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Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass

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Abstract

The responses of tallgrass prairie plant communities and ecosystem processes to fire and grazing are well characterized. However, responses of invertebrate consumer groups, and particularly soil-dwelling organisms, to these disturbances are not well known. At Konza Prairie Biological Station, we sampled soil macroinvertebrates in 1994 and 1999 as part of a long-term experiment designed to examine the effects and interactions of annual fire, mowing, and fertilization (N and P) on prairie soil communities and processes. For nearly all taxa, in both years, responses were characterized by significant treatment interactions, but some general patterns were evident. Introduced European earthworms (*Aporrectodea* spp. and *Octolasion* spp.) were most abundant in plots where fire was excluded, and the proportion of the total earthworm community consisting of introduced earthworms was greater in unburned, unmowed, and fertilized plots. Nymphs of two Cicada genera were collected (*Cicadetta* spp. and *Tibicen* spp.). *Cicadetta* nymphs were more abundant in burned plots, but mowing reduced their abundance. *Tibicen* nymphs were collected almost exclusively from unburned plots. Treatment effects on herbivorous beetle larvae (Scarabaeidae, Elateridae, and Curculionidae) were variable, but nutrient additions (N or P) usually resulted in greater densities, whereas mowing usually resulted in lower densities. Our results suggest that departures from historical disturbance regimes (i.e. frequent fire and grazing) may render soils more susceptible to increased numbers of European earthworms, and that interactions between fire, aboveground biomass removal, and vegetation responses affect the structure and composition of invertebrate communities in tallgrass prairie soils.
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1. Introduction

Tallgrass prairie ecosystems are maintained by periodic disturbances such as fire and grazing (Axelrod, 1985; Knapp et al., 1998a). These disturbances limit the encroachment of woody vegetation into landscapes that would otherwise support forest vegetation (Briggs et al., 1998). Annual spring fire is a common land management practice employed by livestock ranchers to maintain rangeland and maximize production of warm-season forage grasses in the Flint Hills region of eastern Kansas, USA. Additionally, large land areas are mowed annually for hay (as supplemental winter feed for livestock). Changes in plant community species composition in response to fire, mowing, and grazing are documented by Gibson et al. (1993), Collins and Steinauer (1998), Collins et al. (1998), and Knapp et al. (1999), as are ecosystem process level responses to these disturbances (Knapp and Seastedt, 1986; Blair, 1997; Knapp et al., 1998b). However, responses of belowground invertebrates to these important disturbances in tallgrass prairie are less well known (Rice et al., 1998; Blair et al., 2000). These organisms can be important regulators of processes such as plant productivity, nutrient transformation, and organic matter cycling in soil systems (Coleman and Crossley, 1996; Coleman and Hendrix, 2000), and their effects on these processes are often related to their densities.

Earthworms are influential organisms in soil systems where they are abundant. Earthworms affect soil ecosystems

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through their burrowing and feeding behavior, resulting in improved aeration, water infiltration, and incorporation of organic matter (Edwards and Bohlen, 1996). Indeed, earthworms have been referred to as 'ecosystem engineers' because of these profound physical effects on the soil environment (Jones et al., 1994). However, earthworms are also important in terms of biological processes such as nutrient cycling and microbial turnover (Brown, 1995), with increased soil microbial activity and nutrient mineralization in soils where earthworms are present (Scheu, 1987; Lavelle et al., 1992; Zhang and Hendrix, 1995; Saetre, 1998). Although the effects of earthworms on soil systems are relatively well known, most information on earthworm ecology comes from studies of European taxa. Nevertheless, there are numerous species of native North American earthworms in undisturbed soils, and much less is known about these taxa (Hendrix, 1995). Large assemblages of North American earthworm species occur in the Flint Hills region of eastern Kansas (James, 1991, 1995), but European taxa have been introduced to the area and are expanding their ranges into soils occupied by native earthworms (Callaham et al., 1999, 2001). Changes in land management such as exclusion of fire or expansion of forest vegetation in the Flint Hills (Briggs et al., 1998), may facilitate the establishment of exotic earthworms, but interactions (if any) between native and exotic earthworm taxa are poorly understood.

Herbivorous insects make up the majority of arthropod biomass in tallgrass prairie soils (Seastedt, 1984; Seastedt et al., 1986). Previous studies, based on experiments of differing duration (2–5 y), have reported inconsistent responses of these insects to burning and mowing. Herbivorous insects are important regulators of plant productivity in some ecosystems, and they are generally responsive to changes in resource quantity or quality (Schowalter, 2000). Their responses to long-term changes in plant community composition, and plant resource quality are potentially important in tallgrass prairie ecosystems (Blair et al., 2000).

Nutrient limitations play a major role in affecting tallgrass prairie plant communities and consumers, and their effects vary under different fire and grazing regimes (Blair, 1997; Johnson and Matchett, 2001). Nitrogen is generally considered to be the nutrient most limiting to plant productivity in these grasslands (Seastedt et al., 1991; Turner et al. 1997), though soil P availability is also low and can influence plant community composition via plant–mycorrhizal interactions (Hartnett and Wilson, 1999). Frequent fires result in large N losses due to combustion of plant tissues and associated volatilization of N (Ojima et al., 1994; Blair et al., 1998). Mowing and haying can also remove substantial amounts of N in aboveground plant tissues. However, in the absence of these disturbances, soil N availability increases (Blair, 1997), and over the long term, other nutrients such as P may become limiting to primary (or secondary) production in the tallgrass prairie system. Thus, our objectives were to examine influences of annual fire, mowing, and nutrient (N and P) additions on density and biomass of selected taxa of belowground invertebrates (including native and exotic earthworms, and herbivorous insects). We addressed these objectives in the context of a long-term replicated plot experiment by analyzing belowground invertebrate samples collected in 1994 and 1999, after 9 and 14 y of experimental treatment, respectively.

2. Materials and methods

2.1. Site description

This study was conducted at the Konza Prairie Biological Station (KPBS) in the Flint Hills of eastern Kansas. This Long-Term Ecological Research site is owned by the Nature Conservancy and managed by the Division of Biology at Kansas State University. The climate is continental with average annual precipitation of 835 mm (~75% falls during the growing season), and mean monthly temperatures of −4 °C in January and 27 °C in July (Knapp et al., 1998a).

2.2. Experimental design

We sampled soil macroinvertebrates in the Belowground Plot Experiment, a long-term experiment that was initiated at KPBS in 1986. The objective of the Belowground Plot Experiment was to determine the long-term influences of different land management practices and nutrient manipulations on above- and belowground communities and processes (Rice et al., 1998). The experiment is a factorial arrangement of two burning treatments (annual spring burning, or long-term fire exclusion), two mowing treatments (mowed and raked annually in early July, or not mowed), and four different nutrient addition treatments (plots with no nutrients added, plots with 10 g N m^{-2} added as ammonium nitrate, plots with 1 g P m^{-2} added as superphosphate, and plots with both N and P added). Thus, in the 64 total plots (12 m × 12 m in size), there are four replicates for each of 16 treatment combinations arranged in a split-strip plot experimental design. Burning treatments are applied to whole plots, mowing treatments applied to the split-plots, and fertilization treatments applied in opposing strips across mowing treatments (Todd, 1996).

2.3. Field and laboratory methods

The 1994 invertebrate sampling took place over three weeks in October, near the end of the growing season at KPBS. Sampling consisted of digging one monolith (20 × 50, 40 cm deep) from each of the 64 plots and collecting all invertebrates as soil was screened (6 mm) in the field. All specimens were preserved in 70% EtOH. In 1999, we sampled all 64 plots during one week in early June

Table 1
Regression equations for dry mass to ash-free dry mass conversions for various soil invertebrates

Organism	N	Equation	r^2
Earthworms			
Diplocardia spp.	41	$y = 0.526x + 0.00136$	0.853
Aporrectodea trapezoides	60	$y = 0.583x + 0.00494$	0.896
Octolasion spp.	21	$y = 0.396x + 0.00207$	0.991
Cicadas			
Cicadetta spp.	46	$y = 0.978x - 0.00265$	0.977
Tibicen spp.	26	$y = 0.907x + 0.00086$	0.941
Early instar cicadas	20	$y = 0.871x + 0.00111$	0.996
Beetles			
Scarabaeidae	13	$y = 0.993x - 0.00206$	0.998
Curculionidae	18	$y = 0.998x - 0.00002$	0.999
Elateridae	18	$y = 0.978x - 0.00019$	0.999

Equations were derived from specimens collected and ashed in 1999. Terms in the equations are as follows: x = dry mass of individual specimen (60 °C oven dry), y = estimated ash free dry mass of that specimen.

by collecting soil monoliths (25 × 25, and 25 cm deep), and sealing them in plastic bags where they were stored at 4 °C until they could be carefully hand-sorted in the laboratory. Sorting consisted of breaking all soil aggregates into small pieces (< 5 mm) and collecting all organisms encountered. Specimens were preserved and identified as in the 1994 sampling. All native North American earthworm species were identified to genus, and European earthworms were identified to species when possible. Arthropods were identified to family or genus when possible. All identifications (except cicadas) were made using taxonomic keys from Dindal (1990) and Peterson (1967). Final instar cicadas were identified to genus on the basis of their size, as *Tibicen* spp. are 3–4 times larger than *Cicadetta* spp. as adults.

We estimated invertebrate biomass as ash-free dry mass (AFDM), by ashing individuals of each taxonomic group from the 1999 sampling at 450 °C for > 6 h, and subtracting remaining ash mass from dry (50 °C) mass. We used dry biomass and AFDM data from 1999 sampling to generate linear regression equations to estimate AFDM from dry mass values for the 1994 specimens. Equations used to convert dry mass to AFDM are shown in Table 1.

2.4. Statistical analyses

All data were log-transformed to satisfy normality assumptions, and were subjected to mixed model analysis of variance suitable for the analysis of split-strip plot experimental designs (PROC MIXED, SAS Institute), with Burn, Mow, Nitrogen, and Phosphorus as main effects variables. Means separation analysis was by Least Squares Means (LSMEANS/pdiff option, SAS Institute).

3. Results

3.1. Total invertebrate density and biomass

Results from mixed model analysis of variance for all major invertebrate groups collected in 1994 and 1999 are summarized in Tables 2 and 3. Statistically significant treatment interactions characterized the responses of nearly every invertebrate group examined in this study. In 1994, total invertebrate density and biomass were greater in unburned relative to burned plots (Fig. 1A), and there were

Table 2
Results from mixed model analysis of variance for 1994 density and biomass of major soil invertebrate taxa collected from the Belowground Plot Experiment, Konza Prairie Biological Station

Effect	N	*Diplocardia*	*Aporrectodea*	*Cicadetta*	*Tibicen*	Cicada instars	Scarabaeidae	Elateridae	All inverts
B	32	ns	†/†	ns	**/**	**/*	ns	ns	*/**
M	32	ns	†/ns	*/*	ns	*/ns	ns	***/***	†/ns
B × M	16	ns	ns	ns	ns	ns	ns	ns	ns
N	32	ns	ns	*/†	ns	ns	ns/†	**/***	ns/†
B × N	16	ns	ns	ns	ns/†	ns	†/ns	ns	ns
M × N	16	ns	ns	*/†	ns	**/*	ns	†/**	*/ns
B × M × N	8	ns	†/ns	ns	ns	*/ns	ns	ns	ns
P	32	ns	ns	ns	ns	ns	ns	ns	ns
B × P	16	ns	*/*	ns	ns	ns	ns	ns	ns
M × P	16	*/*	ns	ns	ns	ns	ns/†	ns	*/*
B × M × P	8	ns	ns	†/ns	ns	ns	ns	ns	†/ns
N × P	16	ns	ns	ns	ns	ns	ns	ns	ns
B × N × P	8	*/*	ns	ns	ns	ns	ns	ns	*/ns
M × N × P	8	ns	ns	ns	ns	ns/†	ns	ns	ns
B × M × N × P	4	**/*	ns	†/ns	ns	ns	ns	ns	ns

Note. Significant fixed effects of burning (B), mowing (M), N addition (N) and P addition (P), and significant fixed effects of treatment interactions are shown. Number of sample plots used for calculation of means for a given treatment combination is also indicated (column N). For each treatment effect and each taxon, the first symbol in a pair represents density responses and the second symbol represents biomass responses. Levels of significance are indicated by ns: not significant; $^{\dagger}P \leq 0.1$; $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$.

Table 3
Results from mixed model analysis of variance for 1999 density and biomass of major soil invertebrate taxa collected from the Belowground Plot Experiment, Konza Prairie Biological Station

Effect	N	*Diplocardia*	*Aporrectodea*	*Cicadetta*	*Tibicen*	Cicada instars	Scarabaeidae	Elateridae	Curculionidae	All inverts
B	32	ns	†/†	*/*	*/*	†/†	ns	ns	ns	ns/†
M	32	*/*	ns	***/***	ns/*	***/ns	ns	ns	*/**	ns/**
B × M	16	ns	ns	**/**	ns/*	ns	ns	ns	**/*	*/ns
N	32	*/**	†/ns	†/ns	ns/†	ns	*/**	ns	ns/*	ns
B × N	16	ns	ns	ns	ns/†	ns	ns	†/*	ns	ns
M × N	16	ns	ns	ns	*/***	**/*	ns	*/ns	ns/*	*/**
B × M × N	8	ns	ns	ns	*/***	*/*	ns	ns	ns	ns/†
P	32	ns	ns	ns	ns	ns	ns	ns	ns	ns
B × P	16	ns/†	ns	ns	ns	ns/*	ns	ns	ns	ns
M × P	16	ns	ns	ns	†/ns	ns	ns/†	*/ns	ns	ns
B × M × P	8	ns	†/ns	ns	†/ns	ns	ns	ns	†/†	ns
N × P	16	ns	ns	ns	†/†	ns	†/ns	ns	ns	ns/*
B × N × P	8	ns	ns	ns	†/†	ns	ns	ns	ns	ns/†
M × N × P	8	ns	ns	ns/†	ns	ns/†	ns	ns	ns	ns
B × M × N × P	4	ns	ns	ns/†	ns	ns	ns	ns	ns	ns

Note. Significant fixed effects of burning (B), mowing (M), N addition (N) and P addition (P), and significant fixed effects of treatment interactions are shown. Number of sample plots used for calculation of means for a given treatment combination is also indicated (column N). For each treatment effect and each taxon, the first symbol in a pair represents density responses and the second symbol represents biomass responses. Levels of significance are indicated by ns: not significant; $^{\dagger}P \leq 0.1$; $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$.

a number of interactions involving fire, mowing and nutrient manipulations. Invertebrate density (but not biomass) was greater in mowed plots that received N relative to mowed plots with no N added, whereas this effect of N addition was not observed in unmowed plots (Fig. 1B). Interactions between mowing and P addition suggested that mowing negates the positive influence of P addition on invertebrate density and biomass observed in unmowed plots (Fig. 1C). Third-order interactions between burning, mowing and P addition, and also between burning, P addition and N addition, were observed for total invertebrate density in 1994 (data not shown). In both of these higher order interactions, an overriding influence of fire was evident. For example, there was no effect of P addition on the density of invertebrates in plots that were unburned regardless of mowing treatment; whereas in burned plots, the other treatments resulted in responses similar to those in the simpler two-way interaction of mowing and P addition (Fig. 1C). Likewise, fire dominated the interactions among fire, N addition and P addition: in burned plots, N additions resulted in greater densities of invertebrates relative to the control and N + P treatments, but this response to N addition was not observed in unburned plots (data not shown).

In 1999, the responses of total invertebrate density and biomass were less complex than in 1994. The interaction between fire and mowing was statistically significant, and once again revealed that fire induced significant effects of mowing that were not observed in unburned plots. In burned plots, invertebrate density was significantly greater in unmowed plots relative to mowed plots, but there was no such response to mowing in unburned plots (Fig. 1D). Additionally, there was an interaction between mowing and N addition. Total density and biomass were both lower in mowed plots than in unmowed plots in the absence of N addition, and biomass was significantly lowered with N addition in unmowed plots (Fig. 1E). Total invertebrate biomass differed in direction of response to N relative to mowing treatment: biomass was higher in mowed plots that received N, but was lower in unmowed plots that received N (Fig. 1E).

3.2. Earthworms

Native earthworm densities (*Diplocardia* spp.) were affected by significant interactions among treatments in 1994. In the interaction between mowing and P addition, density and biomass of *Diplocardia* were significantly greater in mowed plots with no P added relative to the other three treatment combinations (Fig. 2A). There was a significant third-order interaction between burning, P addition, and N addition in which the addition of one or both nutrients resulted in lower densities of *Diplocardia* in unburned plots, but not in burned plots (not shown). Treatment interaction effects on *Diplocardia* biomass paralleled those of density in 1994 (Fig. 2A).

Density of *Aporrectodea* spp. (an introduced European earthworm) was greater in unmowed plots relative to mowed plots (Fig. 2B), while there was a significant interaction between burning and P addition, with the greatest density and biomass of *Aporrectodea* in unburned plots that received P amendment (Fig. 2C). There was no such influence of P addition in burned plots.

Earthworm biomass data from 1994 showed that the average individual size of European earthworms (*Aporrectodea* spp.) was larger than that of native earthworms in all treatments (Fig. 2A–C). This larger per capita biomass of European earthworms affected the proportion of the total

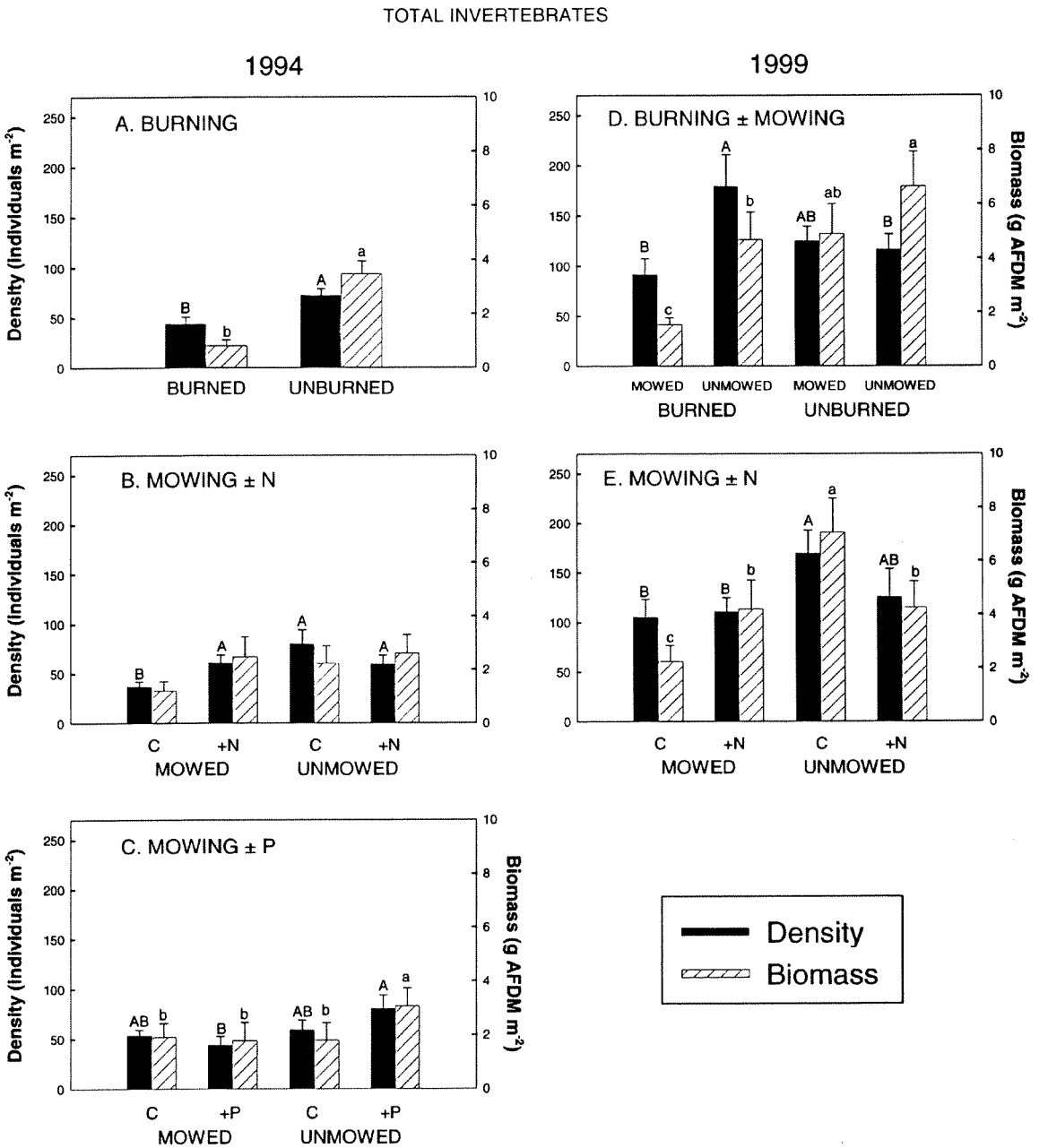

Fig. 1. Statistically significant responses in the mean density (solid bars, scale on left y-axis) and biomass (hatched bars, scale on right y-axis) of all major invertebrate groups to main treatments and treatment interactions in the Belowground Plot Experiment in 1994 and 1999. (A) Burning effects in 1994 ($N = 32$); (B) interaction of mowing and N addition in 1994 ($N = 16$); (C) interaction of mowing and P addition in 1994 ($N = 16$); (D) interaction of burning and mowing in 1999 ($N = 16$); and (E) interaction of mowing and N addition in 1999 ($N = 16$). Treatment effects that were significant at $P < 0.10$ are shown. When significant main effects were contained within a higher-order significant interaction, only the interaction is presented (Tables 2 and 3 for level of significance for specific treatments). Within density or biomass, means with different letters are significantly different from one another. For nutrient treatments C = control (no added nutrients), +N = N added, +P = P added, +NP = both N and P added. Error bars indicate standard error.

earthworm community biomass that consisted of native species in 1994 (Fig. 3A). Burning significantly altered this proportion, and there was a significant interaction between burning, mowing and N addition (Fig. 3A). Specifically, the proportion of the community made up of *Diplocardia* was greater than 75% in all burned plots except those that were unmowed and had N fertilizer added (+N and +N + P plots). In unburned plots, the proportion of earthworm biomass that was *Diplocardia* exhibited high variability ranging from 100% (in unburned, mowed, unfertilized plots) to < 10% (in unburned, mowed, fertilized +N + P) (Fig. 3A).

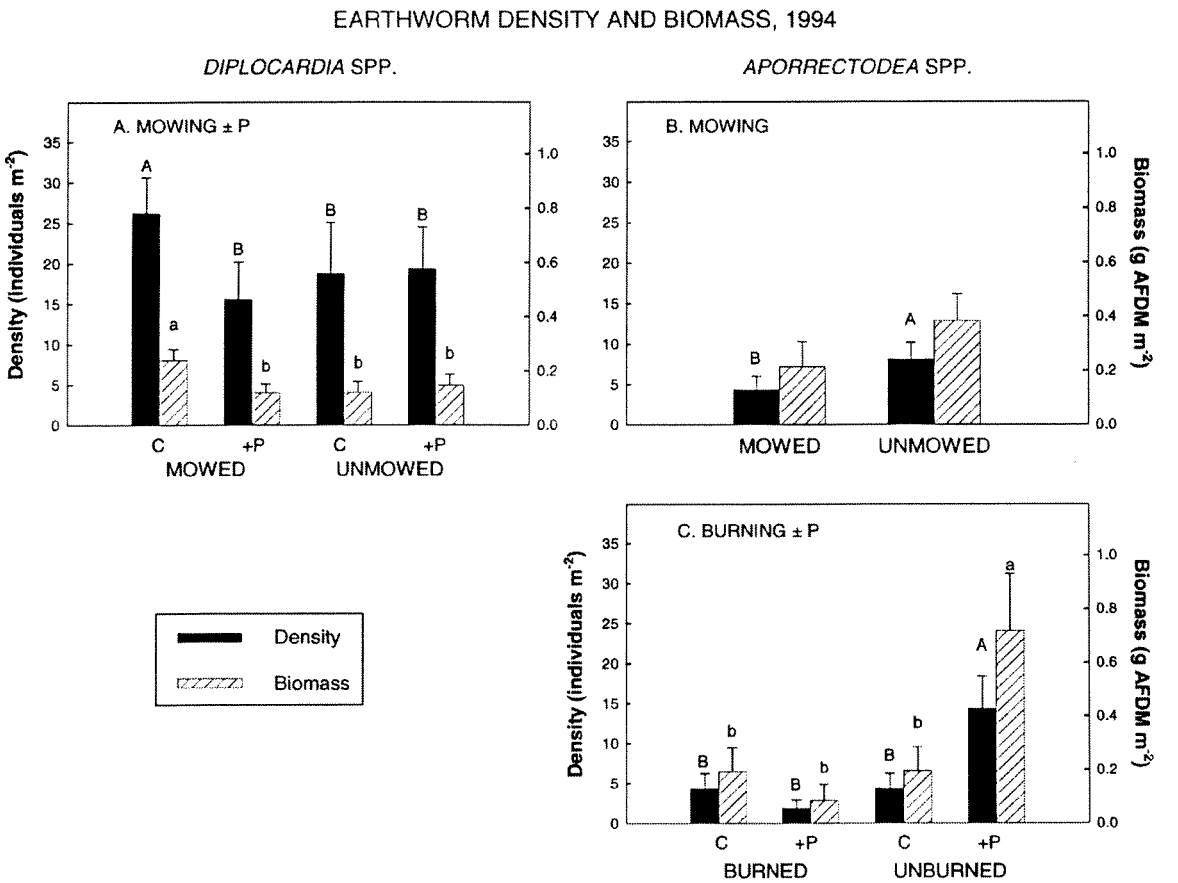

Fig. 2. Statistically significant mean density and biomass responses of earthworms to treatments in the Belowground Plot Experiment in 1994. (A) Interaction of mowing and P addition on *Diplocardia* spp. ($N = 16$); (B) mowing effects on *Aporrectodea* spp. ($N = 32$); and (C) interaction of burning and P addition on *Aporrectodea* spp. ($N = 16$). Treatment effects that were significant at $P < 0.10$ are shown. When significant main effects were contained within a higher-order significant interaction, only the interaction is presented (Table 2 for level of significance for specific treatments). Bars, axes, error bars, and treatment labels as in Fig. 1.

In 1999, earthworms exhibited different trends than in the 1994 sampling. There was a trend for greater abundance and biomass of *Diplocardia* spp. in burned plots relative to unburned plots, but this effect was not statistically significant ($P = 0.11$). However, mowing increased the density and biomass of *Diplocardia* spp. in 1999 (Fig. 4A), while N fertilization had a negative effect on both variables (Fig. 4B). In contrast, *Aporrectodea* spp. had greater abundance and biomass in unburned plots (Fig. 4C), and higher density in plots with N addition (Fig. 4D).

Also of note from the 1999 sampling was the occurrence of another European earthworm genus, *Octolasion* spp., which was not collected in 1994 (data not shown). The distribution of *Octolasion* was not significantly related to any of the experimental treatments, but was significantly related to the block in which sampling occurred. In other words, *Octolasion* was (with the exception of a single individual) collected exclusively from the two blocks on the eastern half of the experimental area. Responses of earthworm biomass to the treatments in 1999 were similar to responses in density, though European earthworms had higher per capita biomass (Fig. 4A–D). The proportion of total earthworm biomass comprised of native earthworms again reflected the larger per capita biomass of European earthworms (Fig. 3B), with a significant decline in this proportion in unburned plots.

3.3. Cicadas

In 1994, cicada nymphs showed clear responses to experimental treatments (Fig. 5A–D). There was a significant interaction effect between mowing and N addition on *Cicadetta* nymphs, with much greater density and biomass in unmowed plots that did not receive N fertilizer (Fig. 5A). In contrast to *Cicadetta*, nymphs of *Tibicen* spp. were collected almost exclusively from unburned plots in 1994 (Fig. 5B). Early instar cicadas were significantly more abundant (density and biomass) in

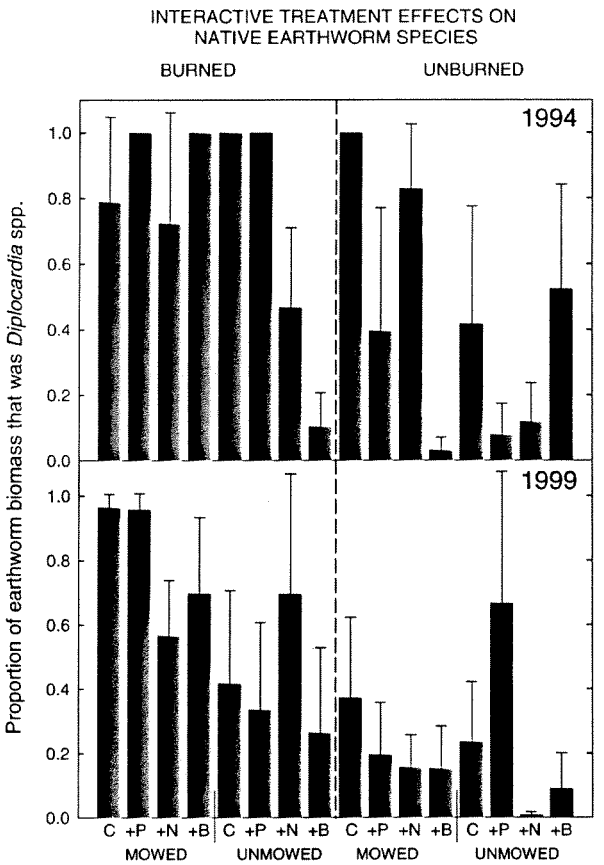

Fig. 3. Treatment effects of burning, mowing, N and P additions on the mean proportion ($N = 4$) of the total earthworm biomass comprised of native species (*Diplocardia* spp.) in the Belowground Plot Experiment in (A) 1994 and (B) 1999. For nutrient treatments C = control (no added nutrients), +N = N added, +P = P added, +B = both N and P added. Error bars indicate standard error.

unburned plots in 1994 (Fig. 5C). Treatment effects on early cicada instars included interactions between mowing and N addition. Nymphs were most abundant in unmowed plots that did not receive N (Fig. 5D). Cicada biomass followed patterns of abundance very closely for both genera and early instars, but *Tibicen* had a much higher per capita effect on biomass per unit area, and as a result, total cicada biomass (at the family level) was significantly higher in unburned plots (Fig. 5B and C).

Responses of cicadas to the treatments in 1999 were somewhat more complex, but generally similar to those in 1994. *Cicadetta* density and biomass was enhanced by N addition (Fig. 6A), and was greater in plots that had been burned and not mowed relative to all other burning and mowing treatment combinations (Fig. 6B). *Tibicen* spp. were again significantly affected by fire with greater abundance in unburned plots (Fig. 6C), but there were also significant interactions among treatments. The interaction between mowing and N indicated that mowing reversed the negative effect of N additions on *Tibicen* density observed in unmowed plots (Fig. 6D). In contrast, the interaction between mowing and P additions showed that mowing removed the positive effect of P amendment on *Tibicen* density observed in unmowed plots (Fig. 6E). There was also an interaction between N addition and P addition. Plots that received P additions alone had significantly greater densities of *Tibicen* than plots that received both N and P additions (Fig. 6F). It is notable that for every two factor interaction observed for *Tibicen* in 1996, there was a corresponding three-way interaction involving burning (Table 3), but these interactions were identical to the two way interactions (except means are exactly twice the values of those shown in Fig. 6D–F), because of the complete absence of *Tibicen* from burned plots.

In a pattern similar to 1994, early instar cicada nymphs were more abundant in unburned, relative to burned, plots in 1999 (Fig. 6G). Significant treatment interactions were also similar between 1994 and 1999, with nearly identical patterns of treatment effects on early cicada instar densities (Figs. 5C–D and 6G,H). Patterns of cicada biomass in 1999 were similar to patterns of density, but with *Tibicen* having a much larger per capita influence on total biomass than *Cicadetta* or early instars (Fig. 6A–H).

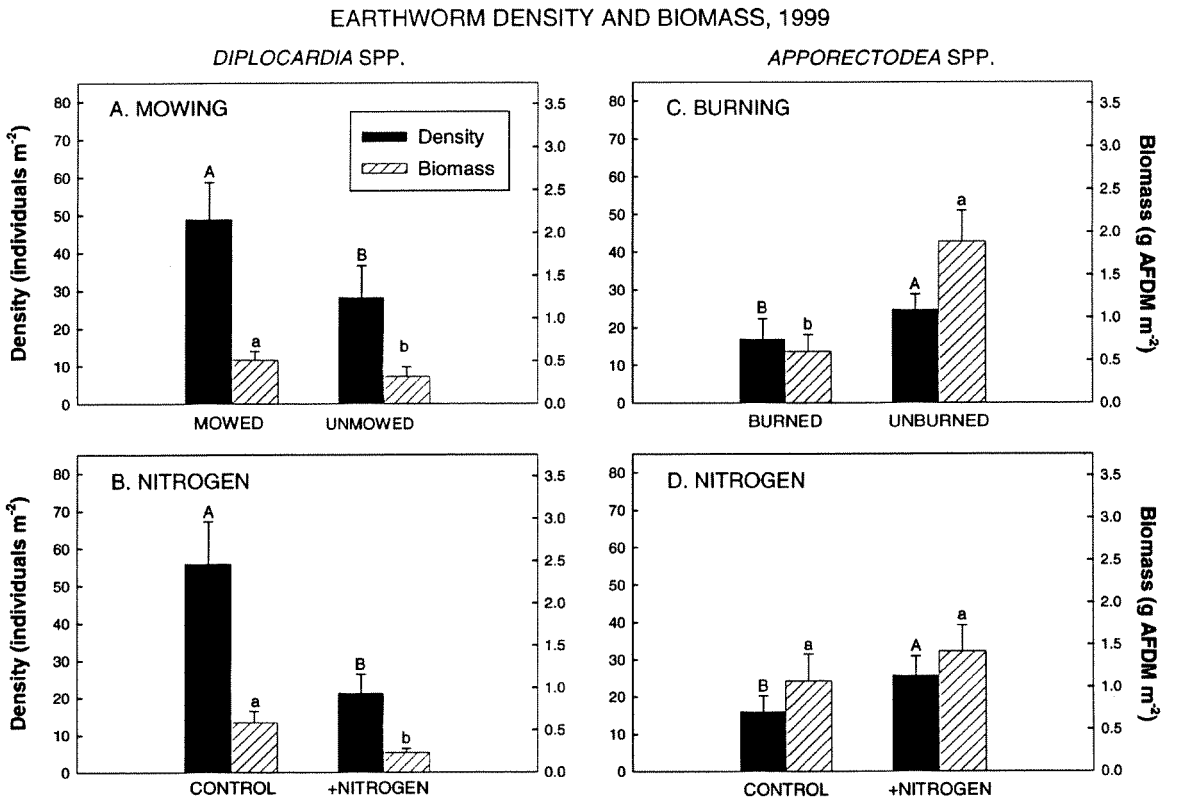

Fig. 4. Statistically significant mean density and biomass responses of earthworms to treatments in the Belowground Plot Experiment in 1999. (A) Mowing effects on *Diplocardia* spp. ($N = 32$); (B) nitrogen effects on *Diplocardia* spp. (N = 32); (C) burning effects on *Aporrectodea* spp. ($N = 32$); and (D) nitrogen effects on *Aporrectodea* spp. ($N = 32$). Treatment effects that were significant at $p < 0.10$ are shown (Table 3 for level of significance for specific treatments). Within density or biomass, bars with different letters are significantly different from one another. Bars, axes, error bars, and treatment labels as in Fig. 1.

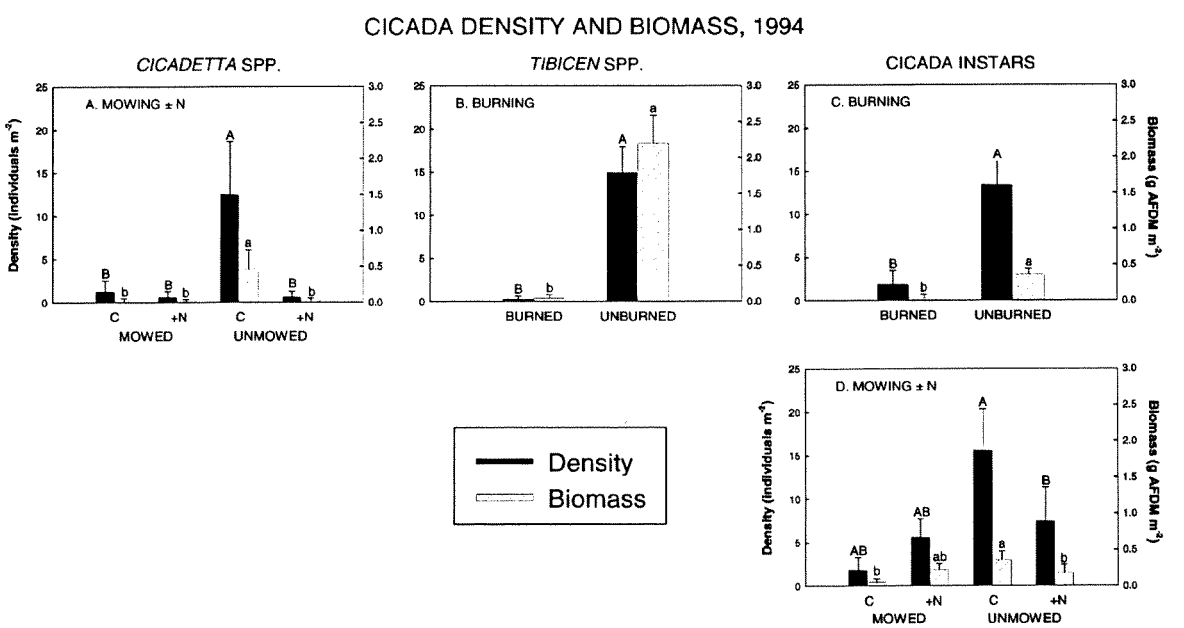

Fig. 5. Statistically significant mean density and biomass responses of cicadas to treatments in the Belowground Plot Experiment in 1994. (A) Interaction of mowing and N addition on *Cicadetta* spp. ($N = 16$); (B) burning effect on *Tibicen* spp. ($N = 32$); (C) burning effect on cicada instars ($N = 32$); and (D) interaction of mowing and N addition on cicada instars ($N = 16$). Treatment effects that were significant at $p < 0.10$ are shown. When significant main effects were contained within a higher-order significant interaction, only the interaction is presented (Table 2 for level of significance for specific treatments). Within density or biomass, bars with different letters are significantly different from one another. Bars, axes, error bars, and treatment labels as in Fig. 1.

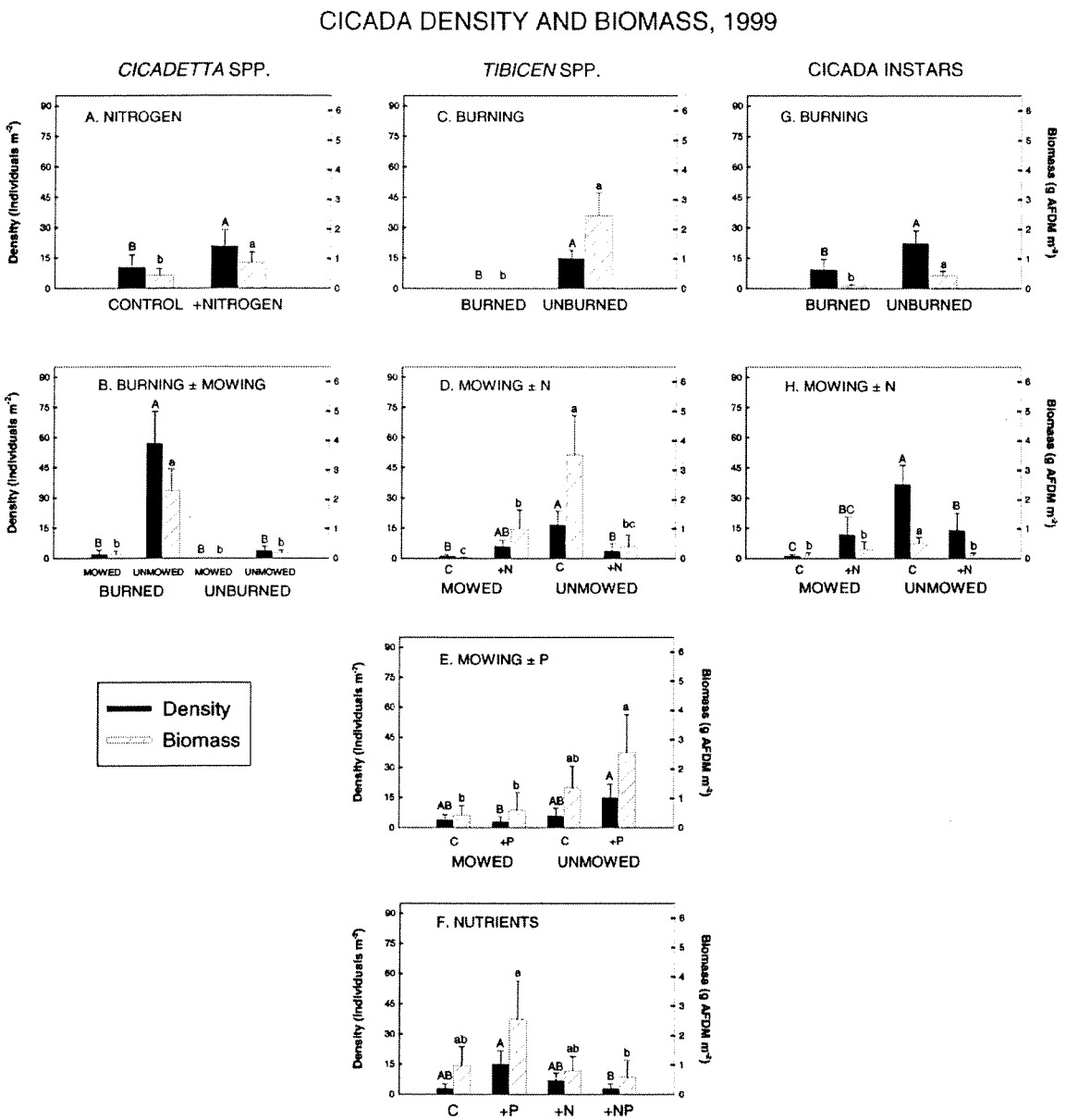

Fig. 6. Statistically significant mean density and biomass responses of cicadas to treatments in the Belowground Plot Experiment in 1999. (A) Nitrogen effects on *Cicadetta* spp. ($N = 32$); (B) interaction of burning and mowing on *Cicadetta* spp. ($N = 16$); (C) Burning effects on *Tibicen* spp. ($N = 32$); (D) interaction of mowing and N addition on *Tibicen* spp. ($N = 16$); (E) interaction of mowing and P addition on *Tibicen* spp. ($N = 16$); (F) interaction of N addition and P addition on *Tibicen* spp. ($N = 16$); (G) burning effects on cicada instars ($N = 32$); and (H) interaction of mowing and N addition on cicada instars ($N = 16$). Treatment effects that were significant at $p < 0.10$ are shown. When significant main effects were contained within a higher-order significant interaction, only the interaction is presented (see Table 3 for level of significance for specific treatments). Within density or biomass, bars with different letters are significantly different from one another. Bars, axes, error bars, and treatment labels as in Fig. 1.

3.4. Herbivorous beetle larvae

Beetle larvae from the family Scarabaeidae (principally *Phyllophaga* spp.) responded positively to N addition in 1994 (Fig.7A). There was also a significant interaction between burning and N addition treatments in 1994, with scarab larvae abundances increased with N addition in unburned plots, but not in burned plots (Fig. 7B). In 1999, scarabs were again significantly more abundant in N addition plots (Fig. 8B). There was also a significant interaction between N and P additions in 1999, with greater scarab abundance in plots that received N or both N and P, relative to plots that received P alone or no nutrient additions (Fig. 8B).

Beetle larvae from the family Elateridae responded strongly to mowing and N addition treatments in 1994, with greatest abundance in unmowed plots that received N (Fig. 7C). In 1999, the response of elaterid larvae was not as straightforward as that of 1994. The only significant effects were interactions involving burning and N, and mowing with the two nutrients. Specifically, densities of elaterid larvae were significantly greater in burned plots without N than in unburned plots without N, but there was no difference between burned and unburned plots that did receive N (Fig. 8C). In contrast to 1994, the interaction between mowing and N addition in 1999 indicated that elaterid larvae were most abundant in unmowed plots, but only those without added N (Fig. 8D). However, P addition in 1999 increased densities of elaterids in unmowed plots, relative to all other mowing and P treatment combinations (Fig 8E).

Beetle larvae from the family Curculionidae were not collected in numbers sufficient for analysis in 1994, but in 1999 several significant treatment effects were observed, including a two factor interaction between burning and mowing. There were significantly greater curculionid densities in burned plots that had not been mowed compared to all other treatment combinations (Fig. 8F). Finally, there was a significant interaction between mowing and N addition with greater biomass of curculionids in unmowed plots that received N fertilization (Fig. 8G).

4. Discussion

4.1. Resource quality and quantity and invertebrate abundance

The treatments examined in this study had individual and interactive effects on the quality and quantity of resources available to soil invertebrates. These effects were manifested largely as changes in plant community composition and both aboveground and belowground plant biomass. In general, annual fire in tallgrass prairie decreases plant community diversity and favors warm-season C_4

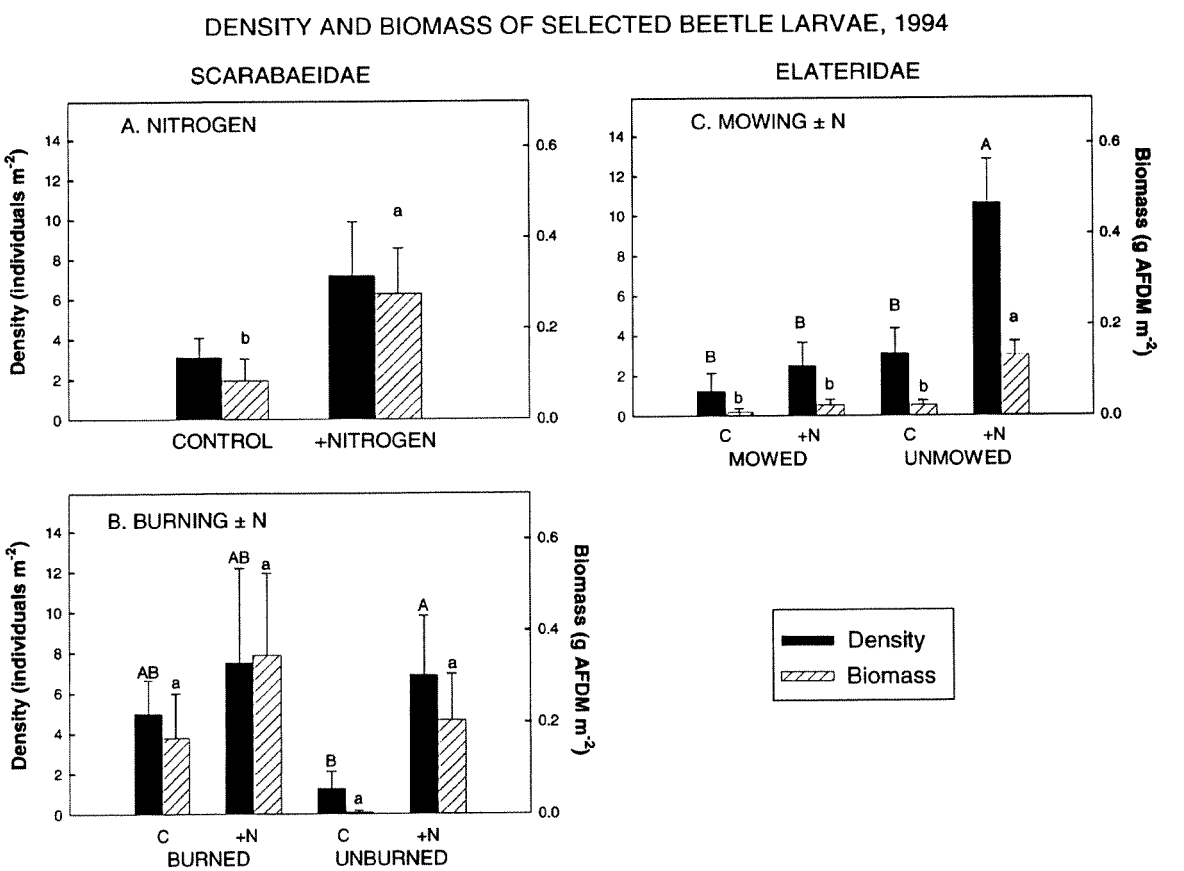

Fig. 7. Statistically significant mean density and biomass responses of beetle larvae to treatments in the Belowground Plot Experiment in 1994. (A) Nitrogen effects on Scarabaeidae ($N = 32$); (B) interaction of burning and N addition on Scarabaeidae ($N = 16$); and (C) interaction of mowing and N addition on Elateridae ($N = 16$). Treatment effects that were significant at $p < 0.10$ are shown. When significant main effects were contained within a higher-order significant interaction, only the interaction is presented (Table 2 for level of significance for specific treatments). Within density or biomass, bars with different letters are significantly different from one another. Bars, axes, error bars, and treatment labels as in Fig. 1.

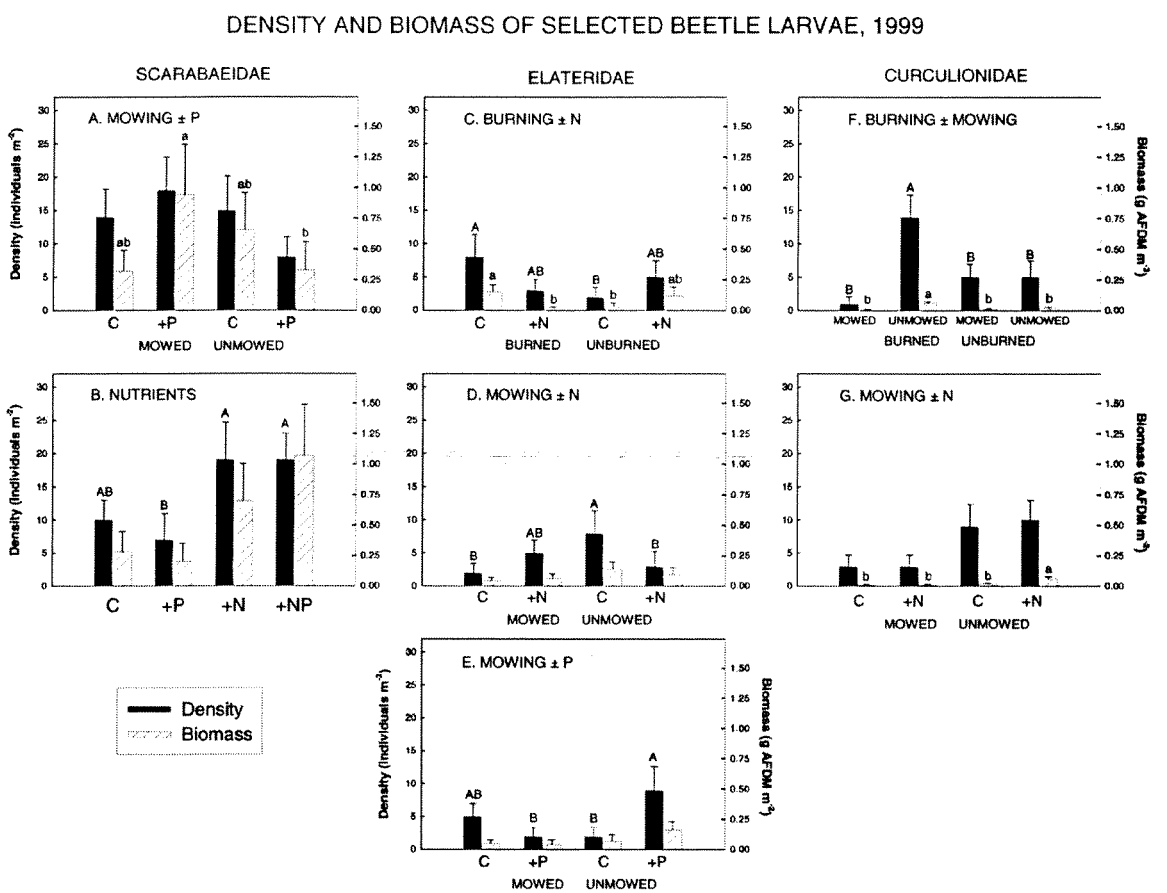

Fig. 8. Statistically significant mean density and biomass responses of beetle larvae to treatments in the Belowground Plot Experiment in 1999. (A) Interaction of mowing and P addition on Scarabaeidae ($N = 16$); (B) Interaction of N addition and P addition on Scarabaeidae ($N = 16$); (C) interaction of burning and N addition on Elateridae ($N = 16$); (D) interaction of mowing and N addition on Elateridae ($N = 16$); (E) interaction of mowing and P addition on Elateridae ($N = 16$); (F) interaction of burning and mowing on Curculionidae ($N = 16$); and (G) interaction of mowing and N addition on Curculionidae ($N = 16$). Treatment effects that were significant at $p < 0.10$ are shown. When significant main effects were contained within a higher-order significant interaction, only the interaction is presented (Table 2 for level of significance for specific treatments). Within density or biomass, bars with different letters are significantly different from one another. Bars, axes, error bars, and treatment labels as in Fig. 1.

grasses (Gibson et al., 1993; Collins et al., 1998), and this affects the quantity and quality of belowground plant inputs. In frequently burned prairie, grass roots are generally more abundant, but because fire reduces soil N availability (Blair et al., 1998), these roots are of lower quality (higher C-to-N ratio) relative to unburned prairie (Blair, 1997; Johnson and Matchett, 2001). Similarly, removal of aboveground plant tissues via mowing and raking results in a net export of nutrients from mowed plots and, over time, tissue quality (in terms of C-to-N ratio) of roots in mowed plots is reduced relative to unmowed plots (D.J. Kitchen, Pers. Comm.). In addition to affecting nutrient relationships, fire and mowing also affect several other soil characteristics. Fire and mowing remove dead plant material from the soil surface and, as a result, soils are generally warmer and drier in burned or mowed plots (Knapp and Seastedt, 1986). In general, the treatments that result in relative nutrient depletion (i.e. burning and mowing) also resulted in decreased invertebrate density or biomass. For example, total invertebrate biomass was significantly less in burned plots in both years (Fig. 1A and D), and was highest in unburned, unmowed plots and lowest in burned, mowed plots (Fig. 1D). Furthermore, when effects of nutrient addition treatments on soil invertebrates were significant, the responses of invertebrate density or biomass were almost always positive. However, we observed several interactions between one of the nutrient depleting treatments (burning or mowing) and nutrient addition treatments. In many cases, the positive effect of nutrient addition was observed only in plots that had also been subjected to some treatment that depleted soil nutrients, whereas there was sometimes a negative effect of nutrient addition to plots that were not subjected to nutrient depletion (see Fig. 1E biomass for 1999 as an example). These generalities suggest that nutrient availability, or plant and litter resource quality, are strong determinants of invertebrate community structure

in tallgrass prairie, but there were several taxon-specific exceptions, and responses of each taxonomic group are discussed below.

4.2. Earthworms

The distribution and abundance of native and introduced earthworm species were affected by experimental treatments in this study. Furthermore, in plots where exotic earthworms were most prevalent, it appeared that displacement of native species may be occurring. Particularly notable were the differences in earthworm community structure between the two most extreme treatments—annually burned, mowed, and without nutrient addition, as opposed to unburned, unmowed, and with supplemental nutrients. For both sampling dates, the proportion of earthworm biomass composed of native taxa was 75% or higher in burned, mowed plots, but this proportion was either variable and erratic (1994) or declined consistently (1999) as treatment combinations became decreasingly 'prairie-like' (Fig. 3A and B). Soil conditions in plots which were annually burned, and mowed with no added nutrients probably most resemble conditions prior to European settlement of the tallgrass prairie region (i.e. frequently burned and with aboveground biomass removal by large ungulates). These plots are also the most typical with respect to floristic and edaphic characteristics of native tallgrass prairie (Knapp and Seastedt, 1986; Collins et al., 1998), and our study demonstrates that native earthworm species comprise the greatest proportion of the earthworm community in these plots as well. Previous studies of earthworm distributions in tallgrass prairie have shown the abundance of *Diplocardia* spp. to be greater in annually burned prairie relative to prairie from which fire had been excluded for 8 y (James, 1982). We found no effect of burning on the absolute abundance of *Diplocardia* spp. in either sampling year, but relative abundance of *Diplocardia* spp. was favored by burning (Fig. 3A and B). One potential explanation for the discrepancy between our study and James (1982) is the virtual absence of exotic taxa in the soils sampled by James (he reports only a single individual of *Aporrectodea* spp.), and therefore effects on distributions arising from interactions between the two taxa were not considered in the earlier study. Interestingly, *Aporrectodea* appears to be expanding its range over time, as there were some treatment combinations with earthworm communities consisting entirely of *Diplocardia* in 1994, but by 1999 there were no treatments combinations without *Aporrectodea* (Fig. 3B).

One effect of suppressing fire, grazing, or mowing in tallgrass prairie is the accumulation of plant litter on the soil surface. The treatments in this experiment essentially resulted in a gradient of surface litter accumulation. Indirect effects of litter accumulation include increased soil moisture and decreased soil temperature, particularly in the early growing season (Knapp and Seastedt, 1986). We suggest that microclimatic consequences of differing land management practices may contribute to changes in the earthworm community in tallgrass prairie. However, it is difficult to decouple the effects of litter accumulation on soil climate and the effects of burning and mowing on plant species composition, belowground plant production, and plant tissue quality. For example, Todd et al. (1992) demonstrated that mowing resulted in significantly less live root biomass, and an increase in the abundance of *Diplocardia* spp. relative to unmowed plots. The results of our 1999 sampling are similar to the findings of Todd et al. (1992), as we found increased abundance of *Diplocardia* spp. related to mowing treatments (Figs. 3A and 4A).

Fire also influences the quality and amount of plant tissue inputs belowground (Blair, 1997), which could affect the distribution of earthworms in tallgrass prairie soil. The amount of live root tissue in annually burned prairie is significantly greater than in unburned prairie, and live roots in annually burned prairie can have C-to-N ratios nearly double that of unburned prairie (Ojima et al., 1994; Blair, 1997; Johnson and Matchett, 2001). Thus, lower quality plant tissue could potentially limit the expansion of exotic earthworms in frequently burned tallgrass prairie.

In spite of the correlative nature of these results, and the difficulty in identifying specific mechanisms underlying the establishment of exotic earthworms, our study demonstrates that departures from natural disturbance regimes can result in detectable changes in the abundances of native and exotic earthworm taxa in these soils. The changes in earthworm community structure may have functional consequences because of differences in the feeding ecology and behavior of these earthworm taxa (James and Cunningham, 1989; James, 1991; Callaham et al., 2001).

4.3. Cicadas

There were profound treatment effects on the density of cicadas (Figs. 5 and 6). Although both species feed on C_4 grasses (Callaham et al., 2000), responses of the two species with respect to the treatments (which differentially affect grass cover (Gibson et al., 1993)) were divergent. The response of *Cicadetta* to treatments was marked by a strong interaction between mowing and N fertilization in 1994 (Fig. 5A), and then by an interaction between burning and mowing in 1999 (Fig. 6B). Responses in 1999 were very similar to another study on cicada responses to land management, where Callaham et al. (2002) found that adults of *Cicadetta* emerged exclusively from burned and unmowed plots, and hypothesized that the distributional pattern of *Cicadetta* resulted primarily from aboveground vegetation structure and the availability of oviposition sites.

In contrast to *Cicadetta*, the responses of *Tibicen* were dominated by a strong negative response to burning. *Tibicen* was collected almost exclusively from unburned plots with only a single individual collected from an annually burned

plot in the two sampling years. The mechanism behind this response is unclear. One potential explanation for *Tibicen* responses to burning is higher belowground resource quality in unburned prairie. In a recent sampling of the belowground plots, root standing stock biomass was observed to be lower in unburned plots relative to burned plots. However, the quality of root tissue (inferred from C-to-N ratios) was better in unburned plots (D.J. Kitchen, Pers. Comm.). Increased root tissue quality in unburned plots relates to changes in plant community composition (Gibson et al., 1993; Collins et al., 1998), or increased N availability in unburned plots (Blair, 1997). Another potential explanation for greater densities of *Tibicen* in unburned plots is that they are attracted to standing dead vegetation for oviposition. Exclusion of fire from tallgrass prairie results in the accumulation of a layer of detritus that can be up to 30 cm deep (Knapp and Seastedt, 1986). This detrital layer may provide protection for adult *Tibicen* from visual predators, or may be selected because of a low probability that this vegetation, along with *Tibicen* eggs, will be eaten by grazers (as senescent vegetation is avoided in favor of fresh forage (Vinton et al., 1993; Coppedge and Shaw, 1998)). Finally, exclusion of fire also results in a greater abundance of forb (non-grass herbaceous plants) vegetation, and *Tibicen* has been observed to oviposit into the stems of forbs as well as grass flowering stalks (M. Whiles, personal observations).

The differential influence of fire and mowing on the distributions of different cicada genera (*Cicadetta* more abundant in burned plots, *Tibicen* more abundant in unburned plots) suggests that these two genera may partition resources spatially by utilizing different parts of the landscape in different years. Interactions between fire and grazers result in a mosaic of burned and unburned vegetation in the landscape (Knapp et al., 1999), and different cicada species appear to have preferences for each component of this mosaic.

4.4. Herbivorous beetles

The responses of herbivorous beetle larvae emphasize the importance of examining both single and interactive effects of these treatments on soil organisms. Previous studies of the responses of herbivorous beetle larvae to fire have produced variable results. For example, Seastedt (1984) found that scarab larvae were significantly more abundant in burned prairie compared to unburned, but in another study Seastedt et al. (1986) found no effect of burning on larval scarab density or biomass. Our results indicated no direct effect of burning on the density of scarab larvae after 9 and 13 y of continuous treatment (Tables 2 and 3). However, N additions were influential (Figs. 7A,B and 8B). The increased scarab abundance observed with N addition in our study contrasts with the lack of scarab response in the only other study to measure soil macroarthropod responses to N addition in tallgrass prairie soils (Seastedt et al., 1988). We observed no significant effect of burning on elaterid larvae density, consistent with the results of Seastedt (1984), but we did observe an interaction that suggested burning had a positive effect on elaterid density in plots with no N amendment (Fig. 8C). We also found several other treatment effects on elaterid larvae including decreased abundance with mowing and increased abundance with N addition (Fig. 7C). Curculionid responses to fire, mowing, or fertilizer have never been reported for tallgrass soils. Our results show that they were strongly influenced by mowing and fire with high densities in burned and unmowed plots, and the highest densities were in burned and unmowed plots that received P fertilizer (Fig. 8F and G). This positive response to P addition was also observed for elaterid larvae in 1999, but the underlying mechanism for this response is unknown. The observed positive response of these, and other taxa (e.g. *Tibicen* and *Aporrectodea*), to P fertilization in this investigation is intriguing, because there have been no vegetation responses to P fertilization observed in the Belowground Plots Experiment (Gibson et al., 1993). Tallgrass prairie systems are generally thought to be dynamically regulated by light, N, or water availability, and the relative limitations of these factors at any given time varies with fire frequency or climatic conditions (Knapp and Seastedt, 1986; Seastedt and Knapp, 1993; Knapp et al., 1998a). Our study demonstrates that P availability is influential, if not limiting, to certain groups of soil invertebrates in this ecosystem that is generally thought of as N limited.

5. Conclusions

Several groups of soil invertebrates responded significantly to treatments imposed in the Belowground Plot Experiment. These responses were characterized by strong interactions between the main effects of burning, mowing and nutrient additions. Native North American earthworm species (*Diplocardia* spp.) were favored by annual burning, and European earthworms (*Aporrectodea*) were more abundant in plots where fire was excluded. The proportion of total earthworm biomass made up of native taxa decreased steadily as the gradient of treatment combinations became more distant from the natural disturbance regime of tallgrass prairie. Cicadas responded differently to treatments depending on genus. *Cicadetta* was more abundant in burned plots that were not mowed, and *Tibicen* was more abundant in unburned plots. This pattern of cicada distribution suggests spatial resource partitioning between the two species. Herbivorous beetles responded variably to the treatments, but were generally more abundant in plots that were not mowed and had received some nutrient amendment (N or P). Our results suggest that disturbances such as fire and aboveground biomass removal are important determinants of soil invertebrate community structure, and that long-term changes in these disturbance regimes may predispose tallgrass prairie earthworm communities to establishment and expansion of exotic taxa. Our

study also provides evidence that altered belowground resource quality (as a function of disturbances and nutrient amendments via fertilizer) has the potential to influence the structure of invertebrate communities in tallgrass prairie soils. Given recent calls for strategies to control the expansion of exotic earthworms in North America (Hendrix and Bohlen, 2002), we suggest that some simulation of natural disturbance regimes in tallgrass prairie could be a viable land management strategy for conservation of native soil organism assemblages.

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