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## THE ROLE OF COMPLEMENTARITY AND COMPETITION IN ECOSYSTEM RESPONSES TO VARIATION IN PLANT DIVERSITY

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**Abstract.** To investigate how plant diversity affects ecosystem-level processes such as primary production and nutrient cycling, I established an experimental plant diversity gradient in serpentine grassland using four functional groups of plants: early season annual forbs (E), late season annual forbs (L), perennial bunchgrasses (P), and nitrogen fixers (N). These groups differ in growth form, phenology, and other traits relevant to nutrient cycling (e.g., rooting depth, litter C:N ratio). Two or three species of each type were planted in single-group treatments, and in two-, three-, and four-way combinations, giving a range of richness from zero to nine species. I tested the hypothesis that, because of complementary resource use, increasing functional group diversity will lead to higher net primary production. At the scale of this experiment ( $\alpha$ -diversity and yearly production), more diverse treatments were not necessarily the most productive. Live plant biomass varied more within than among levels of diversity. In most two-, three-, and four-way mixtures of functional groups, overall productivity did not differ significantly from the average of the yields of component one-group treatments. This pattern apparently resulted from competition: early season annuals and late season annuals reduced the biomass of perennial bunchgrasses (the most productive group in monoculture) below levels expected from monoculture yields.

Relative Yield Totals (RYT) indicated complementary resource use in the EL and LP two-way and ELPN four-way mixtures. In the EL mixture, complementarity appeared to result from temporal rather than spatial partitioning of resources. Because of shifts in root:shoot ratio in mixtures, however, only the LP treatment had consistently significant RYT > 1 when assessing total (roots plus shoots) productivity and nitrogen yield. These results show that (1) composition (the identity of the species present) can be at least as important as richness (the number of species present) in effects on ecosystem processes; (2) competition during critical parts of the growing season may prevent absolute increases in net primary production with increasing diversity, despite complementary resource use at other times of the year; and (3) shifts in belowground allocation in species mixtures can have significant effects on estimates of productivity and resource use as species diversity changes.

**Key words:** *California; ecosystem processes; functional group richness; net primary productivity; complementary plant resource use; plant composition; Relative Yield Total; serpentine grassland; species diversity.*

### INTRODUCTION

We know relatively little about how biological diversity affects the way ecosystems work, either in terms of processes at the ecosystem level, like primary production and nutrient cycling, or in terms of the long term sustainability of natural and managed ecosystems (Schulze and Mooney 1993, United Nations Environmental Programme 1995). Differences in plant species richness could affect ecosystem processes through partitioning of resources (Trenbath 1974, Harper 1977, Vandermeer 1990), whereby plants in more diverse communities may increase total resource capture, and thus increase net primary production. Such complementary resource use may occur in space, in time, or

in types of resources used (Ewel 1986). Species that are deeply rooted have access to water and nutrients not available to more shallowly rooted species (Berendse 1979, Berendse 1982, Chapin et al. 1996). Differences in shoot architectures may allow species to fill aboveground space more efficiently with leaves, increasing overall leaf-area index and light interception (Vandermeer 1990, Naeem et al. 1994, Naeem et al. 1995, Tilman et al. 1996). Phenological differences may allow species to harvest resources at different times of the year (Steiner 1982, Gulmon et al. 1983). Different species may also utilize different nutrient sources, e.g., plants with symbiotic nitrogen-fixing bacteria, plants able to utilize organic nitrogen (Chapin et al. 1993, Kielland 1994, Northup et al. 1995), and plants with mycorrhizal mutualisms that allow greater access to organically bound phosphorus (Hogberg 1989, Perry et al. 1989). While these examples illustrate potential axes for differentiation, plants are also known to compete strongly for a relatively limited suite

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of resources (Tilman 1988). Relatively few experiments have explicitly tested how primary productivity responds to plant diversity in natural ecosystems (McNaughton 1977, McNaughton 1985, Naeem et al. 1994, Tilman and Downing 1994, Naeem et al. 1995, Tilman et al. 1996), and none have directly tested the degree to which complementary resource use is involved.

Whether or not complementary resource use leads to increased productivity in natural systems will depend on several factors, including the relative efficiencies of species in converting resources into biomass, differences in allocation (e.g., to growth, defense, storage, or reproduction; Chapin et al. 1996), and the degree of complementary and competitive interactions among species. Partial complementarity may increase productivity, at least marginally. Reduced competition by this mechanism has been suggested to be a primary reason for improved yields in intercropping (Vandermeer 1990), as well as allowing for species coexistence in diverse natural communities (Grubb 1977, Fowler 1982, Bazzaz 1987, McKane and Grigal 1990). However, because the resource requirements of all plants are fairly similar, the effects of complementary resource use on yearly productivity at the scale of alpha-diversity are thought to saturate at relatively low species richness (Swift and Anderson 1993, Vitousek and Hooper 1993, Field 1995).

In addition to complementary resource use, productivity may increase with increasing diversity because some species can aid the growth of others, either through provision of resources or amelioration of harsh environmental conditions (Bertness and Callaway 1994). Such facilitation is common for nitrogen fixers, which can increase resource availability for other species (Vitousek and Walker 1989, Vandermeer 1990). In other instances, canopy trees and shrubs can facilitate growth of understory species by positive effects on soil moisture, nutrients, and microclimate in both natural and complex agricultural systems (Beets 1982, Steiner 1982, Ewel 1986, Caldwell et al. 1991, Bertness and Callaway 1994). Pathogen/herbivore protection (by various mechanisms), enhanced pollination, and structural attributes could all play facilitative roles for certain species at certain times (Trenbath 1974, Vandermeer 1990, Bertness and Callaway 1994, Lawton and Jones 1995). However, these interactions may change over the course of time (both developmentally and successional) or with plant density (Fowler 1986, Vandermeer 1990, Chapin et al. 1996). Whether facilitative and complementary interactions that increase productivity are a general attribute of increasing species diversity or are idiosyncratic properties of certain mixtures remains an important question (Morgan et al. 1992, Naeem et al. 1995).

Complementary resource use has received much attention in the literature on competition and intercropping (e.g., Trenbath 1974, Fowler 1982, Steiner 1982, Berendse 1983, Vandermeer 1988, McKane and Grigal

1990, Vandermeer 1990, Hetrick et al. 1994). However, most agricultural experiments use only two or three species. Of these, one is often a nitrogen fixer, a functional type for which little doubt remains as to its positive effects on growth of other species (Vandermeer 1990). Despite indications of complementarity, few experimental mixtures other than those with N fixers significantly increase primary production above that of the most productive monoculture, and almost none do so consistently (Trenbath 1974, Berendse 1979, Berendse 1982, Fowler 1982).

Relatively few experiments have been designed to test how plant diversity and complementarity might influence processes at the ecosystem level in natural systems. McNaughton (1977, 1985) and Tilman and coworkers (Tilman and Downing 1994, Tilman 1996) assessed productivity–diversity relationships in response to fertilization, grazing, and drought, but these deal with stability of production in response to disturbance rather than with complementary resource use and “steady state” rates of productivity. Other experiments (Naeem et al. 1994, 1995; Tilman et al. 1996) tested the response of productivity to increasing species richness, but did not control for differences in composition by growing all species in monoculture as well as in mixture. Naeem et al. (1996) observed an increase in average productivity with increasing species richness, but also great variation around that general trend: A given mixture’s total productivity was best predicted by the species-specific responses of all its component species in other mixtures. Elsewhere, in three-way mixtures of different growth forms (grass–shrub–N fixer) in a sagebrush community, grasses inhibited sagebrush growth (the most productive species in monoculture), so that more diverse treatments were not necessarily the most productive (Pendery and Provenza 1987). This indicates that the functional attributes (e.g., competitive ability, size, relative growth rate, response to disturbance) of one or a few species may dominate the ecosystem level response of productivity (Chapin et al. 1996). This is similar to the “idiosyncratic hypothesis” of Lawton (1994) and Naeem et al. (1995). These results illustrate the importance of differentiating between increases in productivity resulting from differences in plant composition (i.e., the identity of species) vs. those resulting from species richness (i.e., the number of species) and complementarity.

The study described here differs from these previous approaches by focusing on plant functional groups rather than species. While functional group classifications are not always clear-cut, categorizing species by physiognomic and life history traits helps to simplify the study, identify mechanisms by which diversity might affect a given ecosystem process, and test whether these mechanisms can be generalized across many species (Hobbie et al. 1993, Körner 1993). Indeed, part of the experiment is to determine the extent to which the classifications used are relevant to the ecosystem pro-

cesses being studied (Vitousek and Hooper 1993). Despite this difference in experimental strategy, however, the mechanistic issues of complementarity and composition just discussed apply to both functional-group and species-based approaches.

To address questions of complementary resource use and the extent to which plant composition and richness affect primary productivity, I used a California serpentine grassland as an experimental system. This system is characterized by small-statured, predominantly annual species with a variety of growth strategies. In addition to stress imposed by regular summer drought in this Mediterranean-type climate, serpentine soils are relatively infertile: nitrogen, phosphorus, or both may limit plant productivity (Turitzin 1982, Kruckeberg 1984, Hobbs et al. 1988, Koide et al. 1988, Huenneke et al. 1990). I investigated effects of plant functional group diversity on productivity by selecting two or three of the most common species within several phenological or functional groups identified by previous research: early season annual forbs, late season annual forbs, perennial bunchgrasses, and nitrogen fixers (Woodmansee and Duncan 1980, Gulmon et al. 1983, Hobbs and Mooney 1985, Mooney et al. 1986, Chiarriello 1989). Because these groups differ in a suite of relevant characteristics, including phenology, rooting depth, root:shoot ratio, size per individual, and leaf nitrogen concentrations (Gulmon et al. 1983, Mooney et al. 1986, Armstrong 1991), I hypothesized that they would use resources in a complementary way, in space, time, or both. I planted each group alone as well as in more diverse combinations, which allowed evaluation of complementarity in two different ways: first, by testing for an absolute increase in productivity with increasing diversity, and second, by measuring Relative Yield Totals (Trenbath 1974, Harper 1977, Vandermeer 1990, Swift and Anderson 1993). In this way, I was able to differentiate between effects in mixtures resulting from complementarity (due to increasing functional group richness) vs. effects resulting from differences in composition (i.e., the presence of particular functional groups).

## METHODS

### *Study site*

I established experimental plots at Kirby Canyon in south San Jose, California (37°15' N, 121°45' W) near a landfill operated by Waste Management, Inc. This region experiences a Mediterranean-type climate, with cool wet winters and a dry season extending from approximately May to October. Average rainfall is ~370 mm/yr (Huenneke et al. 1990), though both the timing and amount are highly variable from year to year (Armstrong 1991, Hobbs and Mooney 1995). Huenneke (1990) has described the native grassland at this site. Because topsoil depth and vegetation history vary greatly over the natural grassland, I chose to restore

TABLE 1. Species classified by functional groups as used in this experiment.

	Functional group	Species
E	Early season annuals	<i>Lasthenia californica</i> Lindley <i>Microseris douglasii</i> (DC.) Schultz-Bip. <i>Plantago erecta</i> E. Morris
L	Late season annuals	<i>Hemizonia luzulaefolia</i> DC. ssp. <i>rudis</i> <i>Lessingia micradenia</i> E. Greene var. <i>glabrata</i> (Keck) Ferris
P	Perennial bunchgrasses	<i>Sitanion jubatum</i> Smith <i>Stipa pulchra</i> Hitchc.
N	Nitrogen fixers	<i>Astragalus gambelianus</i> E. Sheldon <i>Lotus subpinnatus</i> Lagasca

an already denuded area for the experimental plots. Topsoil stockpiled from the landfill was placed over serpentinic subsoil (C horizon) to a depth of ~30 cm, covering an area of ~0.25 ha. This gave a fairly homogeneous substrate on which to plant the experimental treatments. The area was fenced to exclude mammalian herbivores. Soil characteristics are given in Hooper and Vitousek (*in press*).

### *Experimental design*

For manipulations of functional group diversity, I chose species from four distinct phenological and functional categories (Gulmon et al. 1983, Hobbs and Mooney 1985, Mooney et al. 1986, Chiarriello 1989), which are major components of the surrounding grasslands: early season annuals (E), late season annuals (L), perennial bunchgrasses (P), and nitrogen fixers (N) (Table 1). Annual plants germinate in autumn after the first significant rains. Early season annuals flower, set seed, and senesce by the end of the wet season or very early in the dry season (Mooney et al. 1986). Late season annuals persist in rosette form through the wet season, then bolt and flower from the summer dry season through the fall. Perennial bunchgrasses flower in May, senesce aboveground during the dry season, and resprout again from root stock in autumn. N fixers are phenologically similar to E's, but have obvious functional relevance to productivity and nutrient cycling and provide a treatment with well-characterized effects against which to compare results.

Each functional group was planted alone and in various combinations in experimental plots measuring 1.5 × 1.5 m separated by 0.5–1 m buffer strips, using two or three of the most common species from each group (Table 1). Plots were large enough for self-supporting populations of plants: hundreds (late season annuals) or thousands (early season annuals) of individuals are encompassed in a 1 m<sup>2</sup> area in native serpentine grassland (McNaughton 1968, Gulmon et al. 1983). I used

a randomized complete block design with six replicate blocks and a total of 10 treatments in each block. Treatments included a full factorial cross of E's, L's, and P's: bare plots (B), each group alone (E, L, P), all two-way combinations (EL, EP, LP), and the three-way combination (ELP). In addition, there were two treatments including N fixers: a single functional group treatment (N) and a four-way combination (ELPN). This provided a range of functional group richness from zero (bare plots) to four (zero to nine species).

I planted all treatments with a target biomass of 200 g/m<sup>2</sup>, the average from previous studies at nearby natural serpentine grasslands (McNaughton 1968, Turitzin 1982, Huenneke et al. 1990). I derived planting densities for single functional group (SFG) plots by dividing target biomass by the mean size of individuals for each species and by the proportion of seed germination for each species. I aimed for equal proportions by biomass for each species within each functional group. Planting densities of each species in mixture treatments were cut to one-half, one-third, and one-quarter, for the two-, three-, and four-way mixtures, respectively, to maintain consistent overall planting densities in a way analogous to a replacement series design (de Wit and van den Bergh 1965, Harper 1977). Seed was collected from the surrounding native grassland at Kirby Canyon for all species except for *Larthenia californica* (donated by Nona Chiariello), which originated from the serpentine grassland at Jasper Ridge Biological Preserve at Stanford University.

Seeds for all annual species were sown directly onto the plots in January 1992, ~1 mo after the first rains of the season. Perennial bunchgrasses were germinated in greenhouses at Stanford University's Plant Growth Facility, using a mixture of two parts serpentine topsoil to one part perlite in Cone-tainers ("Super Stubbies," Stuewe & Sons, Corvallis, Oregon). Individual grasses were grown for ~3 mo in the greenhouse before transplanting into field plots in February 1992 (64 individuals per species in each single functional group P plot). Planting densities were decreased similarly to annual species in more diverse treatments. I weeded plots regularly throughout each growing season to remove unwanted species, but did not adjust densities of the planted species.

#### *Biomass harvests*

To estimate productivity, plots were harvested for aboveground biomass in 1993, the second growing season after plot establishment. Harvests occurred at peak biomass for each of the functional groups: mid-April for early season annuals and N fixers, mid-May for perennial bunchgrasses, and mid-September for late season annuals (Gulmon et al. 1983, Hobbs and Mooney 1985, Chiariello 1989, Armstrong 1991). In the April harvest, five replicate 10 × 10 cm quadrats were placed randomly throughout the plot, leaving a 10-cm buffer around the outside of the plot to avoid edge

effects. All plants except perennial bunchgrasses were clipped at ground level. These subsamples were then pooled, separated by species, dried at 65°C for >72 h, and weighed.

To minimize removal of perennial bunchgrass individuals, bunchgrasses were nondestructively sampled by: (1) measuring basal circumference, vegetative height, number of reproductive culms, and height of reproductive culms of five randomly selected plants in each plot, and (2) counting the number of bunchgrass individuals by species in each plot. I then harvested one measured individual of each species from each plot and separated live biomass from standing dead. I used principal components analysis to eliminate colinearity among the measured parameters before calculating a regression of live aboveground biomass against the first principal component (Appendix A). I then multiplied the average biomass from the measured individuals by the total number of individuals in each plot for an estimate of total aboveground bunchgrass productivity.

The September harvest was similar to that in April except that three 10 × 20 cm quadrat subsamples were taken from each plot; dead aboveground E's, P's, and N's were counted as litter. All previously harvested quadrats were excluded from later harvests. Measurement of bunchgrasses in autumn 1993 by the same methods as used in the spring indicated no increase in aboveground biomass over the summer dry season. I estimated yearly aboveground productivity as the sum of live biomass of all species at their peak season: spring for E's, N's, and P's; fall for L's.

#### *Core harvests*

To estimate total productivity and plant nitrogen content, I used root biomass and root and shoot nitrogen concentrations from a separate experiment (Hooper 1996). In January 1993, I placed stainless steel cores (30 cm diameter × 40 cm deep) into three replicate blocks of the full factorial E × L × P set of treatments (B, E, L, P, EL, EP, LP, and ELP) for use in an experiment looking at the fates of added tracer <sup>15</sup>N. In April 1993, I removed the cores and their enclosed plants and soil (to a depth of 30 cm) for destructive harvest. Aboveground plant parts were clipped and sorted by species. I harvested soil in 10-cm layers, taking two 300–400 g subsamples from each homogenized layer for estimates of root biomass, percent carbon, and percent nitrogen. These subsamples were washed on a root elutriator (Gillison hydropneumatic elutriation system, Model No. GVF1300, Benzonia, Michigan) at the laboratory of Dr. Louise Jackson at the University of California at Davis Agricultural Extension in Salinas, California. This procedure leaves roots free of mineral soil particles. Roots were further separated from particulate soil organic matter by a series of three floatations in tubs of deionized water with sieving (0.09-mm screen) to capture floating roots. No attempt was made to separate roots by species or functional group. Roots and shoots

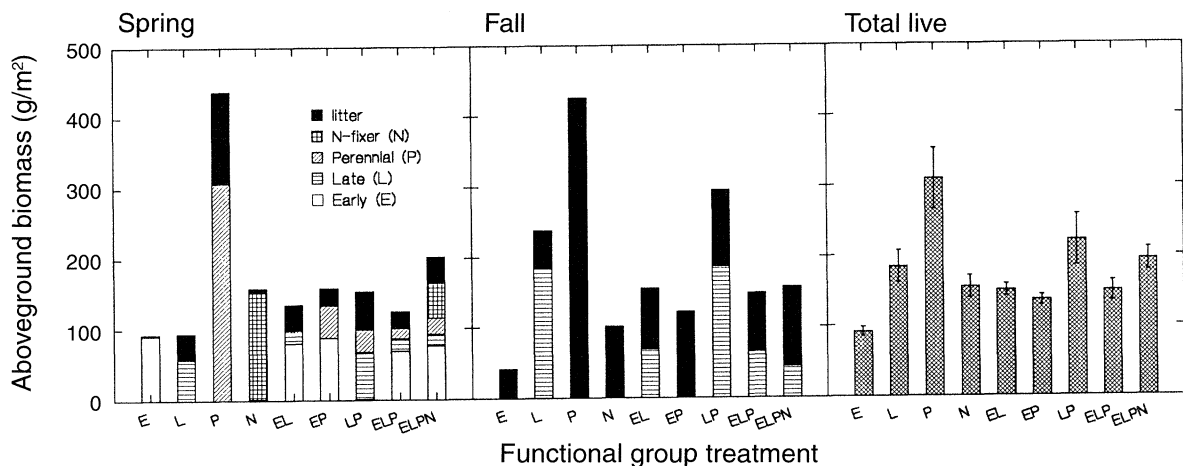


FIG. 1. Aboveground biomass by functional group from harvests in April and September 1993. Functional group designations are E, early season annuals; L, late season annuals; P, perennial bunchgrasses; and N, nitrogen fixers. In fall, all but late season annuals have senesced aboveground. "Total aboveground live" is the summed aboveground biomass (mean  $\pm 1$  SE) from all functional groups at their season of peak biomass: spring for E's, P's, and N's; fall for L's.

were dried at 65°C, weighed, ground to a fine powder, and analyzed for percent carbon and nitrogen in a mass spectrometer (Europa Scientific Tracermass) in the laboratory of Mary K. Firestone, University of California at Berkeley. For roots, these values were corrected for contamination with soil organic matter not removed by the sequential washing procedure by determining correction factors from several intensively separated samples (Hooper 1996).

#### Relative Yield Totals

I used Relative Yield Totals (RYT) to assess the degree of complementary resource use of the functional groups grown in mixture treatments (de Wit and van den Bergh 1965, Harper 1977). Relative Yields and Relative Yield Totals were calculated as follows:

$$RY_{ijk} = Y_{ijk}/(Y_{ik}/n); RY_{jik} = Y_{jik}/(Y_{jk}/n) \quad (1.1)$$

$$RYT_{ijk} = (RY_{ijk} + RY_{jik})/n \quad (1.2)$$

$$RYT_{ij} = \text{mean } RYT_{ijk} \quad (1.3)$$

where  $RY_{ijk}$ ,  $RY_{jik}$  = Relative Yield of functional group  $i$  in mixture with functional group  $j$  in block  $k$ , and relative yield of functional group  $j$  in mixture with functional group  $i$  in block  $k$ ;  $Y_{ijk}$ ,  $Y_{jik}$  = productivity or nitrogen yield of functional group  $i$  in mixture with functional group  $j$  in block  $k$  ( $k = 1-6$ ), and the same for functional group  $j$  in mixture with  $i$ ;  $Y_{ik}$ ,  $Y_{jk}$  = productivity or nitrogen yield of functional groups  $i$  and  $j$  in single functional group plots in block  $k$ ; dividing by  $n$  accounts for differences in planting density; where  $n$  = number of functional groups in mixture;  $RYT_{ijk}$  = Relative Yield Total of mixture with functional groups  $i$  and  $j$  in block  $k$ ;  $RYT_{ij}$  = average Relative Yield Total (across blocks) of mixture with groups  $i$  and  $j$ .

To account for block effects, this approach differs

from former calculations (Trenbath 1974, Harper 1977) in that it calculates relative yields for the components based on SFGs in the same block, rather than by averaging all SFGs. The difference in final RYT values is small, with this approach having slightly higher variance than Harper's (1977).

To calculate RYT based on total plot biomass (roots plus shoots), I used data on root : shoot ratio (calculated on a grams per square meter basis to 30 cm soil depth) from the core tracer experiment (Hooper 1996). However, calculating RYT requires biomass of individual functional groups and it was not possible to separate roots by species or functional group in mixture cores. Therefore, I estimated root biomass for each functional group in mixtures by using the aboveground biomass of that group in the whole-plot biomass harvest and the root : shoot (r:s) ratio of each group from the single functional group cores. Total root biomass in the mixture was constrained by the actual r:s ratio from the mixture cores, using the following formulas:

$$\text{roots}_u = \sum_{i=E,L,P} (b_i r_i) \quad (1.4)$$

$$\text{roots}_i = (b_i r_i)(Y_m r_m / \text{roots}_u) \quad (1.5)$$

where  $\text{roots}_u$  = unconstrained estimate of roots in a mixed plot;  $b_i$  = aboveground biomass of functional group  $i$  in a mixed plot from the biomass harvest;  $r_i$  = average root : shoot ratio of functional group  $i$  from SFG core harvest;  $\text{roots}_i$  = constrained estimate of roots for functional group  $i$ ;  $Y_m$  = total aboveground biomass of mixture treatment  $m$  ( $m = EL, EP, LP, ELP$ ) from the biomass harvest;  $r_m$  = actual root : shoot ratio from core mixture treatment  $m$ .

Because it does not use separate measurements of root : shoot ratio for each functional group in mixtures, this approach assumes that if mixture r:s differs from

the expectation based on SFG treatments (i.e.,  $Y_{mr_m} \neq \text{roots}_i$ ), then all components of the mixture shift allocation in a similar way. While this may not be the case, I used it as the simplest assumption because I have no data to indicate otherwise.

$\text{RYT} = 1$  for a mixture if: (1) the productivity of functional group  $i$  in a two-way mixture with  $j$  is half that of  $i$  in its single-group treatment, and the productivity of group  $j$  in the mixture is half that of  $j$  in its single-group treatment (i.e., the groups do not interact, or interspecific competition is the same as intraspecific competition); or (2) any increase in the relative yield of one is offset by a similar decrease by the other. If groups  $i$  and  $j$  are complementary in their resource use, we would expect that  $\text{RYT} > 1$  due to reduced competition in the presence of plants that effectively partition resources (i.e., interspecific competition is less than intraspecific competition). If groups  $i$  and  $j$  interfere with each other, we expect  $\text{RYT} < 1$ . In practice, RYTs from a variety of competition and intercropping experiments without nitrogen fixers fall in the approximate range 0.5–1.7, with most falling between 0.7 and 1.3 (Trenbath 1974). With nitrogen fixers,  $\text{RYT} > 2$  is possible (Swift and Anderson 1993).

While replacement series designs have been criticized (Inouye and Schaffer 1981, Firbank and Watkinson 1985, Connolly 1986, Taylor and Aarssen 1989, Snaydon 1991, Snaydon 1994; but see also Cousens and O'Neill 1993, Sackville Hamilton 1994), calculation of Relative Yield Totals from them is one measure of complementarity that is robust, as long as certain criteria are met (Connolly 1986, Cousens and O'Neill 1993; T. J. Howard, *unpublished manuscript*). These include planting densities that give constant final yield and adequate time before harvesting to allow individuals to mature and community interactions to develop. Calculating RYT on a yield per area (rather than a yield per individual) basis further buffers it from the vagaries of inadequate planting densities. Using the 1993 productivity estimates, this experiment met these criteria. Furthermore, using experimental plots in the field and a common serpentine topsoil substrate allowed for the full range of expression of different rooting characteristics, while still controlling for differences in productivity which could result solely from soil heterogeneity in intact grassland.

If a single resource such as nitrogen is limiting, the difference in total nitrogen yield ( $D$ ) between mixtures and monocultures should also be a valid measure of complementarity (McGilchrist 1965, Harper 1977). If  $D > 0$  (over-yielding), species in mixtures are able to acquire more total nitrogen than they are in monocultures. If  $D < 0$  (under-yielding), there is less absolute nitrogen in plant biomass in mixture than the average of component single functional group treatments. Aboveground plant nitrogen yields for spring 1993 were calculated from data on total plant percent N (from the core tracer experiment) multiplied by live

plant biomass from the spring 1993 biomass harvest. Root biomass and N content were estimated as above. I calculated  $D$  to evaluate over- or under-yielding in terms of plant nitrogen, in a slight modification of the method of Harper (1977:268–269).

$$D_{ijk} = (Y_{ijk} + Y_{jik}) - [(Y_{ik} + Y_{jk})/n] \quad (1.6)$$

where  $D_{ijk}$  = difference in actual nitrogen yield from mixture  $ij$  in block  $k$  and the estimated nitrogen yield based on  $i$  and  $j$  single functional group treatments in block  $k$ ;  $Y_{ijk}$ ,  $Y_{jik}$ ,  $Y_{ik}$ ,  $Y_{jk}$  = yield of plant nitrogen in functional groups  $i$  and  $j$  in mixture and SFG plots, as in Eqs. 1.4 and 1.5;  $n$  = number of functional groups in the mixture treatment.

This formulation differs from that of Harper (1977) primarily in that it subtracts the mean of the two SFG treatments ( $(Y_{ik} + Y_{jk})/n$ ) from the total mixture yield ( $Y_{ijk} + Y_{jik}$ ). This change makes all  $D$  values positive for cases in which mixtures yield more plant nitrogen than SFGs and negative for the opposite case.

#### Statistics

I did all analyses of variance and regressions using the General Linear Model commands in SYSTAT (SYSTAT 1992). For regression of total plot yield against plot richness (number of functional groups), I used the General Linear Models procedure, coding Block as a categorical variable. For ANOVA by plot composition, analysis of plant biomass or nitrogen yields does not allow evaluation of the full factorial ANOVA model because values for the bare plot are meaningless. I therefore used a combined means and effects model and only included cases from the vegetated treatments. I determined main effects and partial two-way interactions by contrasting the weighted means of all plots containing a given functional group with all plots lacking it, excluding the bare plots. In addition, I used a priori contrasts to compare means of single functional group treatments, and to test if mixture means differed from the average of their component SFG treatments.  $P$  values for a priori contrasts, main effects, and interactions are corrected for family-wide confidence intervals of 90% using Kimball's inequality (Neter et al. 1990), identical to the Dunn-Sidak method of Sokal and Rohlf (1981). The Appendix of Hooper and Vitousek (*in press*) describes these procedures.

For Relative Yield Totals, I used a one-way ANOVA (treatment is PLOT = EL, EP, LP, ELP, or ELPN, plus a block variable) for testing for significance of  $D$  and RYT. Using the pooled variance from the ANOVA, I constructed 95% confidence limits to test whether means of individual treatments differed significantly from zero ( $D$ ) or one (RYT).

#### RESULTS

##### *Treatment confirmation and general patterns*

Plots reflected the intended composition and diversity for all treatments. All species established success-

TABLE 2. Rank order of species and biomass (in grams per square meter, mean  $\pm$  1 SE,  $n = 6$ ) for 1993 aboveground production.

Rank	Treatment					
	E	L	P	N	EL	EP
1	<b>Pla</b> 77.9 $\pm$ 5.8	<b>Les</b> 103.6 $\pm$ 7.4 (38.5 $\pm$ 3.1)	<b>Stp</b> 180.6 $\pm$ 34.2	<b>Lot</b> 143.4 $\pm$ 16.4	<b>Pla</b> 69.7 $\pm$ 5.8	<b>Pla</b> 76.7 $\pm$ 5.8
2	<b>Mic</b> 11.3 $\pm$ 2.0	<b>Hem</b> 80.0 $\pm$ 18.6 (19.1 $\pm$ 4.2)	<b>Sit</b> 127.3 $\pm$ 14.8	<b>Ast</b> 9.4 $\pm$ 2.8	<b>Hem</b> 42.8 $\pm$ 7.9 (9.3 $\pm$ 1.9)	<b>Sit</b> 28.3 $\pm$ 5.9
3	<b>Las</b> 1.62 $\pm$ 0.5	<i>Las</i> 0.06 $\pm$ 0.06	<i>Hem</i> 0.89 $\pm$ 0.89	<i>Les</i> 0.21 $\pm$ 0.21	<b>Les</b> 26.1 $\pm$ 5.6 (8.2 $\pm$ 2.0)	<b>Stp</b> 18.0 $\pm$ 6.2
4	<i>Ast</i> 0.15 $\pm$ 0.12	<i>Stp</i> 0.05 $\pm$ 0.05		<i>Stp</i> 0.09 $\pm$ 0.09	<b>Mic</b> 8.0 $\pm$ 1.6	<b>Mic</b> 9.0 $\pm$ 1.2
5	<i>Les</i> 0.10 $\pm$ 0.05	<i>Mic</i> 0.01 $\pm$ 0.01		<i>Las</i> 0.07 $\pm$ 0.05	<b>Las</b> 2.1 $\pm$ 0.6	<b>Las</b> 1.5 $\pm$ 0.4
6	<i>Hem</i> 0.03 $\pm$ 0.02				<i>Ast</i> 0.06 $\pm$ 0.06	<i>Lot</i> 1.1 $\pm$ 0.7
7					<i>Lot</i> 0.06 $\pm$ 0.06	<i>Ast</i> 0.03 $\pm$ 0.03
8					<i>Sit</i> 0.04 $\pm$ 0.04	<i>Les</i> 0.03 $\pm$ 0.03
9						<i>Hem</i> 0.03 $\pm$ 0.03

Note: Values for a given species are its peak biomass (spring for E's, P's, and N's, fall for L's. Values for L spring biomass are also given in parentheses; daggers ( $\dagger$ ) denote cases that change rank from spring to fall). Species abbreviations, with functional group in parentheses: Ast, *Astragalus* (N); Hem, *Hemizonia* (L); Las, *Lasthenia* (E); Les, *Lessingia* (L); Lot, *Lotus* (N); Mic, *Microseris* (E); Pla, *Plantago* (E); Sit, *Sitanion* (P); Stp, *Stipa* (P). Species abbreviations in bold are sown species; those in italics are "weeds" not intentionally included in specified treatments.

fully and weed biomass was a very small percentage of total plot biomass (Fig. 1, Table 2). Species diversity, as measured by the Shannon-Weiner index (Magurran 1988), increased across levels of functional group richness (data not shown) due to changes in both species richness and evenness of biomass distribution (Table 2). Single functional group (SFG) treatments developed strong differences in aboveground productivity, with perennial bunchgrasses averaging three times the biomass of early season annuals (Fig. 1). In most mixture treatments, early season annuals, particularly *Plantago erecta*, dominated spring biomass in treatments where they were present, whereas late season annuals accounted for equivalent production by the end of the growing season (Table 2). By spring of 1993 (end of the second wet season after establishment), there was a large amount of litter accumulation in treatments containing P's and L's (Fig. 1).

#### Responses of productivity to functional group richness and composition

**Total production.**—To test the expectation that increasing diversity causes increasing productivity, I regressed total aboveground biomass against number of functional groups contained in treatments (Fig. 2). In this approach, functional group richness is not a significant predictor of aboveground productivity (includ-

ing bare treatments,  $P = 0.043$ ,  $R^2 = 0.137$ ; excluding B,  $P = 0.784$ ,  $R^2 = 0.113$ ). Variance in productivity is also much higher at low than at high levels of richness, which calls into question the utility of the standard linear regression. Some subsets of treatments, for example the E-containing plots (E, EL, EP, ELP, and ELPN), do show a significant trend toward increasing productivity with increasing richness (nonlinear regression in Fig. 2). However, when all treatments are considered, none of the mixtures approach the much higher biomass of the P-only treatment.

Because of strong differences in productivity even within levels of functional group richness, functional group composition explains substantially more of the variance than does richness alone (ANOVA by composition,  $R^2 = 0.720$ ). None of the mixture treatments differ statistically from the average of their component SFG treatments (Figs. 1 and 2). While this may appear to be a completely noninteractive mix of plants, the pattern is due to competitive dominance by annuals over perennial bunchgrasses. The biomass of early season annuals changes little across all treatments, while that of bunchgrasses is reduced to between one-fourth and one-third of expected levels in mixtures with E's (Fig. 3). Perennial bunchgrass growth was also greatly below expected values in LP treatments, primarily because of very high over-summer mortality of *Sitanion*



TABLE 2. Extended.

Treatment		
LP	ELP	ELPN
<b>Les</b> 97.1 ± 7.8 (39.4 ± 7.1)	<b>Pla</b> 55.7 ± 5.6	<b>Pla</b> 60.5 ± 4.9
<b>Hem</b> 89.0 ± 36.0 (26.7 ± 4.7)	<b>Les</b> 41.6 ± 3.5 (13.2 ± 3.6)	<b>Lot</b> 43.2 ± 8.0
<b>Stp</b> 17.2 ± 4.3	<b>Hem</b> 23.1 ± 12.1 (4.5 ± 1.6)†	<b>Les</b> 23.1 ± 7.2 (8.2 ± 2.5)†
<b>Sit</b> 14.8 ± 4.5	<b>Mic</b> 9.1 ± 1.4	<b>Hem</b> 21.1 ± 4.9 (7.9 ± 1.2)†
<i>Ast</i> 0.37 ± 0.24	<b>Sit</b> 8.1 ± 2.2	<b>Sit</b> 13.3 ± 2.5
<i>Pla</i> 0.31 ± 0.31	<b>Stp</b> 6.6 ± 1.0	<b>Mic</b> 10.7 ± 1.2
<i>Mic</i> 0.17 ± 0.17	<b>Las</b> 3.1 ± 0.6	<b>Stp</b> 10.1 ± 1.8
<i>Las</i> 0.12 ± 0.06		<b>Ast</b> 6.2 ± 2.5
		<b>Las</b> 3.8 ± 1.0

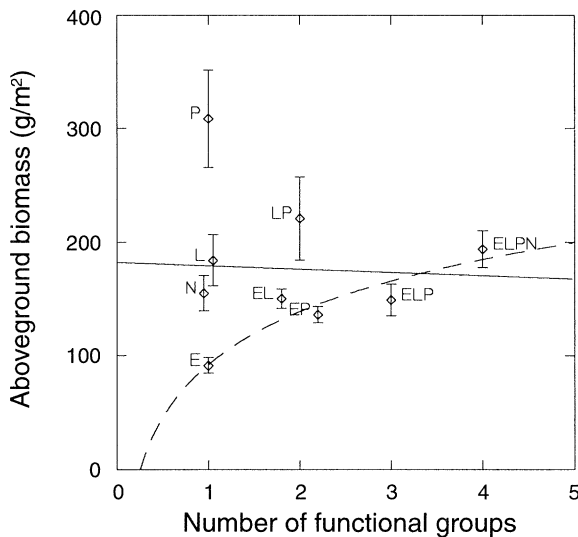


FIG. 2. Total aboveground biomass of treatments plotted as a function of the number of component functional groups (FG). Points are means ± 1 SE, n = 6, and are offset from whole numbers in the abscissa for clarity only. The solid line is a regression through all vegetated treatments (not significant); the dashed line is a nonlinear fit of only those treatments which contain early season annuals: Biomass = 92.13 + 66.72 × log(FG), R<sup>2</sup> = 0.57, P < 0.001. Linear regression for E-only treatments (not shown): ln(Biomass) = 4.408 + 0.216 × FG + BLK, R<sup>2</sup> = 0.66, P < 0.001.

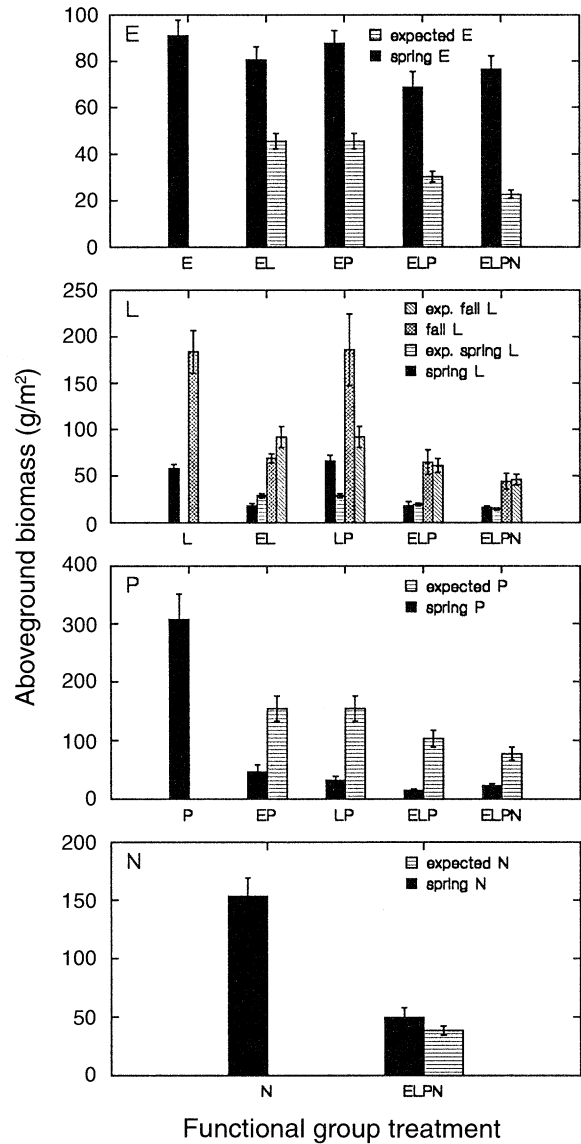


FIG. 3. Actual and expected aboveground biomass in 1993 for each group in single functional group (SFG) and mixture treatments. Expected yields in mixture treatments are SFG yields of a given functional group, divided by the total number of functional groups in the mixture treatment, to correct for planting density (see text: *Methods*). Both spring and fall values are shown for late season annuals.

*jubatum* (Figs. 3 and 4). While these groups differ strikingly in growth form and phenology, it is apparent that competition has as strong an influence on primary production of the entire community, as does complementarity.

*Relative Yield Totals: aboveground production.*—In the regression approach, the influences of competition and complementarity may be confounded with changes in planting density of the components. The design of the experiment replaces half of the planting density of a large growth form (perennial bunchgrasses) with that

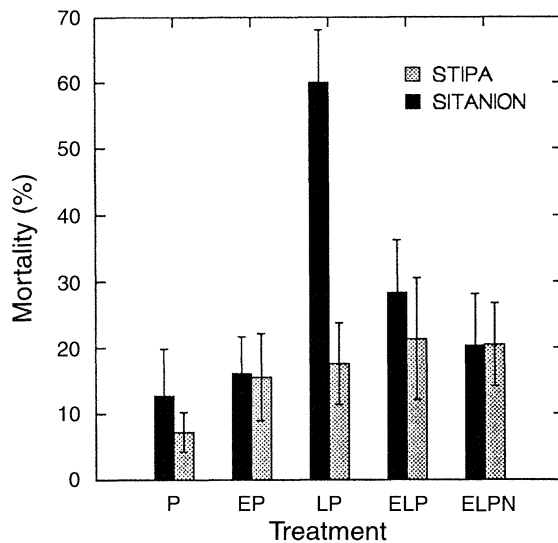


FIG. 4. Bunchgrass mortality from spring 1992 to spring 1993, calculated from the number of planted individuals alive at each sampling and accounting for harvested individuals. For *Sitanion*, mortality in the LP treatment is significantly higher than in other treatments ( $P < 0.05$ , Scheffé post-hoc comparison); no pairwise comparisons among treatments are significantly different for *Stipa*.

of a smaller growth form (early season annuals) when going from single-group to two-way treatments. If we assume as a null hypothesis that interspecific and intraspecific competition are equal, this could explain in part why total plot biomass in more diverse treatments is not greater than that of the most productive single-group treatment. Relative Yield Totals (RYT) offer an alternative to assessing the degree to which species are complementary in their resource use (Trenbath 1974, Harper 1977), i.e., to what extent interspecific competition is less than intraspecific competition (Naeem et al. 1996).

RYTs based on aboveground biomass were significantly  $>1$  for the EL, LP, and ELPN treatments, indicating complementary resource use (Table 3). Con-

sistent with other reports of high RYT in mixtures containing N fixers (Trenbath 1974, Vandermeer 1990, Swift and Anderson 1993), RYT in the ELPN four-way mixture was the highest of all treatments in this experiment. For the EL mixture, the increase in RYT from spring to fall indicates that temporal partitioning of resources may have been important in this treatment. For the LP mixture, increased variance from spring to fall resulted in nonsignificance in the latter, despite no change in RYT. In all cases,  $RYT > 1$  was due primarily to one functional group not declining much in productivity despite lower planting densities (E's or L's), while the other groups were at their predicted values (L's, N's), or were substantially reduced (P's; Table 3, Fig. 3).

*Relative Yield Totals: total production.*—Because substantial allocation goes to roots in this system, particularly for late season annuals and bunchgrasses (Gulmon et al. 1983, Armstrong 1991), I estimated RYT's for total productivity (roots + shoots) using root : shoot ratios determined from a separate experiment (Tables 4 and 5; Hooper 1996). Total biomass RYT showed a different pattern of Relative Yield Totals from values based on aboveground biomass alone, in that LP is the only treatment with a RYT significantly greater than one ( $1.50 \pm 0.14$ ; I have no root biomass data for treatments containing N fixers). Differences in aboveground and total biomass calculations of Relative Yield Totals for LP and EL presumably result from: (1) the substantial increase in root : shoot ratio in the LP treatment compared to the expectation based on SFG treatments, and (2) the decreases in EL (and ELP) r:s relative to expectations (Table 5). The fact that root : shoot ratios in mixtures are not necessarily predictable from those of their component SFG treatments in the EL, ELP, and LP cores indicates that allocation to roots of one, both, or all components shift due to differences in competitive environment. We cannot distinguish between these possibilities. However, differences in the distribution of the belowground biomass primarily affect the Relative Yields for each group, but do not

TABLE 3. Relative Yields of component functional groups in mixtures and Relative Yield Totals (RYT) for those mixtures using aboveground biomass (mean  $\pm$  1 SE,  $n = 6$ ).

Treatment	Aboveground biomass Relative Yields					Relative Yield Totals	
	E	L-Spring	L-Fall	P	N	Spring	Fall
EL	$1.82 \pm 0.16$	$0.66 \pm 0.11$	$0.85 \pm 0.17$	...	...	$1.24 \pm 0.12$	$1.34 \pm 0.14^{\dagger, \S}$
EP	$2.00 \pm 0.23$	...	...	$0.31 \pm 0.06$	...	$1.16 \pm 0.10$	...
LP	...	$2.33 \pm 0.26$	$2.31 \pm 0.59$	$0.24 \pm 0.06$	...	$1.28 \pm 0.11^{\dagger, \ddagger}$	$1.27 \pm 0.27$
ELP	$2.29 \pm 0.21$	$0.88 \pm 0.17$	$1.17 \pm 0.29$	$0.15 \pm 0.02$	...	$1.11 \pm 0.06$	$1.20 \pm 0.09$
ELPN	$3.50 \pm 0.45$	$1.13 \pm 0.13$	$0.98 \pm 0.14$	$0.30 \pm 0.02$	$1.34 \pm 0.21$	$1.57 \pm 0.16^{**}$	$1.53 \pm 0.16^{**}$

Note: Relative Yield Totals are the average of the relative yields for the component functional groups. For treatments with late season annuals, both spring and fall values were calculated.

$\ddagger$  Significant differences from 1 determined by Bonferroni-adjusted confidence limits with error variance from one-way ANOVA of RYT values against plot effects. Spring, 1 SE = 0.1043; Fall, 1 SE = 0.1329.  $\dagger P < 0.10$ ;  $* P < 0.05$ ,  $** P < 0.01$ ,  $*** P < 0.001$ .

$\S$  Overall results indicate that the EL treatment is not significantly greater than 1. However elimination of an LP outlier substantially reduces the pooled error variance making the EL treatment significantly greater than 1 at  $P < 0.05$ .

TABLE 4. Relative Yields by functional group and Relative Yield Totals (RYT) for total biomass (roots ± shoots; mean ± 1 SE, *n* = 6).

Treatment	Total biomass Relative Yields					Relative Yield Totals	
	E	L-Spring	L-Fall	P	N	Spring	Fall
EL	1.65 ± 0.15	0.59 ± 0.10	ND	...	...	1.12 ± 0.11	ND
EP	2.01 ± 0.26	...	...	0.30 ± 0.05	...	1.15 ± 0.12	...
LP	...	2.72 ± 0.33	ND	0.29 ± 0.07	...	1.50 ± 0.14**	ND
ELP	2.25 ± 0.24	0.86 ± 0.17	ND	0.15 ± 0.02	...	1.09 ± 0.07	ND
ELPN	ND	ND	ND	ND	ND	ND	ND

Note: Root biomass by functional group was calculated using average root : shoot ratios from the core tracer experiment for spring 1993, assuming that all functional group root allocations change in a similar fashion (see text, Table 5 for details). No data (ND) was available for root biomass of N fixers or for fall root biomass of late season annuals. Significant differences as in Table 3.

greatly affect the Relative Yield Totals (as demonstrated by the sensitivity analysis below). Taking the simplest assumption, that all components of the mixture shift allocation in a similar way, the significant RYT >1 for the LP treatment is again primarily due to much higher L biomass than expected, at the expense of the P's (Table 4).

Because root : shoot ratios varied substantially among replicates in all three monoculture treatments (high standard error of the mean, Table 5), I performed a simple sensitivity analysis to see how this might affect the outcome of RYT calculations (data not shown). Using the minimum, median, average, and maximum values of the three replicates of the monoculture root : shoot ratios, results for Relative Yield Totals are quite robust to the observed variation in root : shoot ratio. The EL, EP, and ELP Relative Yield Totals were significantly greater than one only when using the lowest measured root : shoot ratios from the single functional group treatments; in contrast, the LP Relative Yield Total was significantly greater than one using all but the highest monoculture root : shoot ratios.

*Nitrogen yield.*—If a single resource, such as nitrogen, limits production, and plants are complementary in their nitrogen use, then total plant nitrogen in mixture treatments should be greater than in single functional group treatments. To test for complementary nitrogen use, I calculated the difference (*D*) between mixture and single

functional group treatments for plant nitrogen yield in aboveground and total biomass (roots plus shoots; Table 6). If there are compensatory trade-offs among species in competition for nitrogen, we expect *D* ≈ 0; complementarity with respect to nitrogen would give *D* > 0. Either interference competition or unequal conversion efficiencies from another limiting resource to total nitrogen capture could give *D* < 0 (Harper 1977). In this experiment, aboveground nitrogen stocks in perennial-containing mixtures always have *D* < 0, i.e., mixtures contain less aboveground plant nitrogen than expectations based on single functional group treatments (Table 6). This difference is even greater when including estimates of root biomass and nitrogen. The slightly higher shoot percent N and significantly higher root percent N in early and late season annuals (see Appendix B) is insufficient to compensate for the overall decline in bunchgrass biomass in mixed treatments relative to expectations from the P treatment. In the EL mixture, the aboveground nitrogen yield indicates that early and late season annuals may be using nitrogen in a complementary manner (*D* > 0). However, nitrogen *D* is not significantly different from SFG averages when root nitrogen is included. As with total biomass Relative Yield Total, this lack of difference appears to result from the shift to lower root : shoot ratio in the mixed plot than expected based on the component groups planted alone.

TABLE 5. Total root and shoot biomass and root : shoot ratios from April 1993 cores (mean ± 1 SE, *n* = 3).

Parameter	Treatment						
	E	L	P	EL	EP	LP	ELP
Shoot biomass (g/m <sup>2</sup> )	117.5 ± 30.2	97.4 ± 22.0	227.6 ± 34.1	148.0 ± 21.0	200.8 ± 2.0	129.6 ± 26.0	162.3 ± 17.0
Root biomass (g/m <sup>2</sup> )	41.5 ± 3.9	43.6 ± 3.6	227.5 ± 18.4	42.1 ± 1.0	117.6 ± 24.2	120.4 ± 12.3	77.0 ± 3.2
Root : shoot ratio	0.41 ± 0.11	0.51 ± 0.13	1.06 ± 0.23	0.30 ± 0.04	0.59 ± 0.12	0.98 ± 0.13	0.48 ± 0.04
Predicted r:s ratio	NA	NA	NA	0.41 ± 0.01†,‡	0.50 ± 0.01	0.67 ± 0.05†	0.59 ± 0.04†

Note: These data were used to calculate RYT for total biomass (Table 4) and *D* for nitrogen (Table 6). Root biomass and root : shoot ratios are overall values per core (i.e., roots were not separated by species). Predicted root : shoot ratios in mixed cores were calculated from root : shoot ratios from single functional group cores times shoot biomass of component functional groups in the mixed cores. These estimates of root biomass for each functional group in the mixture were then summed and divided by total aboveground biomass to give predicted root : shoot ratios. NA = not applicable.

† Significant differences by paired *t* test between actual and predicted root : shoot ratios are indicated as in Table 3.

TABLE 6. Deviations in yield ( $D$ , in grams per square meter) for live plant nitrogen, spring 1993 (mean  $\pm$  1 SE,  $n = 6$ ).

Treatment	Aboveground nitrogen	Total nitrogen
EL	$0.34 \pm 0.12^\dagger$	$0.32 \pm 0.16$
EP	$-0.85 \pm 0.25^{**}$	$-1.44 \pm 0.40^{**}$
LP	$-0.99 \pm 0.23^{**}$	$-1.47 \pm 0.40^{**}$
ELP	$-0.75 \pm 0.18^{**}$	$-1.42 \pm 0.30^{**}$

Note:  $D < 0$  indicates less absolute nitrogen in plant biomass in mixture than the average of component single functional group treatments. Significant differences ( $D \neq 0$ ) are designated as in Table 3. For calculating nitrogen yield for each treatment, aboveground biomass was from the spring 1993 biomass harvest; r:s ratio, root percent N, and aboveground percent N were from the core tracer experiment, spring 1993, as in Table 5 and Appendix B.

#### DISCUSSION

I did not find an absolute increase in productivity with an increase in functional group richness. Instead, composition (the functional attributes of, and interactions between, certain groups) explained more about patterns of productivity than did numbers of functional groups. This was evident both in large differences in productivity among treatments with similar levels of richness, and in the restricted suite of functional group mixtures that showed evidence of complementary resource use when calculating RYTs. While this experiment focused on functional groups, the mechanisms under question should be similar when species are the experimental units. I had anticipated that because of differences in phenological (early, late, and perennial), structural (especially rooting depth), and biogeochemical (N-fixing) traits, these groups would use limiting soil resources in a complementary way. The results from this experiment demonstrate that, even when species or functional groups differ dramatically in phenology and morphological characteristics, other traits (e.g., competitive ability), can have as large an effect on whole community production as complementarity.

While all of the functional groups (and species) used in this experiment commonly co-occur in the natural serpentine grassland, the point was not to try to mimic the natural setting, but to maximize the potential for observing complementarity by using species with dramatically different characteristics. As it turned out, for any given progression of increasing functional group diversity (e.g., B  $\rightarrow$  E  $\rightarrow$  EP  $\rightarrow$  ELP  $\rightarrow$  ELPN, or B  $\rightarrow$  L  $\rightarrow$  LP  $\rightarrow$  ELP  $\rightarrow$  ELPN), the response of productivity was idiosyncratic (Lawton 1994, Naeem et al. 1995) rather than monotonically increasing. Each group had an impact on productivity, but in different directions and for different reasons: (1) early season annuals because of their competitive dominance and small stature; (2) late season annuals because of growth, water, and nitrogen use during the dry season (Gulmon et al. 1983, Chiariello 1989) and potential shifts in root allocation in mixtures; (3) perennial bunchgrasses because of generally greater biomass and

nitrogen accumulation, but a low degree of competitiveness; and (4) nitrogen fixers because of their well-known influence on N availability. Differences in the efficiency of conversion of resources to biomass, potentially due to alternative allocations to growth, reproduction, storage, and defense (Chapin et al. 1990, Armstrong 1991, Chapin et al. 1996) may also limit any additive response of productivity using these different phenological types.

The response of net primary production to changes in plant diversity, in both natural and experimental systems, is likely to be a complex function of the characteristics of the added (or deleted) species, those of the species already present, and the interactions between them (Chapin et al. 1995, Naeem et al. 1996). Other research (focusing on species rather than functional groups) has also observed that mixtures of even very different growth forms may not maximize productivity. In serpentine grassland, Gulmon et al. (1983) found that adding *Hemizonia luzulaefolia* (late season annual) to plots containing *Plantago erecta* (early season annual) does, on average, increase productivity, but that *Hemizonia* alone is more productive than the mixture. Similarly, even under potentially stressful conditions or where facilitation or complementarity is expected, complex interactions among a variety of plant functional traits often lead to net interactions among species that are not positive (Binkley 1992, Morgan et al. 1992, Chapin et al. 1994, Berkowitz et al. 1995). Naeem et al. (1995, 1996) and Tilman et al. (1996), while emphasizing a general trend of greater productivity with greater diversity in their experiments, also observed high variability of productivity within levels of diversity. Both the general trend and the variability are important, however. Productivity, when averaged across all possible combinations of species, may increase with increasing diversity, but predicting the response to gain or loss of any given species is likely to be much more difficult.

Given the large differences in biomass among single functional group treatments and the replacement series design of this experiment, Relative Yield Totals probably offer a better assessment of the degree to which these groups use resources in a complementary fashion than do absolute changes in community production (McGilchrist and Trenbath 1971, Harper 1977). Despite apparently strong competition at critical times of the year (Figs. 3 and 4), Relative Yield Totals show evidence of complementary resource use in some treatments (RYT significantly  $>1$ ; Tables 3, 4, and 6), though mixture yields never approached the substantially higher production in P-only treatments (Fig. 1, Table 2). This is not very surprising with the ELPN plots, as the most common reports of high RYT in the past have come from combinations containing N fixers (Trenbath 1974, Vandermeer 1990; T. Howard, *unpublished manuscript*). In this experiment, nitrogen fixers appear to increase overall nutrient availability (as op-

posed to being only complementary) because absolute as well as relative yields for both E's and P's are equal or higher in ELPN compared to ELP treatments, despite lower planting density in the former.

Of the various mechanisms suggested for complementarity and facilitation (e.g., different growth rhythms, different rooting depths, nutritional complementation, enhanced light use efficiency, "positive allelochemical" effects, climate amelioration, pest/pathogen resistance; Trenbath 1974, Steiner 1982, Vandermeer 1990, Lawton 1994, Lawton and Jones 1995), the response of aboveground production in EL treatments probably reflects seasonal partitioning of resources more than partitioning of nutrients within the wet season by differences in rooting depth. This is suggested by higher RYTs in fall than spring (Table 3) and it agrees with previous work showing competitive effects of *Plantago* on *Hemizonia* in the wet season, but partitioning of water in the dry season (i.e., L's can access deep water in the summer after E's have senesced; Gulmon et al. 1983). It also agrees with results from many intercropping studies that show greater gains in production from seasonal differences in nutrient demand and growth than from spatial partitioning (Steiner 1982).

The negative values for *D* in most treatments (i.e., lower absolute plant nitrogen accumulation in mixture than monoculture; Table 6) indicate that competition for other resources is probably important in this system. For bunchgrasses, competition with L's for water as the soils dry out in late spring may cause high mortality (Fig. 4; Jackson and Roy 1986, 1989, Hooper and Vitousek 1998), thereby limiting bunchgrass biomass and total plant nitrogen pools (Table 6).

In all RYTs, one functional group of a mixture apparently experienced reduced competition and produced more than expected given SFG yields and mixture planting densities, while the opposite occurred for the other(s) (Table 3). This is similar to the pattern described by Trenbath (1974) for the majority (>70%) of the RYTs he reviewed from the agricultural competition literature (excluding N fixers). However, smaller species are not often competitively dominant in mixtures, as the early season annuals are here (Fig. 3; Trenbath 1974, Connolly 1986). This dominance apparently occurs due to competition for nitrogen during the wet season (Hooper and Vitousek, *in press*). Results from this experiment concur, however, with results of Gulmon et al. (1983) and with predictions by Berendse (1979) that species of different rooting depths could coexist if the shallowly rooted species is the more competitive. Strong competition by small-statured species may explain why absolute productivity in this experiment did not increase with increasing diversity (Fig. 2).

Calculations of RYTs used here have three complications. First, spring root and percent N values may underestimate complementarity among E's and L's be-

cause L's can take up significant amounts of nitrogen and water in the dry season after E's have senesced (Woodmansee and Duncan 1980, Gulmon et al. 1983, Chiariello 1989, Hooper and Vitousek 1998). Therefore, the greater complementarity suggested by RYT based on aboveground biomass from the fall (Table 3) may be more accurate than the RYT from total biomass in the spring (Table 4). Second, high litter production in 1993 in the P treatments may feed back to reduce productivity in these plots. In the longer term, bunchgrass production may not differ as dramatically among mixture and SFG treatments as 1993 data indicate. This would lead to an underestimation of the degree of complementarity between E's and P's. Finally, standing biomass may not accurately represent total production for roots. Roots of bunchgrasses are perennial structures; therefore estimates of RYT may be inaccurate if patterns of 2nd-yr root production differ from patterns of root standing biomass (Ares and Singh 1974, Clark 1977, Abbadie et al. 1992). These results highlight the necessity for accurate estimation of root production and turnover for all the functional groups to obtain better estimates of production, Relative Yield Totals, and complementarity (Nadelhoffer et al. 1985, Hendrick and Pregitzer 1993, Pregitzer et al. 1995).

The results from this experiment, from numerous competition experiments (Berendse 1982, Pendery and Provenza 1987; T. Howard, *unpublished manuscript*), from many intercropping studies (Trenbath 1974, Steiner 1982, Vandermeer 1988, Vandermeer 1990), from forestry (Binkley 1992, Morgan et al. 1992, Field 1995), and from some experiments in which diversity is specifically manipulated (Naeem et al. 1995, 1996), lead to the conclusion that plant diversity does not necessarily result in absolute increases in net primary production in any particular system in any particular year. While relative yields may indicate complementary resource use, absolute yields most frequently fall between those of the least and most productive species in monoculture (Trenbath 1974; T. J. Howard, *unpublished manuscript*), except where a relatively limited set of facilitative functional interactions are involved (e.g., N fixing, climate amelioration; Bertness and Callaway 1994, but see also Chapin et al. 1994). Given the restricted suite of fundamental plant resources, even very different species or functional groups presumably are only partially complementary (Vandermeer 1990). These arguments would support contentions that primary production may saturate at relatively low levels of plant richness (Swift and Anderson 1993, Vitousek and Hooper 1993, Field 1995; but see also Tilman et al. 1996), at least when considering only alpha-diversity and production in a single year, which were the scales of this experiment. In addition, responses may be sensitive to the suite of species chosen for investigation, making it important that experiments include all species grown in monoculture, as well as in more diverse assemblages, in order to differentiate between

effects resulting from complementarity and those resulting from differences in composition.

At the same time, further effects of diversity on production may come on longer time scales in response to environmental fluctuation and disturbance (McNaughton 1977, McNaughton 1985, Tilman and Downing 1994, Field 1995, Tilman 1996) or in other processes such as maintenance of soil fertility (Steiner 1982, Swift and Anderson 1993). Many intercropping researchers make the point that traditional farming systems, including some highly complex tropical systems, do not necessarily maximize productivity under favorable conditions. Instead, production advantages of mixed-species systems include reasonable yields over long-term climate variation and in response to pest/pathogen infestations; production of usable food supplies over the course of the year; provision of a variety of necessary staples; and in some cases, better yield per amount of labor invested (Steiner 1982, Altieri 1990). Are there ecological correlates of such factors in natural systems? Might increasing plant diversity have a greater effect on secondary production than on primary production due to provision of a diversity of resources at critical times of the year (Gade and Provenza 1986, Loiselle and Blake 1991, Vinton et al. 1993) or by allowing a keystone species to persist through stress bottlenecks? The results of this experiment suggest that as ecologists pay increasing attention to how biological diversity affects ecosystem function, we should: (1) look at broader levels of diversity, longer time scales, and species that differ substantially in functional characteristics; (2) control for composition effects; and (3) not restrict our views to maximization functions, as these may be neither the most predominant nor the most important ecosystem roles of plant diversity.

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**APPENDIX A**

(A) First principal components and (B) regression equations for determining live and dead perennial bunchgrass biomass. *B*, live aboveground biomass (stems, leaves and seeds, in grams); *C*, basal circumference (cm); *D*, standing dead biomass (g); *F*, number of flowering culms; *H*, vegetative height (cm); *z1*, first principal component of listed variables; “% of var.” refers to the amount of variance accounted for by the first principal component.

A) Principal components		
Species	First component	% of var.
<i>Sitanion</i>	$z1 = 0.8667C + 0.8648 F + 0.8162H$	72
<i>Stipa</i>	$z1 = 0.9631C + 0.9461 F + 0.9091H$	
B) Biomass regressions		
Dependent variable and species	Regression	R <sup>2</sup>
Live biomass		
<i>Sitanion</i>	$\ln(B + 1) = -3.0493 + 1.3327(z1)$	0.91
<i>Stipa</i>	$\ln(B + 1) = -0.1891 + 0.0462(z1)$	0.96
Standing dead biomass		
<i>Sitanion</i>	$\ln(D + 1) = -0.0444 + 0.703(\ln B)$	0.88
<i>Stipa</i>	$\ln(D + 1) = 0.1639 + 0.1262B$	0.94

**APPENDIX B**

Percent nitrogen (mean with 1 SE reported in parentheses; *n* = 3) of aboveground live tissue (leaves, stems, flowers and seeds combined) for individual species and of roots for pooled species from April 1993 cores. This data was used to calculate *D* (deviations in yield) for nitrogen (Table 6). “Average % N” is the percent nitrogen for a given species averaged across all treatments. ND = no data.

Functional group	Species	E	L	P	EL	EP	LP	ELP	Average % N
E	<i>Las</i>	1.25 (0.10)			1.24 (0.07)	1.16 (0.04)		1.00 (0.12)	1.16 (0.04)
	<i>Mic</i>	1.70 (0.20)			1.27 (0.31)	1.30 (0.14)		1.08 (0.21)	1.37 (0.11)
	<i>Pla</i>	1.19 (0.11)			1.20 (0.10)	1.11 (0.11)		0.98 (0.09)	1.13 (0.05)
L	<i>Hem</i>		0.96 (0.02)		1.26 (0.16)		1.09 (0.08)	1.07 (0.16)	1.17 (0.07)
	<i>Les</i>		1.07 (0.01)		1.37 (0.21)		1.23 (0.12)	1.18 (0.08)	1.21 (0.06)
P	<i>Sit</i>			1.16 (0.15)		ND	0.97	ND	1.12 (0.12)
				1.21 (0.20)		1.27 (0.07)	1.03 (0.14)	1.09 (0.10)	1.22 (0.09)
Other	weeds								0.94 (0.06)
	roots	1.36 (0.12)	1.15 (0.03)	0.75 (0.09)	1.37 (0.06)	1.11 (0.02)	0.91 (0.07)	0.85 (0.03)	