.g., addition of carbon) or removal (e.g., planting of selected N-accumulating plant species) to help create the ecosystem conditions favorable to the desired plant community.

Functional groups may be applied to restoration to increase the competitiveness of the community in order to deter the establishment of undesirable species. The experiment conducted by Fargione et al. (2003) showed that when species of different functional guilds were introduced into established diversity plots, the responses to resources of the introduced functional guilds varied (Fargione et al. 2003). Cover of introduced forbs increased with increasing NO<sub>3</sub> and initial bare ground, cover of introduced C3 grasses increased with NO<sub>3</sub> and decreased with increasing light (measured before added seeds emerged), and cover of introduced C4 grasses increased with increasing bare ground and light transmittance. In contrast, the cover of introduced legumes was not strongly associated with any of the environmental variables.

We can apply the knowledge that resident functional guilds can affect resources differentially (Table 2) and that introduced functional guilds can respond differently to the availability of resources (Fargione et al. 2003) in community and ecosystem restoration activities. For example, we can include species in our seed mixes that have the potential to reduce the availability of the resource or resources most likely to lead to invasion. This may be especially effective if we know which exotic species are likely to be problematic. Fargione et al. (2003) provides a good example of this potential. In their study, the abundances of resident and introduced functional guilds were related to each other in very interesting ways. First, the functional guild that was the best competitor for resources, reducing soil N, light, and bare ground, i.e., C4 grasses (Table 2), suppressed introduced species from all functional guilds (Fargione et al. 2003). This highlights that particular functional guilds can be especially dominant and suggests that we must consider the potential importance of keystone species or guilds (Bond 1994). Furthermore, each resident functional guild

Name /wete/2004s\_55

GALLET 200

had the strongest negative association with introduced species from the same functional guild (Fargione et al. 2003). This result indicates important within–functional-guild competitive effects that can be exploited to help reduce the success of invasive species.

10/07/2004 02:21PM Plate # 0-Composite

Functional guilds can be effective tools for testing basic ecological theory through restoration, a need widely recognized (Allen et al. 1997; Jordan et al. 1987). Dividing the species included in the established communities and the species introduced into these communities into functional guilds allowed Fargione et al. (2003) to identify the competitive roles played by each and to test theories of community assembly, leading them to conclude that nonneutral processes were involved in determining the composition of the plant communities in their experiment. Such tests can help improve current theoretical foundations and develop new theoretical foundations of ecology as well as increase the success of the application of theory to community and ecosystem restoration.

Finally, functional types can facilitate comparisons across sites. In systems that are geographically separated, we may be able to design experiments and restoration projects using groups of species that are functionally similar, although the species within each group differ among sites. This approach may allow us to evaluate the generality of effects and responses to environmental conditions and to learn more about the mechanisms underlying the observed patterns by making comparisons among sites.

Functional guilds can be applied to restoration projects and may contribute to their success by simplifying the selection of species, helping to ensure community structure and function, increasing community competitiveness, testing ecological theory, and facilitating comparisons among sites. By virtue of being simple, functional guilds will overlook characteristics of individual species that may be important. Thus, despite the usefulness of functional guilds, we must be mindful that individual species may possess characteristics that are valuable under some conditions, even if such conditions are rare, and that they may interact with other components of the ecosystem in ways that ensure its stability. Greater species richness and redundancy within each functional type can provide insurance against unforeseen future environmental circumstances (Naeem 1998), whether transient or enduring. Although it may not be practical to include every potentially appropriate species in restoration projects, including more species within each functional type may help buffer plant communities

and ecosystems against environmental change. Functional types provide realistic conceptual units to ensure that restored plant communities include species that confer the dominant ecological functions that maintain ecosystem stability.

### ACKNOWLEDGMENTS

I thank Roger Sheley for inviting me to participate in the Invasive Plants in Natural and Managed Systems Conference as well as Joe Fargione and Dave Tilman for their collaboration.

### LITERATURE CITED

- Allen, E. B., W. W. Covington, and D. A. Falk. 1997. Developing the conceptual basis for restoration ecology. Restor. Ecol. 5:275–276.
- Bond, W. J. 1994. Keystone species. In E.-D. Schulze and H. A. Mooney, eds. Biodiversity and Ecosystem Function. Berlin, Germany: Springer-Verlag. Pp. 237–253.
- Box, E. O. 1981. Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography. The Hague, The Netherlands: Junk.
- Bruce, K. A., G. N. Cameron, and P. A. Harcombe. 1995. Initiation of a new woodland type on the Texas coastal prairie by the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb). Bull. Torrey Bot. Club 122:215–225.
- Bruce, K. A., G. N. Cameron, P. A. Harcombe, and G. Jubinsky. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) Roxb. Nat. Areas J. 17: 255–260.
- Craine, J. M., D. Tilman, D. Wedin, P. Reich, M. Tjoelker, and J. Knops. 2002. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. Funct. Ecol. 16:563–574.
- Craine, J. M., D. A. Wedin, F. S. Chapin, and P. B. Reich. 2003. Relationship between the structure of root systems and resource use for 11 North American grassland plants. Plant Ecol. 165:85–100.
- D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Syst. 23:63–87.
- Davis, M. A. and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecol. Lett. 4:421–428.
- DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. Weed Sci. 48:255–265.
- Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. Oecologia 126:563–568.
- Dukes, J. S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. Ecol. Appl. 12:602–617.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proc. Natl. Acad. Sci. USA 100:8916–8920.
- Gitay, H. and I. R. Noble. 1997. What are functional types and how should we seek them? *In* T. M. Smith, H. H. Shugart, and F. I. Woodward, eds. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. Cambridge, UK: Cambridge University Press. Pp. 3–19.
- Gleason, H. A. and A. Cronquist, eds. 1998. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Bronx, NY: The New York Botanical Garden.
- Grime, J. P. 1988. The C-S-R model of primary plant strategies—origins, implications and tests. *In L. D. Gottlieb and S. K. Jain, eds. Plant Evo*lutionary Biology. London: Chapman and Hall. Pp. 371–393.
- Harris, G. A. 1967. Some competitive relationships between Agropyron spicatum and Bromus tectorum. Ecol. Monogr. 37:89–111.
- Hickman, J. C., ed. 1993. The Jepson Manual: Higher Plants of California. Berkeley, CA: University of California Press.
- Hooper, D. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. Ecology 79:704–719.
- Hooper, D. and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. Ecol. Monogr. 68:121–149.

?3

24

?7

?8

?9

#### WEED TECHNOLOGY

Hooper, D. U. and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305.

10/07/2004 02:21PM Plate # 0-Composite

- Jordan, W. R., M. E. Gilpin, and J. D. Aber, eds. 1987. Restoration Ecology. Cambridge, UK: Cambridge University Press.
- Kennedy, T. A., S. Naeem, K. M. Howe, J.M.H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417: 636–638.
- Kindscher, K. and P. Wells. 1995. Prairie plant guilds: a multivariate analysis of prairie species based on ecological and morphological traits. Vegetatio 117:29–50.
- Klemmedson, J. O. and J. G. Smith. 1964. Cheatgrass (Bromus tectorum L.C.). Bot. Rev. 30:226–262.
- Knick, S. T. and J. T. Rotenberry. 1997. Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho (USA). Landsc. Ecol. 12: 287–297.
- Knops, J.M.H., D. Tilman, N. M. Haddad, et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol. Lett. 2:286–293.
- Naeem, S. 1998. Species redundancy and ecosystem reliability. Conserv. Biol. 12:39–45.
- 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.
- Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. J. Biogeogr. 19:117–134.
- Rafferty, D. L. and J. A. Young. 2002. Cheatgrass competition and establishment of desert needlegrass seedlings. J. Range Manag. 55:70–72.
- Raunkiaer, C. 1934. The Life Forms of Plants and Statistical Plant Geography. Oxford University Press. (Translated by Carter, Fausboll and Tansley.)
- Reich, P. B., C. Buschena, M. G. Tjoelker, K. Wrage, J. Knops, D. Tilman, and J. L. Machado. 2003a. Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. New Phytol. 157:617–631.
- Reich, P. B., D. Tilman, J. Craine, et al. 2003b. Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO<sub>2</sub> and N availability regimes? A field test with 16 grassland species. New Phytol. 150:435–448.

- Root, R. B. 1967. The niche exploration pattern of a blue grey gnatcatcher. Ecol. Monogr. 37:317–350.
- Schulze, E. D. and H. A. Mooney, eds. 1994. Biodiversity and Ecosystem Function. Berlin, Germany: Springer-Verlag.
- Shugart, H. H. 1997. Plant and ecosystem functional types. In T. M. Smith, H. H. Shugart, and F. I. Woodward, eds. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. Cambridge, UK: Cambridge University Press. Pp. 20–43.
- Smith, T. M., H. H. Shugart, and F. I. Woodward, eds. 1997. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. Cambridge, UK: Cambridge University Press.
- Stewart, G. and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.): an ecologic intruder in southern Idaho. Ecology 30:58–74.
- Svejcar, T. 1990. Root length, leaf area, and biomass of crested wheatgrass and cheatgrass seedlings. J. Range Manag. 43:446–448.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81:99–109.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7– 13.
- Westoby, M. and M. Leishman. 1997. Categorizing plant species into functional types. In T. M. Smith, H. H. Shugart, and F. I. Woodward, eds. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. Cambridge, UK: Cambridge University Press. Pp. 104– 121.
- Whisenant, S. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. *In* Proceedings of the Symposium of Cheatgrass Invasion, Shrub Dieoff and Other Aspects of Shrub Biology and Management. USFS. Gen. Tech. Rep. INT-276. Pp. 4–10.
- Woodward, F. I., T. M. Smith, and H. H. Shugart. 1997. Defining plant functional types: the end view. *In* T. M. Smith, H. H. Shugart, and F. I. Woodward, eds. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. Cambridge, UK: Cambridge University Press. Pp. 355–359.

26

Name /wete/2004s\_55