
Compatibility of Prescribed Burning with the Conservation of Insects in Small, Isolated Prairie Reserves

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Abstract: *Entomologists have expressed concern that prescribed burning is incompatible with the conservation of insect species richness on small prairie sites. To address this issue, I examined the response and recovery of insect populations after fire within small, isolated tallgrass prairie remnants in northern Illinois, northwestern Indiana, and southeastern Wisconsin. I conducted this research over seven seasons, focused on responses at the species level, distinguished between remnant-dependent and remnant-independent species, and included multiple fire events and sites. I used sweep nets, light traps, sticky traps, and visual searches to gauge population responses and to track negatively affected populations to recovery. Most species (93%) responded consistently to prescribed fires. Postfire responses ranged from positive (26%) to negative (40%) for 151 species representing 33 families and seven orders. Three attributes—remnant-dependence, upland inhabitation, and nonvagility—were significant predictors of negative postfire response. Among negatively affected populations, 68% recovered within 1 year; all 163 populations tracked to recovery did so in 2 years or less. My results support the judicious use of rotational cool-season burning within small, isolated grassland sites.*

Compatibilidad de Incendios Reglamentados con la Conservación de Insectos en Reservas de Praderas Pequeñas y Aisladas

Resumen: *Los entomólogos han manifestado una preocupación con respecto a los incendios reglamentados y la incompatibilidad de los mismos con la conservación de la riqueza de especies de insectos en praderas pequeñas. Para tratar este tema, examiné la respuesta de las poblaciones de insectos post-incendio y su recuperación dentro de remanentes pequeños y aislados de praderas con pastos altos del norte de Illinois, noroeste de Indiana y sureste de Wisconsin. Realicé esta investigación, a nivel de especie, durante siete estaciones, distinguiendo entre especies dependientes e independientes de los remanentes. También incluí eventos de incendios múltiples y sitios. Se emplearon trampas de barrido, trampas de luz, trampas pegajosas y búsquedas visuales para medir las respuestas de las poblaciones y para rastrear aquellas poblaciones que sufrieron un impacto negativo, hasta su recuperación. La mayoría de las especies (93%) respondió consistentemente a los incendios reglamentados. Las respuestas post-incendio variaron desde positivas (26%) hasta negativas (40%) para 151 especies representantes de 33 familias y siete órdenes. Tres atributos—dependencia del remanente, habitación tierras arriba y falta de movimiento—resultaron ser predictores significativos de las respuestas post-incendio negativas. Entre las poblaciones afectadas negativamente, el 69% se recuperó dentro de un año: las 163 poblaciones monitoreadas hasta su recuperación la alcanzaron en dos años o menos. Mis resultados apoyan el uso prudente de quema rotativa durante la estación fría dentro de sitios de pastizal pequeños y aislados.*

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Introduction

The historic role of fire in the establishment and maintenance of tallgrass prairie throughout midwestern North America has been well documented (Gleason 1913; Curtis 1959; Moran 1978; Pyne 1986; Anderson 1990; McClain & Elzinga 1994; Robertson et al. 1997). Fire suppression in this region facilitates invasion by shrubs and trees, culminating in the degradation and eventual loss of native grassland ecosystems (Curtis 1959; Sheldford & Winterringer 1959; Gibson & Hulbert 1987; Leach & Givnish 1996). Systematic burning generally favors prairie plant species and contributes substantially to the control of invasive nonprairie species, both native and exotic (Anderson 1972; Glass 1991; Heidorn 1991; Hutchinson 1992; Wilson & Stubbendieck 1997).

The practice of prescribed burning has become firmly established among Midwestern conservation agencies. Although staunchly supported by botanists and natural-areas managers, the use of fire within fragmented settings has been criticized by entomologists and others whose interests lie in invertebrate conservation (McCabe 1981; Opler 1981; Jackson 1982; Stannard 1984; Orwig 1992; Moffat & McPhillips 1993; Swengel 1994, 1996; Minno & Minno 1996; Pyle 1997; Reed 1997; Williams 1997; Dietrich et al. 1998; Schlicht & Orwig 1992). Although most acknowledge the historical importance of fire, they fear that small, isolated invertebrate populations may be incapable of surviving repeated management burns, given the severely fragmented nature of the modern Midwestern landscape.

Several researchers have examined the short-term effects of fires on prairie-inhabiting insects. Most of these studies were limited to one or two sites and/or seasons, with little or no replication (e.g., Cancelado & Yonke 1970; Nagel 1973; Anderson et al. 1989; Fay & Samenus

1993; Harper et al. 2000), and have been conducted primarily at the tribal, familial, or even ordinal levels (e.g., Cancelado & Yonke 1970; Nagel 1973; Van Amburg et al. 1981; Seastedt et al. 1986; Harper et al. 2000) or have involved primarily wide-ranging, weedy species (e.g., Carpenter 1939; Anderson et al. 1989). These shortcomings notwithstanding, previous studies show that (1) short-term insect responses can range from positive to negative and are unpredictable at higher taxonomic levels (Table 1); (2) populations are seldom eradicated by single fires (Riechert & Reeder 1970; Knutson & Campbell 1974; James 1988; Panzer 1988; Anderson et al. 1989; Dana 1991; Fay & Samenus 1993; Swengel 1998); (3) invertebrate species present beneath the soil surface in the spring and fall when prairies are burned are generally not threatened by the direct effects of fires (Hill 1973; Knutson & Campbell 1974; Lussenhop 1976; Seastedt 1984; James 1988); and (4) postfire recovery is often rapid (Carpenter 1939; Tester & Marshall 1961; Cancelado & Yonke 1970; Van Amburg et al. 1981; Anderson et al. 1989; Hall 1996; Harper et al. 2000; Huebschman & Bragg 2000). Important studies by Dana (1991), Swengel (1996), and Fay and Samenus (1993) demonstrate that remnant-dependent species can respond negatively to prescribed burns. However, data supporting the contention that prevailing burning practices can be expected to result in the loss of insect biodiversity are lacking (Panzer & Schwartz 2000).

I began a study in 1992 to determine the compatibility of modern prescribed burning regimes with the conservation of insect biodiversity within small, widely scattered prairie remnants. Unlike most earlier studies, my study extended over seven seasons, focused on species, included multiple fire events, replicated tests for most species (91%), and distinguished between remnant-dependent and opportunistic, landscape-inhabiting spe-

Table 1. Conflicting reports of short-term postfire responses for higher insect taxa (orders and families) on Midwestern prairies.*

Taxon	Illinois		Missouri	Kansas		Minnesota	
	Rice 1932	Anderson <i>et al.</i> 1989	Cancelado & Yonke 1970	Nagel 1973	Knutson & Campbell 1974	Van Amburg <i>et al.</i> 1981	Tester & Marshall 1961
Coleoptera (beetles)	–	0		0			+
Diptera (flies)	–	0		+			
Miridae (plant bugs)				–		0	
Homoptera (hoppers)	+	–	+				
Cicadellidae (leafhoppers)			+	+		0	
Hymenoptera (bees & wasps)	+	0		+			
Formicidae (ants)	+	+		0		0	
Orthoptera (grasshoppers & katydids)	+	0					
Acrididae (grasshoppers)				+	+	0	0
Tettigoniidae (katydids)				+		–	
Hemiptera (true bugs)	+	0	+				

*Symbols: 0, no response; +, fire-positive response; –, fire-negative response.

cies (Panzer et al. 1997). Broadly speaking, I focused on population response and recovery following fire. More specifically, I used an experimental approach to gauge initial postfire responses among a variety of insect groups, to document recovery rates for fire-sensitive species, and to identify ecological, taxonomic, and natural-history correlates of both fire sensitivity and rapid recovery.

Methods

Study Sites

Burns were conducted from 1992 through 1997 on 21 sites spanning a geographic area of approximately 40,000 km² within the eastern portion of the tallgrass prairie biome (Table 2). Study sites extended from Green County in south-central Wisconsin through northern Illinois to Newton County in northwestern Indiana (Panzer & Schwartz 2000). Study sites ranged in size from 2 to 600 ha, with most (17) falling within the range of 2 to 100 ha. Each site supported one or more plant communities ranging along a hydrological spectrum from xeric prairie to sedge meadow, with most (16) supporting mesic and/or wet-prairie communities (White 1978). All sites are considered to be important examples of presettlement plant communities and are managed as nature preserves.

Insect Groups

Many insect species are restricted in distribution to prairie remnants and are clearly vulnerable to reserve-wide management activities. I included in my study 70 of these remnant-dependent species (Panzer et al. 1997), representing seven families and three orders. Most insect species are vagile and opportunistic and are present within preserves as samples from extensive regional metapopulations (Panzer et al. 1995; Panzer & Schwartz 1998). Eighty-one of these remnant-independent species were included for comparative purposes (see Panzer 1998).

Most of the species I chose for study are characterized by one or more traits that could predispose them to fire sensitivity (Panzer 1998). Seventy species were remnant-dependent, precluding recolonization of burned areas from surrounding developed landscapes. At least 125 were present as eggs or dormant larvae within the highly flammable prairie litter (duff) in the spring and fall when prairies are burned. One hundred and eleven species were univoltine, reducing their potential for rapid recovery. Twenty-one were wingless, presumably limiting their ability to recolonize vacant habitats. Another eight species (*Papaipema* spp.), present in the spring as larvae, were similarly limited in their ability to recolonize recently burned habitats. Univoltine, duff-inhabiting leafhopper, butterfly, and *Papaipema* moth species are considered especially vulnerable to fire-induced extir-

Table 2. Distribution of 52 burns among 6 years and 21 Midwestern nature reserves.

Sites (abbreviation)	Site size ^a (ha)	State ^b	County	Plant community description ^c	Burn year ^d					
					92	93	94	95	96	97
Gensburg Markham Prairie (GMP)	55.0	IL	Cook	sand prairie	x	x	x	x	x	x
Sundrop Prairie (SDP)	25.0	IL	Cook	sand prairie		x	x			
Paintbrush Prairie (PBP)	15.0	IL	Cook	silt loam prairie					x	x
Chicago Ridge Prairie (CRP)	3.0	IL	Cook	gravel prairie					x	x
Shoe Factory Road Prairie (SFP)	3.5	IL	Cook	hill prairie					x	
Wolf Road Prairie (WRP)	25.0	IL	Cook	silt loam prairie				x		
Bluff Spring Fen (BSF)	20.0	IL	Cook	hill prairie and fen						x
Goose Lake Prairie (GLP)	600.0	IL	Grundy	silt loam prairie	x	x	x		x	x
Com Ed Prairie (CEP)	50.0	IL	Grundy	silt loam prairie			x	x		
Grant Creek Prairie (GCP)	32.0	IL	Will	silt loam prairie	x		x			x
Lockport Prairie (LP)	50.0	IL	Will	dolomite prairie			x	x		x
North Shore Prairie (NSP)	8.0	IL	Lake	sand prairie			x			
Illinois Beach Prairie (IBP)	300.0	IL	Lake	sand prairie	x				x	x
Iroquois Prairie (IP)	250.0	IL	Iroquois	sand prairie				x		
Lake in the Hills Fen (LHF)	50.0	IL	McHenry	hill prairie and fen		x		x	x	
Harlem Hills Prairie (HHP)	20.0	IL	Winnebago	hill prairie				x	x	x
Savanna Army Depot prairie enclosure (SAD)	5.0	IL	Carroll	sand prairie				x		x
Thomson Fulton RR Prairie (TFP)	2.0	IL	Carroll	sand prairie					x	
Beaver Lake Prairie (BLP)	80.0	IN	Newton	sand prairie			x	x	x	x
Chiwaukee Prairie (CP)	70.0	WI	Kenosha	sand prairie			x	x	x	
Muralt Bluff Prairie (MBP)	10.0	WI	Green	hill prairie				x	x	x

^a Approximate values for size do not include woodland or old-field habitats.

^b State abbreviations: IL, Illinois; IN, Indiana; WI, Wisconsin.

^c Plant community descriptions follow White (1978).

^d Dates indicate year of the first postburn season.

pation (Hessel 1954; Swengel 1996; Hamilton 1995) and comprised a majority of the remnant-dependant species examined.

Burn Treatments

Fifty-two dormant-season burns were conducted by me or various resource managers. Fires were generally hot, with estimated heat produced ranging between 5 and 8 btu/m² (\bar{x} = 7.20, SD = 0.83, n = 16) on hill and sand prairies and between 60 and 75 btu/m² (\bar{x} = 62.52; SD = 3.3, n = 28) on the denser tallgrass prairies. Estimated rates of spread ranged from 161 to 3018 m/hour (\bar{x} = 1115, SD = 824, n = 16) for hill and sand prairies and from 322 to 4628 m/hour (\bar{x} = 1511, SD = 931, n = 28) for denser tallgrass prairies. Data for eight fires were unavailable (Panzer 1998).

Most fires (79%) were conducted in the spring in either March or April. Each site was subdivided into two or more units, with zero units or one unit burned each year. In most cases recently burned units were spared from fire for 2 or 3 years to facilitate population recovery.

Sampling Protocol

Sampling scales varied among sites, with most data collected within zones that extended from 30 to 300 m in each direction from treatment boundaries. Sampling designs were generally random or stratified random, with samples collected within transects that were 2 m wide and parallel to treatment boundaries (Panzer 1998).

I used a variety of sampling techniques. Standard canvas nets 38 cm in diameter were used to collect random-sweep samples between 1200 and 1800 hours between 15 May and 1 October each year. Certain insect species cannot be sampled effectively with sweep nets (DeLong 1948; Southwood 1966), so I used adhesive-coated plastic plates situated randomly within each treatment to sample these species. This destructive technique was used sparingly to sample leafhoppers in the fall of each year.

Papaipema moth larvae, present as eggs within the duff when prairies are burned, emerge and bore into plant stems each spring. I sampled six species as late-instar larvae along stratified transects that either paralleled burn boundaries or radiated in randomly chosen directions from the centers of large host-plant patches.

I used black-light traps on 3 nights in 1997 to sample three localized moth species on two sites. Traps were randomly placed within host-plant patches situated at least 50 m from burn boundaries. I positioned each trap within dense vegetation to preclude visibility from distant treatments. Traps were operated for 1 night and moved to new locations to avoid recaptures. I established butterfly census routes, designed to traverse predetermined burn units, on seven sites. Censuses were

completed on each site between 1 June and 1 August following the procedures outlined by Pollard (1977). Because butterfly detectability varies as a function of temperature, wind speed, and even time of day, I employed a second sampling approach that incorporated alternating sampling between treatments in 1995–1997 to minimize this potential source of error. Three or four investigators initiated 5-minute counts from randomly chosen points. Investigators typically covered much or most of the suitable habitat within each treatment.

Most sampling was done on a catch, count, and release basis. Voucher specimens were collected for most species and were deposited in the collection at Northwestern Illinois University.

Data Analysis

INITIAL IMPACT

Sizes of sweep-net, sticky-trap, butterfly-count, and light-trap samples were dictated by habitat size, weather conditions, or time constraints and ranged from 8 to 80 per treatment (\bar{x} = 18.08 samples/treatment, SD = 8.58, n = 614). I sampled evenly among treatments within sites. I recorded moth-larvae densities as presence or absence within host plant stems. Sample sizes, dictated by total number of stems present, ranged from 100 to 4700 stems examined per treatment (\bar{x} = 1342, SD = 1848, n = 28). Levels of replication ranged from 1 to 16 tests per species for 151 species, with mean replication at 4.15 (SD = 2.83) tests per species.

I compared mean burned and unburned postfire sample densities using Mann-Whitney two-sample tests for fire effects within years and sites. Binomial exact tests were employed when zero individuals were recorded in one treatment. When prefire sampling was conducted, Fisher's exact tests and chi-square two-way contingency tests were used to compare moth presence and absence data between treatments within sites and years and within sites between years for other species. I used Wilcoxon paired-sample tests to analyze butterfly census-route data. Burned and unburned data from adjacent plots were paired by census date.

Fire responses can be characterized in terms of both direction (e.g., negative response) and magnitude (effect size). I used Fisher's method of combining probabilities to evaluate the generality of the combined tests for individual species (Sokal & Rohlf 1981). Species were arbitrarily categorized as fire-positive ($p \leq 0.05$), fire-negative ($p \leq 0.05$) or fire-neutral ($0.05 < p > 0.05$) based on these combined probability estimates. Species that exhibited mixed responses (significant effects in both directions) were characterized as mixed-response species.

Mean effect sizes were calculated to provide a rough measure of the magnitude of postfire responses for each species. I defined effect size (ES) as the ratio of observed

burned-treatment population size (O_b) to expected burned-treatment population size (E_b) minus 1 ($[O_b/E_b] - 1$), where E_b equals 0.5 of the total individuals recorded. Thus, ES scores could range symmetrically from +1.0, when all individuals are encountered within the burn treatment, to -1.0, when no individuals are encountered within the burn treatment.

RECOVERY OF FIRE-NEGATIVE POPULATIONS

I attempted to track 200 fire-reduced populations to recovery. Comparisons (within site) between burned and unburned populations were repeated for subsequent generations until such time that "recovery" had occurred. Both background variation (sample variation, independent of treatments) and the need to minimize chances of Type II errors must be weighed in the selection of a recovery criterion. With these considerations in mind, recovery was deemed to have occurred when burned populations were at least 80% as large as un-

burned populations ($obs_b/obs_u \geq 0.8$) and where the probability of a Type I error was high ($p \geq 0.5$).

I was unable to track 37 populations to recovery as a result of either unplanned fires or my failure to sample a sufficient number of individuals, due largely to unpredictable population phenologies between sites and years. Estimates of recovery intervals for these unrecovered populations were recorded as greater than or equal to the last year sampled plus 1 (e.g., the recovery interval for an unrecovered population last sampled 1 year after the burn was recorded as ≥ 2 years).

CORRELATES OF FIRE SENSITIVITY AND POSTFIRE RECOVERY

I used Fisher's exact tests to compare levels of fire negativity and recovery times among several suites of species. I used a chi-square contingency analysis to compare levels of fire negativity among insect orders represented by 10 or more species, and a three-way contingency analysis to gauge the strength of two-way and three-way interactions between fire negativity, habitat

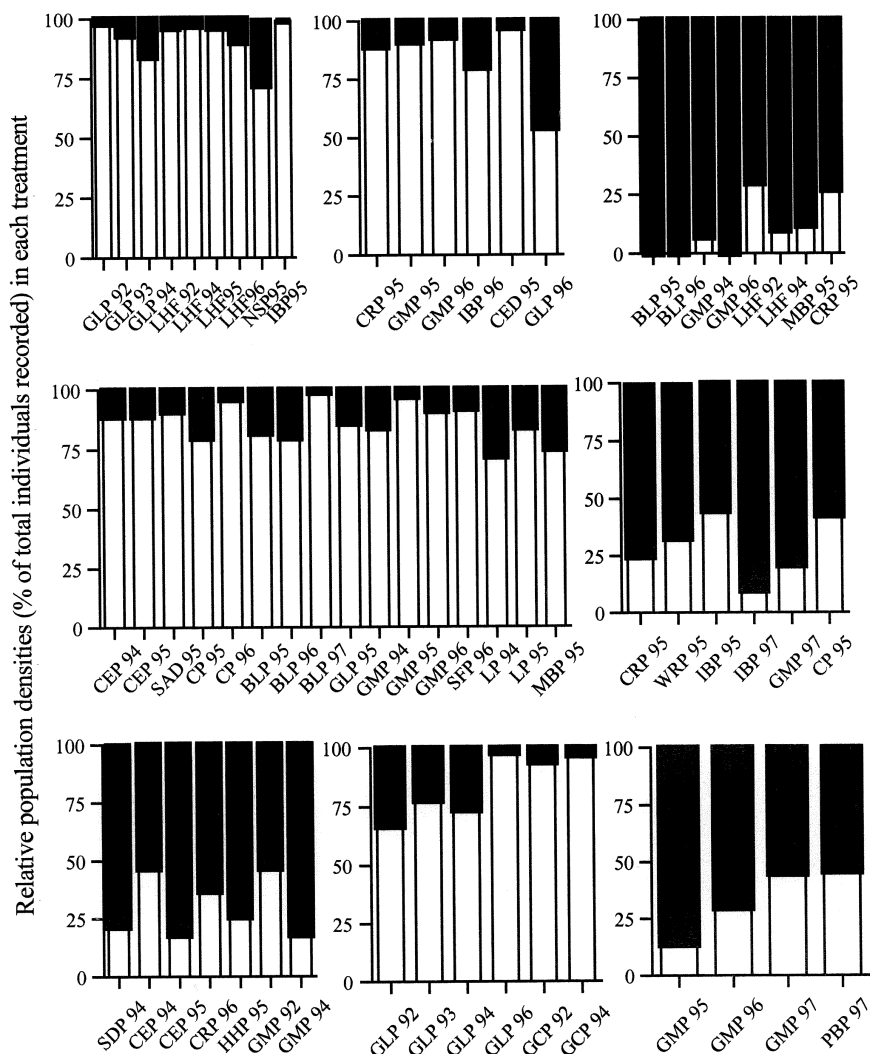


Figure 1. Examples of consistent postfire responses within species across sites and years. Each bar depicts the relative abundance of a species in burned (black) and unburned (white) treatments the summer following a prescribed fire on a specific site. Site abbreviations are explained in Table 2. Top row: Aflexia rubranura, Cribrus shingwauki, Hecalus flavidis. Second row: Polyamia caperata, Diapheromera blatchleyi. Bottom row: Philaenus spumarius, Papaipema eryngii, Problema byssus.

type, and vagility for remnant-dependant species (Fienberg 1980). I used Bonferonni corrections to correct for group size in comparisons of univariate attribute tests.

Results

Initial (Short-Term) Response

Insect species responded consistently to prescribed fires (e.g., Fig. 1). Among 137 species with replicated trials, 87 (64%) never varied in terms of effect direction (positive, neutral, or negative) in any test. If only significant test results (369/642) are considered, 93% of the species examined exhibited consistent responses across sites and years.

Postfire responses ranged from positive (25%) to negative (42%) in 642 trials, and from positive (26%) to negative (40%) for 151 species representing 33 families and seven orders. Sixty-one species exhibited substantial short-term population declines after fire ($p \leq 0.05$) across sites and years. This number rose only slightly to 63 species when $\alpha = 0.1$ was used as the defining (criti-

cal) value for fire negativity. The frequency of fire negativity was similar among native (40%) and exotic (43%) species. For native species, negative responses were more prevalent among remnant-dependent species (54%) than among remnant-independent species (27%) (Fig. 2). Among the five insect orders represented by 10 or more species, the Homoptera exhibited a substantially greater prevalence of fire sensitivity than did Lepidoptera, Orthoptera, Heteroptera, or Coleoptera ($\chi^2 = 16.560$, $df = 4$, $p = 0.0024$).

Natural-history factors such as habitat type and flight capability might be expected to affect the initial response of a species to fire. There were positive two-way associations between fire negativity and both upland inhabitation (adjusted $p < 0.01$) and nonvagility (adjusted $p < 0.05$). In a three-dimensional contingency analysis (Fienberg 1980) of these data, the model of complete independence (model a) revealed substantially nonrandom associations among the three traits (V, vagility; H, habitat; E, fire effect). Inclusion of the two-way interactions EH and EV in the conjoint independence analyses (models b1 and b3) resulted in a reduction in the departures of the data from these model descriptions, but failed to account for much of the nonrandomness present. The VH interaction did not reduce nonrandomness. In the conditional independence analyses, combining the weak VH interaction with either of the strong interactions (models c2 and c3) still left these descriptions at the borderline of significant disagreement with the observed data. Combining the two strong interactions (model c1), however, provided a near-perfect description of the data and obviated the need to consider a more complex model. To summarize, there was no association between habitat and vagility, but the interactions of fire effects with habitat and with vagility were strong and were both needed to account for the substantial

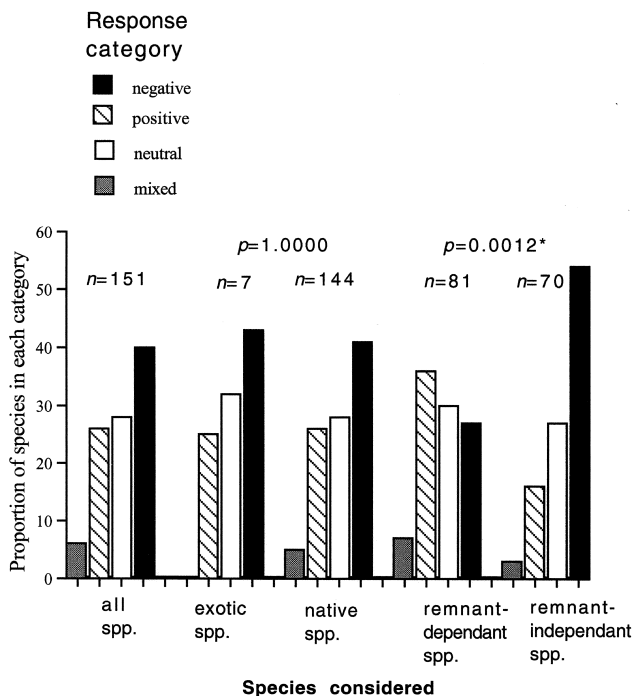


Figure 2. Summary of initial postfire responses for five suites of prairie-inhabiting insect species. Each bar depicts the proportion of n species in each category. Fisher's exact tests were used to compare levels of fire negativity between native and exotic and between remnant-dependant and remnant-independent species. Asterisk indicates that the Bonferonni-corrected critical value for significance is $0.05/2 = 0.025$.

Table 3. Multidimensional contingency analysis of vagility (vagine, nonvagine), habitat (wetland, upland), and fire effects (negative, nonnegative) among 70 remnant-dependant insect species.^a

Model	G^{2b}	df	p
Complete independence model ^c			
(V) (E) (H)	14.9275	4	0.0049
Conjoint independence models			
(V) (E H)	7.5010	3	0.0582
(E) (V H)	13.0558	3	0.0045
(H) (E V)	7.7854	3	0.0507
Conditional independence models			
(H/E) (V/E)	0.3589	2	0.8468 ^d
(E/H) (V/H)	5.6008	2	0.0608
(E/V) (H/V)	5.9116	2	0.0520

^a The model that accounts for (removes) the greatest amount of variation is selected as the best model for the data considered (Fienberg 1980).

^b Asymptotically distributed as χ^2 .

^c V = vagility; E = fire effect; H = habitat.

^d This model removes nearly all the variation in this system.

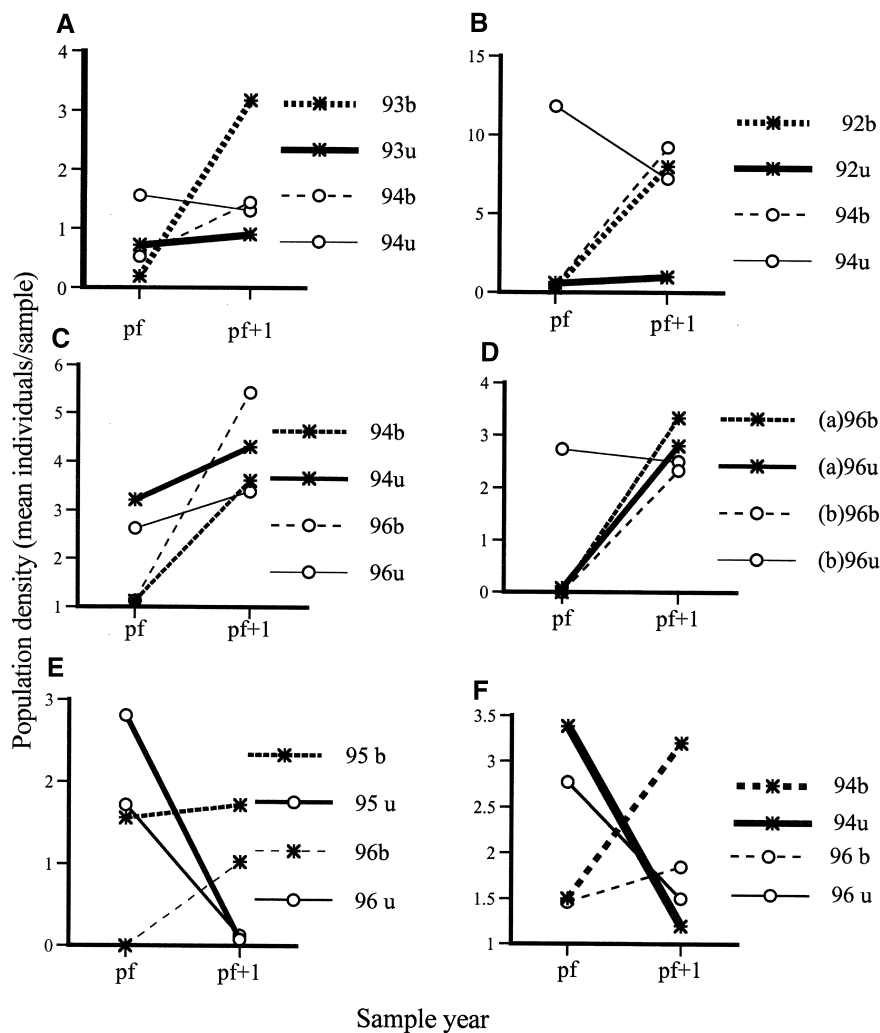


Figure 3. Population trajectories for four remnant-dependant moth (A-D) and two remnant-dependant butterfly (E-F) species following prescribed burns. All initial comparisons between burned and unburned treatments were significantly fire negative ($p < 0.05$). (A) *Papaipema eryngii*, Good Lake Prairie; (B) *Papaipema eryngii*, Grant Creek Prairie; (C) *Papaipema maritima*, Goose Lake Prairie; (D) (a) *Papaipema beeriana*, (b) *Papaipema unimoda*, Gensburg Markham Prairie; (E) *Euphyes bimacula*, Gensburg Markham Prairie; (F) *Speyeria aphrodite*, Sundrop Prairie (94), Beaver Lake Prairie (96). (pf, post-fire abundance; pf + 1, postfire abundance 1 year later; b, burned treatment populations; u, unburned treatment populations.)

nonrandomness of the data (Table 3). A third trait, number of generations per year, was not a significant predictor of species response in two-way tests and was not included in a three-way analysis.

Effect sizes ranged between +1.0 and -1.0 in 630 trials. Effect sizes for fire-negative species ranged between -0.09 and -1.0 for 269 populations and between means of -0.23 and -1.0 for 61 fire-negative species. In other words, mean declines from predicted population densities ranged from 23% to 100% (local extirpation) among fire-negative species. The mean deviation from expected population density for fire-negative species was -67% (SD = 0.20). Relative to unburned populations, postburn populations were, on average, 80% smaller.

Recovery of Fire-Negative Populations

Unplanned fires, considerable regional fluctuations in population sizes, and unpredictable temporal fluctuations in population peaks from year to year can frustrate the tracking of insect populations on multiple sites over

multiple years (Whelan 1995). Despite considerable difficulties, I tracked 200 negatively affected insect populations representing 70 species through at least one postfire season. Of these, 163 populations representing 66 species were tracked to recovery. Recovered population sizes were generally large, in most cases (84%) exceeding those on unburned tracts. The mean population density in burn treatments (b/u) was 2.39 (SD = 3.60). One outlier datum (b/u = 125) was not included in this calculation.

Roughly two-thirds (68%) of those populations tracked to recovery exhibited mean recovery times of ≤ 1 year (e.g., Fig. 3.). All had mean recovery times of ≤ 2 years. The mean recovery time for all species was 1.32 years (SD = 0.47). Thirty-seven populations were tracked initially but were not tracked to recovery. Approximate recovery times for these populations ranged from ≥ 1 year (16 populations) to ≥ 3 years (3 populations).

Mean recovery times for 42 remnant-dependent species and 24 remnant-independent species did not differ significantly (Mann Whitney, $p > 0.2$, $n = 119$ and 44). Mean recovery times for 52 vagile species compared

with those for 14 flight-restricted species were not significantly shorter at this spatial scale ($p > 0.13$, $n = 117$ and 46). Mean recovery times for 19 multivoltine species tended to be shorter than those for 47 univoltine species ($p = 0.038$, $n = 57$ and 46), although differences were not significant at the Bonferonni-corrected significance level of $0.05/4 = 0.0125$.

Discussion

Initial Response

Individual species responded consistently to prescribed fires across sites and years (e.g., Fig. 1). This supports the oft-stated notion that fire plays a major role in determining the short-term structure of insect communities in burned-prairie habitat and supports previous contentions that species can generally be expected to respond predictably to cool-season fires (Swengel 1996; Reed 1997). In contrast, genera responded inconsistently to prescribed fires. Seven of 22 genera represented by two or more species comprised both fire-negative and fire-positive species. This underscores the need to focus fire research at the species level (Panzer et al. 1995).

As expected, initial responses to burning varied among species. Whereas remnant-independent herbivores and flower visitors tended to be fire-neutral or fire-positive, duff-inhabiting, remnant-dependent populations tended to decline sharply following dormant-season fires. Many species (28%) experienced moderately positive or negative fluctuations. These fire-neutral species were commonly encountered in large numbers throughout this study and seem to be well adapted to prevailing burn regimes.

Sixty-one species (40% of total) representing five orders exhibited substantial population declines following fires. Ten of these species have been considered in earlier studies by other investigators. *Laevicephalus minimus* and *Boloria bellona* exhibited similar responses in Illinois (Dietrich et al. 1998) and in the upper Midwest (Swengel 1996). Six remnant-dependent leafhopper species (*Flexamia prairiana*, *F. pectinata*, *F. albida*, *F. inflata*, *Polyamia caperata*, and *Chlorotettix spatulatus*) occurred consistently ($n = 2$) in lesser numbers in burned than in unburned grazed prairie, suggesting similar levels of fire sensitivity in Kansas (Mason 1973). Only two species (*Stirellus bicolor* and *Scaphytopius frontalis*) occurred in greater or similar numbers in burned prairie, in apparent disagreement with my results.

Eighty-two species (54% of total) representing five orders did not exhibit substantial postfire population declines and were classified as either fire-neutral or fire-positive. Sixteen of these species were included in earlier studies (Mason 1973; Evans 1987; Swengel 1996). Results for one grasshopper (*Phoetaliotes nebrascensis*), three leafhoppers (*Endria inimica*, *Hecalus flavi-*

dis, and *Scaphytopius cinereus*), and four butterflies (*Phyciodes tharos*, *Colias eurytheme*, *Danaus plexippus*, and *Limnitis archippus*) were consistent with those I obtained (Mason 1973; Evans 1987; Swengel 1996). Swengel (1996), however, generally indicates a greater prevalence of fire sensitivity among butterflies than I observed (e.g., Fig. 4). Three species that were fire-neutral in my study (*Speyeria aphrodite*, *Boloria selene myrina*, and *Cercyonis pegala olympus*) responded negatively in pairwise tests similar to those I conducted (Swengel 1996). Swengel (1996, 1998) found that another five species (*Lethe eurydice*, *Polites origines*, *Polites themistocles*, *Atrytone logan*, and *Problema byssus*) occur in recently burned treatments in lesser numbers than one would expect, the implication being that they are similarly fire-sensitive. In sharp contrast, I found the latter three species to be demonstrably fire-positive (data for *P. byssus* in Fig. 1). Differences in experimental design and data analysis make it difficult to account for these contrasting results.

Postfire Mortality

Declines in abundance among fire-negative species were substantial, implying high levels of mortality for litter-inhabiting species. Actual mortality levels can be estimated when nonvagile forms are sampled immediately after a prescribed fire (e.g., Dana 1991; Fay & Samenus 1993). Unfortunately, mortality levels for vagile forms can be difficult to assess. Initial postfire responses can result from mortality, habitat choice (emigration or immigration), or a combination thereof. *Papaipema* larvae

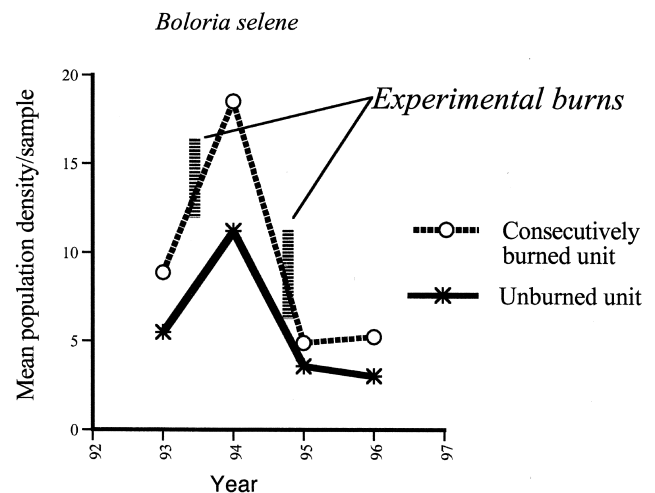


Figure 4. Population trajectories within two management units across 3 years. No significant burn or double-burn effects were detected ($2 \times 4 \chi^2$; $p = 0.36$) for this reportedly sensitive butterfly species. This site had not been burned within the past 20 years.

were sampled within 10 days from the time they emerged as minuscule, essentially immobile caterpillars. For these and a dozen other species that are catchable and identifiable as wingless immatures, postfire responses serve as an unambiguous estimate of fire-related mortality. Effect sizes for this group were generally high ($\bar{x} = -0.71$, $SD = 0.20$, $n = 20$), confirming that cool-season fires can reduce population sizes substantially.

Most of the species I tracked could not be captured or identified until they emerged as adults. Sampling was necessarily delayed 30–90 days beyond periods of post-fire emergence to correspond with adult occurrences for butterflies and many other species. For these species, the underlying mechanisms driving postfire responses are less clear. However, the prevalence of fire-positive responses and the strong association between fire negativity and nonvagility suggest that recolonization among vagile species began well before initial samples were collected for many species. Given the likelihood that initial responses were often estimates of mortality mediated by recolonization, the mean decline in population size of 67% for fire-negative species reported earlier is probably best viewed as an underestimate of mean fire-induced mortality.

Recovery of Fire-Sensitive Species

Establishing the prevalence and distribution of fire sensitivity among insects is important, but this information alone provides limited insights into the role of fire in shaping grassland insect communities. If, for instance, most fire-negative insect populations recover fully within one growing season, rotational fires that occur at 2- or 3-year intervals can be expected to have little effect on species richness or composition.

Postfire recovery can be rapid (Carpenter 1939; Tester & Marshall 1961; Cancelado & Yonke 1970; Van Amburg et al. 1981; Anderson et al. 1989; Hall 1996; Harper et al. 2000). Consistent with these findings, nearly all the populations I tracked recovered in 2 or fewer years (e.g., Fig. 3). At least three populations representing three species failed to recover in 2 years. However, eight or more populations of each species managed to recover in ≥ 2 years in additional trials, suggesting that elapsed recovery times of > 2 years are somewhat rare events.

Several of the species I examined have exhibited similar recovery times in previous studies. Dietrich et al. (1998) and Swengel (1996) reported rapid recoveries for *Laevicephalus minimus* and *Cercyonis pegala*, respectively. Defining recovery as the point at which species occur in recently burned areas in greater numbers than would be expected by chance (my definition), an additional seven species (*Speyeria aphrodite*, *Boloria selene*, *B. bellona*, *Polites themistocles*, *P. origines*, *Atrytone logan*, and *Phycoides tharos*) recovered in ≤ 2 years in the upper Midwest (Swengel 1996). Among the

species examined by both Swengel and me, only *Lethe eurydice* was reported to require > 2 years for recovery (Swengel 1996). Among six remnant-dependent species studied only by Swengel (1996), four also recovered in ≤ 2 years. The remaining two species (*Hesperia leonardus* and *Hesperia arogos*) required 3 or 4 years, respectively. Unfortunately, no direct pairwise (within-site) experiments were conducted to substantiate these findings (Swengel 1996).

Correlates of Fire Sensitivity

Biologists can never hope to document levels of fire sensitivity for each of the several thousand insect species that inhabit Midwestern prairies. It may be possible, however, to identify traits that predispose species to fire sensitivity, and in so doing, to contribute to a predictive understanding of fire susceptibility among grassland insects in general. For native species, fire-negative responses were significantly more prevalent among remnant-dependent species than among remnant-independent species (Fig. 2). Whereas remnant-dependent populations tend to be small and isolated, remnant-independent species are typically present as enormous populations within the “inhospitable” landscapes that surround most preserves. The greater prevalence of fire-negative responses among remnant-dependent species can perhaps be attributed to the general tendency of remnant-independent species to recolonize rapidly from these relatively limitless recolonization sources.

Wetlands typically burn fitfully, often sparing significant amounts of water-soaked duff or stubble. Fires in upland habitats, while frequently less intense, tend to uniformly consume plant debris, often leaving nothing in their wake. Not surprisingly, upland inhabitance was a significant predictor of fire-negative response (adjusted $p < 0.01$).

Insect species with limited dispersal capability are presumed to be especially susceptible to the deleterious effects of fire. Apparently incapable of rapid recolonization, these species are expected to recover slowly and to persist as small populations on frequently burned sites. Nonvagility was a significant predictor of fire-negative response, but this attribute did not affect mean recovery times. Apparently, even nonvagile species can move rapidly across the relatively small temporal and spatial scales considered here.

Species that produce a single generation of adults each year might be expected to recover more slowly than multivoltine species. Swengel (1996) found a strong positive correlation between generations per year (a measure of reproductive potential) and butterfly density within burn age classes. Multivoltine species tended to recover more rapidly in my study as well, although Bonferonni-corrected differences were not significant.

Levels of fire sensitivity can be expected to vary among taxa. Swengel (1996) found fewer butterfly individuals than expected for many species in recently burned units, suggesting a high level of sensitivity for this taxon. Among the five insect orders represented by 10 or more species in my study, the Homoptera exhibited a substantially greater level of fire negativity (55%) than Lepidoptera (29%), Orthoptera (25%), Hemiptera (20%), or Coleoptera (13%). These small, specialized insects, generally present above ground in duff or vegetative tissue during dormant seasons when prairies are burned, may rank among the more fire-sensitive taxa inhabiting small reserves (Hamilton 1995; Siemann et al. 1997).

Management Implications

The advisability of burning isolated patches of once vast ecosystems has become a contentious issue. On one side, many entomologists are advocating the reduction or elimination of burning as a management activity. On the other side, botanists and resource managers, citing both the necessity of maintaining natural processes and the need to counter the escalating invasion of natural areas by exotic plant species, are resisting suggestions to significantly reduce or eliminate prescribed burning (e.g., Schramm 1992; Kline 1997; Packard & Ross 1997; Robertson et al. 1997).

The issue of prescribed burning will be difficult to resolve to the satisfaction of everyone. Given the thousands of insect species that inhabit prairie ecosystems, the contention that specific burning practices may pose a threat to one or more species simply cannot be falsified. Researchers can, however, strive to calculate the likelihood that specific practices will result in appreciable losses in species richness. The data presented here indicate that few (if any) species may be threatened by judicious prescribed burning.

Roughly three-quarters of the insect species that inhabit Midwestern prairie reserves are firmly established within surrounding landscapes and are unlikely to be af-

ected by burning or other management activities (Panzer et al. 1995). Among species incapable of survival outside reserves, roughly half either avoided injury or rebounded within weeks following fires. Among 42 fire-negative species tracked to recovery, 52% recovered in ≤ 1 year. Mean recovery times for the remainder were ≤ 2 years. Highly sensitive species, defined here as those requiring 3 or more years to recover, were not encountered and are presumed to be scarce. These results, summarized in Fig. 5, support the judicious use of cool-season burning within small sites.

As is always the case, managers must establish goals and weigh ecological costs and benefits when establishing management regimes. Some may choose to manage for a narrow range of rare or favored species. In these instances, suitable burn regimes might range from annual fires (e.g., for ants; see Reed 1997), with everything burned as often as possible, to nearly complete fire exclusion. Swengel (1996), for example, recommends that at least 80% of fire-managed sites be spared from fires each year as a means by which to maximize the population densities of a small number of butterfly species.

Few Midwestern reserves are managed for one or a few species. Most are managed as ecosystems, the goal being to preserve authentic, self-sustaining (late-successional) systems replete with indigenous biodiversity. Along with techniques such as shrub removal and re-seeding, frequent burning is used widely as a means by which to maintain high-quality habitat and to facilitate the restoration of requisite plant, vertebrate, and invertebrate habitats within degraded areas.

Ecosystem reserves should be burned on a rotational basis, with sufficient unburned refugia maintained each year. Ideally, important microhabitats will be represented in all units. Rotational burn regimes that allow 2 years for burn-unit recovery (3-year rotations) are compatible with the conservation of prairie-inhabiting bird species (Herkert 1994; Herkert et al. 1996; Swengel 1996). My study suggests that 3-year rotations are compatible with the preservation of insect biodiversity as

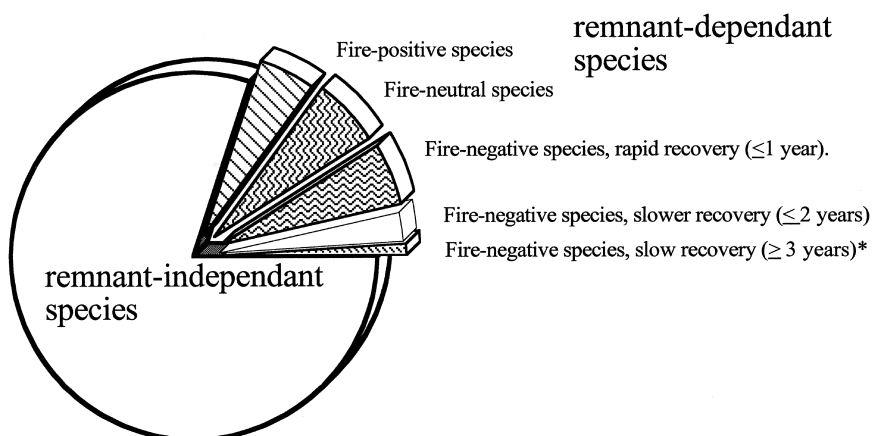


Figure 5. Approximate distribution of fire sensitivity among prairie-inhabiting insect species. Asterisk indicates that no species requiring 3 or more years for recovery were encountered in this study.

well. Regimes that allow 3 years for recovery (4-year rotations) must be considered conservative in terms of insect conservation. In contrast, annual burning of entire sites can be expected to reduce remnant-dependent insect species richness within fragmented landscapes.

Four traits—remnant-dependence, upland inhabitance, low vagility, and probably univoltinism—predispose duff-dwelling, remnant-dependent insects to fire sensitivity. In the absence of empirical data, duff-dwelling species possessing one or more of these characteristics should be presumed to be fire-sensitive. Species of special concern characterized by all four traits should be presumed hypersensitive pending formal study.

Given the thousands of species that inhabit tallgrass prairies, Fig. 5 must be treated as a first approximation of insect response to rotational burning in tallgrass prairie. Levels of remnant-dependence, fuel loads, and insect phenologies can vary geographically, perhaps resulting in contrasting responses for some species. Additional studies should be conducted within contrasting systems to test the generality of the results obtained here. Every effort should be made to include wingless, univoltine, upland-inhabiting, remnant-dependent species in future studies.

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