

genuity to overcome this problem. One approach would be to select several random subsets including 2, 3, . . . , *n* species drawn from a large species pool, sow these under a specific set of ecological conditions, allow community assembly (and potential species loss) to occur, and then measure community resistance and resilience. It would be even better to conduct such an experiment at several sites along climatic and edaphic gradients. Only by breaking down the correlations among diversity, community biomass, climate, edaphic conditions and plant adaptations can we determine whether species richness *per se* is an important determinant of community stability in biomass.

There are plausible arguments for either an increase in stability with diversity (such as greater numbers of functionally interchangeable species or species groups, each susceptible to slightly different perturbations; greater segregation of species into compartments that interact little, if at all) or a decrease in stability with diversity (for example, closer packing of competitors along resource spectra, evolution of species-specific mutualisms in diverse tropical habitats, time lags imposed by more trophic levels). It thus seems likely that diversity and stability (particularly with regard to species composition, as opposed to total biomass) may be related positively in some landscapes, and negatively in others.

It may yet be shown that the observed correlation of stability and diversity in the Tilman–Downing study is causal; there are many reasons why, under a fixed set of conditions, assemblages of 2 or 3 grassland species might be less resistant or resilient to disturbance than sets of 15 or 20 species. But even if the Tilman–Downing finding proves to be an artefact of adaptive shifts induced by fertilization and/or succession, it would have no bearing on the fundamental need to conserve biological diversity. Even if more diverse ecosystems were inherently more fragile to perturbation³, the agricultural, medical, scientific, economic and aesthetic values of biological diversity would still make the conservation of native species, communities, and ecosystems one of the world’s most urgent priorities.

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TILMAN ET AL. REPLY — There are few long-term ecological studies of biodiversity, and even fewer that encompass a major natural disturbance. Our 12-year study^{1,5,12} of 207 permanent grassland plots thus provides a unique record of the relationships between biodiversity and the stability of ecosystem productivity in response to drought. Givnish suggests that the strong relationship that we observed¹

between ecosystem stability and plant species richness might be an artefact caused by changes in root-to-shoot ratios and photosynthetic physiology associated with nitrogen treatments. Because we had similar concerns about collinear variables when we began our analyses, we used multiple regressions to control statistically for effects of over 20 variables¹. Whether we controlled for all of these simultaneously, one at a time, or in various combinations, there remained in all cases a highly significant effect of plant species richness (biodiversity) on ecosystem stability¹.

Although we did not originally control for root:shoot-ratio shifts, we did measure root:shoot ratios in all plots in 1987 at the start of the drought (RSR₁₉₈₇) and in 1993 (RSR₁₉₉₃), by which time plots had returned to pre-drought biomass and composition. When we include RSR₁₉₈₇, RSR₁₉₉₃ and their interaction (product of RSR₁₉₈₇ and RSR₁₉₉₃) as additional covariates in backwards elimination multiple regressions, we find that part of the dependence of drought resistance on biodiversity is explained by 1993 root:shoot ratios ($F=4.85$, $P=0.03$), as Givnish suggests. The effect is in the right direction, but small (the overall R^2 increases from 0.48 to 0.50). But contrary to Givnish’s suggestion, the addition of root:shoot ratios does not eliminate, but rather slightly strengthens, the effect of biodiversity (F increases from 19.25 to 22.53; $P<0.001$ for both). RSR₁₉₈₇ and the interaction term do not significantly contribute to the multiple regression ($F=0.01$, $P=0.92$ and $F=0.25$, $P=0.62$ respectively).

In response to Givnish’s concerns, we have performed other analyses that include root mass, changes in root mass, $\log_e(\text{root mass})$, $\log_e(\text{total biomass})$, biomass of additional plant species, and various interaction terms as additional

covariates. In no single case did the addition of any covariates eliminate the significant residual effect of biodiversity on stability. Thus we doubt if other physiological shifts, as suggested by Givnish, would eliminate the effects of biodiversity on ecosystem stability. Although no single study can eliminate all reasonable doubts about ecosystem functioning, the preponderance of available evidence^{1,13–17} supports the hypothesis that biodiversity influences ecosystem functioning.

We agree with Givnish’s proposal that a cleaner test of the effects of biodiversity on ecosystem functioning would come from direct experimental control of species diversity. In 1993 we began such a study. This 23-acre experiment includes 342 large (13 × 13m) and 147 small (3 × 3m) plots that contain 1–32 species randomly drawn from a pool of native prairie plants. These plots are being sampled to determine the effects of plant diversity on plant productivity, insects, plant pathogens, pollinators, and soil carbon and nitrogen.

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C₆₀ complexation revisited

SIR — In the recent paper by Atwood *et al.*¹ on a purification procedure for C₆₀ and C₇₀ by selective complexation with calixarenes, it was implied that we had previously studied the complexation of C₆₀ with cyclodextrins². In fact, we used calix[8]arenes as the selective host species; but ours were water-soluble rather than the water-insoluble variants used by Atwood *et al.*

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