

PLANT TRAITS THAT INFLUENCE ECOSYSTEM PROCESSES VARY INDEPENDENTLY AMONG SPECIES

VALERIE T. EVINER¹

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Most predictions of plant species effects on ecosystems are based on single traits (e.g., litter chemistry) or suites of related traits (functional groups). However, recent studies demonstrate that predictions of species effects on ecosystems are improved by considering multiple traits. In order to develop this multiple trait approach, it is critical to understand how these multiple traits vary in relation to one another among species. The ecosystem effects of traits that strongly covary can likely be summarized by one of these traits. In contrast, it will be necessary to determine the ecosystem effects of specific trait combinations for those traits that vary independently across species.

In the field, I established monocultures of eight herbaceous species common in California annual grasslands. Plant species significantly differed in their litter quantity and quality, live biomass, and effects on soil labile C, soil temperature, and soil moisture. Species effects on soil moisture and temperature were only significant at the times of the growing season when each of these limited plant and microbial activity. Some of these traits correlated with one another, such as litter biomass and species effects on soil temperature during the winter. However, for the most part, plant species exhibited unique combinations of these traits. For example, species with similar litter chemistry had the largest differences in plant biomass, soil moisture, and soil labile C. Species rankings for many traits changed over the growing season (e.g., biomass), so that the relationship among traits varied seasonally. The independent variation of these traits suggests that predictions of plant species effects on ecosystems will likely be enhanced by an understanding of how the ecosystem effects of plant traits may vary depending on the combination of traits.

Key words: *ecosystem processes; functional groups; functional matrix; litter chemistry; nitrogen cycling; plant traits; species effects.*

INTRODUCTION

Plant species differ in their effects on many biogeochemical processes, including N cycling (Wedin and Tilman 1990, Hobbie 1992), C cycling (Vinton and Burke 1995, Chen and Stark 2000), and decomposition (Melillo et al. 1982, Hobbie 1996, Franck et al. 1997). Understanding these species effects is particularly important because shifts in vegetation composition are widespread due to invasions (Mooney and Hobbs 2000), land management (Schoor and Matson 2000, Eviner and Chapin 2001), and environmental factors (Talbot et al. 1939, Chapin et al. 1995, Hogg et al. 1995, Leadley and Korner 1996). The direct effects of these environmental changes on ecosystem processes can be small compared to the indirect effects mediated by changes in vegetation composition (Kirkby 1995, Hobbie 1996, Verville et al. 1998, Shaw and Harte 2001).

The ecosystem effects of plant species are usually predicted by focusing on one mechanism that is as-

sumed to dominate a plant's effect on a given ecosystem process. The functional group approach is based on the concept that there are suites of related plant traits that can be used to generalize how species affect specific ecosystem processes. For example, species with high litter quality also have high relative growth rates and fast tissue turnover, and all of these traits result in high rates of N cycling (Chapin 1993). This approach assumes that multiple traits covary and reinforce the ecosystem effects of one another, and thus a single trait such as litter chemistry can be used to account for plant effects on ecosystems. Thus, the functional group approach is closely related to the single-trait approach, where traits such as litter lignin/N or C/N ratios are used to predict rates of net N mineralization (Scott and Binkley 1997) and decomposition (Melillo et al. 1982, Taylor et al. 1989, Stump and Binkley 1993). Both the functional-group and single-trait approaches provide large-scale generalizations of the effects of plant species on ecosystem processes because, at a regional scale, environmental conditions select for certain suites of plant traits (Chapin 1993, Diaz and Cabido 1997). However, traits that strongly covary over environmental gradients can vary independently at local scales (Lavorel and Garnier 2002). Within a habitat, differences in traits within a species or among species can be as great as trait differences across the full range of

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¹ Present address: Institute of Ecosystem Studies, P.O. Box AB, Millbrook, New York 12545 USA.
E-mail: evinerv@ecostudies.org



PLATE 1. In a California annual grassland, 1-m² monoculture plots were established to test differences in plant traits across eight different species. Photo credit: V. Eviner.

an environmental gradient (Wright and Westoby 1999, Fonseca et al. 2000).

Thus, it is not surprising that an increasing number of studies have demonstrated that plant species effects on ecosystem processes can be better explained by considering multiple traits rather than litter chemistry alone (Shock et al. 1983, Cheng and Coleman 1991, Verville et al. 1998, Bottner et al. 1999, Eviner and Chapin 2003, Mack and D'Antonio 2003). While plant-litter chemistry is clearly a very important mechanism by which plant species affect ecosystems, plants may also alter ecosystems through other mechanisms such as litter biomass (Aerts et al. 1992, Hobbie 1992), labile C inputs (Newman 1985, Wedin and Pastor 1993, Marschner 1995), root turnover (Aerts et al. 1992, Hobbie 1995), and effects on soil microclimate (Horton 1977, Midmore et al. 1986, Hogg and Leiffers 1991, Van Vuuren et al. 1992, Das et al. 1995, Mack and D'Antonio 2003). Many of these other plant traits are more dynamic than litter chemistry, so the impacts and relative importance of these mechanisms can change over the growing season and with plant age (Eviner and Chapin 2003). For example, species differ in how their exudation patterns vary in response to environmental changes (Biondini et al. 1988), and labile C inputs are likely to shift substantially over the growing season because exudation rates are very sensitive to nutrients, microenvironment, age, and light (Rovira 1959, Smith 1970, Van Veen et al. 1989, Frederick and Klein 1994, Marschner 1995).

A developing mechanistic framework, the functional matrix, predicts the ecosystem effects of multiple traits by accounting for how the relationship between an ecosystem process and a trait may change due to variations in another trait (Eviner and Chapin 2003). For example, there may be a shift in the relationship between decomposition and litter chemistry depending on the availability of labile C and inorganic N (reviewed in Kuzayakov et al. 2000; Eviner, *unpublished manuscript*). A first step toward developing this functional

matrix approach is to determine which plant traits vary independently of one another among species, so that we can focus studies on the ecosystem effects of these trait combinations.

This paper investigates some of the multiple dominant mechanisms by which plant species influence biogeochemical cycling: litter chemistry, biomass, labile C inputs (e.g., from exudation and root turnover), and effects on soil temperature and moisture. I document how these differ among species, and how they are distributed in relation to one another among eight annual plant species.

METHODS

Field site

This research took place in a California annual grassland site at the University of California's Hopland Research and Extension Center in the northern coastal mountains of Mendocino County (160 km north of San Francisco, 39°00' N, 123°04' W; see Plate 1). This area of California experiences a Mediterranean climate, with hot, dry summers and cool, wet winters. Mean annual precipitation is 960 mm, which occurs October through May, with 75% of that falling between November and February. Temperatures also vary seasonally, with a mean temperature of 7.5°C from December through February, while summer temperatures (July through September) average 21°C, with a mean daily maximum temperature of 33°C. The growing season begins in the fall with the first germinating rains and

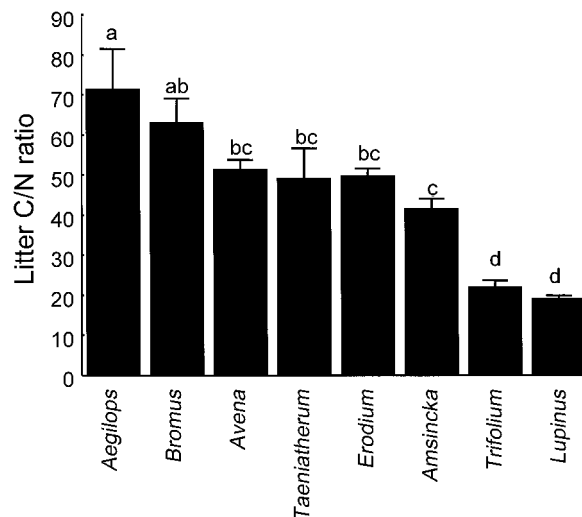


FIG. 1. Litter chemistry of plant species. The litter C/N ratio differs significantly among plant species (ANOVA, $F_{7,63} = 27$, $P < 0.0001$, $n = 8$ replicates per treatment). Different letters above bars indicate significant differences among species (determined by a Tukey-Kramer post hoc test [$P < 0.05$]). Values are means + 1 SE. Species are ordered from high initial litter C/N ratio to low litter C/N ratio. Full species names are *Avena barbata*, *Bromus hordeaceus*, *Aegilops triuncialis*, *Taeniatherum caput-medusae*, *Bromus diandrus*, *Erodium botrys*, *Lupinus bicolor*, and *Trifolium subterraneum*.

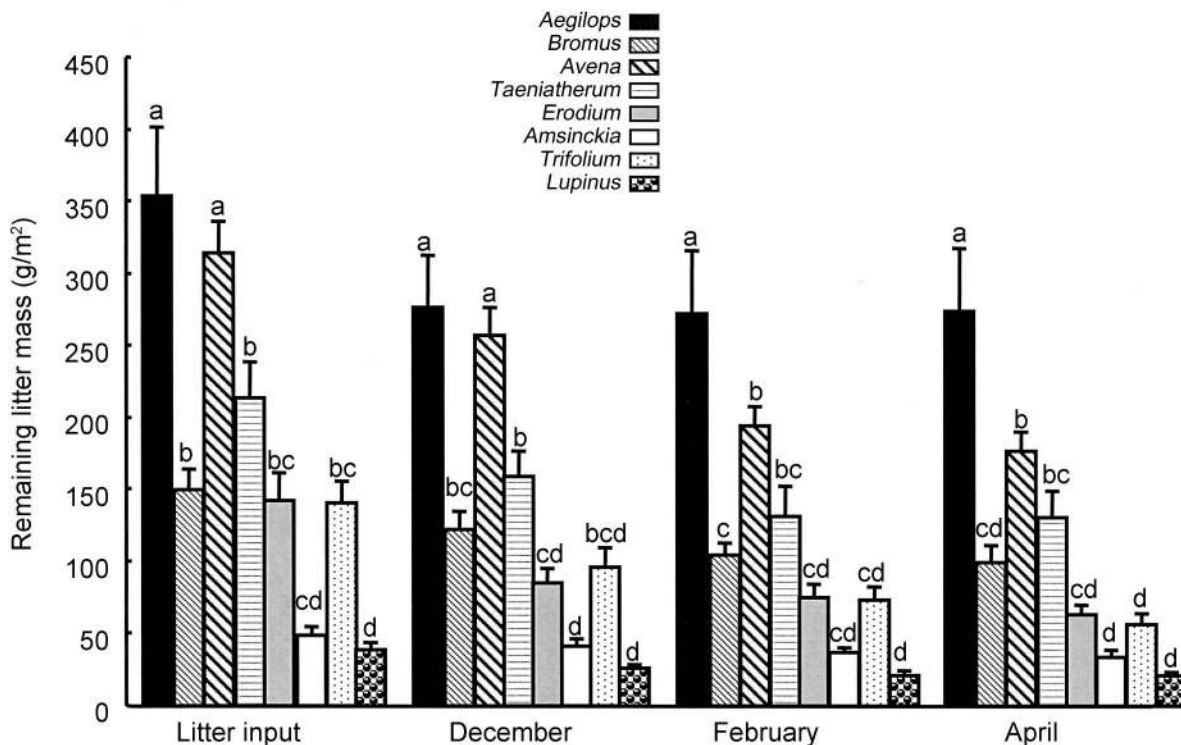


FIG. 2. Species effects on aboveground litter biomass. Plant species differ significantly in their litter inputs (ANOVA, $F_{7,63} = 23$, $P < 0.0001$) and the amount of litter remaining throughout the growing season (MANOVA, species $F_{7,63} = 22.5$, $P < 0.0001$). Different letters above bars indicate significant differences among species at each time (determined by a Tukey-Kramer post hoc test [$P < 0.05$]). Litter mass remaining was computed by multiplying initial litter biomass by the percentage of litter mass remaining from a decomposition experiment. Values are means + 1 SE ($n = 8$ replicates per treatment). Species are ordered from high initial litter C/N ratio to low litter C/N ratio; full species names are as in Fig. 1.

continues until late spring, when the rains cease and most plants senesce. The plots were established at an elevation of 395 m on a west-facing slope of approximately 13° , on a Sutherland soil (a medium-texture loam derived from hard sandstone and shale, classified as an ultic haploxeralf; Gowans 1958). This site is dominated by annual vegetation, including *Avena barbata*, *Bromus hordeaceus*, *Aegilops triuncialis*, *Taeniatherum caput-medusae*, *Bromus diandrus*, *Erodium botrys*, *Lupinus bicolor*, and *Trifolium subterraneum*.

Experimental design

In the summer of 1997, 1-m² monoculture plots were established of eight annual species common in northern California grasslands. These include four species of grasses (barbed goatgrass [*Aegilops triuncialis* L.], wild oats [*Avena barbata* Link.], soft chess [*Bromus hordeaceus* L.], and medusahead [*Taeniatherum caput-medusae* L.]), two forbs (filaree [*Erodium botrys* (Cav.) Bertol.] and fiddleneck [*Amsinckia douglasiana* A. D.C.]), and two legumes (dove lupine [*Lupinus bicolor* Lindey] and maiden clover [*Trifolium microcephalum* Pursch]). Nomenclature follows Hickman (1993). *Amsinckia*, *Trifolium*, and *Lupinus* are native California species, while the other species are exotics that are now

dominant components of these grasslands. Eight replicate plots of each species, as well as eight replicates of an unvegetated treatment, were planted in a randomized block design with a 0.5-m buffer between plots. Plots were blocked along slope position.

These plots were established by minimizing the seed bank on a 30 × 60 m area. The area was mowed, and litter was removed and autoclaved at 200°C for 4 h in order to kill any seeds in the litter layer. This autoclaved litter was bulked, and an equal portion of litter was placed on each plot after seeds were planted. Germination of the soil seed bank was stimulated prior to autumn rains by irrigating with 6.35 cm of water. The resident seed bank was allowed to germinate, as it would in a typical fall germinating rain, and then was killed with glyphosate (Roundup Original Herbicide; Monsanto Company, St. Louis, Missouri, USA). This was repeated once more to ensure minimal quantities of unwanted seeds. Seeds of *Avena*, *Bromus*, *Aegilops*, *Taeniatherum*, and *Erodium* were collected from the field site, while seeds were purchased from California sources for *Trifolium*, *Lupinus* (S&S Seeds, Carpinteria, California, USA) and *Amsinckia* (Valley Seed Service, Fresno, California, USA). Average seed addition rates mirrored typical plant density in the early spring

TABLE 1. Litter chemistry of plant species.

Species†	Litter N (%)	Litter C (%)
<i>Aegilops</i>	0.67 ^a ± 0.09	44.16 ^a ± 0.24
<i>Bromus</i>	0.76 ^{ab} ± 0.08	44.12 ^a ± 0.27
<i>Avena</i>	0.86 ^{ab} ± 0.05	43.38 ^{ab} ± 0.16
<i>Taeniatherum</i>	0.98 ^b ± 0.12	43.91 ^a ± 0.55
<i>Erodium</i>	0.80 ^{ab} ± 0.04	41.03 ^c ± 0.29
<i>Amsinckia</i>	1.01 ^b ± 0.06	40.84 ^d ± 0.34
<i>Trifolium</i>	2.04 ^c ± 0.13	43.38 ^{ab} ± 0.19
<i>Lupinus</i>	2.24 ^c ± 0.12	42.31 ^{bc} ± 0.52

Notes: Plant species differ in litter percentage N (ANOVA, $P < 0.0001$, $F_{7,63} = 71.5$) and percentage C (ANOVA, $P = 0.0007$, $F_{7,63} = 19.5$). Data are presented as means ± 1 SE ($n = 8$). Different letters in columns indicate significant differences among species (Tukey-Kramer post hoc test).

† See *Methods: Experimental design* for full scientific and common names.

(Heady 1958), with an adjustment for each species based on the seed weight necessary to achieve approximately equal biomass per unit area across species, based on greenhouse trials (V. T. Eviner, *unpublished data*). Seeds were raked into the soil, covered with autoclaved litter, and allowed to germinate naturally with the fall germinating rains. Species composition was maintained by weeding of unwanted species throughout the duration of the experiment.

A separate set of monoculture plots (“no-litter plots”) had no vegetation cover for the first year of the

experiment, and was planted in the second year (fall 1998). This allowed a comparison of the immediate effects of plant species on labile C pools and soil microclimate without litter, with the longer-term effects determined by growing plant inputs, litter inputs, and species-induced shifts in soil attributes (e.g., soil aggregation, microbial community composition). There were eight replicate plots of each species/litter treatment. No-litter plots were established for all eight species, although some measurements (e.g., soil moisture, soil respiration) were only performed on a subset of these plots (*Avena*, *Taeniatherum*, and *Trifolium*), and only at one time point, due to time limitations.

Sample collection/harvests

Most sampling was focused on the plots established in the fall of 1997 (“with litter” plots). Soil and plant samples were collected from these plots three times during the second growing season (1998–1999). The first collection of the 1998–1999 growing season occurred in the late autumn (December 1998), three weeks after the first germinating rains. The second collection was late winter (February 1999), just before plants began their aboveground growth spurt. The last sample collection occurred in the late spring (April 1999), when the soil was drier and plants were at peak biomass and beginning to set seed.

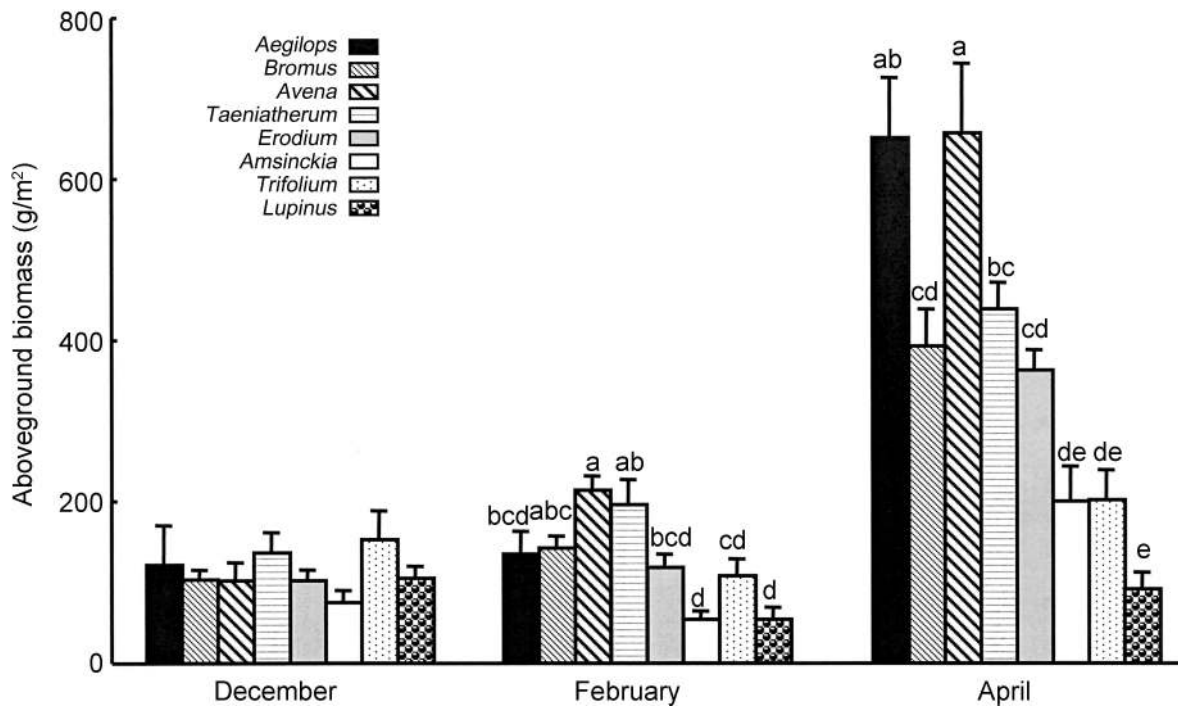


FIG. 3. Aboveground biomass of plant species. Plant species did not differ significantly in aboveground biomass in December (ANOVA, $F_{7,63} = 1$, $P = 0.44$) but did in February (ANOVA, $F_{7,63} = 8$, $P < 0.0001$) and April 1999 (ANOVA, $F_{7,63} = 14$, $P < 0.0001$). Different letters above bars indicate significant differences among species for each time (determined by a Tukey-Kramer post hoc test [$P < 0.05$]). Values are means + 1 SE ($n = 8$ replicates per treatment). Species are ordered from high initial litter C/N ratio to low litter C/N ratio; full species names are as in Fig. 1.

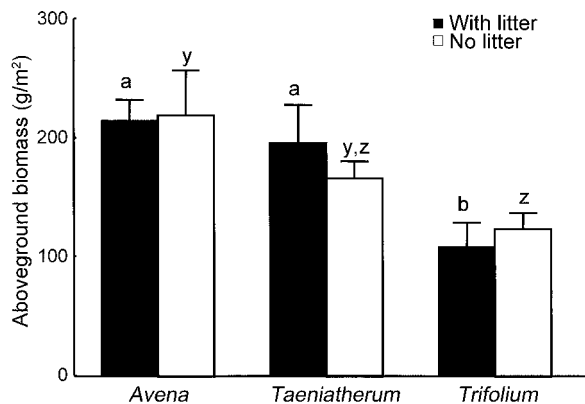


FIG. 4. Aboveground biomass in February of plant species in plots with (solid bars) and without (open bars) litter inputs from the previous growing season. Species differed significantly in biomass, but the presence of litter does not affect live biomass (MANOVA; species $F_{2,23} = 8$, $P = 0.006$; litter $F_{1,22} = 0.005$, $P = 0.9$; species \times litter $F_{2,44} = 0.5$, $P = 0.64$). Significant differences among species for with-litter treatments are indicated by letters a and b above bars, while differences in no-litter treatments are indicated by letters y and z (determined by a Tukey-Kramer post hoc test [$P < 0.05$]). Values are means ± 1 SE ($n = 8$ replicates per treatment). Species are ordered from high initial litter C/N ratio to low litter C/N ratio; full species names are as in Fig. 1.

Plots were divided into 100 10×10 cm quadrats, and for each of these harvests, two random quadrats were selected for sampling, avoiding the quadrats on the plot perimeter, and any that had been previously sampled, covered by litterbags, or disturbed by gophers. In each of these two quadrats, for each harvest, aboveground biomass was clipped from a 10 cm diameter ring. The harvest from one ring was used to determine aboveground biomass, and that from the second was sorted to ensure that the vegetation was a pure monoculture. Aboveground biomass was clipped, dried at 60°C for 48 h and weighed. Soil was harvested from the area beneath each vegetation ring, with a 3.7 cm diameter by 15 cm deep soil core. These two cores for each plot were bulked, mixed, and put on ice. Eight replicate plots were sampled for plant and soil analyses for each treatment, except for the no-litter plots. Time limitations restricted the sampling of the no-litter plots to 3 species; *Trifolium*, *Taeniatherum*, and *Avena* (eight replicates per treatment), and only in February.

Litter quantity and quality

In July 1998, after all species had senesced, a 10 cm \times 1 m strip of aboveground litter was harvested 10 cm from the left-hand edge of each "with litter" plot, dried at 50°C for 48 h, then weighed. Subsamples were placed in four litter bags and returned to the same plot from which the litter was harvested. Mass loss from these litter bags was used to estimate the quantity of litter remaining at the times that litter bags were harvested (December, February, and April). Another subsample of litter was ground in a Wiley mill, milled to a powder

with a rolling mill, and analyzed for C and N on a Carlo Erba CHN auto analyzer. (Carlo Erba Instruments, Milan, Italy).

Soil measurements

All soil measurements were collected three times (fall, winter, and spring), as described above.

Soil moisture.—Soil moisture content was determined gravimetrically by weighing 20–30 g (wet mass) of soil before and after being dried for 24 h in a 105°C oven.

Soil respiration.—Short-term soil respiration measurements were collected as a proxy measure of plant labile C inputs, the C pool that is easily accessible for microbial activity. Roots and rocks were picked out of a soil sample with forceps. Fifty grams (wet weight) of soil was placed into a specimen cup with 12 1.6 mm diameter holes drilled into the bottom. This cup was set inside another with 1.5 cm of space between the bottoms of the two cups, so that excess moisture freely drained from the soil. These cups were placed inside a 1-L mason jar, with an airtight lid that contained a rubber septum for gas sampling. Immediately after sealing the jar, concentrations of CO_2 in the headspace were measured (time 0). A 10-cc (10-cm^3) syringe was used to mix air in the jar by withdrawing and reinjecting air from the jar three times. Gas samples were analyzed for CO_2 on a Shimadzu gas chromatograph, using a thermal conductivity detector (Shimadzu Scientific Instruments, Columbia, Maryland, USA). Soils were incubated in the laboratory at 22°C at their field moisture levels. Accumulated CO_2 was measured at approximately 1, 2, 4, 7, 10, 14, and 30 days, although some of these time steps were missing at some seasons due to time constraints. All seasonal analyses had 4- and 10-day measurements, and these data are presented. After each sampling, jars were opened and allowed to equilibrate to atmospheric CO_2 concentrations for 0.5 h, and time 0 measures were taken once the jars were resealed (Zibilske 1994). CO_2 concentrations were corrected for initial (atmospheric) jar CO_2 concentrations, blanks (jars with cups, no soil), soil moisture, and volume of air (headspace).

In April, soil respiration rates were very low, probably due to low soil moisture content. After incubating these soil samples for 14 days, soil moisture was adjusted to levels common during the wetter times of the year (20% moisture), to determine if these low respiration rates were due to water limitation of microbial activity or lack of labile carbon in the soil.

Soil temperature.—Soil temperature was measured with a Barnant hand-held thermometer using a K-type thermocouple (Barnant Company, Barrington, Illinois, USA) placed at a depth of 5.3 cm, which is in the middle of the most active zone for plant and microbial activity. Daily minimum temperatures were measured before sunrise, and daily maximum temperatures were measured in the midafternoon at the end of the hottest

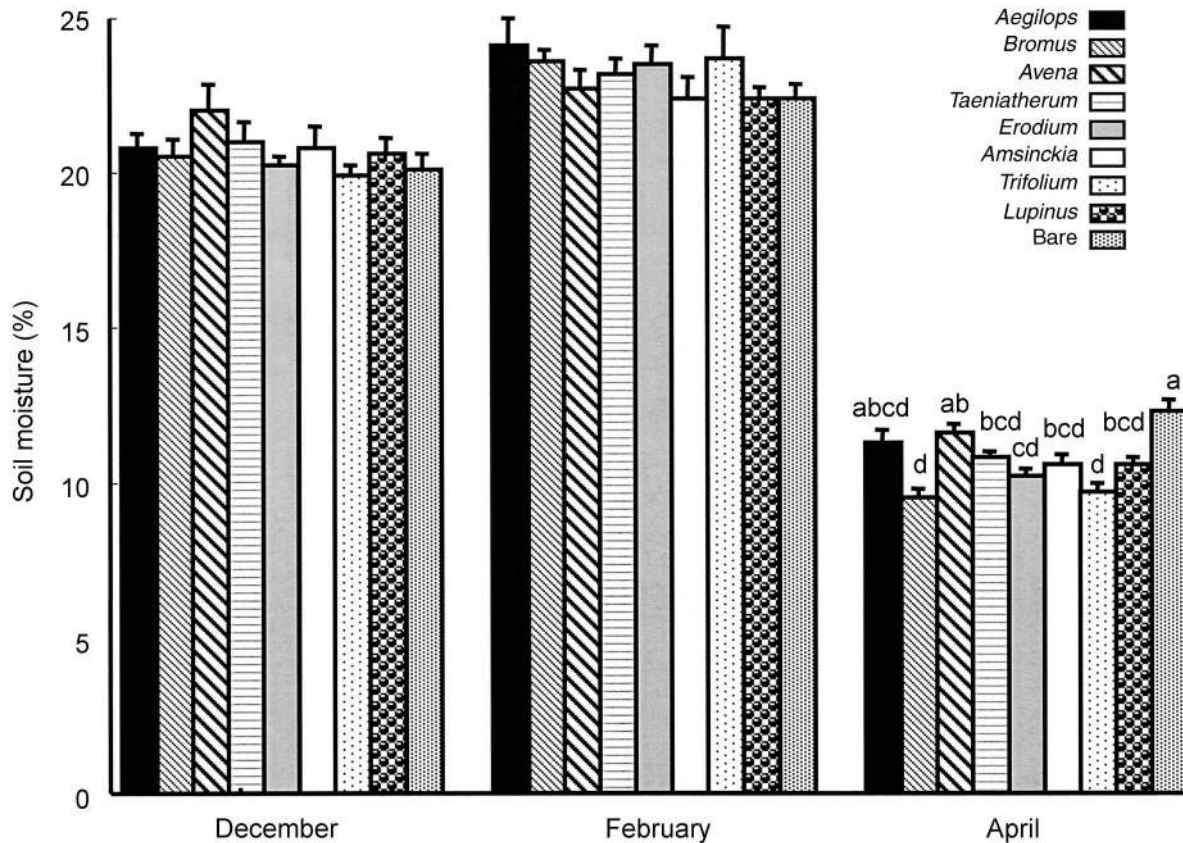


FIG. 5. Seasonal patterns of plant species effects on soil moisture. Soil moisture differs with season (MANOVA; season $F_{1,63} = 8019$, $P < 0.0001$; species $F_{8,63} = 1.1$, $P = 0.35$; species \times season $F_{8,124} = 1.4$, $P = 0.17$). Species did not influence soil moisture in December (ANOVA, $F_{8,71} = 1.1$, $P = 0.36$) or February (ANOVA, $F_{8,71} = 1.3$, $P = 0.28$), but there were significant species differences in April 1999 (ANOVA, $F_{8,71} = 7.6$, $P < 0.0001$), as the system began to dry out. Significant differences among species for April are designated by different letters above bars (determined by a Tukey-Kramer post hoc test [$P < 0.05$]). Data are means + 1 SE ($n = 8$ replicates per treatment). Species are ordered from high initial litter C/N ratio to low litter C/N ratio; full species names are as in Fig. 1.

part of the day. In December and March (one week prior to the April harvest), only four replicate plots could be sampled for soil temperature on a given sample date before diurnal changes in soil temperature began to mask species effects. Only one plot of each treatment was measured in February.

Statistical analyses

All statistics were performed using JMP software (SAS Institute, Cary, North Carolina, USA). ANOVA, followed by a Tukey-Kramer post-hoc test was used to compare plant species traits at each time point. This was an appropriate analysis in this data set because variances were usually equal, and ANOVA is robust even with slight departure from this assumption when the experimental design is balanced (Zar 1996). To determine the effects of with-litter vs. no-litter plots for each species, sequential Bonferroni t tests were performed in order to adjust for the multiple comparisons (Rice 1989). The effects of season and interactions of species with season were determined by multivariate

analysis of variance (MANOVA), using plant species as the independent variable, and seasonal measurements of plant traits as the dependent variables. Unvegetated treatments were considered as a "species" treatment in these analyses.

In order to determine the relationship between plant traits and soil respiration or microclimate effects, stepwise multiple regression was used, making sure that the residuals were normally distributed. Unvegetated plots were excluded from these regressions because in these plots, there were no trait values to relate to these variables.

RESULTS

Plant species differences in traits that influence ecosystem processes

Litter chemistry.—Plant species differed in their litter C/N ratios (Fig. 1; ANOVA, species $F_{7,63} = 27$, $P < 0.0001$). The two legume species had the lowest C/N ratio, but litter chemistry did not differ consistently between grasses and forbs. The grasses *Avena*

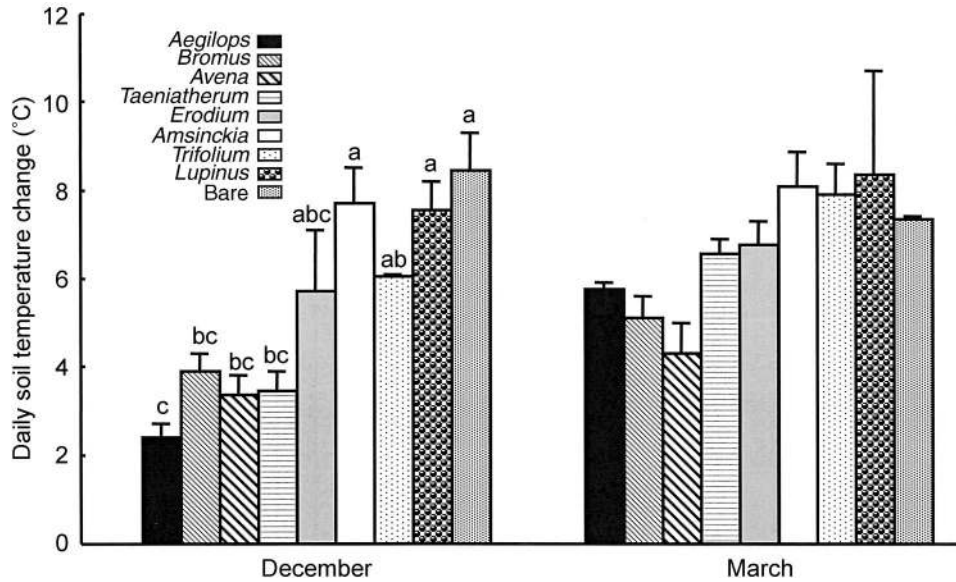


FIG. 6. Seasonal patterns of plant species effects on daily soil temperature fluctuations. The relative effects of plant species change seasonally, and seasons also have a large effect on soil temperatures independent of plant species (MANOVA; species $F_{8,28} = 44$, $P < 0.0001$; season $F_{2,28} = 119$, $P < 0.0001$; species \times season $F_{8,28} = 12$, $P < 0.0001$). Species were significantly different in December (ANOVA, $F_{8,35} = 10$, $P = 0.0012$), and there was a nonsignificant trend of species differences in March (ANOVA, $F_{8,31} = 2.2$, $P = 0.11$). Significant differences among species for December are indicated by different letters above bars (determined by a Tukey-Kramer post hoc test [$P < 0.05$]). Values are means \pm 1 SE ($n = 4$ replicates per treatment). Species are ordered from high initial litter C/N ratio to low litter C/N ratio; full species names are as in Fig. 1.

and *Taeniatherum*, had a C/N ratio similar to forbs, but significantly differed from *Aegilops*, another grass species. These patterns of litter C/N were primarily determined by species differences in litter N concentration (ANOVA, $F_{7,63} = 71.5$, $P < 0.0001$) although C concentration also differed among species (ANOVA, $F_{7,63} = 19.5$, $P = 0.0007$) (Table 1).

Biomass.—Plant species differed dramatically in their quantity of aboveground litter input (Fig. 2; ANOVA, $F_{7,63} = 23$, $P < 0.0001$). The grasses *Aegilops* and *Avena* had the largest litter inputs, about eightfold greater than those produced by the forb *Amsinckia* and the legume *Lupinus*. Early in the growing season (December), the species differences in litter mass were similar to litter inputs. The pattern of species differences in remaining litter mass changed over the growing season because there was greater mass loss in some species (e.g., the forb *Erodium* and the legume *Trifolium*) than in others (e.g., the grasses *Aegilops* and *Taeniatherum*) (Fig. 2; MANOVA, species $F_{7,63} = 22.5$, $P < 0.0001$; season $F_{2,62} = 71.3$, $P < 0.0001$; species \times season $F_{14,124} = 5$, $P < 0.0001$).

Live aboveground biomass differed significantly among species, and the relative ranking among species changed as the growing season progressed (Fig. 3; MANOVA, species $F_{7,63} = 18$, $P < 0.0001$; season $F_{2,62} = 96$, $P < 0.0001$; species \times season $F_{14,124} = 5$, $P < 0.0001$). Aboveground biomass of most species only slightly increased between December and February,

then increased rapidly between February and April. The biomass of each species did not differ between the with-litter and no-litter treatments (Fig. 4; MANOVA, species $F_{2,23} = 8$, $P = 0.0006$; litter $F_{1,22} = 0.005$, $P = 0.90$; species \times litter $F_{2,44} = 0.5$, $P = 0.64$), suggesting that these differences in biomass were characteristic of these species, rather than a consequence of species effects on resource availability.

Soil moisture.—Plant species did not influence soil moisture during the rainy part of the growing season (December and February) because abundant precipitation kept soils saturated. Species effects on soil moisture were significant only in April, when the soil began to dry (Fig. 5; ANOVA, $F_{8,71} = 7.6$, $P < 0.0001$). Unvegetated soils contained relatively high soil moisture in April. Higher soil moisture was also associated with the two species with the most aboveground biomass, *Avena* and *Aegilops*. Soil moisture levels in April were positively but weakly related to the percent litter remaining (stepwise regression, $r^2 = 0.23$, $P = 0.0001$, $n = 64$).

The importance of litter feedbacks on soil moisture could not be verified in the with-litter vs. no-litter comparison, because soil moisture in these plots was only measured in February 1999 under saturated soil moisture conditions (MANOVA; species $F_{2,23} = 0.35$, $P = 0.70$; litter $F_{1,22} = 0.5$, $P = 0.47$; species \times litter $F_{2,44} = 1$, $P = 0.34$, data not shown).

TABLE 2. Effects of plant species on soil temperatures.

Species	December temperature (°C)			
	Morning		Afternoon	
	With litter	Without litter	With litter	Without litter
<i>Aegilops</i>	6.0 ± 0.6	4.5 ± 0.7	8.2 ^{a†} ± 0.2	9.5 ± 0.4
<i>Bromus</i>	4.8 ± 0.5	3.5 ± 0.1	8.7 ^{a*} ± 0.1	10.8 ± 0.4
<i>Avena</i>	4.8 ± 0.9	4.6 ± 0.3	8.4 ^a ± 0.3	9.1 ± 0.7
<i>Taeniatherum</i>	5.1 ± 0.6	4.9 ± 0.8	8.6 ^a ± 0.2	9.8 ± 0.6
<i>Erodium</i>	3.6 ± 1.0	2.9 ± 0.4	9.1 ^{b*} ± 0.2	11.0 ± 0.7
<i>Amsinckia</i>	3.1 ± 0.1	3.4 ± 0.3	10.8 ^{cd} ± 0.5	10.8 ± 0.8
<i>Trifolium</i>	4.1 [†] ± 0.01	3.1 ± 0.3	10.0 ^{bc} ± 0.1	10.5 ± 0.2
<i>Lupinus</i>	3.0 ± 1.1	3.0 ± 0.3	10.3 ^{cd} ± 0.3	10.7 ± 0.6
Bare	NA	3.2 ± 0.6	11.3 ^d ± 0.3	11.3 ± 0.3
Air	2.8 ± 0.2	NA	14.8 ± 0.3	NA

Notes: Significant differences between with-litter and no-litter treatments for each species are indicated by: * $P \leq 0.05$; † $P < 0.10$ (determined by sequential Bonferroni t tests). Different letters indicate significant differences among species within the column. Data are presented as means ± 1 SE ($n = 4$).

Soil temperature.—Plant species had large effects on soil temperature regimes (Fig. 6, Table 2). Soil temperatures varied significantly across species and seasons, and the relative effect of species differed over time (MANOVA, effect on daily temperature change: species $F_{8,28} = 44$, $P < 0.0001$; season $F_{2,28} = 119$, $P < 0.0001$; species × season $F_{8,28} = 12$, $P < 0.0001$. MANOVA, effect on afternoon temperatures: species $F_{8,28} = 40$, $P < 0.0001$; season $F_{2,28} = 1390$, $P < 0.0001$; species × season $F_{8,28} = 6.6$, $P < 0.0001$. MANOVA, effect on morning temperatures: species $F_{8,28} = 1.7$, $P = 0.11$; season $F_{2,28} = 125$, $P < 0.0001$; species × season $F_{8,28} = 1$, $P = 0.45$).

I will focus most of the discussion on daily soil temperature fluctuations, because they best summarize both species effects on soil warming in the day, and soil cooling at night, and because they correlate more closely with species effects on N cycling than do the morning or afternoon temperatures alone (Eviner 2001). In December, grasses had much lower daily soil temperature fluctuations than *Lupinus*, *Amsinckia*, or bare plots, while fluctuations were intermediate in plots of *Erodium* and *Trifolium* (Fig. 6; ANOVA, $F_{8,35} = 10$,

$P = 0.0012$). These daily temperature fluctuations were primarily due to warming in the afternoon (Table 2; ANOVA, $F_{8,35} = 18$, $P < 0.0001$), since minimum morning temperatures did not vary among species (Table 2; ANOVA, $F_{8,35} = 1.9$, $P = 0.15$). The amount of litter remaining negatively correlated with afternoon temperatures and daily temperature changes in December, and positively related to minimum soil temperatures (Table 3), suggesting that in the winter, litter buffered soil temperatures. The importance of litter presence was supported by a comparison of temperature in with-litter and no-litter plots (Fig. 7, Table 2). Litter did not tend to consistently affect soil temperatures in forb and legume plots, the species with high soil temperature fluctuations and little litter. However, in grass plots, the presence of litter decreased soil temperature fluctuations (Fig. 7a) and soil warming (Table 2) in the winter.

The pattern of species differences in daily temperature fluctuations in March was similar to that observed in December, but less pronounced (Fig. 6, Table 2). The litter vs. no-litter plot comparisons indicate that the presence of litter buffered March temperature

TABLE 3. Stepwise multiple regressions relating soil temperature to aboveground biomass and remaining litter ($n = 64$).

Month, time of day	Model			Variables				
	r^2	P	F	Significant factors	SS	P	F	Relationship
December								
Daily change	0.63	<0.0001	99.8	litter mass	141.4	<0.0001	99.8	–
Afternoon	0.51	<0.0001	61.5	litter mass	30.5	<0.0001	61.5	–
Morning	0.54	<0.0001	33.3	litter mass	30.4	<0.0001	59.8	+
				live biomass	1.9	0.06	3.7	+
March								
Daily change	0.51	<0.0001	28.41	live biomass	22.3	<0.0001	19.2	–
				litter mass	5.3	0.04	4.5	–
Afternoon	0.67	<0.0001	59.8	live biomass	12.1	<0.0001	25.1	–
				litter mass	9.0	<0.0001	18.7	–
Morning	NS†							

† Not significant.

TABLE 2. Extended.

February afternoon temperature (°C)		March temperature (°C)			
With litter	Without litter	Morning		Afternoon	
		With litter	Without litter	With litter	Without litter
9.7	9.4	6.9 ± 0.6	6.6 ± 1.0	11.7 ^{a*} ± 0.05	14.5 ± 0.15
9.9	9.9	7.4 ± 0.5	7.4 ± 0.8	12.6 ^{ab†} ± 0.05	15.3 ± 0.8
10.1	NA	7.3 ± 0.7	7.4 ± 1.0	11.7 ^a ± 0.05	13.9 ± 1.4
NA	9.5	7.8 ± 0.6	8.0 ± 0.6	13.8 ^{ab} ± 0.5	13.0 ± 0.04
9.4	9.6	7.1 ± 0.8	7.2 ± 1.0	13.3 ^{ab} ± 0.2	14.1 ± 0.1
NA	9.7	7.1 ± 0.9	7.0 ± 0.9	14.6 ^b ± 0.4	13.6 ± 1.5
9.6	9.7	7.0 ± 1.3	6.7 ± 0.7	14.6 ^b ± 0.5	14.8 ± 0.1
9.2	9.0	7.0 ± 1.1	6.8 ± 1.2	14.6 ^b ± 1.2	14.9 ± 0.5
NA	9.2	NA	6.6 ± 1.1	13.6 ^{ab} ± 0.01	13.6 ± 0.01
9.2	NA	2.8 ± 0.02	NA	13.7 ± 0.1	NA

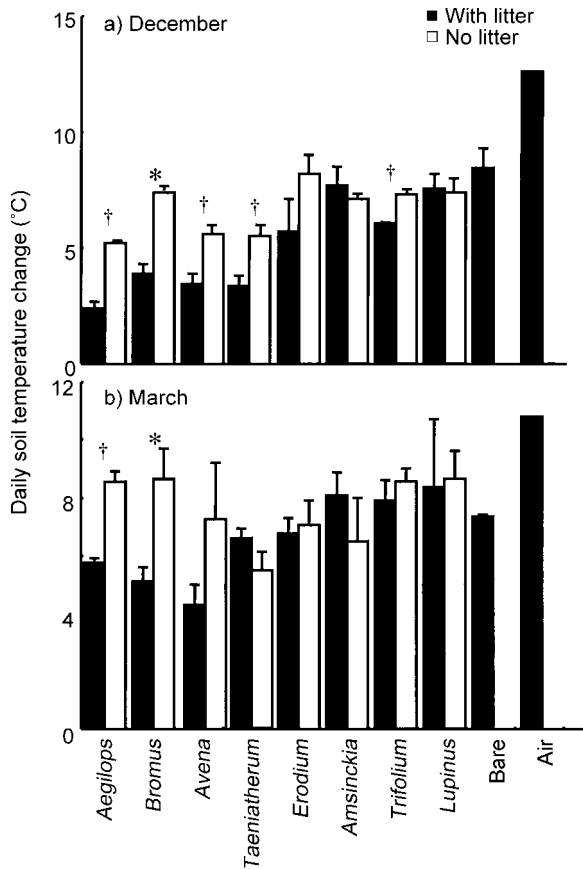


FIG. 7. Plant species effects on daily soil temperature changes in plots with (solid bars) and without (open bars) litter inputs. Significant differences in litter vs. no-litter treatments within a species are indicated by: * $P \leq 0.05$; † $P < 0.10$ (determined by sequential Bonferroni t test). Values are means + 1 SE ($n = 4$ replicates per treatment). Daily temperature fluctuations are presented for (a) December and (b) March. Species are ordered from high initial litter C/N ratio to low litter C/N ratio; full species names are as in Fig. 1.

changes in *Aegilops* and *Bromus*, which had the lowest litter quality, but did not affect soil temperature for the other species (Fig. 7b, Table 2). While species effects on soil temperature were largely mediated by litter mass early in the growing season, by the end of the growing season, when plant biomass was larger and much of the litter had decomposed, plant biomass became the dominant mechanism by which species affected soil temperature (Table 3).

Soil C respiration.—Carbon respiration differed significantly among species and across seasons, (Fig. 8; MANOVA; species $F_{8,63} = 14.3$, $P < 0.0001$; season $F_{2,62} = 96$, $P < 0.0001$; species \times season $F_{16,124} = 2$, $P = 0.04$). Species effects on microbial C use were independent of plant life forms. Grass species with similar litter chemistry had both the highest (*Aegilops*, *Taeniatherum*) and lowest (*Bromus*) soil C respiration rates. The relative ranking of species changed only slightly with growing season and incubation time (Fig. 8). Multiple regression analyses indicated that soil respiration was weakly associated with litter biomass in the early part of the growing season, when seedlings were very small (Table 4). In February, the most labile fraction of C respired (four days) weakly correlated with live biomass, and the less accessible pools (10 days, 30 days) were weakly associated with litter biomass (Table 4). Labile C respiration did not differ between with-litter and no-litter plots (Fig. 9; MANOVA: species $F_{2,42} = 3.4$, $P = 0.04$; litter $F_{1,42} = 1$, $P = 0.31$; species \times litter $F_{2,42} = 1$, $P = 0.38$), suggesting that the C respired early in the incubation was derived from growing plant inputs (e.g., exudates and tissue turnover) and not litter inputs. By the 30th day of incubation, litter tended to have a stronger effect on C respiration, but this trend was not statistically significant.

In April, as the soil dried out, there was a sharp decrease in C respiration (Fig. 8), suggesting a soil moisture limitation. Plant species effects on soil respiration were weakly related to their effects on soil moisture (Table 4). The soil moisture limitation of soil respiration was confirmed by wetting the soil to a moisture level

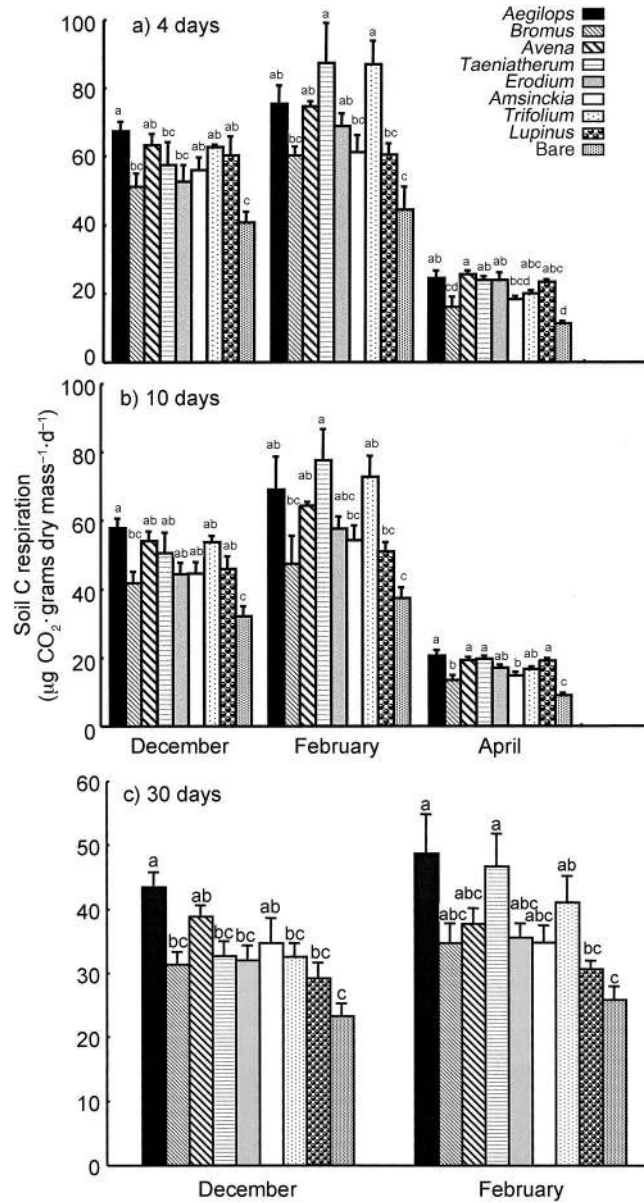


FIG. 8. Seasonal patterns of plant species effects on labile C. Values are means + 1 SE ($n = 8$ replicates per treatment). Species are ordered from high initial litter C/N to low litter C/N; full species names are as in Fig. 1. Significant differences among species for each time are indicated by different letters above bars (determined by a Tukey-Kramer post hoc test [$P < 0.05$]). (a) Rates of soil respiration after four days of incubation. There were significant differences among species and across seasons, and species effects changed with season (MANOVA; species $F_{8,63} = 14$, $P < 0.0001$; season $F_{2,62} = 96$, $P < 0.0001$; species \times season $F_{16,124} = 2$, $P = 0.04$). (b) Rates of soil respiration after 10 days of incubation. There are significant differences among species across seasons, but species effects stay constant over the growing season (MANOVA; species $F_{8,63} = 14$, $P < 0.0001$; season $F_{2,62} = 114$, $P < 0.0001$; species \times season $F_{16,124} = 0.9$, $P = 0.46$). (c) Rates of soil respiration after 30 days of incubation. There are significant differences among species, but no change with season (MANOVA; species $F_{8,63} = 8.7$, $P < 0.0001$; season $F_{2,63} = 4$, $P = 0.07$; species \times season $F_{8,63} = 1$, $P = 0.40$).

comparable to previous seasonal time points. This soil wet-up resulted in significant increases in soil respiration rate for all species treatments (Fig. 10, wet-up effect, ANOVA $F_{1,287} = 129$, $P < 0.0001$), even though the soils had already incubated for 14 days, and theoretically

had respired most of the easily available carbon. Even after five days of incubation under moist conditions, this high respiration rate did not decrease. This suggests that labile C availability was ample at this time, but microbial activity was limited by moisture.

TABLE 4. Stepwise multiple regressions relating soil C respiration to plant traits (litter mass, litter percentage N, litter percentage C, litter C/N ratio, aboveground biomass, soil temperature, soil moisture, microbial P [as an indicator of microbial biomass]).

Month and no. days	Overall model			Variables				Relationship
	r^2	P	F	Factors	ss	P	F	
December								
4 days	0.17	0.012	3.96	litter mass	822	0.02	6	+
				litter C/N ratio	684	0.03	5	-
				microbial P	656	0.03	4.8	+
10 days	0.28	0.0002	7.7	litter mass	1073	0.001	12	+
				microbial P	874	0.003	9.7	+
				litter C/N ratio	510	0.02	5.7	0
30 days	0.23	0.0003	9.1	live C/N ratio	528	0.002	10.6	+
				soil moisture	186	0.06	3.7	+
February								
4 days	0.2	0.0011	7.6	live biomass	2698	0.003	9.5	+
				microbial P	992	0.07	3.5	-
10 days	0.22	0.003	5.2	litter mass	2499	0.008	7.5	+
				live biomass	1845	0.022	5.5	+
30 days	0.16	0.002	11	litter mass				+
April								
4 days	0.19	0.002	7.2	soil moisture	166	0.01	6.5	+
				live biomass	102	0.05	4.0	+
10 days	0.21	0.0002	16	soil moisture				+
Feb, no litter								
4 days	0.32	0.004	10.5	biomass				-

Notes: Accumulated CO₂ was measured at 4, 10, and 30 days after soil collection. Sample sizes: $n = 64$ for "with-litter" plots; $n = 24$ for "no litter" plots.

Relationships among plant characteristics that influence biogeochemistry

While some of the mechanisms by which plant species can influence ecosystem processes correlated (e.g., litter biomass and soil temperature), many of these mechanisms varied independently among plant species (Fig. 11). Species differences in these mechanisms and the relationships among these mechanisms varied through time (season, plant age). The fact that plant species significantly differed in their effects on soil temperature in the winter and soil moisture in the spring suggests that species effects on soil microclimate were most pronounced when those environmental conditions were most constraining to ecosystem processes.

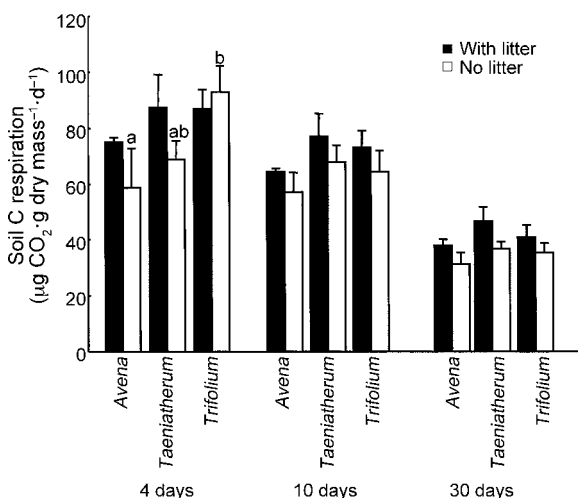


FIG. 9. Plant species effects on labile C in plots with (solid bars) and without (open bars) litter inputs in February at 4, 10, and 30 days. Litter does not significantly influence respiration or species effects on respiration (MANOVA; species $F_{2,42} = 3.4$, $P = 0.04$; litter $F_{1,42} = 1$, $P = 0.31$; species \times litter $F_{2,42} = 1$, $P = 0.38$; time $F_{1,41} = 392$, $P < 0.0001$; time \times species $F_{2,82} = 2.1$, $P = 0.08$). Significant differences among species for no-litter treatments are designated by different letters (determined by a Tukey-Kramer post hoc test [$P < 0.05$]). Values are means \pm 1 SE ($n = 8$ replicates per treatment). Species are ordered from high initial litter C/N ratio to low litter C/N ratio; full species names are as in Fig. 1.

DISCUSSION

The present study clearly demonstrates that plant species differed in a number of traits that can influence ecosystem processes, including litter chemistry, litter biomass, live biomass, labile C inputs, and effects on soil temperature and moisture. All of these traits impact plant species effects on biogeochemical cycling (e.g., litter quantity [Aerts et al. 1992, Hobbie 1992], soil temperature [Midmore et al. 1986, Majid and Jusoff 1987, Das et al. 1995], soil moisture [Van Vuuren et al. 1992, Mack 1998, Mack and D'Antonio 2003], and labile C [Newman 1985, Wedin and Pastor 1993]).

Many of these traits varied independently of one another across species. For example, the quantity of

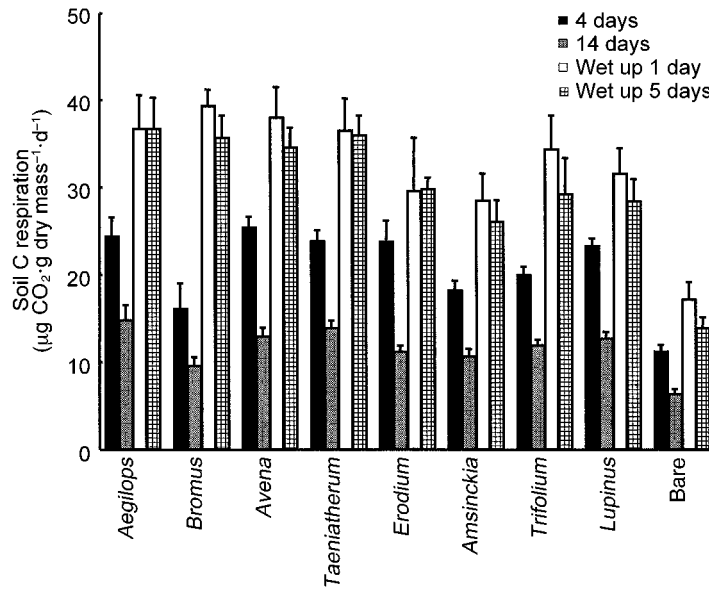


FIG. 10. Effects of soil moisture on labile C in April. In order to test whether low rates of CO₂ respiration in April were due to soil moisture constraints, soils were wet up to typical rainy season moisture levels (20% moisture). Solid bars represent rates of soil respiration at field moisture four days after soil collection; stippled bars represent rates of soil respiration at field moisture 14 days after soil collection. After respiration measurements were made on day 14, soils were wet up. Open bars represent soil respiration one day after soil wet up, and hatched bars represent soil respiration five days after soil wet up. Soil moisture significantly increased rates of CO₂ respiration (MANOVA; species $F_{8,260} = 17$, $P < 0.0001$; moisture $F_{1,260} = 129$, $P < 0.0001$; moisture \times species $F_{8,260} = 1.6$, $P = 0.05$). Values are means + 1 se ($n = 8$ replicates per treatment). Species are ordered from high initial litter C/N ratio to low litter C/N ratio; full species names are as in Fig. 1.

labile C in soil differed significantly among species, but these differences did not correspond to differences in litter chemistry or functional groups based on life form. This is because these labile C inputs were largely independent of litter, but instead derived from growing plant inputs, such as exudation and tissue turnover. The independence of litter and labile C inputs is verified by similar respiration rates from plots with and without litter inputs.

Some of the traits studied weakly correlated with one another. For example, species effects on soil moisture in the spring were weakly related to the quantity of litter remaining, but were independent of species differences in litter chemistry and labile C. The weak relationships among species attributes may be due to the fact that multiple traits often determine a given species characteristic. While the presence of litter can increase soil moisture by decreasing surface evaporation (Heady 1956), soil moisture is also strongly influenced by water use, which is determined by traits such as plant phenology, water uptake per unit root biomass, and rooting morphology (Mueller-Dombois 1973, Gordon et al. 1989, Gordon and Rice 1993, Brown 1998). Similarly, biomass of the litter layer is determined by initial litter mass and decomposition rate, as determined by litter chemistry. Species with similar litter chemistry differed two- to threefold in their litter inputs, so it isn't surprising that even though these two traits determined remaining litter biomass over the

growing season, remaining litter mass did not closely correlate with either trait across species.

Because the correlations among many traits are so weak, it is more useful to consider these as independent traits. Another argument for considering multiple independent traits rather than suites of traits is that the relationships among traits change over the growing season. For some traits, such as labile C and remaining litter mass, the trait values change seasonally, but the relative ranking of species remains somewhat constant. However, patterns of species differences in other attributes change substantially over the growing season (e.g., aboveground live biomass, soil moisture, and soil temperature). This is not surprising, because a given species characteristic is influenced by multiple traits, and these traits can change independently within and across species over the growing season. In addition, the relative importance of these traits in determining a species characteristic can shift seasonally. For example, species effects on soil temperature were mediated by the mass of remaining litter during the cold winter. High litter mass buffers soil temperature fluctuations, a pattern that has been well documented in a number of systems including California grasslands (Heady 1956, Evans and Young 1970), and tropical (Mack 1998) and boreal ecosystems (Hogg and Leiffers 1991). However, the patterns of species differences in soil temperature shifted in the spring, when aboveground biomass played an increasingly important role in buff-

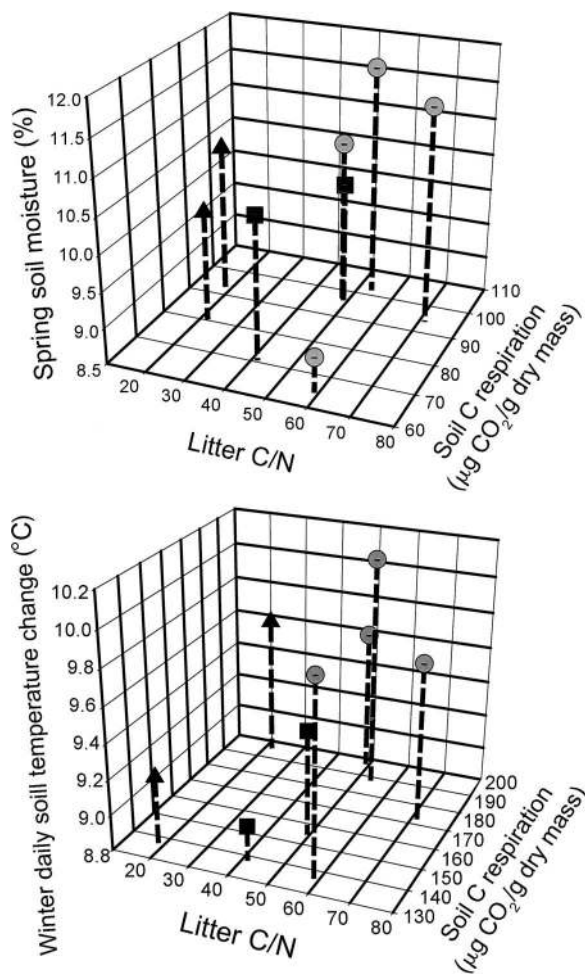


FIG. 11. Mechanisms that determine plant species effects on ecosystem processes vary independently among species. Grass species are represented by circles, forb species by squares, and legumes by triangles. Labile C measurements are from the four-day incubations. (a) Independence of key mechanisms determining plant species effects on biogeochemical cycling in the dry spring. (b) Relationship of key mechanisms in the cold winters.

ering soil temperature, and the buffering role of litter decreased.

This study clearly shows that, overall, many plant attributes that influence ecosystems are largely independent of one another. Other studies have also shown that many plant traits vary independently among species (Wardle et al. 1998) and across groups of species (Garnier 1991, 1992). Even plants within the same functional group can have up to a 10-fold difference in traits (Wardle et al. 1998), explaining why the same plant species can be grouped into many different functional groups (Wilson 1999). Even when some traits do strongly covary among species (e.g., flowering phenology, life span, size, tissue percent N), other traits show no correlation (e.g., shoot:root ratio, seed allocation, leaf area, root length) (Wardle et al. 1998). In

addition, the current study demonstrates that some suites of traits (e.g., soil temperature and litter biomass in the winter) are only seasonal.

The independence of plant traits suggests that we may need to rethink how we predict plant species effects on ecosystem processes. A number of studies have shown that plant species effects on biogeochemical cycling can best be predicted by accounting for these multiple plant traits (Shock et al. 1983, Verville et al. 1998, Wardle et al. 1998), rather than focusing on one trait such as litter chemistry. For example, species effects on N cycling (Mack 1998, Eviner and Chapin 2003, Mack and D'Antonio 2003) and decomposition (Cheng and Coleman 1991, Bottner et al. 1999, Eviner 2001) are determined by litter chemistry, labile C inputs, and effects on soil temperature and moisture. Given the independent distribution of multiple plant traits that can influence ecosystem processes, our ability to predict plant species effects on ecosystems may be greatly improved by moving beyond single traits or functional groups based on a suite of covarying traits. The functional matrix (Eviner and Chapin 2003) provides such an approach, where the focus is on understanding how the relationships among key traits and ecosystem processes vary depending on the values of other key traits. For example, the relationship between litter chemistry and decomposition or nitrogen cycling depends on availability of inorganic N and labile C (reviewed in Eviner and Chapin 2003; Eviner, *unpublished manuscript*).

The study described in this paper is a major step toward a stronger predictive framework for plant species effects on ecosystems. By determining which traits vary independently of one another, we can focus future studies on determining the ecosystem effects of these specific trait combinations.

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