

## Annual Fire, Mowing and Fertilization Effects on Two Cicada Species (Homoptera: Cicadidae) in Tallgrass Prairie

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**ABSTRACT.**—In tallgrass prairie, cicadas emerge annually, are abundant and their emergence can be an important flux of energy and nutrients. However, factors influencing the distribution and abundance of these cicadas are virtually unknown. We examined cicada emergence in plots from a long-term (13 y) experimental manipulation involving common tallgrass prairie management practices. The plots were arranged in a factorial experimental design, incorporating annual burning, mowing and fertilization (10 g N m<sup>-2</sup> and 1 g P m<sup>-2</sup>). One cicada species, *Cicadetta calliope*, responded positively to fire, but negatively to mowing, and was most abundant in plots that were burned, unmowed and fertilized. Increased density of *C. calliope* in this treatment combination is related, in part, to increased availability of oviposition sites aboveground. Furthermore, *C. calliope* females from fertilized plots were significantly larger in body size relative to females from unfertilized prairie. Another cicada species, *Tibicen aurifera*, emerged only from unburned plots. The mechanism underlying this negative response to fire is unclear, but may be related to the presence of standing dead vegetation or improved quality (*i.e.*, N content) of belowground plant tissue in unburned plots. In contrast to *C. calliope*, the density of *T. aurifera* was not affected by mowing or fertilization. However, like *C. calliope*, the body size of *T. aurifera* females was significantly greater in fertilized plots. Cicada emergence resulted in N flux ranging from 0.05–0.16 g N m<sup>-2</sup> in unburned plots, but N flux (as cicada biomass) from annually burned plots was negligible.

### INTRODUCTION

Periodic disturbances, such as fire and grazing by American bison (*Bos bison*), are credited, in part, for the original development (and subsequent maintenance) of the grassland biome in North America (Axelrod, 1985). Because precipitation along the eastern edge of the grassland biome is sufficient to support forest vegetation, a principal role of disturbances in these “tallgrass” prairie ecosystems is the prevention of woody plant encroachment (Briggs *et al.*, 1998; Hoch and Briggs, 1999). However, aside from biome-level influences, disturbances (or the absence thereof) in these grasslands affect many other levels of ecological organization, ranging from the physiology of individual blades of grass (Knapp, 1985; Knapp and Seastedt, 1986) to plant community species composition (Collins and Steinauer, 1998; Knapp *et al.*, 1999) to ecosystem primary productivity and nutrient cycling (Blair, 1997; Knapp *et al.*, 1998a).

In the present-day tallgrass prairie landscape disturbances continue to be influential, but are best considered in terms of land use and land management. Grazing of cattle (*Bos taurus*) is the principal land use in tallgrass prairie of the Flint Hills region of eastern Kansas, and one common management practice for maintenance of these rangelands is prescribed burning of detritus in the spring of each year. Fire is used as a range management tool because the removal of grass litter from the soil surface results in increased

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productivity of warm-season grasses and, thus, increases the amount of forage for livestock (Knapp and Seastedt, 1986; Knapp *et al.*, 1998a). Another important and widespread land use is mowing of large areas of tallgrass vegetation in midsummer for hay production. Although the effects of these different land management practices on plant community composition and aboveground primary productivity are well documented (Knapp and Seastedt, 1986; Gibson *et al.*, 1993; Collins *et al.*, 1998; Knapp *et al.*, 1998a), the effects of these practices on various consumer groups, and particularly those inhabiting soil, are not well characterized (Rice *et al.*, 1998).

Cicadas are long-lived belowground herbivores that are abundant in tallgrass prairie soils (Beamer, 1928). Annual emergence of these large insects can result in a significant flux of energy and nutrients from belowground to aboveground (Callaham *et al.*, 2000). Topographic position in the tallgrass prairie landscape has been shown to influence the distribution and abundance of different cicada species (Callaham *et al.*, 2000), but the influences of land management practices, such as annual burning or cutting hay on cicadas at the species level have yet to be examined. However, there have been investigations of the effects of disturbances on the whole belowground invertebrate community, with variable results. For example, Seastedt (1984) found no differences between the densities of cicada nymphs in plots that had been either burned annually or left unburned for 5 y. In another study, Seastedt *et al.* (1986) found that cicada nymphs (and other belowground herbivores) were more abundant in burned plots than in mowed plots, but there was still no difference in cicada abundance between burned and unburned plots. It is notable that these studies of nymphal cicada responses to disturbance addressed changes in the entire belowground invertebrate community, and did not determine cicada responses at levels of taxonomic resolution below that of family. Additionally, these studies were all conducted with short-term experimental manipulations relative to the typical cicada life cycle. For grassland cicadas, the typical life cycle is 4–6 y (Beamer, 1928), and population-level cicada responses to experimental treatments of five or fewer years may not have sufficient time to be fully realized. For example, fire-induced changes in plant community composition—which may underlie belowground herbivore responses—are indirect and accrue through time (Knapp *et al.*, 1998b; Collins and Steinauer, 1998). Thus, it is possible that species-specific responses to imposed treatments may have been outside the purview of previous studies.

Our objectives for this study were to examine the responses of cicadas, at the species level, to long-term (13 y) burning, mowing and fertilization treatments. We hypothesized that in the context of long-term experimental manipulation, we would be able to detect differences (if any) in the density and biomass of two common cicada species, *Tibicen aurifera* (Say) and *Cicadetta calliope* (Walk.), in response to different land management practices.

#### METHODS

*Site description and experimental design.*—The study site was located in the Flint Hills region of eastern Kansas. The Flint Hills region represents the largest contiguous tract of tallgrass prairie vegetation remaining in North America. More than 95% of the land area once covered in tallgrass prairie has been converted to agricultural or urban use in the last 150 y (Samson and Knopf, 1994), but the Flint Hills region escaped large-scale conversion to row-crop agriculture because of its relatively steep topography and rocky soils. This study was conducted at the Konza Prairie Biological Station (KPBS), a Long-Term Ecological Research site owned by The Nature Conservancy and operated by the Division of Biology at Kansas State University. The climate at the site is continental, with average annual precipitation of 835 mm (75% of which falls during the growing season). Mean monthly tem-

peratures are  $-4$  C in January and  $27$  C in July (Knapp *et al.*, 1998a). For this study we selected plots from the Belowground Plot Experiment, an experimental manipulation that had been underway at KPBS since 1986. The long-term objective of the Belowground Plot Experiment has been to determine the influences of different land management practices on belowground communities and processes (Rice *et al.*, 1998). The treatment structure of the experiment is a three-way factorial arrangement of two burning treatments (either annual spring burning or not burned), two mowing treatments (either mowed to a height of  $\sim 5$  cm and raked annually in early July or not mowed) and four different nutrient-addition treatments (plots with no nutrients added, with  $10$  g N  $m^{-2}$  added, with  $1$  g P  $m^{-2}$  added and with both N and P added). Thus, in the 64 total plots, there are 4 replicates for each of 16 treatment combinations, arranged in a split-strip plot experimental design with burning treatments applied to whole plots, mowing applied to half of each sub-plot and fertilization treatments applied in opposing strips within the plots (Todd, 1996). Each individual plot measures  $12$  m  $\times$   $12$  m. For our study we used a subset of half of all possible treatment combinations by using plots that were burned or not burned, mowed or not mowed and fertilized with both N and P or not fertilized.

*Study organisms.*—We examined two cicada species in this study: *Tibicen aurifera* (Say) and *Cicadetta calliope* (Walk.). These are grass-feeding species, and both are more abundant in upland prairie than in lowland prairie (Callaham *et al.*, 2000). *Cicadetta calliope* is the smaller of the two (mean body length  $\sim 14$  mm vs.  $\sim 24$  mm for *T. aurifera*), and *C. calliope* emerges in late June/early July, whereas *T. aurifera* emerges in early August through mid-September (Callaham *et al.*, 2000). Within a few days of emergence, adult cicadas mate and females oviposit inside the flowering stems of grasses (for *C. calliope*) and/or stems of some forbs (for *T. aurifera*). Eggs hatch in the same season that they are laid, and first instar nymphs drop to the soil surface where they immediately make their way into the soil (Beamer, 1928; pers. obs.). Information on the full life cycles of these insects is scarce, but the best information suggests that their life cycles are variable from 4–6 y, with a cohort of individuals emerging every year (Beamer, 1928).

*Field and laboratory methods.*—During the growing season of 1999 we determined densities of emerging cicadas by trapping adults as they emerged from the soil (as in Whiles *et al.*, 2001). Traps were constructed of wire-mesh ( $\sim 3$  mm aperture) cylinders with a circumference of  $1.75$  m (basal area of  $\sim 0.25$   $m^2$ ). Three traps were placed in each plot and traps were checked for cicadas every 2 or 3 d throughout the growing season. We also collected the shed exuviae from emerged cicadas inside each trap and used these to verify the total number of adults trapped during the growing season. At the end of the growing season (mid-October), when traps were removed from the plots, we carefully searched the vegetation and soil surface inside the traps for any dead individuals or exuviae that may have been missed during the summer.

Twice during the 1999 growing season we assessed vegetation in plots where the trapping occurred. Sampling dates were chosen to coincide approximately with periods of oviposition for the different cicada species (06 July for *Cicadetta calliope* and 06 October for *Tibicen aurifera* [Callaham *et al.*, 2000]). Vegetation assessment consisted of counting stems of grasses and forbs in three  $10 \times 20$  cm quadrats randomly positioned within the experimental plots. In addition to total stem counts, we counted the number of stems in the quadrats that were suitable sites for cicada oviposition. This stem count provided an estimate of the number of available oviposition sites under different treatments. These cicada species appear to use any vegetation that fits certain size requirements for oviposition (stems and stalks approximately 3–7 mm in diameter, personal observations) and, thus, for our esti-

mates, oviposition sites were defined as any grass flowering stalk (culm) or forb stem within the sampling quadrat.

To assess the effects of fertilizer application on cicada body size, we measured individual cicadas from fertilized and reference plots, using a dissecting microscope fitted with an ocular micrometer (for *Cicadetta calliope*) or manual calipers (for *Tibicen aurifera*). We used length of body parts, rather than individual body mass, as a conservative measure of size because females can lose body mass rapidly as a consequence of oviposition. Three measurements were made for each individual: head width at the eyes, total body length and forewing length. For *C. calliope*, we measured 10 females from fertilized plots and compared them to 10 females collected from similar (unfertilized) grasslands >1 km off-site because too few individuals were collected from the unfertilized experimental plots to allow effective comparison. For *T. aurifera* and male *C. calliope*, we compared individuals from fertilized plots to individuals from unfertilized plots. Additionally, we performed tissue nitrogen analysis for a subset of male and female individuals from fertilized and unfertilized plots. Individual cicadas were freeze-dried and pulverized with mortar and pestle and tissue N content was determined by coupled combustion and gas chromatography (Carlo-Erba NA1500).

*Statistical analyses.*—Densities (number of individuals  $m^{-2}$ ) were estimated by averaging emergence over the three traps in a given plot. Plot averages were used in statistical analyses (*i.e.*  $N = 4$  for a given experimental treatment combination). We tested for differences in means by subjecting the data to mixed model analysis of variance (PROC MIXED, SAS Institute, Cary NC) suitable for analyzing split-strip plot experimental data. Energy and nutrient fluxes ( $g$  biomass  $m^{-2}$  and  $g$  N  $m^{-2}$ , respectively) were estimated by multiplying average mass of final instar nymphs collected from fertilized and unfertilized plots (Callahan, 2000) by density and tissue N concentration of emergent individuals of each species from fertilized and unfertilized plots.

Because body size measurements are often highly correlated with one another, we used multivariate analysis of variance (MANOVA) to analyze the body size data (simultaneous analysis of all measured variables). Because MANOVA results showed significant differences (Wilks' Lambda, likelihood ratio test,  $\alpha < 0.05$ ) in body size means due to fertilization treatments for both cicada species, we proceeded with univariate tests of individual measurements (Johnson, 1998). Results of the univariate tests of fertilization effects are reported.

Linear regression analysis was used to explore relationships between plant community structure and cicada emergence patterns. We performed regressions relating cicada density to all of the parameters collected during the sampling described above (grass stems, forb stems, oviposition sites and proportion of total stems that were potential oviposition sites). Regressions were also used to relate cicada emergence to the percent cover of selected plant species (data from KPBS Belowground Plot Experiment data archive), including the dominant warm-season grasses, *Andropogon gerardii* Vitman (big bluestem), *Sorghastrum nutans* (L.) (Indian grass), *Schizachyrium scoparium* (Michx.) Nash (little bluestem) and *Panicum virgatum* L. (switchgrass).

## RESULTS

*Cicada densities.*—Three cicada species were captured in emergence traps during the study. Two species, *Cicadetta calliope* and *Tibicen aurifera*, were numerous and are the focus of analyses in this study. The third species, *Tibicen dorsata* (Say), was represented by only a few individuals and did not warrant extensive examination. We found clear differences in the densities of cicadas with respect to the treatment combinations (Figs. 1a, b). *Cicadetta calliope* emerged first and was significantly influenced by fire with higher densities in burned

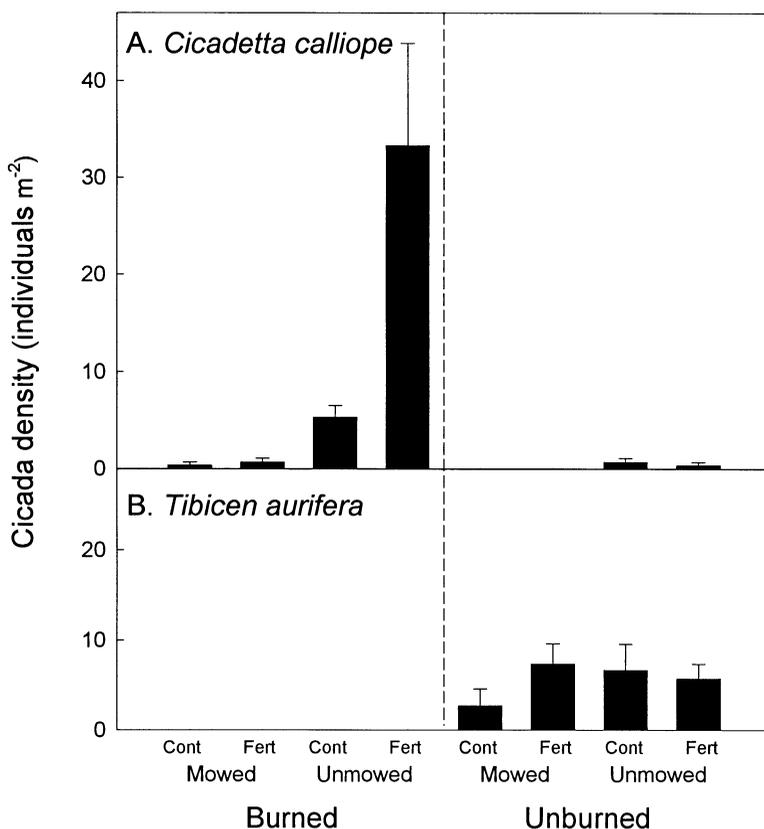


FIG. 1.—Mean densities of A. adult *Cicadetta calliope* and B. adult *Tibicen aurifera* emerging from selected plots in the Belowground Plot Experiment, Konza Prairie Biological Station, Summer 1999. Bars indicate one standard error

plots than in unburned plots ( $P < 0.01$ ). However, a significant interaction between fire and mowing for this species was evident, such that larger numbers of *C. calliope* were captured in plots that were burned but not mowed, compared to burned plots that were mowed ( $P < 0.0001$ ). Furthermore, maximal *C. calliope* densities were observed in plots that were burned, not mowed and which had received fertilizer additions (Fig. 1a). This effect was also significant, with densities of *C. calliope* being  $\sim 4\times$  greater in burned, unmowed and fertilized plots, compared to the treatment combination with the next greatest densities (burned, unmowed, unfertilized plots).

The response of *Tibicen aurifera* to different land management treatments was less complex than that of *Cicadetta calliope*, but no less pronounced (Fig. 1b). Densities of *T. aurifera* in plots that had not been burned were significantly greater than in burned plots (in fact, *T. aurifera* were not encountered at all in burned plots) (Fig. 1b). Density of *T. aurifera* was not significantly influenced by mowing or fertilization.

*Cicada body size and tissue C and N content.*—Because of significant effects of fire and mowing on distributions of cicadas, we were unable to test for effects of fire and mowing on body size or tissue chemistry—too few individuals were collected from some of the

TABLE 1.—Body measurements of two cicada species trapped from fertilized (treatment +), and unfertilized (treatment -) plots, summer 1999. All measurements are in millimeters. Level of significance for differences between means of fertilizer treatments within sex are indicated by P-values (Least Squares means separation procedure LSMEANS/pdiff option, SAS Institute, Cary, NC)

Species	Sex	Treatment	N	Head width	Body length	Wing length
<i>C. calliope</i>	Male	+	7	4.24	13.26	16.30
	Male	-	4	4.18	12.43	15.16
				P = 0.51	P = 0.07	P = 0.01
<i>C. calliope</i>	Female	+	10	4.64	15.90	17.30
	Female	-	10	4.45	14.27	15.76
				P = 0.01	P = 0.01	P = 0.01
<i>T. aurifera</i>	Male	+	7	10.91	24.93	31.09
	Male	-	7	10.62	25.47	30.12
				P = 0.13	P = 0.35	P = 0.12
<i>T. aurifera</i>	Female	+	7	10.71	24.20	30.67
	Female	-	7	10.36	22.94	29.06
				P = 0.06	P = 0.04	P = 0.01

treatments to perform measurements. However, we were able to test for differences in body size and tissue chemistry in response to fertilizer effects. Fertilizer effects on cicada body size were evident in females of both species (Table 1). *Cicadetta calliope* females were significantly ( $P < 0.0001$ ) larger than males, and females collected from plots receiving nutrient additions were significantly larger than those collected from unfertilized plots. This increase in size was observed in all of the body measurements. Male *C. calliope* were less responsive than female *C. calliope* to fertilizer additions, but still showed indications of larger size with significantly larger wings ( $P < 0.01$ ). *Tibicen aurifera* also responded to fertilization (Table 1), but for this species, differences were statistically significant only for females and were not significant ( $P = 0.06$ ) for head width (Table 1). Results of tissue chemistry analyses of cicadas revealed that individuals (of both species and both sexes) collected from fertilized plots had lower percent N (as % dry mass of body tissue), compared to individuals collected from unfertilized plots (Table 2).

*Energy and nitrogen flux.*—Cicada emergence resulted in biomass and N fluxes ranging from  $\sim 0.5$  to  $1.3$  g biomass  $m^{-2}$  and  $0.05$  to  $0.16$  g N  $m^{-2}$ , respectively, in unburned plots (Figs. 2a, b). Biomass of *Tibicen aurifera* was responsible for  $>99\%$  of the total cicada related N flux from unburned plots. Nitrogen fluxes from burned plots were negligible with the exception of burned, unmowed and fertilized plots where *Cicadetta calliope* density was highest. From these plots, the N flux from belowground to aboveground was similar to the largest fluxes from unburned plots ( $\sim 0.16$  g N  $m^{-2}$ ).

*Cicada distribution and plant parameters.*—Analyses examining the relationships between cicada abundance and various plant parameters showed that, of the many plant species examined, the percent cover of the warm-season grass species *Panicum virgatum* was best correlated with abundance of *Cicadetta calliope* in the plots ( $r^2 = 0.79$ , plot not shown). However, oviposition site availability, measured as grass flowering stalk and forb density, was an even better correlate of *C. calliope* density (Fig. 3a). We found no significant relationships between the density of *Tibicen aurifera* and any of the plant parameters examined in this study (e.g., Fig. 3b).

TABLE 2.—Tissue nitrogen (N) and carbon (C) concentrations (% dry mass) and C/N of male and female *Cicadetta calliope* (N = 5 for each sex) and *Tibicen aurifera* (N = 7 for each sex). Individuals were collected from fertilized (+nutrients) or unfertilized (−nutrients) plots. Values are means ( $\pm$ SE). Within species, sex and element, means followed by \* are significantly different from one another ( $P < 0.05$ ), and † ( $P < 0.10$ ) (Least Squares means separation procedure LSMEANS/pdiff option, SAS Institute, Cary NC)

Species	Sex	%N				%C				C/N	
		+Nutrients	−Nutrients	+Nutrients	−Nutrients	+Nutrients	−Nutrients	+Nutrients	−Nutrients	+Nutrients	−Nutrients
<i>C. calliope</i>	Male	10.90 (0.53)	11.74 (0.99)	54.42 (0.89)	53.23 (1.44)	5.09 (0.40)	4.62 (0.52)				
<i>C. calliope</i>	Female	9.00 (0.14)*	10.97 (0.48)	56.68 (0.72)†	54.29 (0.94)	6.30 (0.11)	5.00 (0.31)				
<i>T. aurifera</i>	Male	11.57 (0.27)	11.75 (0.40)	53.97 (0.43)	53.82 (0.48)	4.68 (0.12)	4.61 (0.18)				
<i>T. aurifera</i>	Female	11.39 (0.17)†	11.85 (0.12)	56.33 (0.35)*	55.02 (0.23)	5.20 (0.09)	4.84 (0.09)				

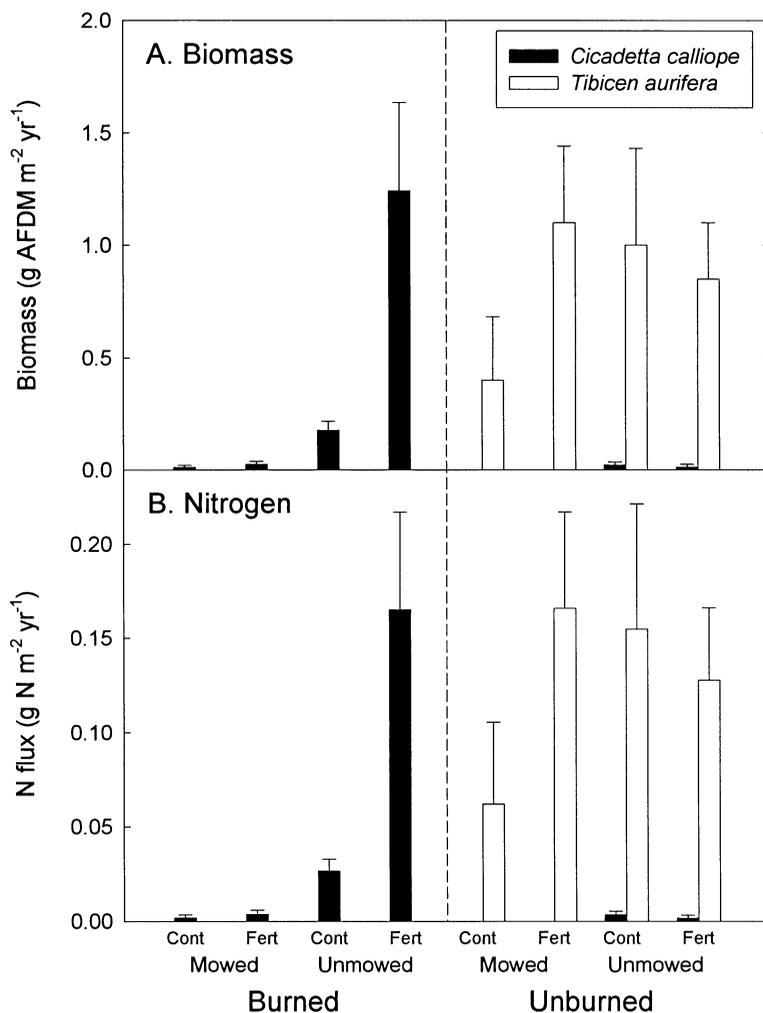


FIG. 2.—A. mean biomass flux and B. mean nitrogen flux associated with cicada emergence from the Belowground Plot Experiment, Konza Prairie Biological Station, Summer 1999. Bars indicate one standard error. Note differences in y-axis scales

#### DISCUSSION

*Land management and cicada density.*—The experimental treatments in this study had clear effects on the density of both cicada species examined (Figs. 1a, b). Although both species feed on the roots of C<sub>4</sub> grasses (Callaham *et al.*, 2000), the experimental treatment combinations that maximized C<sub>4</sub> grass production did not similarly affect abundance of both cicada species. Rather, the two cicada species were affected in fundamentally different ways, with fire having an overwhelming effect. *Tibicen aurifera* was collected exclusively from unburned plots, whereas *Cicadetta calliope* was collected almost exclusively from burned plots (Figs. 1a, b). The experimental design of the Belowground Plot Experiment does not allow identification of the specific mechanisms underlying these responses, but below we

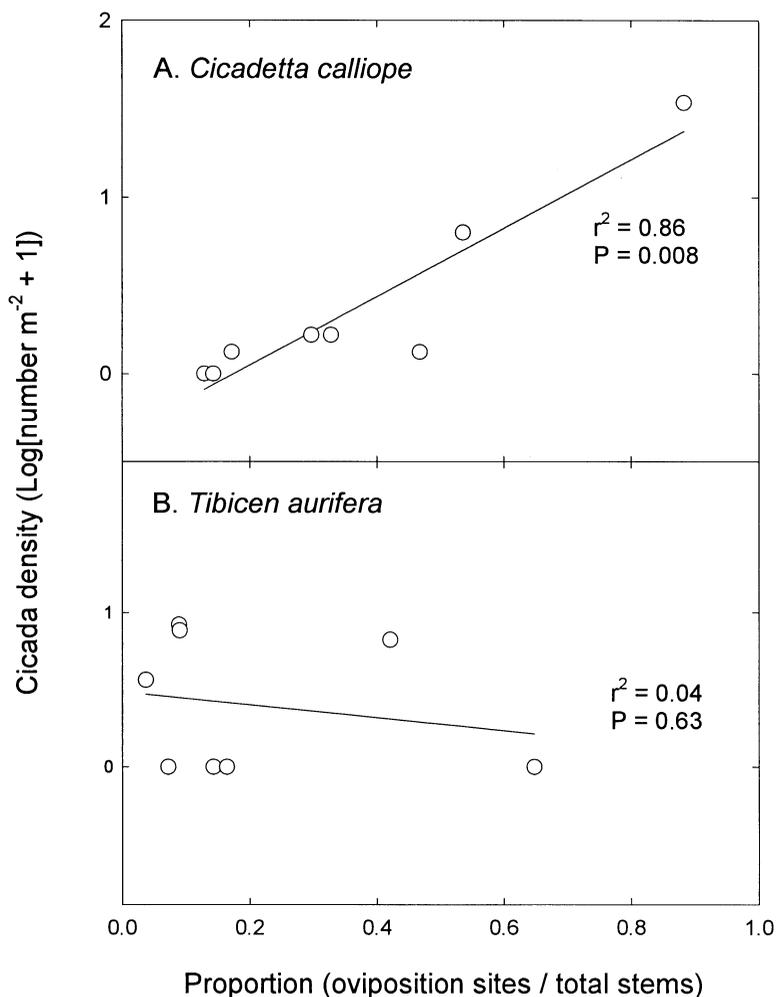


FIG. 3.—Relationship between oviposition site availability and cicada density for A. *Cicadetta calliope* and B. *Tibicen aurifera* (bottom), Summer 1999. Oviposition site availability was defined as the proportion of grass flowering stems and forb stems suitable for oviposition out of the total number of stems in sampling frames. Oviposition site availability was assessed in July for *C. calliope* and in October for *T. aurifera*. Note: y-axis is log scale

provide discussion of the most likely explanations for the observed responses for each cicada species.

The response of *Cicadetta calliope* was characterized by a significant interaction among burning, mowing and fertilization (Fig. 1a). The availability of oviposition sites showed similar interactive responses to this treatment combination, providing one potential explanation for the *C. calliope* response. The density of grass stems and the proportion of these stems suitable for oviposition (*i.e.*, flowering stems) were increased by the same combination of treatments that maximized *C. calliope* density (Fig. 3a). These findings are similar to other studies of cicada abundance, including Glinski and Ohmart (1984) who noted a

significant relationship between oviposition site availability and abundance of Apache cicadas (*Diceroprocta apache*) in the American southwest, and also Yeates and Lee (1997) who hypothesized that increased availability of oviposition sites was related to increased abundance of cicadas in burned tussock grasslands of New Zealand. Alternatively, increased cicada abundance in plots with increased availability of oviposition sites could be the result of better cicada survivorship under soil conditions which coincidentally promote high availability of oviposition sites in the plant community (e.g., high nutrient availability). However, the absence of any fertilizer effect on *C. calliope* abundance in burned and mowed plots (Fig. 1a) is further evidence indicating the importance of oviposition site availability (mowing removes nearly all potential oviposition sites).

*Tibicen aurifera* was collected exclusively from unburned plots, contrasting markedly with the responses of *Cicadetta calliope*. The mechanism for this response is unknown, but could involve either belowground resource quality or aboveground vegetation structure. In a recent sampling (unrelated to the present study) of the Belowground Plot Experiment, root standing stock biomass was observed to be lower in unburned plots relative to burned plots, but root tissue quality (inferred from lower relative C/N) was greater in unburned plots (D. J. Kitchen, pers. comm.). This difference in root tissue quality is partly due to fire-induced changes in plant community composition (Gibson *et al.*, 1993; Collins *et al.*, 1998), and partly due to increased availability of mineral nitrogen in unburned plots (Blair, 1997). Another potential explanation for the increased density of *T. aurifera* in unburned plots is that the insects are attracted to standing dead vegetation. Exclusion of fire from tallgrass prairie results in the accumulation of a layer of up to 30 cm of detritus (Knapp and Seastedt, 1986). This detrital layer may provide protection for *T. aurifera* adults from visual predators such as birds or rodents (Steward *et al.*, 1988; Krohne *et al.*, 1991) or standing dead vegetation may be selected by *T. aurifera* because senescent vegetation is of lower nutritional quality and is frequently avoided by grazers (Vinton *et al.*, 1993; Coppedge and Shaw, 1998). Finally, exclusion of fire also results in a greater abundance of forb vegetation and *T. aurifera* has been observed to oviposit into the stems of forbs (such as *Aster* spp., *Solidago* spp. and *Liatris* spp.) as well as grass flowering stalks (pers. obs.). Thus, *T. aurifera* abundance in unburned plots may be explained in part by availability of forb stems.

*Body size and tissue C and N content.*—In addition to the increase in density of *Cicadetta calliope* in fertilized plots, the body size of individuals collected from these plots was significantly greater (Table 1). Furthermore, even though we found no influence of fertilization on density of *Tibicen aurifera*, this species also responded to fertilization with larger females emerging from the fertilized plots. Presumably, this increase in body size is the result of increased quality and/or quantity of food resources available for cicada consumption in fertilized plots. Results from tissue analysis indicated that cicadas from unfertilized plots had greater N content (as a percentage) than did cicadas from fertilized plots (Table 2). However, because cicadas from fertilized plots were larger in size, the absolute N content (total mass) of cicada tissues was similar between treatments on a per individual basis.

*Nitrogen flux.*—The emergence of cicadas represents a significant flux of N from belowground to aboveground in unburned and unfertilized plots (Fig. 2b). This flux is due primarily to the emergence of *Tibicen aurifera* from these plots. *Tibicen aurifera* is a relatively large-bodied cicada (~4x the size of *Cicadetta calliope*), and has a much larger per capita influence on nutrient flux (Callaham, 2000). Cicada emergence from unburned plots resulted in fluxes of 0.05–0.16 g N m<sup>-2</sup> y<sup>-1</sup> which is equivalent to ~10% of the total annual input of N via bulk precipitation in these tallgrass systems (Blair *et al.*, 1998). The only burned plots that exhibited a significant flux of N in cicada biomass were those that were unmowed and fertilized. However, the fact that these plots received fertilizer at a rate of 10

$\text{g N m}^{-2} \text{y}^{-1}$  renders the flux of cicada biomass negligible (<1.5% of the total annual input). Cicada-mediated fluxes of N from the burned plots in this experiment were similar to those observed for *T. aurifera* and *C. calliope* in lowland tallgrass prairie (Callaham *et al.*, 2000).

The fate of N associated with cicada emergence is unknown, but much of it likely returns to soil pools when cicadas die. However, this N returns to the soil in a less homogeneous manner than would occur with rainfall deposition. The influence of this increased heterogeneity of N inputs to soil on plants or other components of the N cycle remains to be examined. Additionally, some fraction of cicada N is transferred to higher trophic levels as cicadas are commonly preyed upon by other arthropods (spiders and ants) as well as birds and mammals, but the magnitude of such transfer has not been estimated.

*Resource partitioning among cicadas.*—Differential use of burned and unburned areas by different cicada species, as observed in this plot level study, represents spatial and temporal niche partitioning among cicadas. This idea, although unsubstantiated at the landscape scale, allows for the formulation of hypotheses that are testable in the context of long-term, landscape-level, experimental grazing and fire manipulations such as those ongoing at Konza Prairie Biological Station. In particular, sampling in grazed watersheds, and watersheds with different fire return intervals, should provide further information about cicada community structure in tallgrass prairie soils. Such data would be useful for linking aboveground disturbances and belowground community responses, as well as for development of fine resolution energy and nutrient models in the tallgrass prairie ecosystem

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