RESEARCH ARTICLE

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Importance of In Situ Survival, Recolonization, and Habitat Gaps in the Postfire Recovery of Fire-Sensitive Prairie Insect Species

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ABSTRACT: I investigated the roles of in situ survival and recolonization in the postfire recovery of fire-sensitive insect species within isolated tallgrass prairie remnants in Illinois, northwest Indiana, and southeast Wisconsin, USA. I examined the extent to which commonly encountered habitat gaps suppress recovery among several taxa and tested the pivotal assumption that small populations are readily extirpated when their requisite habitats are completely burned. Both in situ survival and recolonization were found to contribute appreciably to postfire recovery within the spatial and temporal scales examined. Combined recovery times for 22 species separated from unburned units by roads or other barriers were not greater than those for populations in burn units abutting unburned tracts. The flightless leafhopper *Aflexia rubranura* (DeLong) and the sedentary moth *Papaipema eryngii* Bird readily crossed habitat gaps as large as 36 m and 25 m, respectively. When 6-m gaps were covered with tar paper in the *Aflexia* experiment, colonization of outlying patches was reduced, but not stopped. I conclude that burn unit designs that provide adjacent or nearby refugia, coupled with procedures that promote patchiness within burned units, can be expected to contribute appreciably to the rapid recovery of fire-sensitive species.

Importancia de la Supervivencia In Situ, la Recolonización, y los Gaps en el Hábitat en la Recuperación Posterior al Fuego de Especies de Insectos de Llanura Sensibles al Fuego

RESUMEN: Investigué los roles de la supervivencia in situ y la recolonización en la recuperación post quema de especies de insectos sensibles al fuego dentro de remanentes aislados de pastos altos en Illinois, noroeste de Indiana, y sudeste de Wisconsin, USA. Examiné hasta que punto los gaps de hábitats comúnmente encontrados suprimen la recuperación en varias especies y analicé la asumpción pivote que las poblaciones pequeñas son prontamente extirpadas cuando sus requisitos de hábitat son completamente quemados. Ambas, la supervivencia in situ y la recolonización contribuyeron apreciablemente a la recuperación post fuego dentro de las escalas espaciales y temporales examinadas. El tiempo combinado de recuperación para 22 especies separadas de unidades no quemadas por rutas u otras barreras no fueron mayores que los de las poblaciones en unidades quemadas linderas con los caminos no quemados. Insectos no voladores como *Aflexia rubranura* (DeLong) y la mariposa nocturna sedentaria *Papaipema eryngii* Bird rápidamente cruzaron los gaps tan largos como 36 m y 25 m respectivamente. Cuando los gaps de 6 m fueron cubiertos con papel con alquitrán en el experimento de *Aflexia*, la colonización de parches lejanos estuvo reducida, pero no detenida. Concluí que los diseños de unidades quemadas que proveyeron refugios adyacentes o cercanos, fueron similares a los procedimientos que promovieron los parches dentro de las unidades quemadas, puede esperarse que contribuya apreciablemente a la rápida recuperación de las especies sensibles al fuego.

Index terms: Homoptera, Lepidoptera, prairie insects, prescribed burning, tallgrass prairie

INTRODUCTION

Tallgrass prairie remnants can support hundreds of insect species (Hendrickson 1930, Evans 1975, Risser et al. 1981, Panzer 1988), many of which are incapable of inhabiting the human-dominated landscapes within which reserves are situated (Panzer et al. 1995). Isolated as small populations on what are essentially small habitat islands, these remnant-dependent (r-d) organisms (Panzer et al. 1997) must contend with frequent management fires conducted predominantly for the benefit of vascular plants (Panzer and Schwartz 2000).

Studies by Dana (1991), Fay and Samenus (1993), Swengel (1996), Harper et al. (2000) and Panzer (2002), have shown that r-d insect species can respond negatively to management burns, with postfire declines often appproaching 100%. Given sufficient time between fires, fire-impacted populations generally recover quickly, often within 1 y (Carpenter 1939, Tester and Marshall 1961, Cancelado and Yonke 1970, Hill 1973, Van Amburg et al. 1981, Anderson et al. 1989, Hall 1996, Panzer 2002). The means by which recovery occurs, however, is unclear. Some species may be eradicated from burn units and rely entirely on recolonization from unburned refugia. Others may rely predominantly on in situ survival and rapid population growth. This topic has important

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implications for the design and implementation of management burn regimes, especially within severely fragmented landscapes where recolonization from outside sources is unlikely. 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 (Panzer and Schwartz 2000, Panzer 2002). In the work reported here, I used an experimental approach to determine the relative importance of postfire recolonization versus in situ population growth, to gauge the extent to which habitat gaps retard recovery, and to test the pivotal assumption that small populations are readily extirpated when their requisite habitats are completely burned.

METHODS

Sites

Prescribed burns were conducted from 1992 through 1997 on 21 reserves spanning a geographic area of approximately 40,000 km^2 within the eastern portion of the tallgrass prairie biome, USA (Table 1). Study sites extended from Green County in south-central Wisconsin through northern Illinois to White County in northeast Indiana. Study sites ranged in size from 3- to 600-ha, with most (17) falling within the 3 to 100 ha range. Each site is known to support 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 (see White 1978).

Table 1. Distribution of 52 burns among 6 years and 21 nature reserves in the midwestern United States.

Sites	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 & 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 & fen		x		x	x	
Harlem Hills Prairie (HHP)	20.0	IL	Winnebago	hill prairie				x	x	x
Savanna Army Depot prairie exclosure (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] IL = Illinois; IN = Indiana; WI = Wisconsin

[c] Plant community descriptions follow White (1978).

[d] Dates indicate year of the first postburn season.

Insect Groups

I included 151 insect species representing 33 families and 7 orders in this assessment (see Panzer 1998). Many insect species persist as small, isolated populations within isolated reserves and are clearly vulnerable to reserve-wide management activities. Seventy of these remnant-dependent species representing 14 families and 5 orders were included in this study. Most insect species are vagile and opportunistic, and are present within preserves as samples from extensive regional metapopulations (Panzer et al. 1995). Eighty-one of these "remnant-independent" (r-i) species were included for comparative purposes.

Insect species present as eggs or dormant larvae within the highly flammable prairie duff in the spring and fall are expected to experience high levels of postfire mortality. Duff-inhabiting leafhopper, butterfly, and *Papaipema* moth species comprise a majority of the r-d species examined here. Flight-limited (wingless and/or sedentary) species are most likely to rely heavily on in situ survival. Twenty-one flight-limited species were included as well. The distribution of pertinent life history traits among the taxa considered is shown in Table 2.

Burn Treatments

Fifty-two dormant season burns were conducted by myself and/or by various resource managers (Table 1). In many cases, fires were conducted according to preexisting burn schedules. Burn schedules were modified on 10 sites to accommodate this study. Each site was subdivided into two or more units with zero or one unit burned each year. Burn units on five sites were separated by narrow habitat gaps (10–40 m), including roads (three sites), a gravel pit, a gravel trail, a gravel railroad bed, and a tree-lined ditch. In most cases recently burned units were spared from fire for 2 or 3 y to facilitate population recovery.

Thirteen mathematical fire fuel models are widely used by burn managers to predict fire behavior (Anderson 1982). Model 1 is applied for hill and sand prairies where vegetation is sparse and grasses are gener-

Table 2. Distribution of life history traits among the taxa considered in this study.

Taxon	Species Totals	r-d Species	Exotic Species	Univoltine Species[a]	Flight-limited Species	Duff-inhabiting Species[b]
HOMOPTERA	**76**					
Cercopidae	4	2	1	3	1	4
Membracidae	2	0	0	2	0	2
Caliscelidae	3	2	0	3	3	3
Dictyopharidae	3	0	0	3	1	3
Issidae	1	0	0	1	0	1
Delphacidae	2	0	0	2	1	2
Cicadellidae	61	36	3	39	8	61
LEPIDOPTERA	**31**					
Hesperiidae	8	3	0	4	0	8
Pieridae	1	0	0	0	0	1
Lycaenidae	1	1	0	1	0	1
Nymphalidae	6	4	0	2	0	6
Satyridae	2	1	0	2	0	2
Daniidae	1	0	0	0	0	0
Noctuidae	6	12	0	12	0	12
ORTHOPTERA	**16**					
Tettigoniidae	3	1	0	3	2	3
Acrididae	8	3	0	8	2	1
Phasmatidae	1	1	0	1	1	1
Oecanthidae	3	0	0	2	0	3
Grylidae	1	0	0	1	1	1
COLEOPTERA	**15**					
Chrysomelidae	8	2	0	7	0	?
Curculionidae	2	1	0	2	0	1
Scarabidae	2	0	1	1	0	2
Meloidae	1	0	0	1	0	?
Cantharidae	1	0	0	1	0	?
Coccinellidae	1	0	1	1	0	?
HEMIPTERA	**10**					
Lygaedae	3	1	0	2	0	?
Pentatomidae	2	0	0	1	0	2
Reduviidae	2	0	0	0	1	?
Scutelleridae	1	0	0	2	0	2
Coreidae	1	0	0	1	0	?
Alydidae	1	0	0	1	0	1
DIPTERA	**2**					
Otididae	2	0	0	1	0	0
DERMAPTERA	**1**					
Forficulidae	1	0	1	1	0	1
Totals	**151**	**70**	**7**	**111**	**21**	**≥113**

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[a] Determination of generations/year based on both the literature and the data generated in this study.

[b] Question marks indicate that the stratum within which species are present when prairies are burned is unknown.

ally less than 0.76 m (2.5 feet) tall. Model 3 is used for tallgrass prairies where vegetation is dense and grasses are always greater than 0.76 m tall. These models were used to generate rough estimates of rate of spread, heat per unit area, fire line intensity, and flame length for 44 fires following the nomogram procedures outlined in Rothermel (1983). Air temperature, wind speed, and relative humidity data gathered at the time of each fire were used in these calculations (Table 3).

Sampling Protocol

Sampling scales varied among sites, with most data collected within zones that extended from 30 m to 300 m in each direction from burn/unburned boundaries. A variety of sampling techniques were employed to gauge postfire population densities within burned and unburned treatments. Standard 38-cm-diameter canvas nets were used to collect random sweep samples between the hours of 12:00 and 18:00 between 15 May and 1 October each year (1992–1998). Sampling frequencies for each population varied from twice to five times each year, with most samples collected between mid-June and late September. *Papaipema* moth larvae, present as eggs within the duff when prairies are burned, emerge and bore into plant stems each spring. Six species were randomly sampled as third, fourth, or fifth instar larvae along stratified transects that either paralleled burn boundaries or radiated in randomly chosen directions from the centers of large host plant patches.

Butterfly census routes, designed to traverse predetermined burn units, were established on seven sites. Censuses were completed on each site between 1 June and 1 August following the procedures outlined by Pollard (1977). The census taker proceeded at a uniform pace (1 h/census), conducted surveys between the hours of 10:00 and 17:00, surveyed only on days with < 50% cloud cover, surveyed only on days with light to moderate winds (5–13 kph), and recorded all individuals sighted within approximately 10 m of the route transect.

Butterfly detectability varies as a function of temperature, wind speed, and even time of day. A second sampling approach that incorporated alternating sampling between treatments was employed in 1995–1997 to minimize these potential sources of error. Haphazard 5-min counts were initiated from randomly chosen points by three or four investigators. Counters were subject to the same weather constraints and 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 have been deposited in the collection at Northeastern Illinois University

Aflexia Experiment

I conducted a manipulative release-recapture experiment designed to gauge the ability of the rare, flightless, fire-sensitive leafhopper (see Panzer 2002) *Aflexia rubranura* (DeLong) to recolonize requisite host plant patches across habitat gaps (although a small proportion of *A. rubranura* adults can be macropterous, these individuals seem to be incapable of flight). This experiment was conducted within a retired agricultural field at Goose Lake Prairie State Park, Grundy County, Illinois. Four experimental northern dropseed (*Sporobolus heterolepis* A. Gray) arrays, each consisting of 2-m^2 central patches with 1-m^2 outlier patches situated 2, 4, 8, and 16 m from the central patches, were planted in 1994. Outlier patch distances were increased to 6, 12, 18, and 24 m in 1995, and to 6, 18, and 36 m in 1996. Four of eight 6-m gaps were covered with tar paper in the last year to create an inhospitable dispersal barrier. Two hundred and fifty brachypterous *A. rubranura* individuals were captured within the nearby Goose Lake Prairie Preserve and were released within the central patches of each array on two occasions each year. Outlier patches were subsequently sampled for colonists at least eight times between 15 June and 15 September each year. Successful colonists were tallied and removed to avoid recounts.

Table 3. Descriptive statistics for 44 dormant season fires conducted in 1992–1997. SD=standard deviation.

	Model 1 Short Grasses[a] (n = 16)			Model 3 Tall Grasses[a] (n = 28)		
	mean	**range**	**SD**	**mean**	**range**	**SD**
Rate of spread (m h^{-1})	1115	161–3018	824	1511	322–4628	931
Heat per unit area (btu m^{-2})	840	592–969	97	7244	6997–8611	388
Fireline intensity (btu m^{-1} s^{-1})	259	33–898	230	3133	656–9841	1998
Flame length (m)	0.9	0.3–1.8	0.3	3	1.5–5.0	0.9

[a] Model 1 is applied for hill and sand prairies where vegetation is sparse and grasses are generally < 0.76 m (2.5 feet) tall. Model 3 is used for tallgrass prairies where vegetation is dense and grasses are always > 0.76 m feet tall (Anderson 1982). Data for eight fires were unavailable.

Host Plant Gap Experiment

Vagility, the propensity for individuals to move about and to cross ecological barriers, is often low for insect species with narrow host plant requirements (Ehrlich 1961, Arnold 1983, Cappucino and Kareiva 1984, Wourms 1984, Klein 1989). Extensive inventories for the monophagus prairie moth *Papaipema eryngii* Bird have suggested that this prairie species is relatively sedentary (Panzer, unpubl. data), seldom straying from established colonies. If this is the case, this moth may be disinclined to traverse habitat gaps devoid of host plants to recolonize burned tracts. I translocated a founding population of this species to the Gensburg Markham Prairie Nature Preserve, Cook County, Illinois, in 1994 as a means by which to assess its ability and/or inclination to disperse across a heterogeneous landscape. Sixty-nine fresh adults were placed within damp and dark containers, transferred, and released within a large host plant patch between 15 September and 1 October. I returned in early June to search for evidence of larval presence, an unambiguous indicator of female movement (larvae emerge in the spring and bore into *Eryngium yuccifolium* Michx. plants within inches of the point where eggs were deposited.). Larval distances from the release point were measured and plotted throughout the host plant patch. Linear regression was used to characterize the spatial distribution of *P. eryngii* larvae throughout the host plant patch.

Patch Survivorship Experiment

The pivotal assumption that small populations of duff-inhabiting species are readily eliminated by single fires (Moffat and McPhillips 1993) was tested directly on three sites by burning 100% of the requisite habitat for 40 small populations of r-d leafhoppers, moths, and one true bug species isolated within tiny, disjunct habitat patches less than 0.01 ha in size. All of the patches chosen were situated at least 200 m from potential recolonization sources. In every case, postfire sampling was conducted before vagile species were capable of flight, precluding the likelihood that recolonization had occurred.

Table 4. Insect species included in recolonization, gap, and survival trials.

Species	Recolonization	Recovery across Gaps	Small Population Survivorship
grasshoppers			
Phoetaliotes nebrascensis[a] (Thomas)	●		
Pseudopomala brachyptera brachyptera[a] (Scudder)	●		
katydids			
Conoephalus saltans[a] (Scudder)	●	●	
true bugs			
Ishnodemus falicus (Say)		●	●
leafhoppers			
Flexamia prairiana DeLong	●	●	
Flexamia reflexa (Osborn and Ball)		●	
Flexamia pectinata (Osborn and Ball)	●	●	
Flexamia delongi (Ross and Cooley)	●		
Flexamia albida (Osborn and Ball)	●		
Flexamia inflata (Osborn and Ball)	●		
Graminella aureovitatta Sanders and DeLong		●	
Aflexia rubranura[a] (DeLong)	●	●	●
Chlorotettix spatulatus Osborn and Ball	●	●	
Dorydiella kansana Beamer		●	
Extrusanus oryssus[a] Hamilton		●	
Laevicephalus minimus (Osborn and Ball)	●		
Laevicephalus unicoloratus (Gillette and Baker)	●	●	
Cribrus shingwaukee[a] (Beamer and Tuthill)	●	●	●
Polyamia caperata[a] Ball	●	●	
Mesamia straminea (Osborn)	●		
Neohecalus Lineatus[a] (Uhler)	●	●	●
Memnonia panzeri[a] Hamilton	●	●	●
Gyponana contana DeLong	●	●	
froghoppers			
Philaenarcys killa[a] Hamilton	●	●	
planthoppers			
Bruchomorpha dorsata[a] Fitch	●		
moths			
Papaipema eryngii Bird	●	●	●
Papaipema maritima Bird		●	
butterflies			
Euphyes bimacula (Grote and Robinson)		●	
Speyeria aphrodite (Fabricius)		●	
beetles			
Pachybrachis EGR.26[b]	●	●	

[a] flight-limited species

[b] unnamed species, determined by Edward G. Riley, Texas A & M University

Recolonization Analysis

Recolonization from unburned refugia may play an important role in postfire insect recovery. If this is the case, postfire population densities are expected to vary inversely with distance from unburned recolonization sources. As previously reported, 163 negatively-impacted populations representing 66 families were tracked to recovery following dormant-season fires (Panzer 2002). Samples were collected at increasing distances along transects paralleling burn boundaries, and linear regression was employed to test for negative density/distance relations for 90 populations representing 22 species. A 2 × 3 Chi-square contingency test was used to compare density/distance trends among three distance classes. Mann-Whitney two-sample tests were used to compare recovery times in disjunct and contiguous habitats for a second subset of 22 species (Table 4). Test results were considered to be significant at $p \leq 0.05$ in each case.

RESULTS AND DISCUSSION

In Situ Survival

One or more putative survivors were encountered in 568 of 617 (92%) initial burn response trials involving 151 species. In the case of vagile species, it is not possible to rule out the possibility that "survivors" were early emigrants from unburned refugia. However, survivorship among nonvagile species was nearly as high (88%), suggesting that numerous individuals had, in fact, survived in situ. In the patch survivorship experiment, two or more individuals survived in at least 37 of 40 tests in which their relatively minuscule isolated host plant patches were burned in their entirety (Table 5). These lines of evidence suggest that in situ survival can contribute appreciably to the postfire recovery of prairie-inhabiting insect species.

Recolonization

Forty-two of 151 species responded positively to rotational burns, occurring in high numbers in recently burned tracts early in the first postburn season (Panzer 2002). These "fire-positive" species are clearly capable of rapid recolonization from nearby refugia.

For negatively affected species, an inverse distribution of population density and distance from burn boundaries in postfire populations can be construed as evidence of recolonization. Recolonization effects of this nature persist briefly within limited temporal and spatial scales, however, and can be difficult to detect. Despite this difficulty, inverse density/distance trends were detected among 22 species for 73 of 90 recovering fire-negative populations. All significant regressions (24/90) were negative. These inverse density/distance relations held up in 87% of the trials with data from the 1–10 m zone excluded. Moreover, there was no significant difference in the prevalence of recolonization effects detected in data sets that extended 30–60 m, 100–120 m, or 200–400 m from burn boundaries (χ^2=0.0427, df=2, p=0.979). In accord with the findings of Harper et al. (2000), these results suggest that recolonization contributes substantially to the postfire recovery of insect species at this spatial scale.

Movement Across Gaps

Mader et al. (1990) reported that carabid beetle movements were reduced appreciably by linear obstacles such as paved and gravel field tracks and a railway line. However, in this study similar obstacles generally did not increase recovery times for disjunct insect populations. Combined mean recovery times for 22 species separated from unburned refugia by roads or other barriers ($\bar{x}$ years=1.2, SE =0.09, n=37) were not higher than those for populations in units abutting unburned tracks ($\bar{x}$ years =1.3, SE = 0.09, n = 50; Mann-Whitney, p = 0.27). Mean recovery times were higher for only 5 of 22 species. However, small sample sizes ($n \leq 5$) precluded the use of statistical comparisons for individual species.

In the *P. eryngii* translocation experiment, numerous larvae survived the winter and bored into the lower stems of their requisite host plant. I managed to locate 261 bored plants distributed within 120 m of the adult release point, as illustrated in Figure 1. One or more females had managed to traverse both a 25-m gap devoid of host plants and a 1.8-m-high chain link fence 30 m distant. No inverse relation between larval density and distance was detected (r^2 = 0.027, df = 97, p= 0.10), suggesting that this moth may be quite capable of recolonization at this spatial scale.

In the related *Aflexia* colonization experiment, individuals managed to cross old field habitat gaps as large as 36 m. As the vegetation surrounding host plant outlier patches grew denser (years 2 and 3), colonization of outlying patches was reduced but not stopped. When four of eight 6-m gaps were covered with tar paper (1995),

Table 5. Postfire survivorship among 40 small populations within small disjunct host plant patches following complete burns. Response variable is number of populations surviving/number of populations burned.

		Approximate Host Patch size			
Species	**Host Plants**	**≤ 4 m²**	**4 m² <X ≤ 8 m²**	**8 m² <X ≤16 m²**	**≤32 m²**
Aflexia rubranura	*S. heterolepis*	2/2	3/4	4/4	—
Memnonia panzeri	*S. heterolepis*	1/2	2/2	2/2	3/3
Papaipema eryngii	*E. yuccifolium*	—	1/2	2/2	2/2
Cribrus shingwauki	*C. canadensis*	—	3/3	2/2	3/3
Neohecalus lineatus	*S. pectinata*	—	—	1/1	2/2
Ishnodemus falicus	*S. pectinata*	—	2/2	1/1	1/1

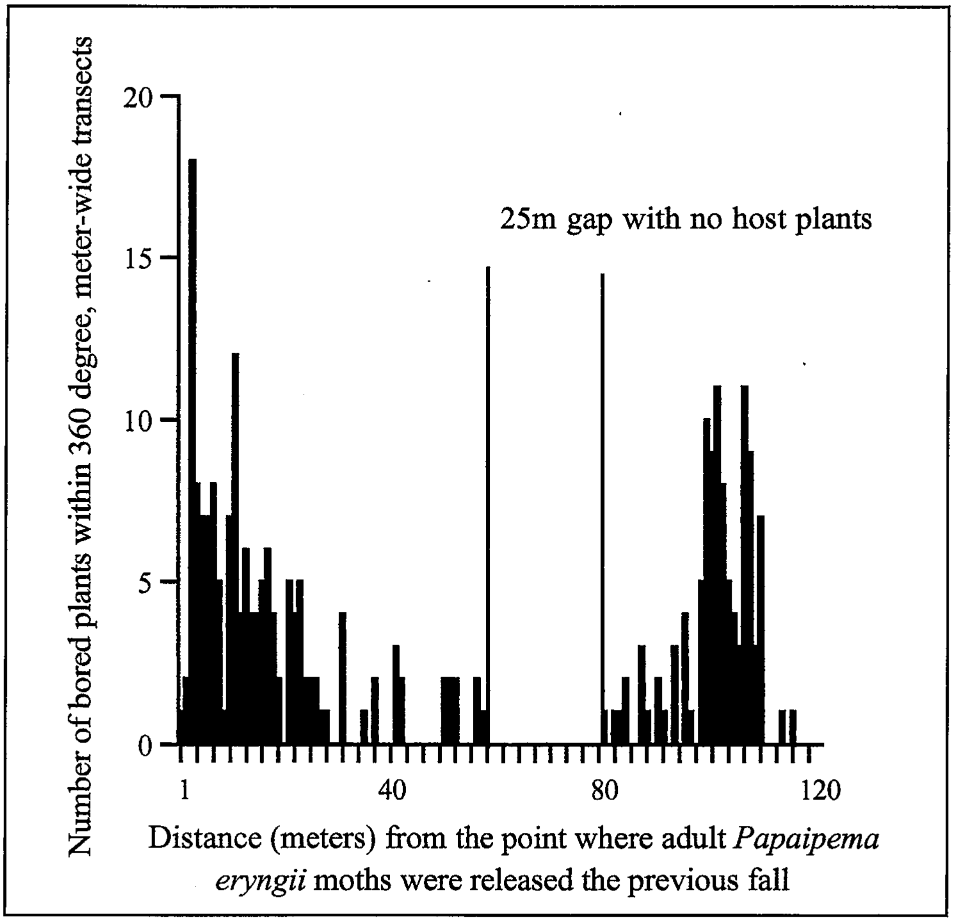

Figure 1. Distribution of *P. eryngii* larvae within a large patch of *Eryngium yuccifolium* on the Gensburg Markham Prairie, Cook County, Illinois, USA, in the Spring of 1994.

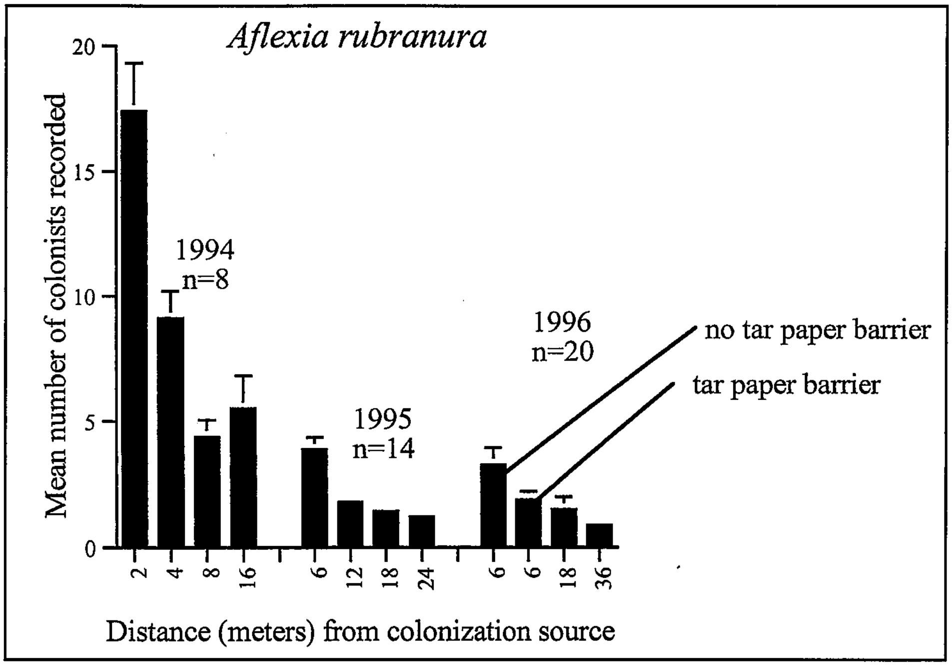

Figure 2. Mean number of colonists captured (±SE) within host plant patches situated 2–36 m from central release points. Four of eight 6-m gaps were covered with tar paper in 1996; n = number of samples taken each year.

colonization was reduced yet was not stopped (Figure 2). These results suggest that even wingless species may routinely traverse inhospitable habitat gaps at this small scale.

Management Implications

Harper et al. (2000) used exclosures effectively to demonstrate that the recovery of the leafhopper *Laevicephalus minimus* (Osborn and Ball) and several additional "morphospecies" was due primarily to recolonization from unburned tracts. The prevalence of inverse postfire population density/burn boundary distance ratios reported here suggest similarly that recolonization from unburned units plays an important and perhaps crucial role in the recovery of many species at this spatial scale. Clearly, prudent management burning will require the maintenance of unburned refugia to ensure the rapid recovery of fire-sensitive species within small, isolated reserves. Burn programs that fail to provide sufficient (see Panzer 2002) contiguous or nearby sanctuaries each season will likely contribute to the loss of fire-sensitive species, especially on smaller sites.

Harper et al. (2000) found survivorship to be very low within miniscule 0.78-m plots on two sites in Illinois. The presence of one or more survivors in most of my substantially larger postfire samples suggests, however, that in situ survivorship does play a role in the recovery of many, perhaps most, species. Consistent with this evidence, rates of survivorship were high even when requisite habitats of exceedingly small populations were completely burned. Populations of duff-inhabiting species restricted to patches as small as 8 m^2 usually survived the complete incineration of their habitat (Table 5). Burn procedures that promote patchiness (e.g., burning under cool or damp conditions) within burned units can be expected to increase in situ survival and, in so doing, contribute to the rapid recovery of vulnerable species. Proactive techniques that promote patchiness (e.g., Hall 1996) should probably be considered in situations involving imperilled species and/or tiny (<2 ha) sites. Naturally occurring unburned "skips" should generally be left intact (Panzer et al. 1988).

Fire-managed reserves should be burned on a rotational basis, with sufficient unburned refugia maintained each year (Harper et al. 2000, Panzer 2002). Disjunct fire units isolated by putative barriers less than 40 m in width may not require special treatment. However, units separated by greater distances should perhaps be treated as separate reserves until such time that more data addressing insect recolonization capabilities are made available.

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