

Plant Diversity and Productivity Experiments in European Grasslands

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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 approximately matched background levels of diversity in comparable unmanipulated seminatural 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 or mixture 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: $F_{12,185} = 7.01$, $P < 0.001$ (Table 3)] (22). Because there was no location-by-species richness interaction, differences in slopes between sites were not

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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.

Site	Country	Latitude	Longitude	Altitude (m asl)	January mean (°C)	July mean (°C)	Annual rain (mm)	Previous land use	Site preparation	Harvests	Biomass (g m ⁻²)
Bayreuth	Germany	50°N	12°E	350	-0.1	18.2	630	Arable	Steam	2	802.2
Riverstick	Ireland	52°N	08°W	75	5.4	15.6	1130	Grazing	Bromide	2	767.5
Silwood	UK	51°N	01°W	50	3.7	16.9	652	Grazing	Bromide	1	683.4
Sheffield	UK	53°N	01°W	137	4.5	17.2	788	None	Sand	1	675.0
Lupsingen	Switzerland	47°N	08°E	439	0.7	18.3	1046	Arable	Hand	2	605.5
Lezirias	Portugal	39°N	09°W	25	9.4	26.1	588	Grazing	Heat	1	432.3
Umeå	Sweden	64°N	20°E	12	-7.0	16.1	600	Arable	Hand	1	402.9
Mytilini	Greece	39°N	27°E	30	9.6	26.5	682	Fallow	Bromide	1	336.5

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.

	Species richness										
	1	2	3	4	8	11	12	14	16	18	32
Germany	20	14		10	10				6		
Ireland	20	16	4	20	10						
Silwood	22	12		12	10	10					
Sheffield	24	10		8	8		4				
Switzerland	20	14		16	10						4
Portugal	28	10		10	4			4			
Sweden	24	12		12	6		4				
Greece	14	12		10	8					8	
Functional richness											
1	172	32		14	6	2					
2		68		40	18	4					
3			4	44	42	4	8	4	6	8	4

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 assemblage term against the assemblage-by-location interaction, and the assemblage-by-location interaction against the overall residual. Nonsignificant block effects and locality-by-diversity interactions are omitted.

Source of variation	d.f.	s.s.	% s.s.	m.s.	F	P
Locality	7	12,413,386	28.3	1,773,341	24.73	1.32 × 10 ⁻¹⁰
Total richness effect	12	7,769,673	17.7	647,473	7.01	1.93 × 10 ⁻¹⁰
Species richness	10	6,599,591	15.1	659,959	7.15	1.72 × 10 ⁻⁷
Log-linear contrast	1	5,089,222	11.6	5,089,222	55.13	4.01 × 10 ⁻¹²
Deviation	9	1,510,369	3.5	167,819	1.82	0.0675
Functional group richness	2	1,170,082	2.7	585,041	6.34	0.0022
Linear contrast	1	966,878	2.2	966,878	10.47	0.0014
Deviation	1	203,204	0.5	203,204	2.20	0.1396
Assemblage	185	17,079,328	38.9	92,321	1.29	0.2133
Locality × assemblage	29	2,079,864	4.8	71,719	3.77	1.83 × 10 ⁻⁸
Residual	235	4,465,007	10.2	19,000		
Total	468	43,807,258	100.0	93,605		

significant [$F_{2,29} = 1.25, P = 0.287$ (Table 3)]. The overall effect of decreasing species richness was best described by a linear rela-

tion between productivity and the natural logarithm of the number of plant species [$F_{1,185} = 55.13, P < 0.001$ (Fig. 1A)], which

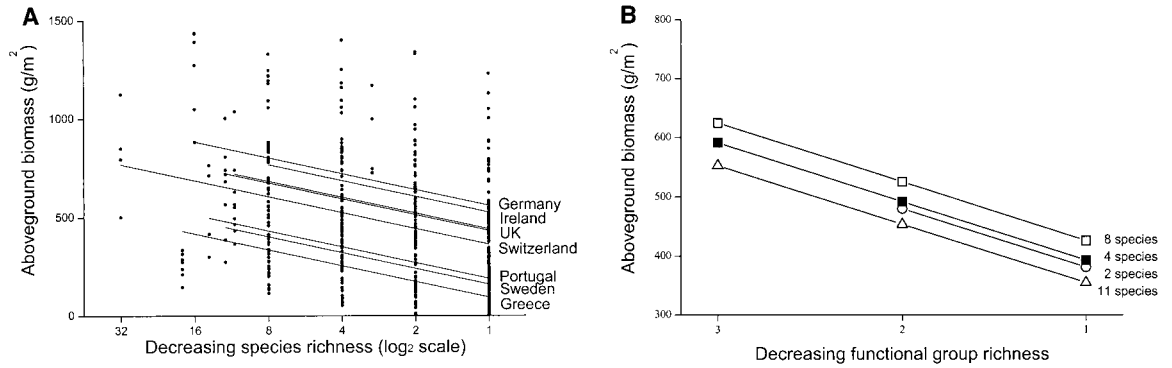
is similar to patterns reported from previous single-location experiments (4, 5) and predicted by theory (17, 23). The log-linear relation corresponds to an initially weak but increasing reduction of productivity with decreasing species richness. Each halving of the number of plant species reduced productivity 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

Fig. 1. Productivity declines with the loss of plant diversity. **(A)** Overall log-linear reduction of above-ground biomass with the simulated loss of plant species richness. **(B)** Linear reduction with the loss of functional group richness within species richness levels. Points in **(A)** are total aboveground biomass for individual plots; lines are slopes from the multiple regression model using species richness on a \log_2 scale. Silwood and Sheffield are labeled together as UK. In **(B)**, assemblages with 11 species occurred only at Silwood, whereas assemblages with 2, 4, and 8 species are represented at all sites, including the more productive, and therefore have a higher average biomass.



reveal 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 [$F_{1,85,29} = 1.29, P = 0.21$ (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.

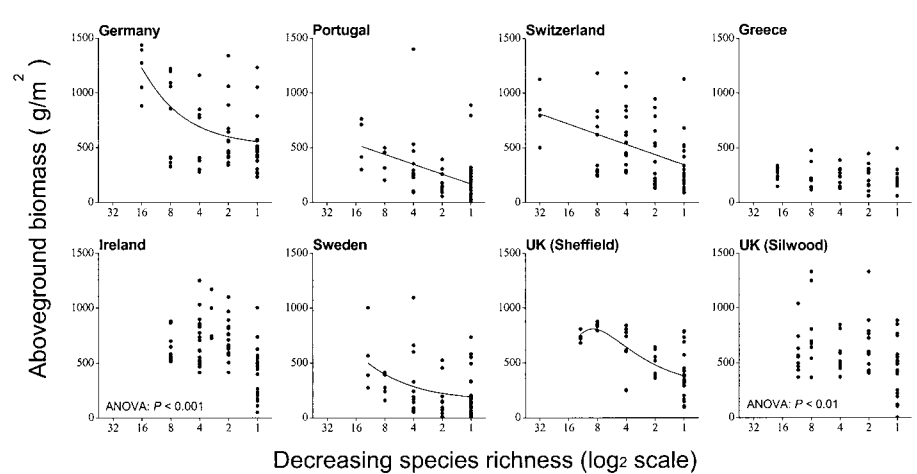


Fig. 2. Biomass patterns at each site (displayed with species richness on a \log_2 scale for comparison with Fig. 1A). Best-fit models from individual sites based on adjusted R^2 are as follows: log-linear in Switzerland and Portugal; linear (untransformed species richness) in Germany and Sweden; quadratic in Sheffield; ANOVA with five species richness levels (significant treatment effects with no simple trend) in Ireland and Silwood; and no significant effect in Greece.

Table 4. Summary of regression analyses of the aboveground biomass of individual species across the species richness gradients. Slopes are from simple regressions analyzing change in estimated biomass per individual sown of a species with increasing \log_2 number of species, after adjusting for differences between blocks and sites. “Plots” gives the sample size for each regression, and “sites” gives the number of locations from which they were derived.

Species	Sites	Plots (n)	Slope	SE
<i>Achillea millefolium</i>	4	35	0.44	0.277
<i>Agrostis capillaris</i> †	3	68	-0.15	0.087
<i>Alopecurus pratensis</i> †	5	63	0.01	0.025
<i>Anthoxanthum odoratum</i>	5	54	0.10	0.079
<i>Arrhenatherum elatius</i> †	3	74	1.17*	0.220
<i>Dactylis glomerata</i>	5	61	0.42*	0.113
<i>Festuca rubra</i>	3	56	-0.12	0.057
<i>Holcus lanatus</i> †	5	86	0.37*	0.134
<i>Lolium perenne</i>	2	37	0.47*	0.135
<i>Lotus corniculatus</i>	5	59	0.49*	0.212
<i>Plantago lanceolata</i> †	6	92	0.56*	0.114
<i>Rumex acetosa</i>	4	43	0.02	0.046
<i>Trifolium pratense</i> †	4	41	0.60*	0.180
<i>Trifolium repens</i>	6	85	0.28*	0.066

*Significant change in aboveground biomass, with species richness $P < 0.05$. †Significant location-by-species richness interaction, $P < 0.05$.

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

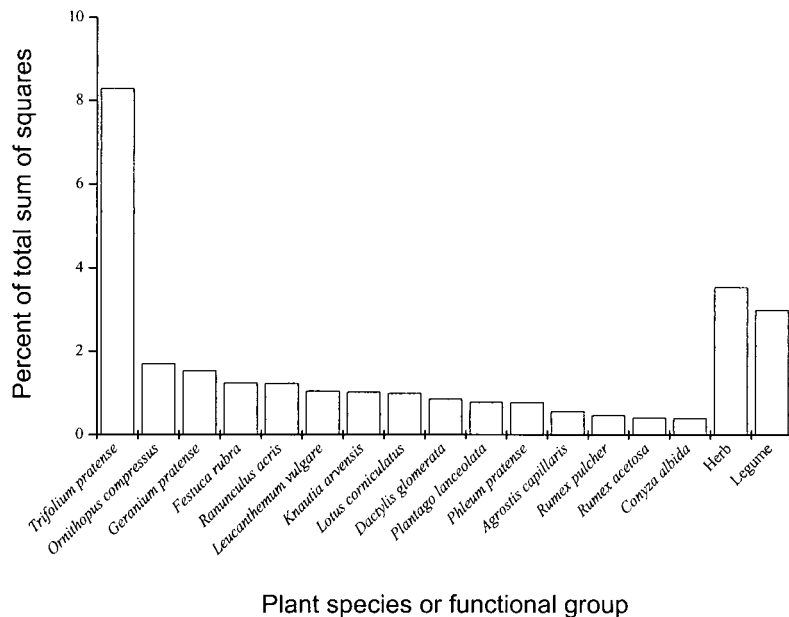


Fig. 3 Percentages of the total sums of squares explained by the effects of individual species and functional groups. Twenty-nine species had significant effects ($P < 0.05$); the 15 most highly significant species ($P < 0.001$) are shown.

diverse synthesized plant communities have a higher probability of containing, and becoming dominated by, a highly productive species (10, 23); (ii) niche complementarity, where ecological differences between species lead to more complete utilization of resources in intact communities relative to depauperate versions (2, 4, 6, 17, 23); (iii) a reduction in positive mutualistic interactions between species in simplified assemblages (6). Distinguishing (ii) from (iii) will require detailed local experiments, nor is separating the sampling effect from complementary and positive interactions straightforward (6, 12, 13, 30). However, the sampling effect predicts that the dominance of some species in high-diversity mixtures should be compensated for by reductions in the biomass of subordinate species. In contrast, fewer species declined in performance in polycultures than increased, which is consistent with a reduction of competition in mixtures of species relative to monocultures due to niche complementary or positive species interactions or both (Table 4) (31). Similar results have been reported elsewhere (5).

Only niche complementarity and positive species interactions can generate “overyielding,” where the total biomass of a mixture of species exceeds the monoculture biomass achieved by the highest yielding of the component species (32). We adapted (13) well-established techniques from agricultural and plant competition experiments (33) and used data from our replicated monocultures to test for overyielding in individual plant assemblages. As in the productivity analysis, overyielding differed significantly between sites ($F_{7,136} = 6.59$; $P < 0.001$), but there was a

consistent average decrease in overyielding with the simulated loss of species richness (slope = -0.021 , SE = 0.0075 , $F_{1,126} = 6.09$, $P < 0.05$) and with declining number of functional groups within species richness levels (slope = -0.143 , SE = 0.0544 , $F_{1,126} = 5.08$, $P < 0.05$). These results are again consistent with the occurrence of complementary and positive interactions within our mixtures of plant species and provide a second line of evidence indicating that our productivity patterns cannot be explained solely by the sampling effect.

Our results demonstrate multiple control of the productivity of experimental plant communities by geographic location and by the richness and composition of plant species and functional groups. Biomass patterns predict a log-linear decline in productivity with the loss of plant species richness, in which reductions of niche complementary or positive species interactions or both appear to play a role.

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16. Field experiments were established in 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 assemblage. 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.
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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 , $n = 480$, $R^2 = 0.95$, $P < 0.001$). 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: $F_{1,5} = 3.19$, $P = 0.134$; quadratic term: $F_{1,5} = 40.47$, $P = 0.001$, $R^2 = 0.86$). When included in a model with the linear effect of latitude, July temperature also had a significant effect on productivity (July temperature: $F_{1,5} = 11.64$, $P = 0.019$; temperature and latitude model: $R^2 = 0.73$).
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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 quadrat 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,

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 26. Data from the third year of the experiment have been processed for all sites except Portugal. Although there still appears to be no response in Greece, much of the other variation shown in Fig. 2 has disappeared, and the overall pattern appears to match the general log-linear relation more closely than in year two.
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 28. Composition effects are a combination of the effects of particular species and of interactions between species in polycultures. An assemblage-by-location interaction indicated that where the same species or mixture of species occurred at more than one site, they generally achieved significantly different biomasses at different locations [$F_{29,235} = 3.77$, $P < 0.001$ (Table 3)].
 29. Each species or functional group was added individually to the multiple regression models in Table 3. Fitting each species or group separately meant that the effect attributed to each was maximized. Our ability to test the effects of the grass functional group was limited, because most of the assemblages included grasses.
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 31. We performed simple regressions of the estimated per-plant biomass of 14 species across a gradient of increasing species richness (on a \log_2 scale) after adjusting for differences between locations and blocks by taking residuals from analyses with these terms [seven of the species showed significantly different responses at different sites (Table 4)]. We expected slopes of zero where intraspecific competition was equal to competition with other species and expected positive and negative slopes where it was more and less intense, respectively. Under the sampling hypothesis, we expected approximately equal distributions of positive and negative slopes. In contrast, 12 of the 14 species had slopes that were positive; 8 significantly so. Two species had slopes that were negative, but neither was significantly different from zero.
 32. J. L. Harper, *Population Biology of Plants* (Academic Press, London, 1977).
 33. We identified the species with the highest biomass in each plant assemblage and, where data were available (271 of the 308 polycultures), compared their average monoculture biomass with the biomass of the total assemblage using the overyielding index D_{max} [M. Loreau, *Oikos* **82**, 600 (1998)], where $D_{max} = (\text{total biomass of a plant assemblage} - \text{average monoculture biomass of the dominant species in that assemblage}) / \text{average monoculture biomass of the dominant species in that assemblage}$. We analyzed D_{max} after transformation using natural logarithms (after adding 1 to make all values positive) to meet the assumptions of parametric analyses.
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REPORTS

Hydrogen Storage in Single-Walled Carbon Nanotubes at Room Temperature

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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 (H_2) 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 H_2 storage and transportation have yet been developed. Of the problems to be solved for the utilization of hydrogen energy, how to store H_2 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 H_2 uptake. Dillon *et al.* (1) first

measured the H_2 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 H_2 adsorptivity for pure SWNTs of 5 to 10 weight % (the weight of H_2 adsorbed divided by the weight of SWNTs plus the H_2 adsorbed by the SWNTs), and predicted that SWNTs with a diameter of between 1.63 and 2 nm would come close to the target H_2 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 H_2 , respectively, at room temperature and at a pressure of 12 MPa. More recently, Chen *et al.* (4) reported that a high H_2 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 H_2 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 H_2 .

We measured the H_2 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 H_2 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, $\sim 80\%$ of the adsorbed H_2 can be released at room temperature. These results indicate that SWNTs are highly promising for H_2 adsorption even at room temperature.

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