

## Plant functional type effects on trace gas fluxes in the shortgrass steppe

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**Abstract.** Plant community structure is expected to regulate the microbial processes of nitrification and denitrification by controlling the availability of inorganic N substrates. Thus it could also be a factor in the concomitant release of NO and N<sub>2</sub>O from soils as a result of these processes. C<sub>3</sub> and C<sub>4</sub> plants differ in several attributes related to the cycling of nitrogen and were hypothesized to yield differences in trace gas exchange between soil and atmosphere. In this study we estimated fluxes of NO, N<sub>2</sub>O and CH<sub>4</sub> from soils of shortgrass steppe communities dominated by either C<sub>3</sub> plants, C<sub>4</sub> plants or mixtures of the two types. We collected gas samples weekly from two sites, a sandy clay loam and a clay, throughout the growing seasons of 1995 and 1996. Plant functional type effects on gas fluxes at the clay site were not apparent, however we found several differences among plant communities on the sandy clay loam. CH<sub>4</sub> uptake from atmosphere to soil was significantly greater on C<sub>4</sub> plots than C<sub>3</sub> plots in both years. NO fluxes were significantly greater from C<sub>4</sub> plots than from C<sub>3</sub> plots in 1995. NO fluxes from C<sub>3</sub> and mixed plots were not significantly different between 1995 and 1996, however fluxes from C<sub>4</sub> plots were significantly greater in 1995 compared to 1996. Results indicate that under certain environmental conditions, particularly when factors such as moisture and temperature are not limiting, plant community composition can play an important role in regulating trace gas exchange.

### Introduction

Trace gas constituents of the atmosphere play crucial roles in atmospheric processes and in interactions between atmosphere and biosphere. Biologically mediated trace gases such as NO, N<sub>2</sub>O and methane (CH<sub>4</sub>) have a variety of atmospheric influences (Graedel & Crutzen 1989). NO in the atmosphere results in acid deposition and N redistribution (Logan 1983; Williams et al. 1992), NO and CH<sub>4</sub> are both regulators of tropospheric oxidants such as ozone and hydroxyl (Logan 1983; Williams et al. 1992, Graedel & Crutzen 1989), N<sub>2</sub>O and CH<sub>4</sub> are important greenhouse gases (Rodhe 1990; Duxbury et al. 1993), and N<sub>2</sub>O leads to stratospheric ozone depletion (Crutzen 1970).

Microbiological processes contribute to the exchange of these gases between atmosphere and biosphere. For example, nitrification and denitrification lead to net emission of NO and N<sub>2</sub>O from soil (Firestone & Davidson 1989). Methane is generated in soils by reduction of CO<sub>2</sub> during anaerobic respiration (Mooney et al. 1987; Ojima et al. 1993), whereas sinks for atmospheric CH<sub>4</sub> are common in more arid regions where CH<sub>4</sub> is oxidized by some soil bacteria (Whittenbury et al. 1970; Lidsurom & Stirling 1990). These microbial processes and the concomitant gas exchange are driven predominantly by soil moisture and temperature, soil aeration and the availability of reactive substrates to microbes (Parton et al. 1988; Davidson et al. 1993; Corre et al. 1995; Dunfield et al. 1995). The interactions among these controls of trace gas fluxes are complex (Robertson 1989; Firestone & Davidson 1989).

NH<sub>4</sub><sup>+</sup> availability in soils is a key proximal control of nitrification (Haynes 1986), as is NO<sub>3</sub><sup>-</sup> availability for denitrification (Tiedje 1988). Plant community structure can be an important regulator of these two microbial processes, because it influences the levels of inorganic N in soils (Hooper & Vitousek 1997; Tilman et al. 1996, 1997). Mechanisms include, but are not limited to, NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> uptake by plants, and litter quality controls over N mineralization (Jackson et al. 1989; Wedin & Tilman 1990; Janssen 1996). Other potential effects of plant community structure on microbial activity are organic C inputs, and transpiration effects on soil water content and O<sub>2</sub> diffusivity (Robertson 1989). Because CH<sub>4</sub> exchange is influenced by the cycling of N and is controlled by many of the same factors that govern nitrogen gas fluxes (Mosier et al. 1991), plants may also play a role in CH<sub>4</sub> consumption. Despite the assumed importance of plant community structure (Robertson 1989), there have been few empirical attempts to quantify its influence on soil-atmosphere trace gas exchange (e.g. Mosier et al. 1986; Haider et al. 1987; Bronson & Mosier 1993).

Some aspects of plant community structure are species composition or functional type composition. Plant species and functional types differ in a variety of attributes including phenologies, rates of growth, productivity potentials, nutrient and water use efficiencies, and allocations of nutrients among plant tissues (Hobbie 1992; Jones & Lawton 1995; Hobbie 1996). These differences in plant characteristics lead to differences in functions of ecosystems, such as soil organic matter accumulation, decomposition rates and nutrient availability (Melillo et al. 1982; Pastor et al. 1984; Vitousek et al. 1987; Binkley 1994). An important example in many grassland ecosystems is the difference between perennial grasses that possess the C<sub>3</sub> vs. the C<sub>4</sub> photosynthetic pathway. These plant functional types differ in timing of growth (Tieszen 1970; Kemp & Williams III 1980; Monson et al. 1983), water

use efficiencies (Caldwell et al. 1977; Pearcy & Ehleringer 1984; Monson et al. 1986), N use efficiencies (Brown 1978) and thus tissue N concentrations (Field & Mooney 1986; Wedin & Tilman 1990; Hunt et al. 1996). Resulting differences in tissue C:N ratios influence both the availability of inorganic soil N and the amount of N taken up by plants (Wedin & Tilman 1990; Wedin & Pastor 1993; Wedin 1995; Garnier et al. 1995).

Our objective was to determine whether differences in N cycling as a function of C<sub>3</sub> and C<sub>4</sub> plant composition yielded temporal differences in NO, N<sub>2</sub>O and CH<sub>4</sub> fluxes. General assumptions we considered were that C<sub>3</sub> plants are less efficient in their use of nitrogen (Brown 1978), have potentially greater tissue N concentrations (Cook et al. 1977; Wedin & Tilman 1990; Hunt et al. 1996), and initiate growth earlier in the growing season (Monson et al. 1983) than C<sub>4</sub> plants. Conversely, C<sub>4</sub> plants are more active than C<sub>3</sub> plants during hot summer months (Björkman et al. 1975). Our main hypothesis was that, given identical weather conditions and soil type, a relatively more active plant community will assimilate more inorganic N and thus minimize gaseous N losses. Because of phenological differences, we hypothesized that nitrogen gas fluxes would be less from C<sub>3</sub> communities in the spring compared to C<sub>4</sub> communities and comparatively greater for C<sub>3</sub> communities in the summer compared to C<sub>4</sub> communities. Plants compete well with nitrifying and denitrifying bacteria for NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> (Verhagen et al. 1995), but does this competition alter the availability of inorganic substrate to microbes enough to limit trace gas fluxes? Differential litter quality between C<sub>3</sub> and C<sub>4</sub> plants could also lead to different rates of N mineralization (Wedin & Tilman 1990) which may influence the temporal patterns and magnitudes of NO, N<sub>2</sub>O and CH<sub>4</sub> fluxes.

## Methods

Our experiments were conducted at the Central Plains Experimental Range (CPER), a shortgrass steppe site in northeastern Colorado, 60 km northeast of Fort Collins. Mean annual precipitation is 321 ± 98 mm (52 year mean ± 1 SD), with 83% falling between April and September, and mean annual temperature is 8.6 ± 0.6 °C (Lauenroth & Sala 1992). The site is characterized by highly variable precipitation during the growing season, but with predictable peaks during May and June (Sala et al. 1992). Vegetation is dominated by C<sub>4</sub> grasses, but there is substantial cover of C<sub>3</sub> species, particularly in lowland and fine-textured sites (Lauenroth & Milchunas 1992). The site is less than 20 km from the continental transition between C<sub>3</sub> and C<sub>4</sub> dominance (Epstein et al. 1997b), making it an appropriate location for this study. The CPER is administered by the Agricultural Research Service of the USDA and is a

National Science Foundation Long-Term Ecological Research site (Franklin et al. 1990; Lauenroth & Sala 1992).

We located two sites at the CPER, separated by approximately 4 km; both sites were situated at a swale landscape position and were moderately grazed by cattle during summer months. The predominant soil texture for one site was a sandy clay loam, the other a clay (Table 1). The dominant  $C_3$  species located at our sites were *Agropyron smithii* Rydb. and *Carex eleocharis* (Bailey) Hultén; the dominant  $C_4$  species were *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. and *Buchloë dactyloides* (Nutt.) Engelm. Our plant community treatments for this study were native plots of the dominant  $C_3$  species, native plots of the dominant  $C_4$  species, and a mixture of the two plant functional types. Within each site there were no significant differences in either soil texture (percentage sand and clay) or total soil N among plots of the three plant community types (Epstein et al. 1997a). Additional factors, such as population dynamics, that might influence the spatial distribution of  $C_3$  and  $C_4$  plants within a site were not important with respect to the hypotheses being tested.

Polyvinyl chloride chamber anchors of 20 cm in diameter and 10 cm in depth were permanently inserted 8 cm in soils (Mosier et al. 1991) in plots of  $C_3$  plants,  $C_4$  plants, and mixtures of  $C_3$  and  $C_4$  plants. At each site, we established three sets of sampling locations; sets were approximately 30–40 m apart. Within a set, chamber anchors were randomly located and inserted for two occurrences of each plant community treatment ( $C_3$ ,  $C_4$ , mixed). Sampling locations within a set were separated by approximately 2–5 m. Thus at each of two sites, we had six spatially distributed anchors for each plant community treatment, giving a total of 36 sampling locations.

We collected samples for  $NO$ ,  $N_2O$ ,  $CH_4$  and  $CO_2$  analysis approximately weekly for 17 weeks between May 16 and October 6 in both 1995 and 1996; the same sampling locations were used for both years of the study. Samples were collected at the same time each week, between 10 AM and 2 PM. One implication of taking regular measurements was that peak fluxes were not always captured. Opaque vented chambers, constructed from polyvinylchloride with reflective tops (Hutchinson & Mosier 1981), 7.5 cm in height, were placed onto the anchors, and gas samples were taken in polypropylene syringes after 0, 15 and 30 minutes. Samples were analyzed for  $N_2O$ ,  $CH_4$  and  $CO_2$  within 24 hours of sampling by gas chromatography, using flame ionization detection for  $CH_4$  analysis and electron capture detection for  $N_2O$  and  $CO_2$  analysis (Mosier & Mack 1980). Leakage rates for our syringes were less than 1% for a 24 hour period with double ambient levels of  $N_2O$  (Mosier & Hutchinson 1981).  $NO$  fluxes were analyzed *in situ* using a luminol-based chemiluminescence detector (Wendel et al. 1983; Schiff et al. 1986).  $CO_2$

Table 1. Site soil properties (0–15 cm).

| Site number | Site name       | Sand, % | Clay, % | Bulk density, g/cm <sup>3</sup> | Total N, % | Total C, % | Gravimetric soil water content at WFPS kg/kg (×100) |      |      |
|-------------|-----------------|---------|---------|---------------------------------|------------|------------|---|------|------|
|             |                 |         |         |                                 |            |            | 0.2   | 0.4  | 0.6  |
| 1           | Sandy clay loam | 54      | 30      | 1.24                            | 0.146      | 1.39       | 8.6   | 17.2 | 25.8 |
| 2           | Clay            | 37      | 43      | 1.27                            | 0.115      | 1.20       | 8.2   | 16.4 | 24.6 |

accumulating in the opaque chambers is the sum of  $\text{CO}_2$  from soil respiration and  $\text{CO}_2$  from plant respiration in the absence of photosynthesis; we therefore used  $\text{CO}_2$  flux to represent gross ecosystem respiration (Odum 1969; Schlesinger 1991).

Soil temperature at 5 cm depth was measured at approximately 40 minute intervals during each sampling period. Air temperatures used in the gas flux calculations were taken approximately every 20 minutes during the time of sampling. Soil moisture to 15 cm depth was estimated gravimetrically for three locations with mixed  $\text{C}_3$  and  $\text{C}_4$  composition at each site on every sampling date and converted to proportion of water-filled pore space (WFPS) (Linn & Doran 1984).

We tested for significant differences among plant community treatments within each site and year combination. At each site, we had six gas flux estimates for each plant community treatment on every sampling date; therefore the number of observations for each treatment was six multiplied by the number of sampling dates for the year being tested. Because the trace gas data were not easily normalized using common data transformations, we used the non-parametric Wilcoxon ranked sum procedure (SAS 1991) to compute the test statistic. We conducted *t*-tests with pooled standard errors *a posteriori* to compare means across soil texture and year, comparisons that were not part of our initial hypotheses. Linear and nonlinear regressions were used to relate the fluxes of  $\text{NO}$ ,  $\text{N}_2\text{O}$  and  $\text{CH}_4$  to WFPS and soil temperature. A more complex function was used only when it provided a significantly better fit to the data (Huisman et al. 1993). Given the limited nature of the statistical design, we caution readers when making inferences beyond our sites of study.

## Results

### *Environmental conditions: Soil moisture and temperature*

The growing seasons of 1995 and 1996 at our sites were climatically different (Figure 1). The spring of 1995 was uncommonly wet, with 138 mm of precipitation falling in May and 108 mm in June; WFPS to 15 cm approached 0.8 at the clay site, and peaked greater than 0.6 at the sandy clay loam site, through the first week in June. WFPS then declined to less than 0.2 at both sites during late August and mid September, until precipitation in late September. Soil temperatures were cool in the spring of 1995, approximately  $10^\circ\text{C}$  on May 18. However, soils became relatively hot later in the growing season, peaking at greater than  $30^\circ\text{C}$  in late August before dropping in late September.

In contrast, the spring of 1996 was warm and dry. Soil temperatures were greater than  $25^\circ\text{C}$  on May 16, and WFPS was less than 0.2 at both sites on

## Soil Moisture and Temperature

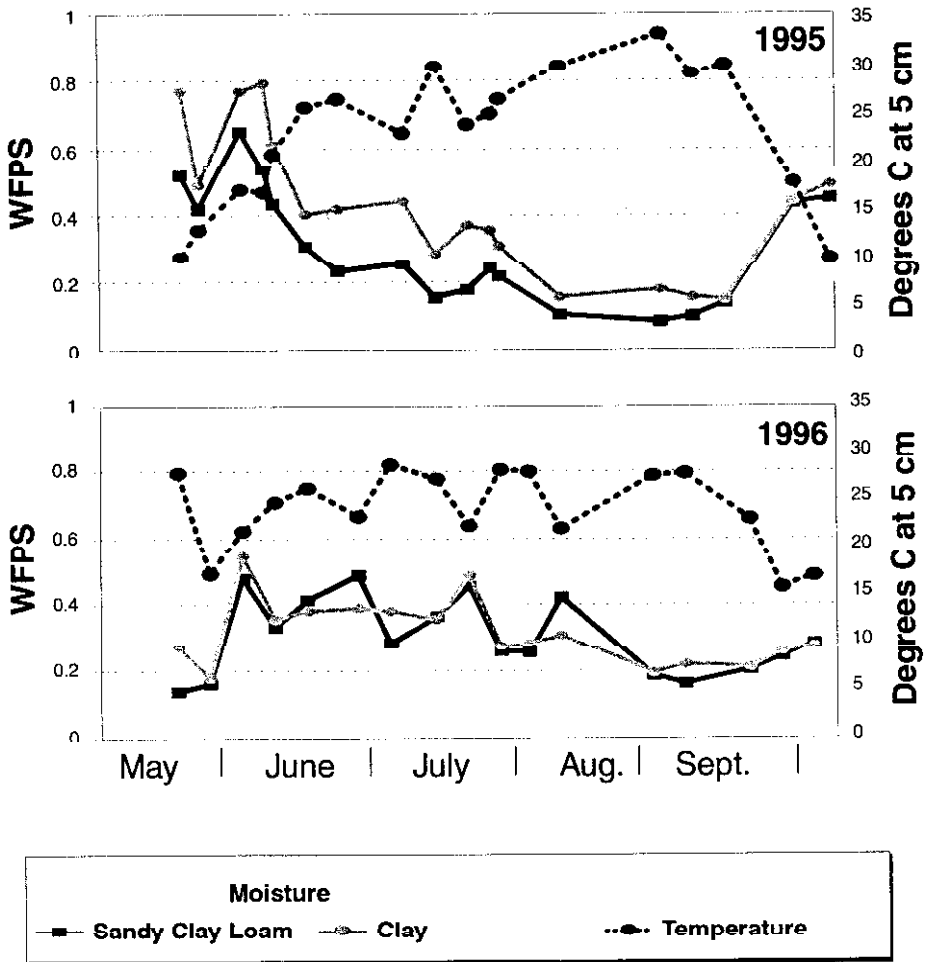


Figure 1. Seasonal patterns of proportion of water-filled pore space and soil temperature at 5 cm depth on a sandy clay loam and a clay, for 1995 and 1996. Soil temperatures were very similar between sites, therefore only the average of the two sites is presented.

May 23. Beginning in late May the moisture and temperature regimes were relatively consistent throughout the remainder of the growing season; soil temperatures were between 20 and 30 °C, and WFPS was between 0.2 and 0.5. There was a dry period from late August to mid September, and soil temperatures dropped below 20 °C beginning late September.

### *Trace gas fluxes*

NO, N<sub>2</sub>O and CH<sub>4</sub> fluxes were all significantly related to WFPS and soil temperature ( $p < 0.05$  for all relationships) (Figure 2a–f). Skewed curves were fitted to relationships between NO flux and both WFPS and soil temperature. N<sub>2</sub>O flux increased linearly with WFPS and decreased linearly with soil temperature. CH<sub>4</sub> uptake decreased linearly with WFPS, and a skewed curve was fitted to the relationship between CH<sub>4</sub> uptake and soil temperature. While all three plant communities exhibited similar seasonal patterns of NO, N<sub>2</sub>O and CH<sub>4</sub> fluxes, there were some differences in the magnitude of trace gas fluxes among plant community types; these differences were found only for certain years and sites. Because the temporal patterns of trace gas fluxes were similar between sites, we present the seasonal flux data for only the sandy clay loam site.

High soil water content in the spring of 1995, and dry conditions late in the growing season of both years, generally constrained NO fluxes (Figure 3a–b). NO fluxes peaked at greater than 40 gN ha<sup>-1</sup> d<sup>-1</sup> on the sandy clay loam site in 1995. Mean NO fluxes were 9.7 and 5.7 gN ha<sup>-1</sup> d<sup>-1</sup> on the sandy clay loam for 1995 and 1996, respectively; mean NO fluxes were 3.9 and 2.6 gN ha<sup>-1</sup> d<sup>-1</sup> on the clay site for 1995 and 1996, respectively (Figure 4). In 1995, NO fluxes from C<sub>4</sub> plots (13.6 gN ha<sup>-1</sup> d<sup>-1</sup>) were significantly greater than fluxes from C<sub>3</sub> (6.0 gN ha<sup>-1</sup> d<sup>-1</sup>) and mixed plots (9.4 gN ha<sup>-1</sup> d<sup>-1</sup>) on the sandy clay loam ( $p < 0.05$ ), but in 1996, there were no significant differences among plant communities. Additionally, NO fluxes from C<sub>4</sub> plots were significantly greater in 1995 compared to 1996 ( $p < 0.05$ ). There were no significant differences among plant communities on the clay site in either year.

N<sub>2</sub>O fluxes were greatest during times of high WFPS, approaching 6 gN ha<sup>-1</sup> d<sup>-1</sup> on the sandy clay loam site during the very wet spring of 1995 (Figure 5a–b); the maximum flux at the clay site was ~3 gN ha<sup>-1</sup> d<sup>-1</sup>. N<sub>2</sub>O fluxes at both sites were close to zero during the driest parts of both years. Average N<sub>2</sub>O fluxes on the sandy clay loam were 1.4 and 1.2 gN ha<sup>-1</sup> d<sup>-1</sup> for 1995 and 1996, respectively, and on the clay were 1.0 and 0.5 gN ha<sup>-1</sup> d<sup>-1</sup>, respectively (Figure 6). There were no significant differences in N<sub>2</sub>O fluxes among plant community types on the sandy clay loam in either year. N<sub>2</sub>O fluxes on mixed plots were significantly lower than on C<sub>3</sub> plots ( $p < 0.05$ ) at the clay site in 1996.

CH<sub>4</sub> uptake at the sandy clay loam site was least during periods with high WFPS, less than 1 gC ha<sup>-1</sup> d<sup>-1</sup> during the spring of 1995 and on the wettest sampling date in 1996 (Figure 7a–b). It was greatest when the soil was drying and remained relatively high during dry periods. The uptake rate reached ~4 gC ha<sup>-1</sup> d<sup>-1</sup> in July of 1995 and was greater than 4 gC ha<sup>-1</sup> d<sup>-1</sup> for several



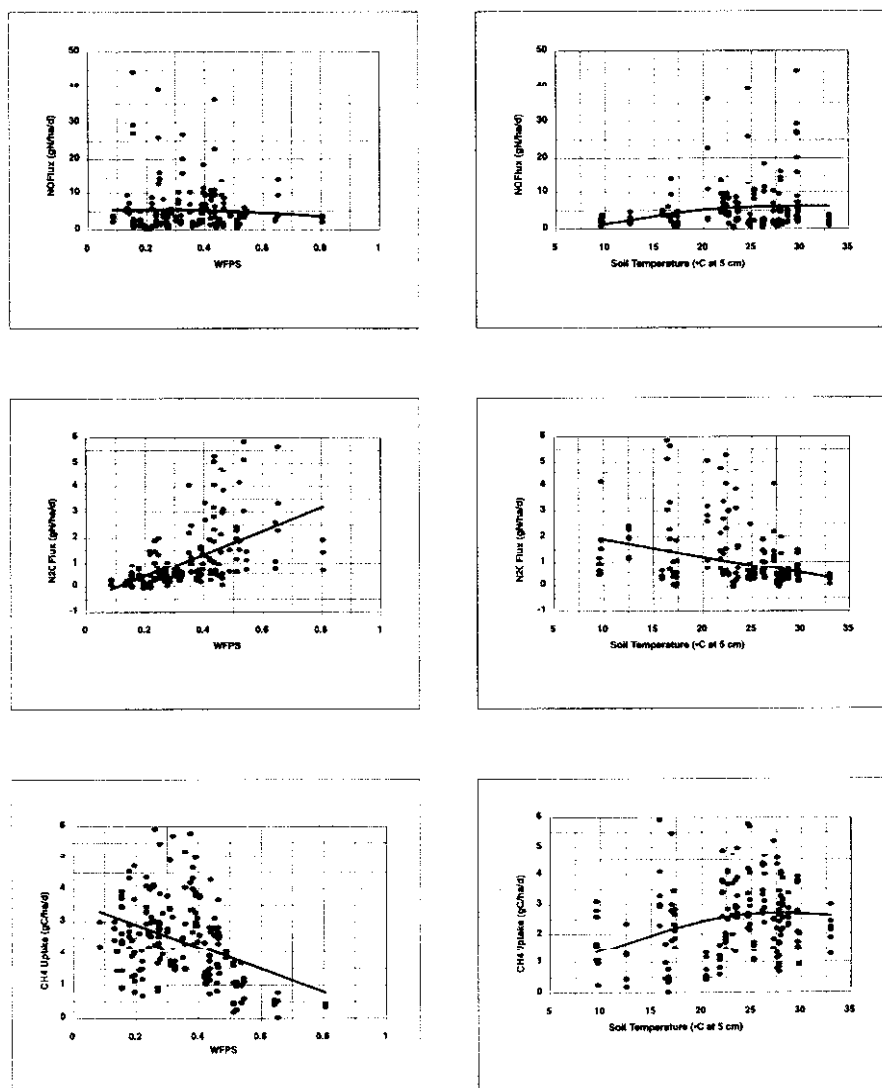


Figure 2. Relationships between (a) NO flux and water-filled pore space (WPFS);  $\text{NO} = 10.8 / ((1 + e^{(-2.2 + 3.0 * \text{WPFS})}) * (1 + e^{(-0.3 - 1.1 * \text{WPFS})}))$ ,  $r^2 = 0.10$ , (b) NO flux and soil temperature (TEMP);  $\text{NO} = 6.2 / ((1 + e^{(4.1 - 0.3 * \text{TEMP})}) * (1 + e^{(9.4 - 702.4 * \text{TEMP})}))$ ,  $r^2 = 0.08$ , (c) N<sub>2</sub>O and WPFS;  $\text{N}_2\text{O} = -0.5 + 4.6 * \text{WPFS}$ ,  $r^2 = 0.29$ , (d) N<sub>2</sub>O and soil temperature;  $\text{N}_2\text{O} = 2.6 - 0.1 * \text{TEMP}$ ,  $r^2 = 0.10$ , (e) CH<sub>4</sub> uptake and WPFS;  $\text{CH}_4 = 3.6 - 3.5 * \text{WPFS}$ ,  $r^2 = 0.16$ , (f) CH<sub>4</sub> and soil temperature;  $\text{CH}_4 = 20.8 / ((1 + e^{(0.8 + 0.03 * \text{TEMP})}) * (1 + e^{(2.4 - 0.1 * \text{TEMP})}))$ ,  $r^2 = 0.20$ . All relationships are statistically significant ( $p < 0.05$ ).

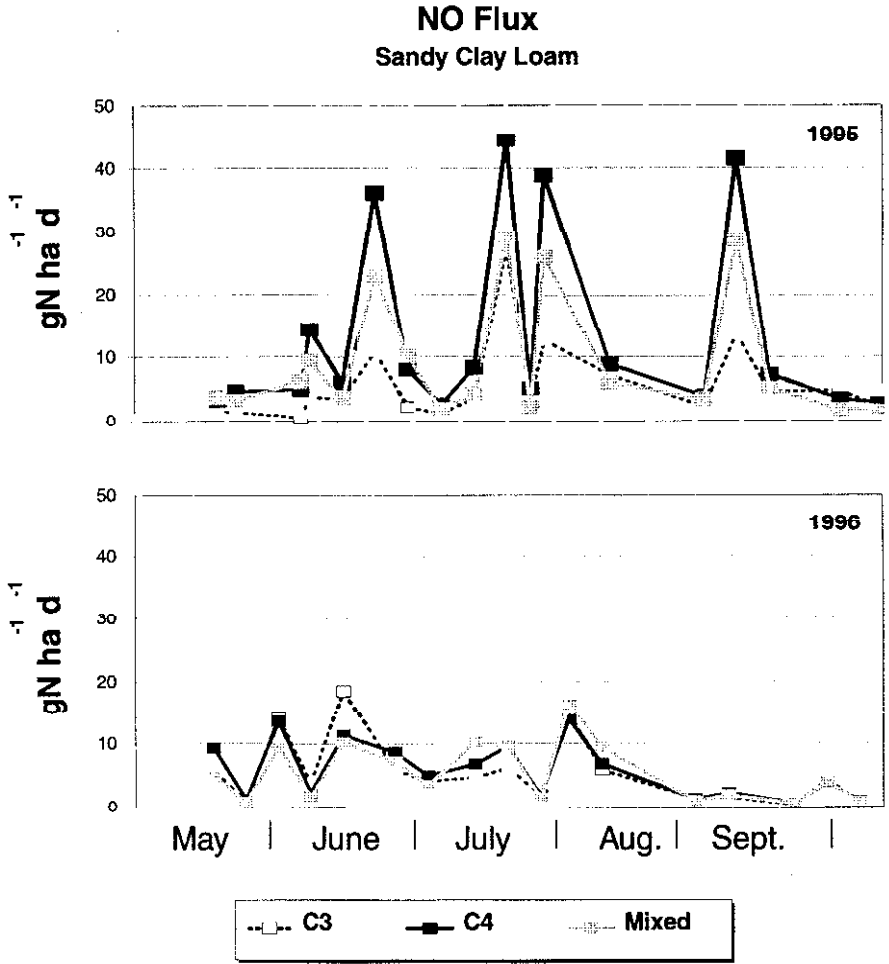


Figure 3. Seasonal patterns of NO fluxes on a sandy clay loam in shortgrass steppe from C<sub>3</sub>, C<sub>4</sub> and mixed plots, for 1995 and 1996.

sampling dates during 1996. CH<sub>4</sub> uptake averaged 2.2 and 2.9 gC ha<sup>-1</sup> d<sup>-1</sup> on the sandy clay loam in 1995 and 1996, respectively, and 2.0 and 2.6 gC ha<sup>-1</sup> d<sup>-1</sup> on the clay in 1995 and 1996, respectively (Figure 8). CH<sub>4</sub> uptake on the sandy clay loam was significantly greater in C<sub>4</sub> plots than C<sub>3</sub> plots for both 1995 and 1996 ( $p < 0.05$ ), averaging 2.4 and 2.6 gC ha<sup>-1</sup> d<sup>-1</sup> on C<sub>4</sub> plots in 1995 and 1996, respectively, compared to 1.9 and 2.2 gC ha<sup>-1</sup> d<sup>-1</sup> on the C<sub>3</sub> plots. There were no significant differences in CH<sub>4</sub> uptake among plant communities on the clay site in either year.

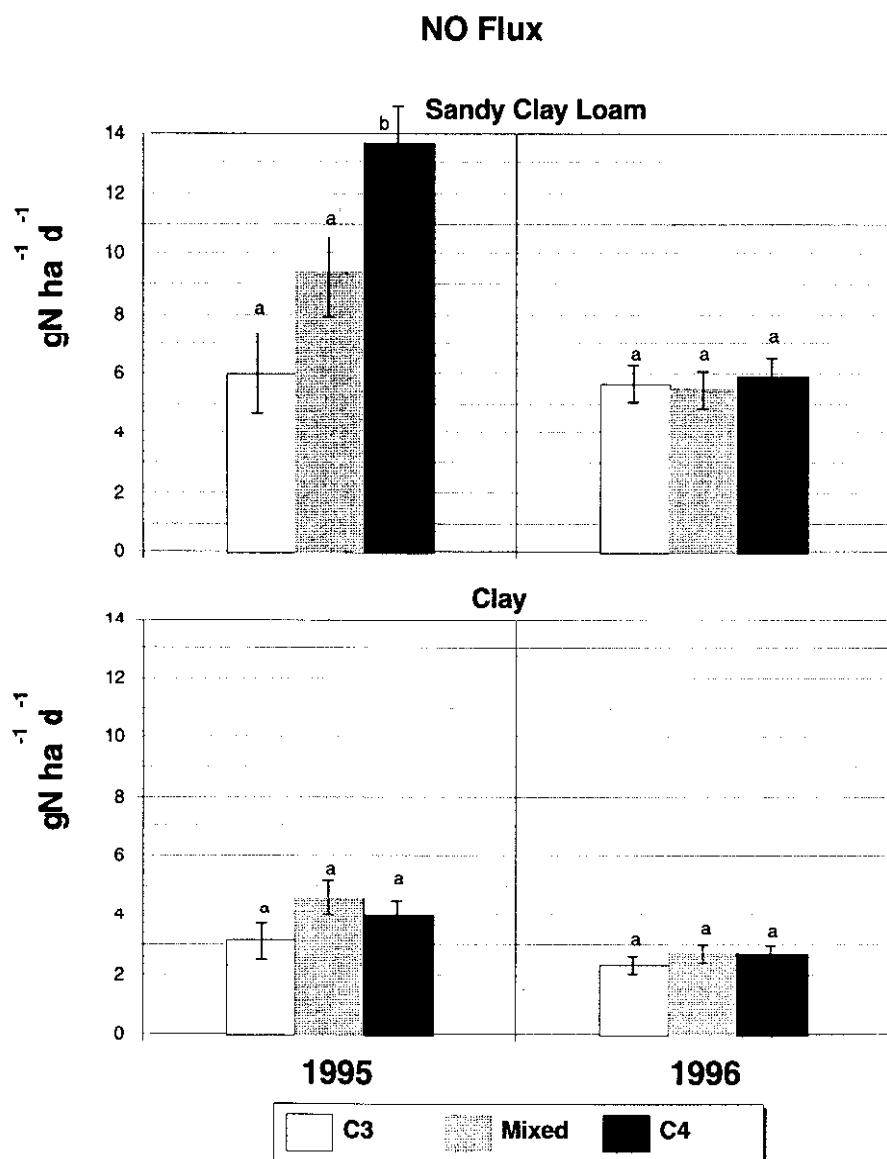


Figure 4. Mean NO flux for three shortgrass steppe plant communities (C<sub>3</sub>, C<sub>4</sub> and mixed) in 1995 and 1996 on a sandy clay loam and a clay. Bars are one standard error. Different letters represent significant differences within each year.

### Gross ecosystem respiration

CO<sub>2</sub> fluxes peaked during mid June in 1995, but in 1996 the peak CO<sub>2</sub> flux was observed in mid July (Figure 9a–b). Mean CO<sub>2</sub> fluxes were significantly

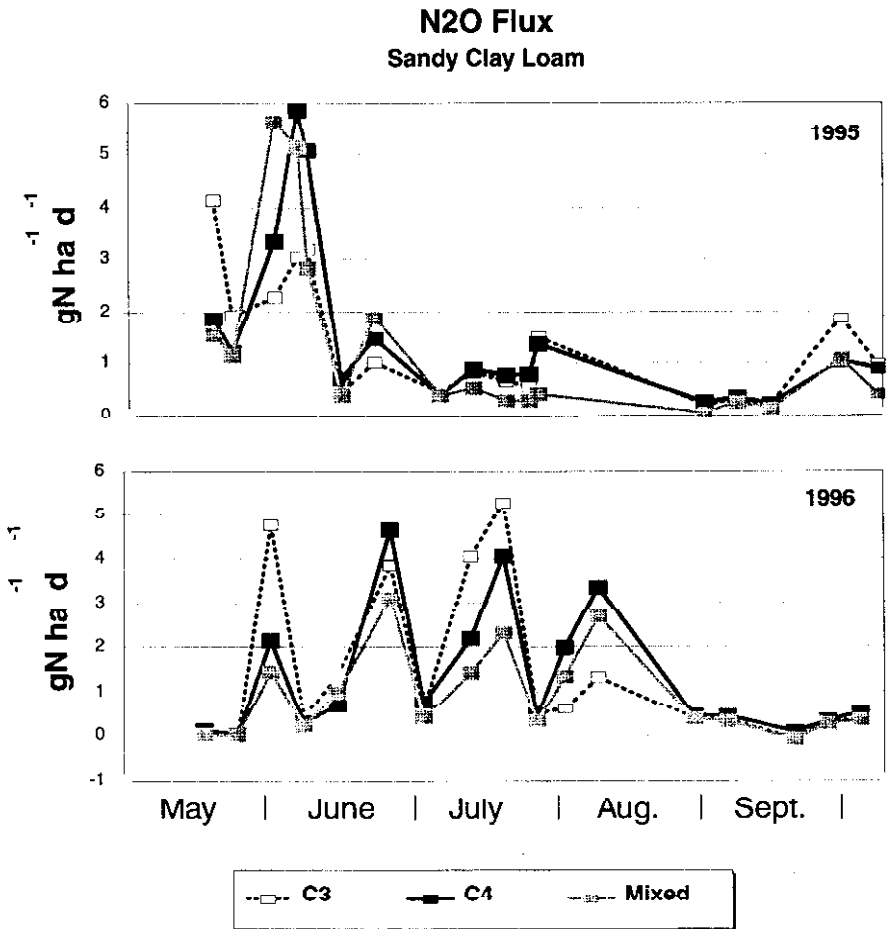


Figure 5. Seasonal patterns of N<sub>2</sub>O fluxes on a sandy clay loam in shortgrass steppe from C<sub>3</sub>, C<sub>4</sub> and mixed plots, for 1995 and 1996.

greater from C<sub>3</sub> plots than C<sub>4</sub> plots on the sandy clay loam during 1995, but the reverse was true on the same site during 1996 ( $p < 0.05$ ) (Figure 10). There were no significant differences in CO<sub>2</sub> fluxes among plant communities on the clay site for either year.

**Discussion**

Soil moisture and soil temperature explained between 8% and 29% of the variation in fluxes of NO, N<sub>2</sub>O and CH<sub>4</sub> uptake. We fit skewed curves to the relationships between NO flux, and WFPS and soil temperature. Williams and

## N<sub>2</sub>O Flux

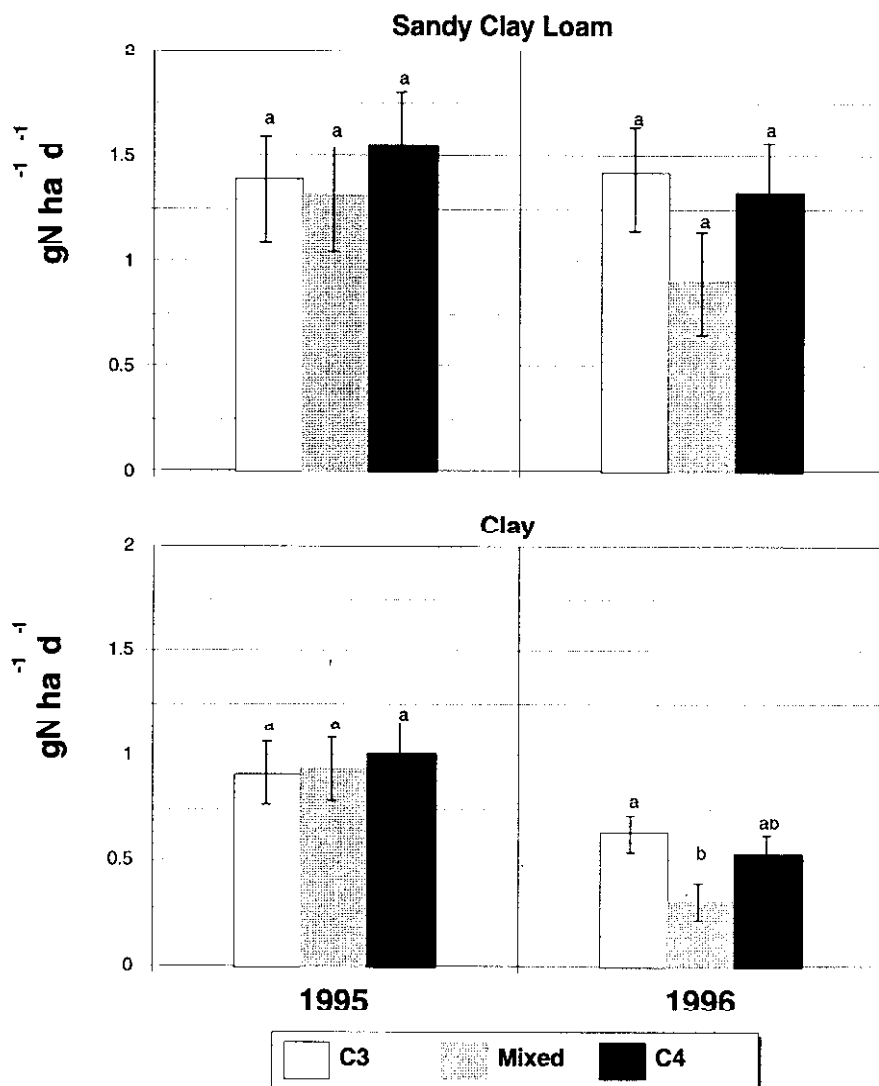
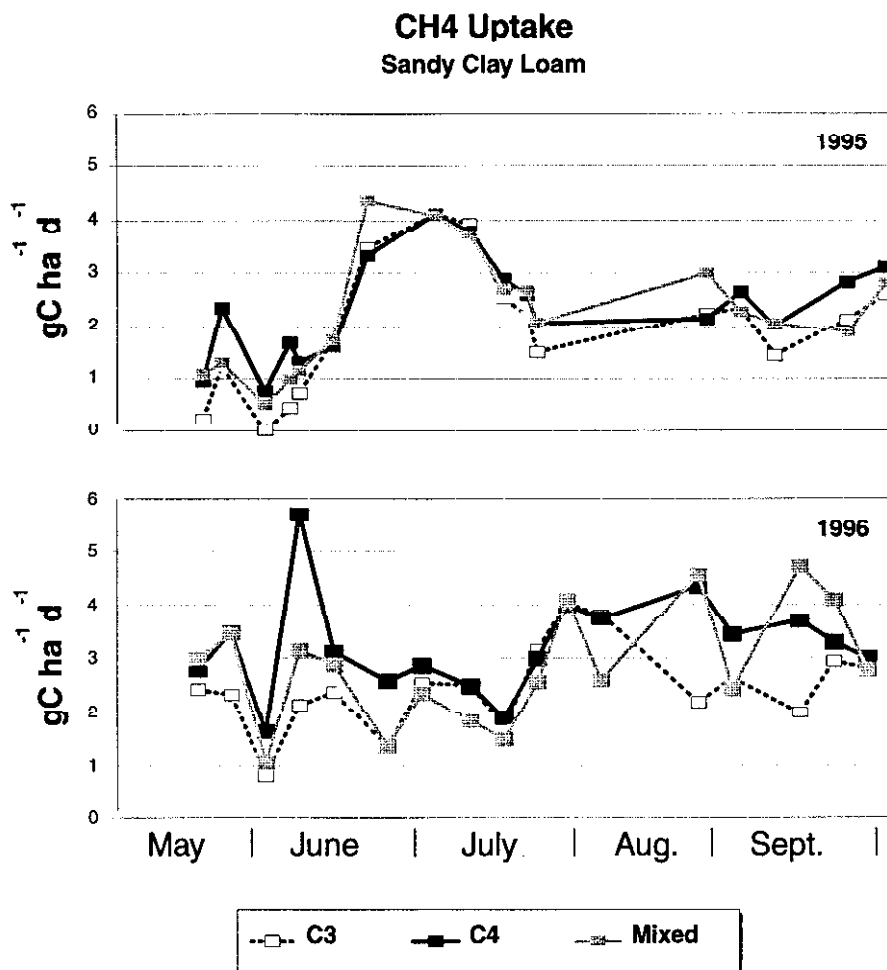


Figure 6. Mean N<sub>2</sub>O flux for three shortgrass steppe plant communities (C<sub>3</sub>, C<sub>4</sub> and mixed) in 1995 and 1996 on a sandy clay loam and a clay. Bars are one standard error. Different letters represent significant differences within each year.

Fehsenfeld (1991) show NO emissions increasing with soil moisture (% of dry weight) within a soil moisture range from 1% to 9% when soil temperatures were normalized to 30 °C. Other studies show field fluxes and laboratory



*Figure 7.* Seasonal patterns of CH<sub>4</sub> uptake on a sandy clay loam in shortgrass steppe from C<sub>3</sub>, C<sub>4</sub> and mixed plots, for 1995 and 1996.

incubations of NO decreasing linearly with soil moisture over ranges from 6% to 50% gravimetric soil moisture (Davidson et al. 1993; Yamulki et al. 1995). Studies have shown NO fluxes increasing with soil temperature (Williams & Fehsenfeld 1991; Yamulki et al. 1995). Several studies concur that N<sub>2</sub>O emissions increase with WFPS and soil moisture (Parton et al. 1988; Davidson et al. 1993; Mosier et al. 1996). Mosier et al. (1996) show N<sub>2</sub>O fluxes increasing with soil temperature when WFPS was greater than 0.3. Mosier et al. (1996) fit a skewed curve to the relationship between CH<sub>4</sub> uptake and WFPS, and they show CH<sub>4</sub> uptake increasing linearly with soil temperature when WFPS was between 0.15 and 0.25.

## CH<sub>4</sub> Uptake

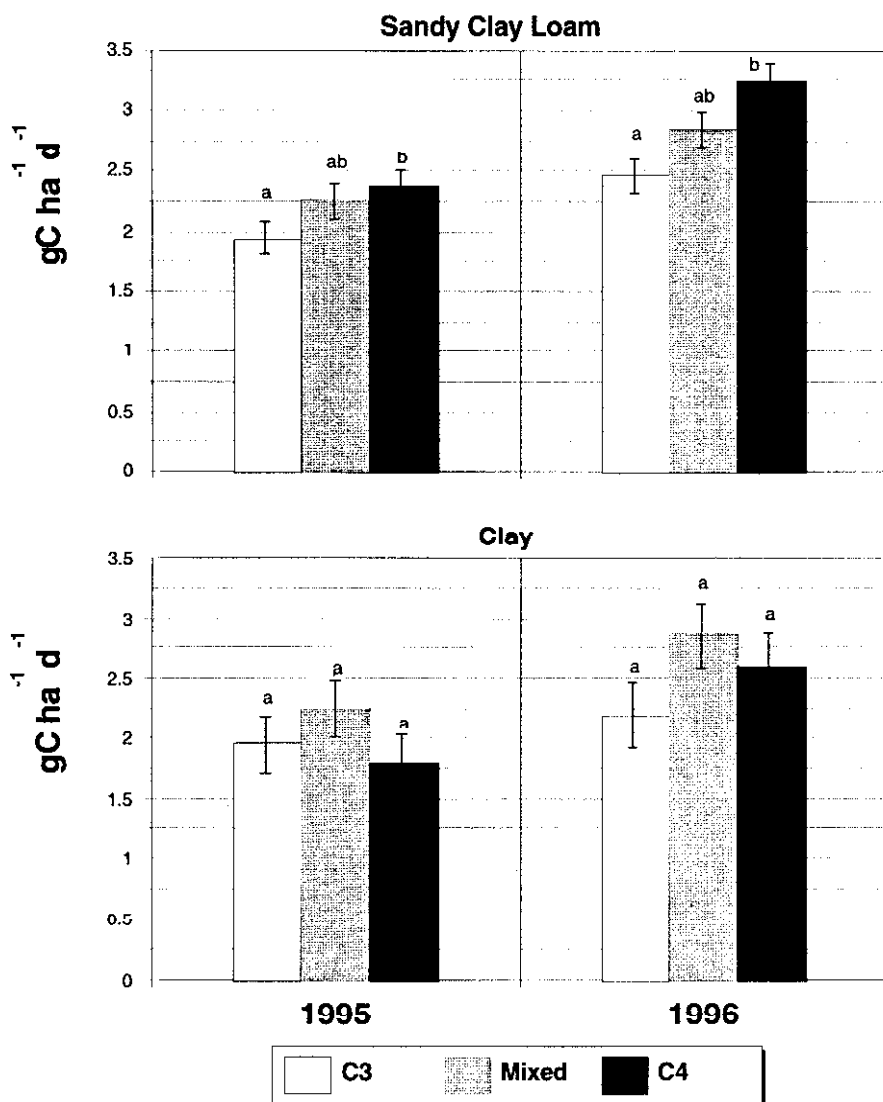


Figure 8. Mean CH<sub>4</sub> uptake for three shortgrass steppe plant communities (C<sub>3</sub>, C<sub>4</sub> and mixed) in 1995 and 1996 on a sandy clay loam and a clay. Bars are one standard error. Different letters represent significant differences within each year.

Our results indicated that under certain environmental conditions plant community structure does play a significant role in the regulation of trace gas fluxes between atmosphere and biosphere. Our initial hypothesis, that the seasonal patterns of trace gas fluxes would differ among plant community

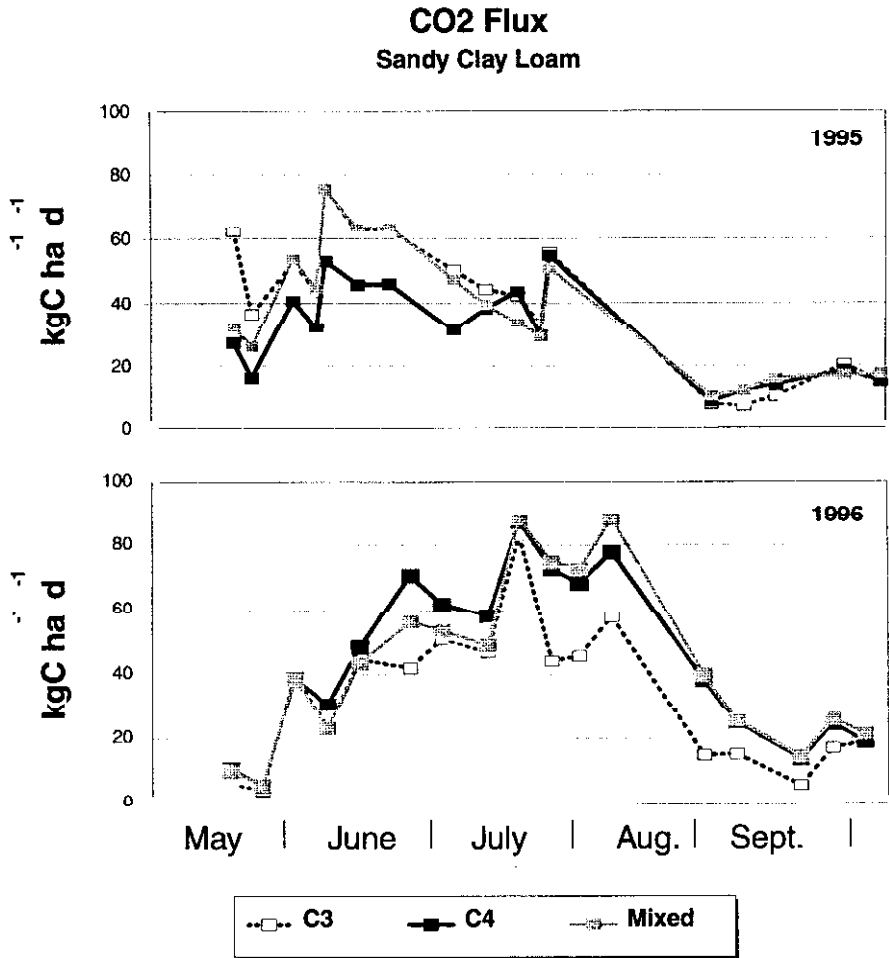


Figure 9. Seasonal patterns of CO<sub>2</sub> fluxes on a sandy clay loam in shortgrass steppe from C<sub>3</sub>, C<sub>4</sub> and mixed plots, for 1995 and 1996.

types because of plant phenology differences, was only partially supported. Intraseasonal patterns of trace gas fluxes were similar among plant community types, however, there were several statistically significant differences in the magnitudes of fluxes among plant communities.

There was only one instance (Figure 6) of a significant difference among plant communities at the clay site. Greater WFPS (0–15 cm) at this site than at our sandy clay loam likely limited soil gas diffusivities, including that of O<sub>2</sub>, a proximal controlling factor of the microbial processes that drive NO, N<sub>2</sub>O, and CH<sub>4</sub> production and consumption. Slower decomposition rates (Jenkinson 1977; Monreal et al. 1991) and greater N immobilization



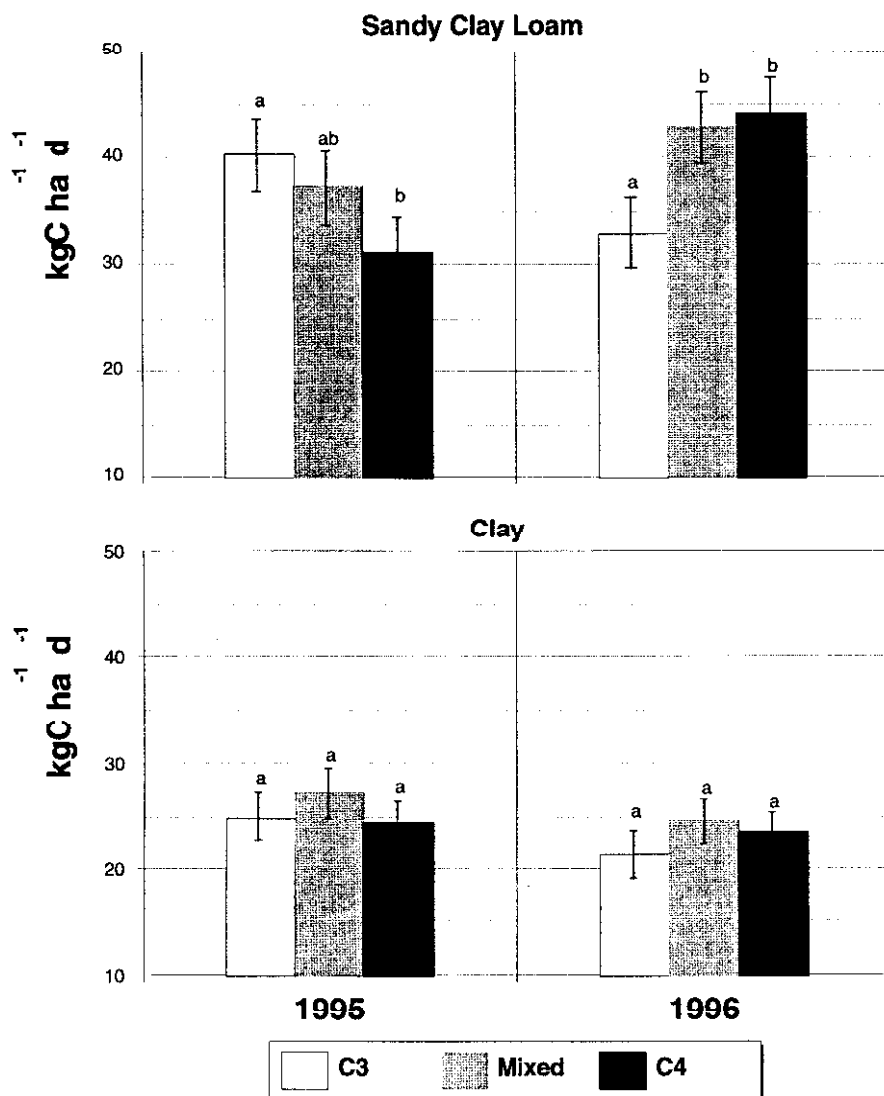
CO<sub>2</sub> Flux

Figure 10. Mean CO<sub>2</sub> flux for three shortgrass steppe plant communities (C<sub>3</sub>, C<sub>4</sub> and mixed) in 1995 and 1996 on a sandy clay loam and a clay. Bars are one standard error. Different letters represent significant differences within each year.

(Schimel et al. 1985; Schimel 1988) on fine-textured soils could also limit the availability of inorganic N substrates for nitrification and denitrification. Supporting this possibility, Schimel and Parton (1986) found significantly

lower net N mineralization rates on a fine-textured soil in the shortgrass steppe compared to a coarse-textured soil. Lower soil gas diffusivities and reduced inorganic N availability probably both contributed to the absence of significant differences in NO and CH<sub>4</sub> fluxes among plant communities on the clay site.

NO fluxes were significantly greater from C<sub>4</sub> plots than from mixed or C<sub>3</sub> plots on the sandy clay loam site in 1995. Plants, and both autotrophic and heterotrophic microbes, compete for available NH<sub>4</sub><sup>+</sup> (Jackson et al. 1989; Verhagen et al. 1995). The high activity of C<sub>3</sub> plants in the spring of 1995 (Epstein et al. 1997a) potentially could have constrained NO fluxes, by sequestering more inorganic N than the other communities and limiting microbial nitrification rates. In a separate study conducted on the same sites, N uptake by C<sub>3</sub> plants during May was almost three times that of C<sub>4</sub> plants; total N uptake by C<sub>3</sub> plants for the growing season of 1995 was estimated to be 30% more than N taken up by C<sub>4</sub> plants (Epstein et al. 1997a). The additional N uptake by C<sub>3</sub> plants is likely enough to account for greater N mineralized in C<sub>3</sub> communities (Wedin & Tilman 1990; Epstein et al. 1997a).

The dominant C<sub>3</sub> grass at our sites, *Agropyron smithii*, has been shown to have higher protein concentrations in green forage (Cook et al. 1977) and higher N concentrations in crowns and large roots (Hunt et al. 1996) than the dominant C<sub>4</sub> grass, *Bouteloua gracilis*. Hunt et al. (1996) report crown N concentrations of 1.47% and 0.85%, and large root N concentrations of 1.28% and 0.94%, respectively for *A. smithii* and *B. gracilis*. Epstein et al. (1997a), however, did not find significant differences in tissue N concentrations between C<sub>3</sub> and C<sub>4</sub> plants. Aboveground biomass has also been shown to be significantly greater in *A. smithii* than *B. gracilis* (Hunt et al. 1996). Whereas greater N use by C<sub>3</sub> plants in 1995 could have limited NO fluxes from C<sub>3</sub> plots, there were no significant differences in NO fluxes among the plant communities in 1996. Lower, and more evenly distributed, precipitation in 1996 compared to 1995 could have limited NO fluxes such that potential effects of plants were not evident.

CH<sub>4</sub> uptake rates on the sandy clay loam were substantially less than a 4-year average on a comparable site (Mosier et al. 1996), likely because of above average rainfall during the years of our study. CH<sub>4</sub> uptake was significantly greater on C<sub>4</sub> plots than C<sub>3</sub> plots on the sandy clay loam in both years. Laboratory studies suggest that NH<sub>4</sub><sup>+</sup> can inhibit CH<sub>4</sub> consumption by methanotrophs and nitrifiers (Whittenbury et al. 1970; Bronson & Mosier 1994), through competition with CH<sub>4</sub> for the active enzyme sites in methane oxidation and nitrification (Bédard & Knowles 1989). However, several investigators have found that high N turnover rates, rather than NH<sub>4</sub><sup>+</sup> levels, may be the important controlling factor (Mosier et al. 1991; Hütsch et

al. 1993). Studies in grassland ecosystems have found greater net N mineralization rates in  $C_3$  than  $C_4$  communities (Wedin & Tilman 1990; Wedin & Pastor 1993; Epstein et al. 1997a), providing support for the inhibition of  $CH_4$  oxidation in  $C_3$  plots. Differences in N turnover have been attributed in some studies to differences in  $C_3$  vs.  $C_4$  plant litter quality, or C:N ratios (Hobbie 1992; Wedin 1995). Epstein et al. (1997a), however, did not find significant differences in C:N ratios between  $C_3$  and  $C_4$  plants.

$N_2O$  fluxes on the sandy clay loam were approximately 60% greater than a 4-year average measured by Mosier et al. (1996) on a comparable site. The difference is likely due to above average precipitation during the years of our study and the fact that our measurements were made only during the growing season. There was no site from Mosier et al. (1996) comparable to our clay site. There was only one combination of year and site where plant community had a significant effect on  $N_2O$  fluxes, which are more likely controlled by the availability of  $O_2$  than by other factors (Tiedje 1988; Firestone & Davidson 1989; Robertson 1989). On the clay site in 1996, mixed plots had significantly lower  $N_2O$  fluxes than either  $C_3$  or  $C_4$  plots. This is a situation where diverse plots, in terms of plant functional types, potentially constrained a vector of N loss from the system. Other studies have found that communities of high species or functional type richness have greater nutrient use by plants (Ewel et al. 1991; Hooper & Vitousek 1997; Tilman et al. 1997) and can limit the leaching of  $NO_3^-$  below the rooting zone of plants (Tilman et al. 1996). However, with our simple experimental design (diverse plots of two functional types), we found no other evidence to support reduced nutrient losses in plots with greater functional type diversity.

There have been relatively few studies that examined the effects of plants on trace gas fluxes. Several studies have examined whether root exudate C from actively growing plants stimulates denitrification, resulting in gaseous N loss; results have been contradictory, with some studies finding increased denitrification in the rhizosphere of actively growing plants (e.g. Woldendorp 1962), while others show no effect of root exudates even when  $NO_3^-$  is non-limiting (Haider et al. 1987). In a study by Mosier et al. (1986), total  $N_2O + N_2$  emissions from a corn field ( $C_4$  crop) were three times those from a barley field ( $C_3$  crop). The spring of the barley growing season was uncommonly wet, which could have enhanced denitrification, but the process may have been constrained by relatively low soil temperatures; high recovery of applied nitrogen by the barley may also have played an important role in limiting gaseous N losses.  $N_2O$  fluxes were also greater from an irrigated corn system ( $C_4$  crop) than from an irrigated wheat system ( $C_3$  crop) when nitrogen fertilizer was added (Bronson & Mosier 1993).

Our study provides some insight into the complex interactions among climate, plant community structure and the ecosystem processes that drive trace gas fluxes. We have identified some conditions under which the composition of C<sub>3</sub> and C<sub>4</sub> plant functional types in a shortgrass steppe community influenced the exchange of trace gases between soil and atmosphere. Our results indicate that plant functional type effects on trace gas fluxes can be observed over annual times scales, when other factors such as moisture and temperature are not limiting. Changes in temperature and precipitation will likely affect the magnitude of trace gas fluxes (Peterjohn et al. 1994; Hantschel et al. 1995; Torn & Harte 1996), as well as the function of C<sub>3</sub> and C<sub>4</sub> plants (Hunt et al. 1996). An understanding of how plants can influence soil microbial processes and the resultant gas exchange may be an important inclusion for predictions of trace gas budgets.

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