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The influence of plant species, fertilization and elevated CO_2 on soil aggregate stability

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Abstract

We tested the effects of plant species, fertilization and elevated CO_2 on water-stable soil aggregation. Five annual grassland species and a plant community were grown in outdoor mesocosms for 4 years, with and without NPK fertilization, at ambient or elevated atmospheric CO_2 concentrations. Aggregate stability (resistance of aggregates to slaking) in the top 0.15 m of soil differed among plant species. However, the more diverse plant community did not enhance aggregate stability relative to most monocultures. Species differences in aggregate stability were positively correlated with soil active bacterial biomass, but did not correlate with root biomass or fungal length. Plant species did not affect aggregate stability lower in the soil profile (0.15–0.45 m), where soil biological activity is generally decreased. Elevated CO_2 and NPK fertilization altered many of the factors known to influence aggregation, but did not affect water-stable aggregation at either depth, in any of the plant treatments. These results suggest that global changes will alter soil structure primarily due to shifts in vegetation composition.

Introduction

Soil aggregation is a critical regulator of ecosystem functioning. It determines the distribution of soil pore sizes, and thus water infiltration, microbial predation, aeration, root growth, and the heterogeneity of redox conditions in the soil. These factors, in turn, greatly influence biogeochemical cycles (Oades, 1984). Soil macro-aggregates (0.25–2 mm) can also promote soil carbon storage by protecting soil organic matter from decomposition (Elliot, 1986, Van Veen and Kuikman, 1990). Because of the critical role that soil aggregation plays in hydrology, biogeochemistry, C storage, and erosion control (Degens, 1997), modifications of soil aggregation could have important consequences for the functioning of ecosystems. However, predictions of ecosystem response to environmental changes rarely account for the consequences of possible changes in soil aggregation. To do this, we must understand how soil aggregate stability is affected by multiple types of environmental changes. This can be a challenge, as demonstrated by the varied responses of aggregation to fertilization. In response to N fertilization, aggregate stability may decrease (Ram and Zwerman, 1960), not change (Aoyama et al., 1999, Biederbeck et al., 1996), or vary depending on the vegetation composition (Latif et al., 1992) or the amount of fertilizer added (Roberson et al., 1995). These varied responses emphasize the need for a mechanistic approach to understanding what drives changes in soil aggregation.

Many factors influence soil aggregate stability, including microbial extracellular polysaccharides (Roberson et al., 1995), glomalin derived from arbuscular mycorrhizae (Wright et al., 1999), fungal hyphae (Tisdall, 1991), soil microbial biomass, plant roots, plant carbon and nitrogen inputs, and aromatic humics (Degens, 1997, Jastrow et al., 1998, Lynch and Bragg, 1985, Tisdall and Oades, 1982). These factors have been shown to shift in response to many types of environmental changes. For example, elevated CO_2 can alter root mass, plant nutrient content, exudation, mycorrhizal infection, soil microbial community composition, and belowground carbon al-

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location (for a review of studies, see Diaz, 1996, O'Neill, 1994). Likewise, N fertilization has a significant impact on these same plant (Burke et al., 1992, Kuzyakov and Domanski, 2000) and microbial (Bardgett et al., 1999a; Biederbeck et al., 1996; Henriksen and Breland, 1999; Johnson, 1993) characteristics. In addition, changes in the vegetation community composition can alter the factors that influence aggregation (Chiariello and Field, 1996; Jongen and Jones, 1998; Leadley et al., 1999).

Plant species differ in a number of factors that are responsible for binding soil particles, including root characteristics (e.g., biomass and length) (Aerts et al., 1992; Miller and Jastrow, 1990), soil carbon inputs in the form of exudates (Gransee and Wittenmayer, 2000; Klein et al., 1988) or litter (Melillo et al., 1982; Tilman and Wedin, 1991)), and associated soil biota (Bardgett et al., 1999b; Lawley et al., 1982; Priha et al., 1999; Springett and Gray, 1997). Plant species can also alter soil physical conditions that can initially form soil aggregates, such as soil moisture (Gordon and Rice, 1993) and freeze-thawing (Hogg and Lieffers, 1991). Environmental changes such as elevated CO_2 can alter plant traits that influence soil aggregation, but the response of these traits is often species-specific (Cotrufo and Gorrison, 1997; Monz et al., 1994; Paterson et al., 1996).

Thus, there are many factors that influence soil aggregate stability, and all of these can potentially change in response to environmental changes. It is crucial to understand how aggregation may change in response to shifts in the above factors. Our objective in this study was to identify some of the mechanisms through which soil aggregation responds to plant species, NPK fertilization and elevated CO_2. We hypothesized that soil aggregation should differ among plant treatments due to their differences in C inputs, rooting characteristics, and effects on soil microbes. Changes in soil aggregation in response to elevated CO_2 and NPK fertilization were expected to be determined by shifts in these same mechanisms.

Materials and methods

Experimental set-up

This experiment was conducted at the Jasper Ridge Biological Preserve of Stanford University in northern California. Plants were grown for 4 years in a factorial combination of ambient and elevated CO_2, and ambient and enhanced nutrients in MECCAs (microecosystems for climate change analysis) (Field et al., 1996). The MECCA facility consisted of 20 open-topped chambers, half of which were exposed to ambient CO_2, the other half exposed to ambient +350 μmol mol^{-1} CO_2. Approximately 30 mesocosms were tightly-packed on square platforms (1.2 × 1.2 m), and surrounded by a 1 m high plywood enclosure. This was topped with a 1.65 m tall polyethylene film (0.15 mm thick) chamber, with a polyethylene mesh top to evenly distribute rainfall over the enclosure. Single-species mesocosms were planted in 0.2 m diameter × 0.95 m deep polyvinyl chloride (PVC) tubes. Community mesocosms were planted in 0.4 m diameters × 0.95 m deep PVC tubes. In order to mimic the natural serpentine soil profile, the top 0.15 m were filled with shredded serpentine topsoil from Kirby Canyon landfill (25 km SE of our field site), and the bottom 0.8 m were filled with subsoil, consisting of a mix of serpentine and non-serpentine crushed rock. These mesocosms were rain-fed, and drained freely through perforated bottoms.

Seeds were collected near the field site and planted at a density typical of adult density in the field (approximately 7500 m^{-2} for most plant treatments) (see Chiariello and Field, 1996, for complete details). Monocultures were planted with representatives of the major functional types of plants that occur on serpentine soils, and include: (1) grass (*Bromus hordeaceus*, flowers mid-March to July), (2) early-season forbs (*Plantago erecta* and *Lasthenia californica*, flower mid-March to June), a late-season forb (*Hemizonia congesta* spp. *Luzilifolia*, flowers July through November), and a legume (*Lotus wrangelianus*, flowers mid-March through June). The species in the community mesocosms were seeded to mimic the proportion of these species in the typical field community. Species composition of the community mesocosms differed with treatment due to competitive interactions and differential survival, but potentially included the species discussed above, as well as *Avena fatua, Bromus diandrus, Lolium multiflorum, Vulpia microstachus* (all flower mid-March through June) and *Calycadenia multiglandulosa* (flowers May through November). Low-nutrient communities were dominated by *Plantago, Lotus*, and *Vulpia*, while high-nutrient treatments were dominated by *Lolium, Avena*, and *Bromus diandrus*. All mesocosms were weeded to eliminate unwanted plant species. Within each of the CO_2 treatments, these plant treatments were grown at ambient nutrients, or with additions of N,P, and K at a

rate of 20 g m^{-2} of each element applied as Osmocote 120-day slow-release fertilizer. There were four replicates of each treatment (species × nutrients × CO_2) (see Chiariello and Field, 1996; Field et al., 1996, for further details).

Sample harvest

After 4 years of growth under their designated treatments, the mesocosms were harvested. This harvest occurred in April, which corresponded to the time of maximum community biomass in the field, and peak flowering time for all species except *Hemizonia*. Aboveground biomass was clipped, and root biomass was determined by washing roots from a 75 mm diameter 150 mm deep soil core. Plant biomass was oven dried (60 °C for 48 h) and weighed. Soil remaining in each mesocosm was bulked at 0–0.15 m depth, and soil from plant monocultures was also bulked at the 0.15–0.45 m depth. The bulked soil was used to determine soil aggregation and bacterial and fungal biomass. Labile carbon and soil moisture were determined from 35 mm diameter × 150 mm deep soil samples collected 9 days prior to the biomass and aggregation harvest.

Water stable aggregation

Bulked soil samples were air-dried, passed through a 2 mm sieve, and analyzed for resistance of aggregates to slaking. In our experiment, slaking resistance is the best indicator of soil aggregate stability since it mimics the drying-wetting cycles experienced seasonally by California grassland soil. In addition, slaking resistance of aggregates is one of the most important and dynamic properties of soils in relation to erosion control, and best accounts for the effects of small roots, root hairs and fungal mycelia (Yoder, 1936). Thus, this measure of aggregate stability is best suited to study the effects of different vegetation types. Five grams of aggregates (0.3–2.0 mm diameter) were placed on a 0.3 mm sieve, and covered with filter paper (100 mm diameter) to minimize the direct impact of falling water. A PVC cylinder (43 mm diameter × 100 mm high) was placed over the aggregates and filter paper, and pressed firmly against the sieve. This essentially sealed off the system, allowing us to maintain a constant head of 100 mm while pouring 2.5 l of water over the aggregates (Roberson, 1991; Roberson et al., 1995; Sarig et al., 1993). Aggregates remaining were then oven dried at 105 °C for 48 h (until constant mass) and weighed. Water stable aggregation was expressed as the percentage of the original soil mass that remained after the treatment. This method of slaking resistance correlates well with the Yoder (1936) measure of aggregate stability (Roberson, 1991), which is the basis for most current measures of aggregate stability (Kemper and Rosenau, 1986).

Other measures

Soil moisture at harvest was determined gravimetrically, by drying the soil for 48 h at 105 °C. Subsamples of the same soils used to determine aggregation were measured for active and total bacterial biomass and fungal length. These were determined by the Soil Microbial Biomass Service (Corvallis, OR) on a subset of the treatments (all CO_2 and fertilization treatments in the community and *Plantago*, and only low-fertility treatments in *Lotus* and *Bromus*). Active fungal length and bacteria were determined by FDA staining (Ingham and Klein, 1984; Lodge and Ingham, 1991). Phase-contrast microscopy was used to determine total fungal length (Ingham and Klein, 1984), and FITC (fluorescein isothiocyanate) for total bacterial biomass (Babiuk and Paul, 1970). Labile C was determined on all unfertilized treatments. Fifty grams of soil were incubated under constant temperature and moisture conditions (21 °C, 200 mg g^{-1} soil moisture) in an air-tight mason jar (Zibilske 1994). CO_2 production measurements were taken at 23 and 108 h and run on a Shimadzu gas chromatograph (Shimadzu Scientific Instruments, Columbia, MD).

Statistical analyses

MANOVAs were used to determine differences among the plant, fertility and CO_2 treatments. Regression analysis was used to determine the relationship of soil aggregation with microbial community characteristics and plant traits.

Results

Soil aggregate stability

Plant species differed in the percentage of aggregates resistant to slaking in the top 0.15 m of soil (Figure 1). Aggregate stability in the soil under the forb species (*Plantago, Lasthenia, Hemizonia*) was significantly higher than under the grass and legume species ($P<0.0001$), and the plant community was not significantly different from the forb treatments. There

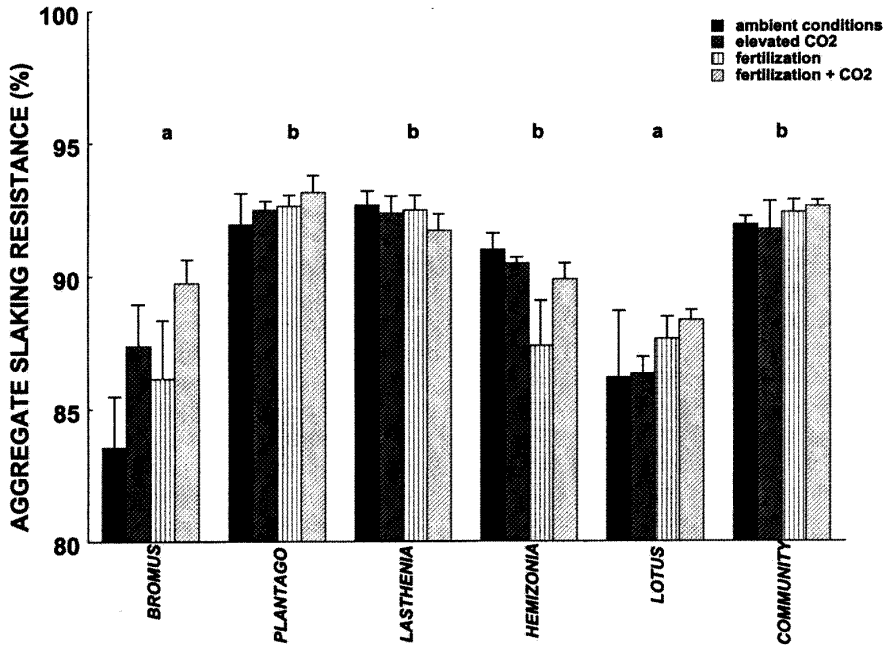

Figure 1. Percentage of aggregates (0.3–2 mm diameter) resistant to slaking at 0–0.15 m depth as a function of plant species, elevated CO_2 and NPK fertilization ($n = 4$). Error bars represent standard errors of the means. Significant differences between plant treatments ($P < 0.0001$) are indicated with different letters. Aggregate stability under ambient CO_2 and nutrient conditions are in the solid bars, elevated CO_2 and ambient nutrients in the dark hatched bars, ambient CO_2 and fertilized treatments in the striped bars, and elevated CO_2 and fertilized treatments in the light hatched bars. MANOVA results show that there were no significant effects of CO_2 and NPK treatments on water stable aggregation (MANOVA: CO_2, F=3.5, $P = 0.07$; Nutrients, $F = 0.75$, $P = 0.4$; Species, $F = 20.2$, $P < 0.0001$; $CO_2 \times$ nutrients, $F = 0.3$, $P = 0.6$; $CO_2 \times$ species, $F = 1.8$, $P = 0.14$; Species $\times$ nutrients, $F = 2.2$, $P = 0.08$; $CO_2 \times$ nutrients $\times$ species, $F = 0.33$, $P = 0.85$).

were no species differences in aggregate stability at the 0.15–0.45 m depth (Figure 2). Fertilization and elevated CO_2 had no significant effect on aggregate slaking resistance in any plant treatment, at any depth. (Figures 1 and 2).

Factors explaining soil aggregate stability

Plant and microbial characteristics that influence aggregation differed among plant species, elevated CO_2 treatments, and fertilization treatments (Table 1). Plant species significantly differed in their aboveground and root biomass, as well as their effects on total fungal length, soil moisture, and labile C. There were also strong trends of plant species differences in active bacterial biomass and fungal length (Table 1). Regression analysis of aggregation in the absence of fertilization indicated that active bacterial biomass correlated with aggregate stability (Table 2). Species differences in active bacterial biomass (Figure 3) followed species patterns of aggregate stability (Figure 1), with the plant community and *Plantago* being greater than *Bromus* and *Lotus*. The correlation between active bacteria and aggregation disappeared when plant species were used as a covariate in the regression, indicating that the bacteria may be one of the mechanisms by which plant species alter soil aggregation. There were no significant correlations between any of these factors and aggregate stability in fertilized treatments.

Elevated CO_2 altered some of the traits that influence aggregate stability, including labile C and root biomass (Table 1). Fertilization altered plant biomass and soil moisture (Table 1).

Discussion

Differences among plant species can significantly alter water-stable soil aggregation. Scott (1998) found that differences in soil aggregate stability between tree species were related to fungal biomass. Other studies examining the effects of plant species on aggregate

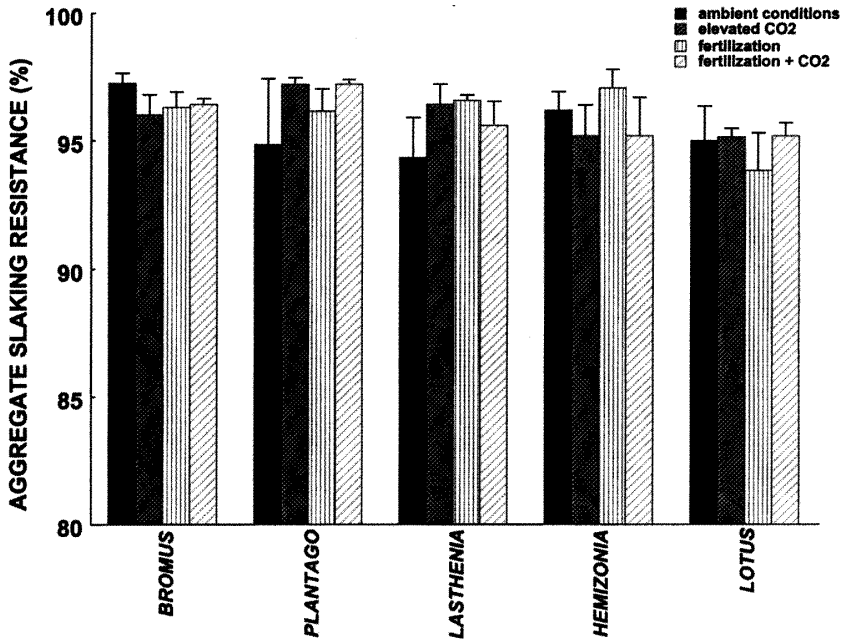

Figure 2. Percentage of aggregates (0.3–2 mm diameter) resistant to slaking at 0.15–0.45 m depth as a function of plant species, elevated CO_2 and NPK fertilization ($n = 4$). Error bars represent standard errors of the means. Aggregate stability under ambient CO_2 and nutrient conditions are in the solid bars, elevated CO_2 and ambient nutrients in the dark hatched bars, ambient CO_2 and fertilized treatments in the striped bars, and elevated CO_2 and fertilized treatments in the light hatched bars. There were no significant differences between plant species, CO_2 or NPK treatments (MANOVA: CO_2, $F = 0.2$, $P = 0.66$; Nutrients, $F = 0.18$, $P = 0.67$; Species, $F = 2.0$, $P = 0.11$; $CO_2 \times$ nutrients, $F = 0.34$, $P = 0.56$; $CO_2 \times$ species, $F = 1.4$, $P = 0.24$; Species $\times$ nutrients, $F = 0.34$, $P = 0.85$; $CO_2 \times$ nutrients $\times$ species, $F = 0.85$, $P = 0.5$).

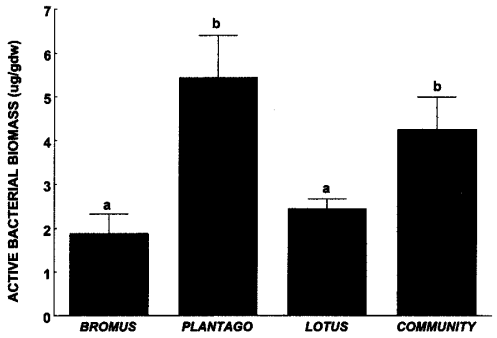

Figure 3. Plant treatment effects on active bacterial biomass (μg/g dw soil), CO_2 treatments are pooled ($n = 8$). Error bars represent standard errors of the means. Significant differences between plant treatments are indicated with different letters ($P = 0.0065$).

stability have shown that grass species tend to be associated with greater aggregate stability than other vegetation groups, most likely due to the higher root and fungal biomass associated with graminoids. This is true in both annual (Degens et al., 1994; Rillig et al., 2002; Tisdale and Oades, 1979) and perennial grassland systems (Jastrow, 1987). In contrast, in our annual system, grass and legume species had lower stable aggregation than did the forb species. Almost all factors known to influence water-stable aggregation differed between plant species in our study, but only species' effects on active bacteria were associated with aggregate stability. However, the relationship of active bacteria to aggregate stability ($r^2 = 0.27$) only explains a portion of the plant species' effects on aggregation ($r^2 = 0.63$). It is not clear what other factors may be responsible for plant species effects on aggregation, because plant C inputs, readily available soil C, effects on soil moisture and fungal length were not related. A number of other factors were measured in these same mesocosms but also did not relate to aggregation patterns, including: percent root infection of arbuscular mycorrhizal and non-mycorrhizal fungi (Rillig et al., 1998), litter quality (Franck et al., 1997), and plant and microbial N (Hungate et al., 1996). This demonstrates

Table 1. *F* ratios and *P* values of the effects of elevated CO_2, species and nutrients on factors known to influence aggregate stability. Biomass and soil moisture statistics are from MANOVAs using CO_2, nutrient, and plant treatments as the main factors. Statistics on other variables are from MANOVAs, using CO_2 and plant treatment as the main effects within each unfertilized plant treatment

	Factor	DF	F ratio	p value
Active bacterial biomass	Species	4	2.4	0.06
	CO_2	1	0.01	0.92
	CO_2 × species	4	0.7	0.55
Total bacterial biomass	Species	4	1.6	0.19
	CO_2	1	1.7	0.20
	CO_2 × species	4	1.0	0.41
Active fungal length	Species	4	2.3	0.07
	CO_2	1	0.0001	0.99
	CO_2 × species	4	1.1	0.39
Total fungal length	Species	4	6.5	0.0003
	CO_2	1	2.5	0.12
	CO_2 × species	4	2.2	0.08
Labile C	Species	6	18.8	<0.0001
	CO_2	1	6.4	0.01
	CO_2 × species	6	0.5	0.8
Soil moisture	Species	5	2.4	0.04
	CO_2	1	0.13	0.72
	Nutrients	1	137.7	<0.0001
	CO_2 × species	5	1.4	0.22
	CO_2 × nutrients	1	0.23	0.63
	Species × nutrients	5	3.8	0.004
	Species × nutrients × CO_2	5	1.2	0.32
Aboveground biomass	Species	5	34.1	<0.0001
	CO_2	1	2.3	0.13
	Nutrients	1	101.8	<0.0001
	CO_2 × species	5	1.4	0.24
	CO_2 × nutrients	1	1.8	0.18
	Species × nutrients	5	28.0	<0.0001
	Species × nutrients × CO_2	5	1.1	0.34
Belowground biomass	Species	5	23.4	<0.0001
	CO_2	1	6.7	0.01
	Nutrients	1	80.9	<0.0001
	CO_2 × species	5	0.65	0.66
	CO_2 × nutrients	1	2.7	0.11
	Species × nutrients	5	15.3	<0.0001
	Species × nutrients × CO_2	5	0.56	0.73

that, although we understand some of the factors that *can* influence aggregate stability, there is still a lot to learn about controls of aggregation.

Other factors may be responsible for determining plant effects on aggregation in this experiment because it was performed on an unusual soil type. Serpentine soil tends to be sparsely vegetated, low in nutrients, and toxic due to high levels of chromium, nickel or other heavy metals (Walker, 1954). Similarly, a study in a sandy soil was unable to determine the mech-

Table 2. Correlations of different factors with soil aggregate stability in unfertilized treatments

	Correlation with aggregation (r^2)	Significance value (p)
Plant species	0.634	<0.0001
Active bacterial biomass	0.267	0.0068
Total bacterial biomass	0.039	0.2584
Active fungal length	0.052	0.1932
Total fungal length	0.001	0.8577
Aboveground plant biomass	0.0006	0.8597
Belowground plant biomass	0.022	0.3699
Soil moisture	0.038	0.2688
Labile carbon	0.013	0.4277

anisms that accounted for plant species' effects on aggregate stability, finding no correlation with soil carbohydrate C, organic C, microbial biomass, hyphal length or root length (Degens et al., 1994). These studies suggest that the mechanisms by which plants alter aggregation may vary among soil types.

Factors that have been shown to influence soil aggregates also varied in response to fertilization and elevated CO_2. Despite these changes in factors that may influence aggregation, 4 years of exposure to elevated CO_2 or NPK fertilization had no effect on aggregate stability. In contrast, elevated CO_2 was shown to increase soil aggregation in serpentine field plots at our site (Rillig et al., 1999). This increase in soil aggregation was associated with an increase in glomalin, a glycoprotein associated with arbuscular mycorrhizal fungi. Differences in aggregation responses between the field plots and the mesocosms may have resulted from a lower fungal length in the mesocosms, due to the disturbance associated with their construction. Such soil disturbance has been shown to substantially decrease fungal biomass in annual grassland soil (Balser, 2000).

Although there is a solid understanding of the biological factors that can play a role in soil aggregation (Degens, 1997; Lynch and Bragg, 1985), we need a better understanding of how factors interact to determine aggregate stability. All of our treatments altered many of the factors cited to influence aggregation, but these shifts either did not affect aggregation or did not clearly relate to the aggregation patterns we found. Although environmental changes have the potential to alter soil aggregation, it is uncertain what types of shifts may alter aggregate stability. What magnitude of change in factors such as root biomass and fungal length is necessary to alter aggregate stability? How do these different biological factors interact to determine aggregate stability? These are questions that may help us elucidate the mechanisms determining soil aggregate stability.

Plant species significantly altered aggregate stability, and these species effects were unchanged by exposure to elevated CO_2 and fertilization. This is consistent with the findings that plant species effects on aggregation (Dapaah and Vyn, 1998) and soil microbial activity and biomass (Bardgett et al., 1999a) were larger than the effects of fertilization. Therefore, it is likely that changes in soil structure in response to global changes may be largely due to shifts in vegetation composition.

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