

## Does diversity beget stability?

**SIR**—Tilman and Downing<sup>1</sup> present data which they argue support the hypothesis that more diverse plant communities are more stable. This finding, if well founded, would shed light on long-standing questions about the relationship between the diversity and stability of ecological communities<sup>2-4</sup>, and provide added motivation to conserve biological diversity. But this finding may be premature.

Tilman and Downing studied grasslands that developed different levels of vascular plant species richness (number of species per 0.3 m<sup>2</sup>) largely as a result of different amounts of nitrogen fertilization. Fertilization decreases species richness in this system<sup>5</sup>, paralleling a general tendency for grassland diversity to decrease with increasing soil fertility<sup>6,7</sup>. Community stability in response to drought was measured using the proportional rate of change in total above-ground biomass ( $1/B \times dB/dt$ ), estimated from the logarithm of the ratio of single harvests in successive years. More diverse quadrats showed greater resistance to drought, with less reduction in  $B$  heading into the drought year 1988; and greater resilience to drought, with faster recovery in  $B$  after 1988.

As expected from various economic models<sup>8-10</sup>, greater soil fertility generally favours plants with lower allocation to roots versus leaves, higher stomatal con-

ductance, and greater photosynthetic capacity. But plants with low allocation to roots and high stomatal conductance usually have low drought resistance, and plants with high photosynthetic capacity often do. Hence, the fact that quadrats with low species richness had the greatest drop in above-ground biomass during the 1988 drought may be a result of such quadrats having been those most heavily fertilized, and consequently those most likely to be dominated by drought-sensitive plants. The correlation of community resistance to drought and species richness may thus be illusory, reflecting the indirect effects of high soil fertility (in promoting drought-sensitive species or phenotypes) more than the effects of low diversity itself. A similar argument might apply to community resilience, which increased with species richness<sup>1</sup>. Plants adapted to low-diversity, high-fertility sites may have been most damaged by drought, and hence the slowest to recover.

Tilman and Downing<sup>1</sup> did attempt to control for possible shifts in the functional groupings of plants caused by shifts in soil fertility along their 'diversity' gradient by examining partial correlations of resistance and resilience with the number and abundance of C4 versus C3 species. But C4 grasses comprise only a small fraction of species richness in Tilman's experimental grasslands<sup>5</sup>, and controlling for their abundance would not screen effectively for systematic shifts in other drought adaptations along the fertility gradient. Furthermore, given that diversity and nitrogen levels are so closely related across plots<sup>5,10</sup>, it seems highly probable that some within-plot (among-quadrat) variation in diversity is tied to within-plot variation in nitrogen levels and root:shoot ratio; the latter were not measured. Thus, attempts to control for among-plot differences in nitrogen, C3 versus C4 abundance, or 1993 root:shoot ratios (see reply from Tilman *et al.*) are unlikely to eliminate completely the confounding effects of fertility on drought sensitivity.

Some of the variation in species richness among the Tilman-Downing plots reflects a difference in successional age: older fields tend to be more diverse<sup>5,10</sup>. These older, more diverse fields are known to be dominated by plants with a higher root:shoot ratio than those seen in younger fields<sup>10,11</sup> (perhaps reflecting more intense competition for nutrients in older fields), which may account for some additional portion of the apparent correlation between stability and diversity.

The underlying problem in the Tilman-Downing study is that diversity, community biomass, soil fertility, and (presumably) species sensitivity to drought are inter-correlated along the experimental gradient. It will require considerable in-

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