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- To prepare for planting, a field at Cedar Creek Natural History Area, in Minnesota, was treated with herbicide and burned in August 1993, and had the upper 6 to 8 cm of soil removed to reduce the seed bank, was plowed and repeatedly harrowed, and divided into 342 plots, each 13 m by 13 m (only the inner 11 m by 11 m was sampled). Plots were seeded in May 1994 and again in May 1995. To test for effects of species diversity, we determined composition of each of 167 plots by random draws of 1, 2, 4, 8, or 16 species from a core pool of 18 species (four species each of C₃ grasses, C₄ grasses, legumes, and forbs; two woody species), with 29 to 35 replicates at each level of species diversity. To better distinguish between effects of species and functional diversity, we assigned combinations of 1, 2, or 3 functional groups containing 2, 4, or 8 species to 76 more plots, with compositions chosen by random draws of functional groups followed by species. When needed, we used a pool of 16 additional species (four in each of the nonwoody functional groups). Another 46 plots were created with 32 of these 34 species. Four plots were kept bare. These 289 plots uncouple species diversity, functional diversity, and functional composition, but have a weak correlation between these and species composition. There is no such correlation in the 167-plot random species subexperiment. The 289 plots have the following numbers of plots assigned to species and functional diversity classes:

		Species per plot						
		0	1	2	4	8	16	32
Functional groups per plot	0	4	–	–	–	–	–	–
	1	–	34	11	12	14	–	–
	2	–	–	33	13	14	–	–
	3	–	–	–	20	14	–	–
	4	–	–	–	10	18	1	16
	5	–	–	–	–	11	34	30
- Unless noted otherwise, all analyses use treatment species diversity, treatment functional diversity, and treatment functional composition. In each plot we estimated the percent cover of each species in four subplots (0.5 m by 1 m each). We measured peak aboveground living plant standing crop (an estimate of plant productivity) by clipping, drying, and weighing four 0.1 m by 3.0 m strips per plot. We measured % N in this aboveground biomass (plant % N), its total N (plant total N), soil NH₄ and soil NO₃ extractable in 0.01 KCl [four soil cores (2.5 cm by 20 cm depth) per plot], and the proportion of incident light (PAR) that penetrated to the soil surface. In 1996, plots contained mature, flowering plants, but the relative abundances of species may still be changing.
- Linear regressions for effects of species diversity: productivity, $r = 0.20$, $P < 0.01$, $n = 289$; plant % N, $r = -0.24$, $P < 0.001$, $n = 286$; plant total N, $r = 0.10$, $P = 0.08$, $n = 286$; soil NH₄, $r = -0.11$, $P = 0.06$, $n = 289$; soil NO₃, $r = -0.18$, $P < 0.01$, $n = 289$, light penetration, $r = -0.24$, $P < 0.001$, $n = 288$. For effects of functional diversity: productivity, $r = 0.30$, $P < 0.001$, $n = 289$; plant % N, $r = -0.33$, $P < 0.001$, $n = 286$; plant total N, $r = 0.16$, $P < 0.01$, $n = 286$; soil NH₄, $r = -0.19$, $P = 0.01$, $n = 289$; soil NO₃, $r = -0.29$, $P < 0.001$, $n = 289$, light penetration, $r = -0.34$, $P < 0.001$, $n = 288$.
- Regressions (as in 13), multiple regressions (as in Table 1), ANOVAs (as in Table 2), and MANOVAs that used only the 167 plots of the random species subexperiment (17) had similar results and generally higher r^2 values, indicating that results are not caused by the weak correlation between diversity and species composition in the full 289-plot experiment.
- The 1996 average percent cover of each species or functional group in each plot was used to calculate its effective species or functional diversity as $e^{H'}$, where H' is the Shannon-Wiener diversity index for species or functional groups. Trends found using treatment diversity variables also occurred when using 1996 effective diversity.
- There were 32 different combinations of five functional groups drawn 0, 1, 2, 3, 4 or 5 at a time. All 32 combinations were represented in the experiment. For the nested ANOVAs, each plot with a given level of functional diversity was further classified by which of the 32 combinations it contained. Similar results occurred when plots with bare soil or with 32 species were excluded.
- In the MANOVA, $P < 0.0001$ for both functional diversity and functional composition using Wilks' Lambda, Pillai's Trace, Hotelling-Lawley Trace, or Roy's Greatest Root.
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The Effects of Plant Composition and Diversity on Ecosystem Processes

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The relative effects of plant richness (the number of plant functional groups) and composition (the identity of the plant functional groups) on primary productivity and soil nitrogen pools were tested experimentally. Differences in plant composition explained more of the variation in production and nitrogen dynamics than did the number of functional groups present. Thus, it is possible to identify and differentiate among potential mechanisms underlying patterns of ecosystem response to variation in plant diversity, with implications for resource management.

Recent experiments have shown increasing net primary productivity (NPP) and nutrient retention in ecosystems as the number of plant species increases (1, 2). Ecosystem response to plant richness could occur via complementary resource use if plant species differ in the ways they harvest nutrients, light, and water (3, 4). Complementarity could happen in space, for example, because of differences in rooting depths; in time, for example, because of differences in phenology of plant resource demand; or in nutrient preference, for example, nitrate versus ammonium versus dissolved organic N. Greater plant diversity would then allow access to a greater proportion of available resources, leading to in-

creased total resource uptake by plants, lower nutrient losses from the ecosystem, and increased NPP, if the resources in question are limiting growth. However, differences in plant composition (the identity of the species present) may have large effects on ecosystem processes if the traits of one or a few species dominate (5). For example, if one species or group of species reduces soil nutrients to a lower level than do other species, then this species (or group) may dominate pools of available soil nutrients in mixtures (6). Such effects of composition could also lead to lower soil nutrient pools and greater nutrient retention as diversity increases because of an increasing probability of including the dominant species at higher levels of richness. In this case, however, increased ecosystem nutrient retention results from the presence of only one species rather than from niche differentiation and complementary resource use among many.

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Table 1. Statistics for productivity and inorganic N (inN) (13). Productivity data were natural log-transformed before ANOVA to improve normality. Models used for nonlinear regression are also shown.

ANOVA			Regression by richness			
R ²	Composition effects*	Richness effects†	R ²	Linear	R ²	Nonlinear
<i>Productivity</i>						
0.72	+E < -E***‡ +P > -P** E×L (0.053) L×P (0.039)	NS (1 = 2 = 3 = 4)	0.13	All§ Intercept = 5.04*** Slope = 0.02 (NS) BLK (NS)	—	All ND¶
			0.66	E only Intercept = 4.408 Slope = 0.216*** BLK (NS)	0.57	E only B = 92.13 + 66.72 * log(FG)
<i>Inorganic nitrogen pools</i>						
0.75	+E < -E*** +N ≥ -N (0.046) E×L (0.014)	B > 2, 3, 4* 1 > 2, 3* 1 > 4 @	0.29	All# Slope = 1.359*** Intercept = -0.296*** BLK (NS)	0.20	All inN = x ₁ + x ₂ * e ^(x₃*FG) x ₁ = -0.081 x ₂ = 1.617 x ₃ = -0.364
			0.37	E only# Slope = 0.43 (NS) Intercept = 0.002 (NS) BLK*	—	E only ND

*Composition effects: significant main effects and interactions from ANOVA. †Richness effects: differences among levels of functional group richness [B (bare), 1, 2, 3, or 4 functional groups] without accounting for composition. ‡Significance for a priori ANOVA tests is denoted by the following: NS, not significant; @, Bonferroni family-wide $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$. Because the Bonferroni correction is conservative, when the uncorrected P value is lower than 0.10 but greater than the Bonferroni corrected P for family-wide confidence, the significance value is listed. § Regression including all treatments. Model is $\ln(B) = a + b \cdot FG + BLK$, where B is biomass in g/m², a and b are the intercept and slope, respectively, FG is number of functional groups, and BLK is a categorical variable for block. ||Regression including only E-containing treatments; see Fig. 1. Model is the same as for All. ¶ND, analysis was not done because no trend was evident. #Regression model is $\ln N = a + b \cdot FG + BLK$.

Until now, a direct test to resolve these mechanisms has not been reported.

We describe an experiment that examined how richness and composition of plant functional groups (7) affect nutrient cycling in a serpentine grassland in California. We assessed how plant diversity affects productivity, resource availability to plants, and N leaching losses. The experiment focused on both the plant and microbial mechanisms responsible for such effects. Species from four functional groups defined by traits that are potentially relevant to nutrient cycling were used: early season annual forbs (E), late season annual forbs (L), perennial bunchgrasses (P), and N-fixers (N) (8). In the Mediterranean-type climate of the San Francisco Bay region, annual plants germinate in the fall after the first significant winter rains. E's set seed and senesce by April or May, the beginning of the summer dry season. L's continue to grow and flower through the summer, senescing the following autumn. P's senesce aboveground in late May and resprout from roots at the beginning of the following rainy season. N's are phenologically similar to E's, but were included for their relevance to nitrogen cycling. In addition to phenology, these groups differ in other characteristics relevant to nutrient retention and turnover, including rooting depth, root-to-shoot ratio, competitive ability, size, and foliage C/N ratio (9, 10). E's, L's, and P's were planted in a factorial combination, and two

treatments containing N-fixers were also included: N's alone, and N's combined with all other groups (11). A disturbed serpentine grassland site was used, in which serpentine topsoil was layered over the preexisting subsoil to provide a common substrate on which to plant the experimental treatments.

Aboveground biomass, used here to estimate primary productivity, did not correlate with increasing functional group richness (Table 1) (12). However, there were significant differences among treatments having the same number of functional groups (Fig. 1A) (13). In general, composition (the identity of the functional groups present) explained much more variance than did richness (the number of groups present) (Table 1). Complementarity may be evident in some subsets of the treatments; for example, the E-containing treatments showed an increase in productivity as more functional groups were included (E < EL, EP ≤ ELP < ELPN; Fig. 1A). However, mixture yields never approached the substantially higher biomass of the perennial-only treatment. Although these groups differ in both phenology and rooting depth, competitive interactions in mixture treatments had a strong effect on total plant biomass. In mixtures, the smaller E's and L's reduced the biomass of P's substantially below the levels expected on the basis of planting density and yields in single-group treatments (Fig. 1B). Our results do not

address year-to-year variability in production in response to pests, disturbance, or climatic variability (4, 14, 15). However, for NPP in this one year, traits of certain functional groups, such as competitiveness of E's and L's in mixture and large biomass of P's in monoculture, outweighed the effects of complementarity due to differences in phenology and rooting depth.

If nutrient use among plants is complementary, the expectation is that functional group mixtures will be able to reduce pools of available N in soil to lower levels than will single functional group treatments. On the other hand, if one group is dominant, this group alone (and all mixtures containing it) should have the lowest soil N levels. We measured pool sizes of inorganic N in the top 10 cm of soil in February during the wet mid-winter growing season (16). Increasing functional group richness was correlated with reduced soil inorganic N pools in the experimental plots (Fig. 1C and Table 1). However, E's alone reduced inorganic N pools to the lowest level of any single functional group treatment, and all more diverse treatments containing E's had equally low pool sizes. This pattern is consistent with Tilman's R* hypothesis (6, 17), in which the most competitive species reduces resource pools to the lowest level. Because a greater proportion of the treatments contained the dominant E's as diversity increased, this led to lower average N pool sizes as well. As with productivity,

composition explained substantially more of the variance in the data than did functional group richness alone (Table 1).

To obtain an integrative measure of how plant composition and diversity affect N losses from the ecosystem, we added tracer amounts of the stable isotope ^{15}N and followed its fate over the course of a growing season (18). Unlike the single time-point

measurement of inorganic N, increasing functional group richness did not significantly affect ^{15}N retention; total losses were similar for all treatments except for significantly lower retention in bare plots (Fig. 2 and Table 2). In all treatments, most ^{15}N was recovered in soil. Other experiments looking at ecosystem N retention have yielded similar results, implying that, in the short term, microbial immobilization is a more important pathway for N retention than plant uptake (19). However, the presence of microbes alone is not sufficient; microbial immobilization relies on C inputs from plants, resulting in low soil retention in bare plots in this and other experiments (Fig. 2) (20).

Composition, but not richness, of plant functional groups affected the distribution of ^{15}N between plants and soil (Fig. 2 and Table 2). If plant ^{15}N uptake were complementary between all three groups, we would expect to see a general increase in plant

retention as diversity increased. Instead, where differences among treatments occurred, they resulted from interactions among certain combinations of groups, as with productivity (Table 2). Complementarity among these functional groups apparently had a smaller effect on ecosystem N retention than did other attributes, such as litter quality and root turnover, that affected microbial immobilization.

In summary, we observed two patterns for the response of ecosystem processes to changes in plant functional group richness and composition. For productivity and ^{15}N retention, there was no response to changes in functional group richness, although within a given level of richness, treatments of different composition differed from each other. For inorganic N, we observed a decrease in soil pool sizes as plant functional group richness increased. However, the mechanism by which this occurred was not complementary nutrient use resulting from functional group richness per se; rather, it resulted from the dominant effects of one functional group, the early season annuals, in all mixtures of which it was a component.

These results point to two primary conclusions. First, differences in functional group composition can have a larger effect on ecosystem processes than does functional group richness alone. The effects of differences in composition are widely recognized in intercropping and agroforestry, where much time and expense are invested in finding species or genetic varieties that combine in more diverse agroecosystems to improve total yield (4, 14, 21). This suggests that the functional properties of particular species and combinations of species, more than richness per se, control yields and nutrient use (2, 22). Second, because differences in species composition can be correlated with differences in species richness, we need to look at all species or func-

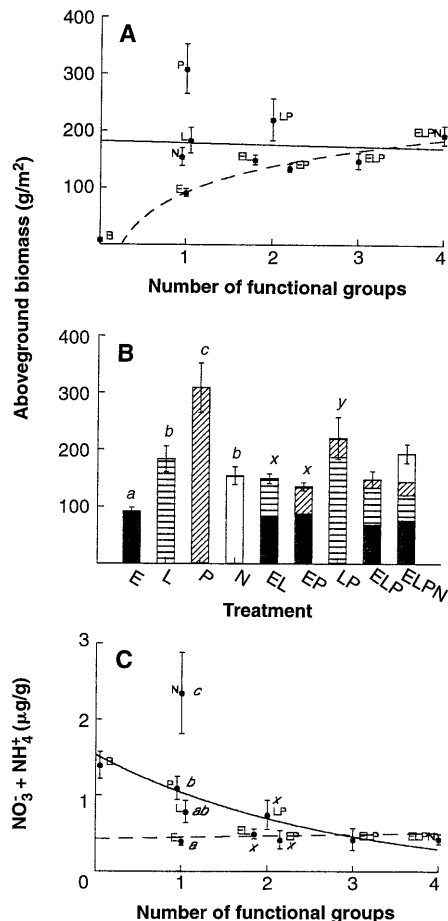


Fig. 1. Response of (A) aboveground biomass to functional group richness (mean \pm 1 SE, $n=6$), (B) aboveground biomass in 1993 to functional group composition, and (C) soil inorganic N (microgram of N per gram of soil) in February 1993 to functional group richness. Treatments are B = bare plots, E = early season annuals, L = late season annuals, P = perennial bunchgrasses, N = N-fixers, EL = earlies plus lates, EP = earlies plus perennials, LP = lates plus perennials, ELP = earlies plus lates plus perennials, and ELPN = earlies plus lates plus perennials plus N-fixers. In (A) and (C), points are offset from whole numbers for clarity only. The solid line is the regression through all data points, and the dashed line is the regression through only those treatments that contain early season annuals. See Table 1 for regression parameters. In (B), stacked bars show the average functional group composition of each treatment ($n = 6$, ± 1 SE of the total plot biomass). In (B) and (C), means within one level of richness with the same nonlabel letter (*a*, *b*, *c*, *x*, and *y*) are not significantly different at Bonferroni-corrected $P < 0.10$.

Table 2. ANOVA results for ^{15}N retention. Regressions were not performed because no trends were evident. Soil ^{15}N data were natural log-transformed before ANOVA to improve normality. NS, @, *, **, and *** as in Table 1.

R^2	Composition effects	Richness effects
	<i>Plant ^{15}N</i>	
0.50	L×P (0.030) (E + ELP \leq EL + EP)	NS
	<i>Soil ^{15}N</i>	
0.69	+E \geq -E (0.012) +L > -L@ +P \leq -P (0.019)†	NS
	<i>Total ^{15}N recovery</i>	
0.87	+E \geq -E** +L > -L** E×L@ E×P* L×P* (Due to low recovery in B)	NS

†Post-hoc test including only vegetated treatments: $3(P+EP+LP+ELP) = 4(E+L+EL)$.

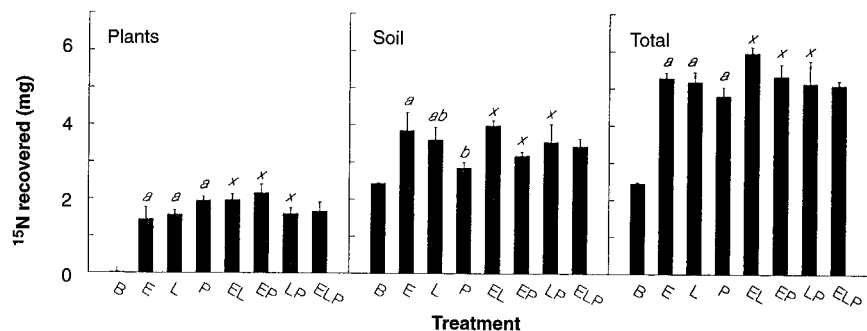


Fig. 2. Recovery of ^{15}N in plants (roots, shoots, and litter) and soil (soil organic matter, microbial biomass, and inorganic nitrogen pools). "Total" is the sum of plant and soil recovery. Treatments are as in Fig. 1, except no treatments with N-fixers were used with this experiment. Bars are means \pm 1 SE, $n = 3$. Differences of means within levels of richness are designated as in Fig. 1. See Table 2 for additional statistics.

tional groups grown alone as well as in more diverse combinations to understand mechanisms of diversity effects on ecosystem processes. As diversity changes, complementarity or facilitation among species are possible, but so are many other effects that may counteract these (23, 24).

The implications of the effects of richness and composition on ecosystem processes cut both ways for conservation and land management. If the only goal is the short-term maximization of production, in some cases less diverse cropping systems may perform as well as more diverse systems, as seen in agriculture and forestry. However, higher production in monocultures often comes only with the added expense of energy, fertilizer, and pesticides over the longer term, along with the external environmental costs of such inputs (25). On the other hand, knowledge of the functional characteristics of component species can aid in sustainable management of low-diversity intercropping systems. The results of our experiment also indicate that in aiming to protect natural ecosystems, we cannot just manage for "species diversity" alone—as measured by richness or the Shannon-Wiener index, which ignore species composition. The functional characteristics of the component species in any ecosystem are likely to be at least as important as the number of species for maintaining critical ecosystem processes and services.

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- Functional groups are groupings of species based on physiology, morphology, life history, or other traits relevant to controls on an ecosystem process; classification will depend on the process under investigation. Although functional groups are not always clearcut, they help to elucidate mechanisms by which species influence ecosystem processes, help to generalize such mechanisms across species, and help to simplify studies in systems with a large diversity of species [P. M. Vitousek and D. U. Hooper, in *Biodiversity and Ecosystem Function*, E.-D. Schulze and H. A. Mooney, Eds. (Springer-Verlag, Berlin, 1993), pp. 3–14; S. E. Hobbie, D. B. Jensen, F. S. Chapin III, *ibid.*, pp. 385–408; C. Körner, *ibid.*, pp. 117–140].
- Early season annuals: *Lasthenia californica* DC. ex Lindley, *Microseris douglasii* (DC.) Schultz-Bip., and *Plantago erecta* (Morris); Late season annuals: *Hemizonia luzulaefolia* (DC.) ssp. *rudis* and *Lessingia micradenia* E. Greene var. *glabrata* (Keck) Ferris; Perennial bunchgrasses: *Stipa pulchra* Hitchc. and *Sitanion jubatum* Smith; N-fixers: *Lotus subpinnatus* Lag. and *Astragalus gambellianus* Sheldon.
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- There were a total of 10 treatments at five levels of plant diversity: B (bare plots); E, L, P, and N (1-group); EL, EP, and LP (2-group); ELP (3-group); and ELPN (4-group) (species richness thus ranged from 0 to 9 species). We aimed for a planting density of 200 g/m² in 1-group treatments, based on previous measurements of aboveground biomass in undisturbed serpentine grassland [S. J. McNaughton, *Ecology* **49**, 962 (1968); S. N. Turitzin, *Am. Midl. Nat.* **107**, 95 (1982)]. In mixture treatments, 1-group planting densities were cut to one-half, one-third, or one-fourth to maintain constant overall planting density. Because of the small stature of most serpentine species, they attained self-supporting populations within relatively small plots (9). Plots were located near the Kirby Canyon Landfill (Waste Management Inc.), on an area that was originally bare of topsoil. Serpentine topsoil was graded over the subsoil to a depth of approximately 30 cm. Treatments were planted in 1.5 m by 1.5 m plots (0.5 to 1 m buffer zone between plots) in a randomized complete block design, with 10 treatments per block and six replicates of each treatment. Treatments were planted in the winter of 1991–92, and measurements were made in the following growing season (winter/spring 1993).
- We measured aboveground biomass by clipping annual species at the soil surface in five randomly placed 10 cm by 10 cm quadrats in each plot. For P's, we measured diameter and height of random individuals within each plot, then determined regressions for these measurements, with aboveground biomass on randomly harvested individuals [D. U. Hooper, *Ecology*, in press]. Clippings were sorted by species, dried at 65°C, and weighed. Total aboveground biomass is the sum of measurements made at peak biomass for each functional group: April for E's and N's, May for P's, and September for L's.
- Data were analyzed in two ways, using SYSTAT [SYSTAT Inc., SYSTAT for Windows: *Statistics, Version 5 Edition* (Evanston, IL, 1992)]. First, the effects of functional group richness alone were tested, using linear and, where appropriate, nonlinear regressions (See Table 1). Second, the effects of composition were tested, using analysis of variance (ANOVA) with the following model: $var = CONST + E + L + P + E \times L + E \times P + L \times P + E \times L \times P + N + E \times L \times P \times N + BLK$, where *var* is the response variable of interest; CONST is a constant; E, L, P, N, and combinations thereof are main effects and interactions of the functional groups; and BLK is a categorical variable representing the experimental blocks. In addition to ANOVA main effects and interactions, the following a priori comparisons were tested: differences among levels of functional group richness and differences among treatments within a level of functional group richness for the 1-group and 2-group levels. Probability levels were corrected by Bonferroni adjustment (see Table 1). For productivity and plant ¹⁵N, where values for the bare plot are meaningless, we used a means model coding for the ANOVA to avoid confounding the results. In these cases, ANOVA main effects and interactions were tested with balanced comparisons among the remaining treatments [For details, see D. U. Hooper and P. M. Vitousek, *Ecol. Monogr.*, in press].
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- Three random soil samples 5 cm in diameter and 10 cm deep were composited from each plot. A 20-g subsample was extracted in 0.5 M K₂SO₄, filtered after 36 hours in refrigeration, and the filtrate was measured colorimetrically for ammonium and nitrate on an Alpkem RFA/2 autoanalyzer (Perstorp Analytical, Silver Spring, MD).
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- Near the beginning of the growing season (January 1993), stainless steel cores (30 cm in diameter by 40 cm long) were inserted to a depth of 30 cm into randomly selected quadrats within experimental plots in three of the six replicate blocks. No treatments that included N-fixers were used for this experiment. After 2 weeks, we added tracer amounts of ¹⁵N as ammonium sulfate (26.4 mg ¹⁵N, ~65% enriched, total N addition = 5.6 kg N/ha) in solution with deionized water (a total of 18 ml). The solution was spread onto the soil surface then watered in by slowly adding ~1000 ml of deionized water. Cores were harvested at the beginning of the dry season in April 1993. Aboveground biomass was separated by species, dried (65°C for 3 days), weighed, ground, and analyzed for percent N, and percent ¹⁵N on a Europa Scientific Tracer mass spectrometer (in the laboratory of M. K. Firestone, University of California, Berkeley). Root biomass was estimated by washing subsamples of soil (400 g) on a root elutriator (Gillison hydropneumatic elutriation system, model GVF1300, Benzonia, MI) at the laboratory of L. Jackson at the University of California Davis Agricultural Extension in Salinas, CA. Roots were not separated by species; they were analyzed as above for N and ¹⁵N content. Soil moisture was measured gravimetrically. Dried soil samples were ground on a roller mill and analyzed for N and ¹⁵N as above. See [D. U. Hooper, thesis, Stanford University, Stanford, CA (1996)] for more details.
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