Plant Diversity and Productivity Experiments in European Grasslands


At eight European field sites, the impact of loss of plant diversity on primary productivity was simulated by synthesizing grassland communities with different numbers of plant species. Results differed in detail at each location, but there was an overall log-linear reduction of average aboveground biomass with loss of species. For a given number of species, communities with fewer functional groups were less productive. These diversity effects occurred along with differences associated with species composition and geographic location. Niche complementarity and positive species interactions appear to play a role in generating diversity-productivity relationships within sites in addition to sampling from the species pool.

Because species differ in their ecological attributes, the loss of biodiversity from local communities may be detrimental to the ecosystem goods and services on which humans ultimately depend (1). This issue has been the subject of major recent research efforts using experimental plant assemblages (2–6). However, differences in aims and approaches, and the fact that experimental manipulations of diversity have been restricted to single localities, limit the ability of ecologists to make generalizations and predictions. The design, analysis, and interpretation of these experiments are also complex (7), and the view that the loss of plant species can be detrimental to ecosystem functioning remains contentious (8–11). In particular, the mechanisms underlying the relationship between species richness and ecosystem functioning are still the subject of debate because of the difficulty in identifying and interpreting the importance of niche complementarity versus “sampling effects” (8, 12, 13). Here we report patterns of aboveground plant biomass from the most extensive experiment to date in terrestrial ecosystems, and we examine the underlying mechanisms.

We used standardized protocols to establish experimental assemblages of grassland species (grasses and forbs) that varied in species richness, and we measured aboveground plant biomass production at two localities in the United Kingdom and at single sites in Germany, Ireland, Greece, Portugal, Sweden, and Switzerland (14, 15). Sites differed widely in climate and other major environmental factors (Table 1). We simulated the loss of plant species by removing the existing vegetation and seedbank and reestablishing plant communities from seed (16). At each site, we established five levels of species richness, ranging from monocultures of grasses or forbs to higher-diversity assemblages that approximated background levels of diversity in comparable unmanipulated semi-natural grasslands at each site (Table 2). If reducing the number of species reduces productivity because of a decrease in functional diversity and therefore the amount of niche space occupied in the resulting depauperate community (2, 4, 6, 17), then we expect, for a given number of species, that productivity will also be lower in communities with fewer functional groups. To test this, we categorized species into three functional groups: graminoids (grasses), nitrogen-fixing legumes, and other herbaceous species (herbs) and established communities containing one, two, or three of these groups. To replicate plant diversity, each level of species richness and functional group richness was represented by several different plant assemblages at each site (18). Each assemblage contained a different species mixture or species of species. We used constrained random selection from the local pool of grassland species (14, 15) to form experimental plant assemblages where all polycultures contained at least one grass. To investigate the effects of species composition, each assemblage was replicated in a minimum of two plots including monocultures of many of the species involved. In total, the experiment comprised 480 plots and 200 different plant assemblages (19).

Aboveground biomass patterns. Aboveground plant biomass in the second year of the experiment (an estimate of net annual aboveground primary production) differed significantly between sites ($F_{7,185} = 24.73, P < 0.001$ (Table 3)). The productivity of plots with eight species (the highest richness common to all sites) ranged from 337 g m$^{-2}$ in Greece to 802 g m$^{-2}$ in Germany (Table 1) and was driven by environmental differences among sites. Extreme northern and southern locations in Sweden, Portugal, and Greece, where growing seasons are short and productivity is often limited by temperature and water (20, 21), had the lowest biomass.

Species richness and functional group richness had highly significant effects on aboveground biomass; overall, assemblages with lower diversity were less productive on average [combined effect of species richness and functional group richness: $F_{3,185} = 7.01, P < 0.001$ (Table 3)] (22). Because there was no location-by-species richness interaction, differences in slopes between sites were not significant between sites ($F_{7,185} = 2.04, P = 0.053$ (Table 3)).
Diversity terms are tested against the plant assemblage term, the site differences and the quadratic and higher order polynomial terms (shown indented). Our experiment has multiple error terms of the experiment.

Our experiment has multiple error terms of the experiment.

We present the combined effect of decreasing species richness. Each halving of the number of plant species reduced productivity by approximately 80 g m$^{-2}$ on average.

Plant cover was reduced by loss of plant species richness ($F_{1,185} = 3.84, P < 0.001$). Cover and aboveground biomass are likely to be correlated, and biomass patterns may not occur after controlling for differences in cover ($8, 24$). However, highly significant reductions in aboveground biomass with declining plant species richness remained in multiple regressions which included cover as a covariate, and when plots with less than 80% cover were excluded.

For a given number of species, assemblages with fewer functional groups were less productive ($F_{2,185} = 6.34, P < 0.01$ (Fig. 1B)). A multiple regression using the (untransformed) number of functional groups, after accounting for species richness (Table 3), revealed that the omission of a single functional group reduced productivity by approximately 100 g m$^{-2}$ on average.

### Importance of scale

When all sites were analyzed together, the lack of a significant location-by-species richness interaction determined that the log-linear regression with parallel slopes provided the best overall model (Table 3 and Fig. 1A). However, when the data for individual sites are plotted separately, they look different, and when analyzed alone, produce a variety of different models (Fig. 2) corresponding to alternative qualitative relationships between species richness and ecosystem processes (25). There are two explanations for this result: (i) all sites conform to the same underlying model, and apparent differences between sites are due to the lower sample sizes and statistical power at each site; (ii) sites differ in their responses, but the analysis is not powerful enough to

### Table 1. Details of the eight field sites, including location [site, country, degrees of latitude and longitude, and altitude above sea level [asl]]; climate (mean January and July temperatures and annual precipitation); previous land use (arable crops, horse grazing, fallow land, or none); method of site preparation (methyl bromide fumigation or steam sterilization of the soil, hand weeding only, or use of a sterile sand substrate); number of biomass harvests; and mean aboveground biomass of the plant assemblages with eight species. Aboveground biomass comprised all living and standing dead plant material above 5 cm, harvested in two quadrats 20 cm by 50 cm once or twice each season around the times of peak biomass (where two harvests were taken, the values reported are the sum totals per plot). For brevity, we refer to accumulated net annual aboveground biomass as productivity but note that it provides only an estimate of the aboveground component of this process. All vegetation was cut to a height of 5 cm at the times of harvest and the clippings were removed. Plots received no fertilizer during the first 2 years of the experiment.

**Table 1.** Details of the eight field sites, including location [site, country, degrees of latitude and longitude, and altitude above sea level [asl]]; climate (mean January and July temperatures and annual precipitation); previous land use (arable crops, horse grazing, fallow land, or none); method of site preparation (methyl bromide fumigation or steam sterilization of the soil, hand weeding only, or use of a sterile sand substrate); number of biomass harvests; and mean aboveground biomass of the plant assemblages with eight species. Aboveground biomass comprised all living and standing dead plant material above 5 cm, harvested in two quadrats 20 cm by 50 cm once or twice each season around the times of peak biomass (where two harvests were taken, the values reported are the sum totals per plot). For brevity, we refer to accumulated net annual aboveground biomass as productivity but note that it provides only an estimate of the aboveground component of this process. All vegetation was cut to a height of 5 cm at the times of harvest and the clippings were removed. Plots received no fertilizer during the first 2 years of the experiment.

<table>
<thead>
<tr>
<th>Site</th>
<th>Country</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Altitude (m asl)</th>
<th>January mean (°C)</th>
<th>July mean (°C)</th>
<th>Annual rain (mm)</th>
<th>Previous land use</th>
<th>Site preparation</th>
<th>Harvests</th>
<th>Biomass (g m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bayreuth</td>
<td>Germany</td>
<td>50°N</td>
<td>12°E</td>
<td>350</td>
<td>-0.1</td>
<td>18.2</td>
<td>630</td>
<td>Arable Steam</td>
<td>2</td>
<td>802.2</td>
<td></td>
</tr>
<tr>
<td>Riverstick</td>
<td>Ireland</td>
<td>52°N</td>
<td>08°W</td>
<td>75</td>
<td>5.4</td>
<td>15.6</td>
<td>1130</td>
<td>Grazing Bromide</td>
<td>2</td>
<td>767.5</td>
<td></td>
</tr>
<tr>
<td>Silwood</td>
<td>UK</td>
<td>51°N</td>
<td>01°W</td>
<td>50</td>
<td>3.7</td>
<td>16.9</td>
<td>652</td>
<td>None Sand</td>
<td>1</td>
<td>675.0</td>
<td></td>
</tr>
<tr>
<td>Sheffield</td>
<td>UK</td>
<td>53°N</td>
<td>01°W</td>
<td>137</td>
<td>4.5</td>
<td>17.2</td>
<td>788</td>
<td>Grazing Heat</td>
<td>1</td>
<td>432.3</td>
<td></td>
</tr>
<tr>
<td>Lupsingen</td>
<td>Switzerland</td>
<td>47°N</td>
<td>08°E</td>
<td>439</td>
<td>0.7</td>
<td>18.3</td>
<td>1046</td>
<td>Arable Hand</td>
<td>2</td>
<td>605.5</td>
<td></td>
</tr>
<tr>
<td>Lezirias</td>
<td>Portugal</td>
<td>39°N</td>
<td>09°W</td>
<td>25</td>
<td>9.4</td>
<td>26.1</td>
<td>588</td>
<td>Fallow Bromide</td>
<td>1</td>
<td>336.5</td>
<td></td>
</tr>
<tr>
<td>Urnä</td>
<td>Sweden</td>
<td>64°N</td>
<td>20°E</td>
<td>12</td>
<td>-7.0</td>
<td>16.1</td>
<td>600</td>
<td>Fallow Bromide</td>
<td>1</td>
<td>402.9</td>
<td></td>
</tr>
<tr>
<td>Mytilini</td>
<td>Greece</td>
<td>39°N</td>
<td>27°E</td>
<td>30</td>
<td>9.6</td>
<td>26.5</td>
<td>682</td>
<td>Arable Steam</td>
<td>2</td>
<td>802.2</td>
<td></td>
</tr>
</tbody>
</table>

### Table 2. The experimental design at each location, showing numbers of plots per species richness level and for each level of functional group richness. Plant assemblages (where an assemblage is a particular species or mixture of species) were replicated in two plots at each site, with the same assemblage sometimes occurring at more than one site.

<table>
<thead>
<tr>
<th>Species richness</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>8</th>
<th>11</th>
<th>12</th>
<th>14</th>
<th>16</th>
<th>18</th>
<th>32</th>
</tr>
</thead>
<tbody>
<tr>
<td>Germany</td>
<td>20</td>
<td>14</td>
<td>10</td>
<td>10</td>
<td></td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ireland</td>
<td>20</td>
<td>16</td>
<td>4</td>
<td>20</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Silwood</td>
<td>22</td>
<td>12</td>
<td>12</td>
<td>10</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheffield</td>
<td>24</td>
<td>10</td>
<td>10</td>
<td>8</td>
<td>8</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Switzerland</td>
<td>20</td>
<td>14</td>
<td>10</td>
<td>10</td>
<td></td>
<td>4</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Portugal</td>
<td>28</td>
<td>10</td>
<td>10</td>
<td>4</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sweden</td>
<td>24</td>
<td>12</td>
<td>12</td>
<td>6</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greece</td>
<td>14</td>
<td>12</td>
<td>10</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Functional richness</td>
<td>1</td>
<td>172</td>
<td>32</td>
<td>14</td>
<td>6</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>68</td>
<td>40</td>
<td>18</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>4</td>
<td>44</td>
<td>42</td>
<td>4</td>
<td>8</td>
<td>4</td>
<td>6</td>
<td>8</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

### Table 3. Summary of the analysis of second-year aboveground biomass. We present the combined effect of the two richness terms and partition the separate species and functional group richness effects from initial analysis of variance (ANOVA) into a linear contrast (regression) and a deviation from linearity; that is, the quadratic and higher order polynomial terms (shown indented). Our experiment has multiple error terms: Diversity terms are tested against the plant assemblage term, the site differences and the quadratic and higher order polynomial terms (shown indented). The overall effect of decreasing species richness was best described by a linear relationship between productivity and the natural logarithm of the number of plant species ($[F_{1,185} = 55.13, P < 0.001$ (Fig. 1A)]), which is similar to patterns reported from previous single-location experiments ($4, 5$) and predicted by theory ($17, 23$). The log-linear relation corresponds to an initially weak but increasing reduction of productivity with decreasing species richness. Each halving of the number of plant species reduced productivity by approximately 80 g m$^{-2}$ on average.

Plant cover was reduced by loss of plant species richness ($F_{1,185} = 3.84, P < 0.001$). Cover and aboveground biomass are likely to be correlated, and biomass patterns may not occur after controlling for differences in cover ($8, 24$). However, highly significant reductions in aboveground biomass with declining plant species richness remained in multiple regressions which included cover as a covariate, and when plots with less than 80% cover were excluded.

For a given number of species, assemblages with fewer functional groups were less productive ($F_{2,185} = 6.34, P < 0.01$ (Fig. 1B)). A multiple regression using the (untransformed) number of functional groups, after accounting for species richness (Table 3), revealed that the omission of a single functional group reduced productivity by approximately 100 g m$^{-2}$ on average.

Importance of scale. When all sites were analyzed together, the lack of a significant location-by-species richness interaction determined that the log-linear regression with parallel slopes provided the best overall model (Table 3 and Fig. 1A). However, when the data for individual sites are plotted separately, they look different, and when analyzed alone, produce a variety of different models (Fig. 2) corresponding to alternative qualitative relationships between species richness and ecosystem processes (25). There are two explanations for this result: (i) all sites conform to the same underlying model, and apparent differences between sites are due to the lower sample sizes and statistical power at each site; (ii) sites differ in their responses, but the analysis is not powerful enough to
revel a significant location-by-species richness interaction when sites are analyzed together. Much of the individual site deviation from the overall log-linear model may be due to lower within-site replication. There may also be transient effects at this early stage of the experiment that largely disappear by the following year (26). For these reasons, and for parsimony, we favor the more general and powerful combined analysis, which shows that differences between locations are not significant and suggests that there may be a single general relationship between species richness and diversity across all sites.

Our results highlight the importance of considering scale when studying relationships between diversity and productivity (14), as predicted by theory (23). Despite large differences in productivity between locations and no clear relationship between productivity and maximum within-site species richness (Fig. 1A), within a site, productivity generally declines as species are lost, reconciling apparent contradictions in the literature (27).

Multiple influences on productivity. Our experiment reveals the relative roles of richness, location, and species composition as determinants of productivity; these key variables explained approximately 18, 28, and 39% of the total sums of squares, respectively (Table 3). Although it accounted for a large amount of the total variation, species composition was not statistically significant \( F_{185,29} = 1.29, P = 0.21 \) (Table 3) (28). However, when we tested the presence in an assemblage of a particular plant species or functional group (29), of the 71 more commonly occurring species, 29 had significant \( P < 0.05 \) effects on productivity, although virtually all these effects were small (Fig. 3).

Only one species, the nitrogen-fixing Trifolium pratense, had particularly marked effects. On average, the omission of this species reduced productivity by approximately 360 g m\(^{-2}\). We also found highly significant effects from the presence of legumes and herbs when considered collectively as functional groups.

Evidence for niche complementarity and positive species interactions. There are three processes through which the loss of plant species richness could decrease productivity: (i) the “sampling effect” (17) or “selection probability effect” (8), in which more...
Plant species or functional group

Fig. 3 Percentages of the total sums of squares explained by the effects of individual species and functional groups. Twenty-nine species had significant effects ($P < 0.05$); the 15 most highly significant species ($P < 0.001$) are shown.

References and Notes

16. Field experiments were established the spring 1995 in Switzerland, in autumn 1996 in Portugal, and in spring 1996 at all other sites. Plots 2 m by 2 m were seeded with 2000 seeds per square meter, divided equally between the number of species in each plant assembly. Seeds were collected locally as far as possible or otherwise were purchased from national commercial sources, avoiding agricultural cultivars. Plots were regularly weeded to remove unwanted species.
19. The numbers of functional groups in our assemblages were exactly as planned. A few plant species failed to establish, particularly in the higher-diversity assemblages, but realized richness was highly correlated with initial number of species sown. In the second year, realized species richness was 10% lower on average than planned richness (slope = 0.9, SE = 0.007, $n = 480, R^2 = 0.05, P < 0.001$). The analyses reported here use the planned number of species. Analyses using actual numbers of species present in the second year of the experiment are not presented but also reveal highly significant effects of species richness and functional group richness.
20. Correlations of environmental parameters with average productivity per site for assemblages with eight species support reduced productivity in northern and southern sites by revealing a significant quadratic effect of latitude (linear term: $F_{1, 76} = 40.47, P = 0.001, R^2 = 0.86$). When included in a model with the linear effect of latitude, July temperature also had a significant effect on productivity (July temperature: $F_{1, 76} = 0.019, P = 0.019$; temperature and latitude model: $R^2 = 0.73$).
22. Because species richness and functional group richness are uncorrelated, in statistical analyses it is impossible to unequivocally distinguish their relative effects [G. W. Allison, Am. Nat. 153, 26 (1999)]. We present the sequential analysis determined by our experimental design and a priori hypotheses, which addressed the effects of (i) species richness and (ii) functional group richness for a given number of species. Analyses used sequential backward selection of terms from the maximal model, which included sites, blocks within sites, species richness, functional group richness (within-species richness levels), plant assemblage, the locality-by-assemblage interaction, and the overall residual variation between plots within the above treatments. Locality-by-diversity interactions, the interaction of species, and functional group richness were also included but were never statistically significant and, for brevity, are not reported here.
24. The percent of plant cover in each plot was visually estimated several times during each growing season and by the presence or absence of rooted individuals in 50 cells of a permanent quadrant measuring 1 m by 0.5 m. Productivity patterns could be associated with poor cover in low diversity assemblages, which may arise from poor plant establishment [M. A. Huston,
RESEARCH ARTICLES

Hydrogen Storage in Single-Walled Carbon Nanotubes at Room Temperature


Masses of single-walled carbon nanotubes (SWNTs) with a large mean diameter of about 1.85 nanometers, synthesized by a semicontinuous hydrogen arc discharge method, were employed for hydrogen adsorption experiments in their as-prepared and pretreated states. A hydrogen storage capacity of 4.2 weight percent, or a hydrogen to carbon atom ratio of 0.52, was achieved reproducibly at room temperature under a modestly high pressure (about 10 megapascal) for a SWNT sample of about 500 milligram weight that was soaked in hydrochloric acid and then heat-treated in vacuum. Moreover, 78.3 percent of the adsorbed hydrogen (3.3 weight percent) could be released under ambient pressure at room temperature, while the release of the residual stored hydrogen (0.9 weight percent) required some heating of the sample. Because the SWNTs can be easily produced and show reproducible and modestly high hydrogen uptake at room temperature, they show promise as an effective hydrogen storage material.

Hydrogen (H₂) has attracted a great deal of attention as an energy source. Once it is generated, its use as a fuel creates neither air pollution nor greenhouse gas emissions. However, no practical means for H₂ storage and transportation have yet been developed. Of the problems to be solved for the utilization of hydrogen energy, how to store H₂ easily and cheaply has been given high priority on the research agenda.

Recently, carbon nanotubes and carbon nanofibers were reported to be very promising candidates for H₂ uptake. Dillon et al. (1) first measured the H₂ adsorption capacity of an as-prepared soot containing only about 0.1 to 0.2 weight % SWNTs at 133 K, from which they extrapolated an H₂ adsorptivity for pure SWNTs of 5 to 10 weight % (the weight of H₂ adsorbed divided by the weight of SWNTs plus the H₂ adsorbed by the SWNTs), and predicted that SWNTs with a diameter of between 1.63 and 2 nm would come close to the target H₂ uptake density of 6.5 weight %. Ye et al. (2) reported that a ratio of H to C atoms of about 1.0 was obtained for crystalline ropes of SWNTs at a cryogenic temperature of 80 K and pressures >12 MPa. Instead of SWNTs, Chambers et al. (3) claimed that tubular, platelet, and herringbone forms of carbon nanofibers were capable of adsorbing in excess of 11, 45, and 67 weight % of H₂, respectively, at room temperature and at a pressure of 12 MPa. More recently, Chen et al. (4) reported that a high H₂ uptake of 20 and 14 weight % can be achieved for Li-doped and K-doped multi-walled carbon nanotubes (MWNTs) in milligram quantities, respectively, under ambient pressure. The K-doped MWNTs can adsorb H₂ at room temperature, but they are chemically unstable, whereas the Li-doped MWNTs are chemically stable, but require elevated temperatures (473 to 673 K) for maximum adsorption and desorption of H₂.

We measured the H₂ storage capacity of SWNTs synthesized by a hydrogen arc-discharge method, with a relatively large sample quantity (about 500 mg) at ambient temperature under a modestly high pressure. A H₂ uptake of 4.2 weight %, which corresponds to a H/C atom ratio of 0.52, was obtained by these SWNTs with an estimated purity of 50 weight %. Ye et al. (2) reported that a ratio of H to C atoms of about 1.0 was obtained for crystalline ropes of SWNTs at a cryogenic temperature of 80 K and pressures >12 MPa. Instead of SWNTs, Chambers et al. (3) claimed that tubular, platelet, and herringbone forms of carbon nanofibers were capable of adsorbing in excess of 11, 45, and 67 weight % of H₂, respectively, at room temperature and at a pressure of 12 MPa. More recently, Chen et al. (4) reported that a high H₂ uptake of 20 and 14 weight % can be achieved for Li-doped and K-doped multi-walled carbon nanotubes (MWNTs) in milligram quantities, respectively, under ambient pressure. The K-doped MWNTs can adsorb H₂ at room temperature, but they are chemically unstable, whereas the Li-doped MWNTs are chemically stable, but require elevated temperatures (473 to 673 K) for maximum adsorption and desorption of H₂.

We measured the H₂ storage capacity of SWNTs synthesized by a hydrogen arc-discharge method, with a relatively large sample quantity (about 500 mg) at ambient temperature under a modestly high pressure. A H₂ uptake of 4.2 weight %, which corresponds to a H/C atom ratio of 0.52, was obtained by these SWNTs with an estimated purity of 50 weight %. Also, ~80% of the adsorbed H₂ can be released at room temperature. These results indicate that SWNTs are highly promising for H₂ adsorption even at room temperature.

1Institute of Metal Research, Chinese Academy of Sciences, 72 Wenhua Road, Shenyang 110015, China.
2State Key Lab for Rapidly Solidified Non-equilibrium Alloys, Institute of Metal Research, Chinese Academy of Sciences, 72 Wenhua Road, Shenyang 110015, China.
3Department of Physics and Department of Electrical Engineering and Computer Science, Massachusetts Institute of Technology, Cambridge, MA 02139, USA.

*To whom correspondence should be addressed. E-mail: cheng@imr.ac.cn (H.M.C.) and millie@nmr.mitt.edu (M.S.D.)