

Responses of Prairie Insects and Other Arthropods to Prescription Burns

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ABSTRACT: The results of many field studies provide ample evidence that burning has a major influence on the presence and persistence of arthropod species on prairie sites. The variation in fire tolerance of species and the changes in the physical environment and plant communities following burns result in the development of distinctly different arthropod communities on frequently burned sites compared to sites protected from burning. Changing successional stages following burns also support distinctive arthropod species and groups. In general, a landscape containing sites at different successional stages, and sites varying in burn frequency, will support the most species; if a single site is burned at intervals, a cycle of arthropod species richness, species composition, and numbers of individuals will occur. It is possible to predict the responses of a prairie arthropod community or of a single species to a controlled burn or a series of burns if the fire history of the site, and the burn tolerance, colonizing ability, and basic biology of the species present, are known.

Index terms: insect conservation, fire management, prairie insects; prairie burning

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INTRODUCTION AND METHODS

Whether, when, and how frequently to burn prairie preserves have become increasingly difficult decisions for managers. Controlled burns have been used to maintain prairie vegetation and prevent the invasion of woody plants, but concern has developed that these burns may damage or even endanger arthropod species. Many have studied the effects of controlled burns on plants, but arthropod responses to burning have not been well understood. Natural features of the prairie arthropod community challenge researchers. Populations are difficult to census, especially those of species with short flight periods such as many butterflies and specialist bees. Patchy dis-

tributions of species among available sites and wide fluctuations of populations from year to year are common among arthropods. The small size of many prairie preserves has limited the areas available for well-replicated studies. A few groups, primarily butterflies, have been relatively well studied, but many taxa have received little or no attention from researchers.

Despite these limitations, many field studies of arthropod responses to burning have been completed in a variety of prairie habitats. (A bibliography of 176 published and unpublished reports and the literature survey on which this paper is based [Reed 1995a] are available from the author.) I reviewed these studies with the goals of

identifying general patterns in the responses of arthropod species and arthropod communities to burning. I used a descriptive model of the burn process and postburn succession to aid in organizing the information. The model allows identification of the information needed to predict the responses of arthropod species and communities to burning. The conditions under which responses to burning vary among sites and among species can be predicted, and possible trade-offs related to management for multiple species or groups can be identified.

RESULTS AND DISCUSSION

Phases of a Burn

Warren et al. (1987) reviewed the responses of grassland arthropods to burning, from a pest management perspective, and divided the burn into phases. Burn phases include the preburn phase, the combustion phase (the burn itself), the shock phase (time until the vegetation starts regrowth), and the recovery phase (time until the system returns to the preburn state or reaches a new steady state). Fire characteristics, the arthropod species, the timing of the burn relative to arthropod phenology, host/parasite and predator/prey ratios following the fire, postburn weather, and the direction and extent of postburn succession can influence a species' response to burning and must be understood in order to predict this response. The mortality, reproduction, immigration, and emigration of arthropod taxa during each phase determine the species composition of any site.

The Preburn Phase

The insect species composition of prairie areas is poorly known. Tallgrass prairie sites contain a mixture of rare and common species, including prairie obligates, grassland species, woodland species, and widespread species, as observed for bees (Reed 1995b); butterflies (Swengel 1996);

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leafhoppers (Hamilton 1995); grasshoppers, crickets, and katydids (Ballard and Greenlee 1994); and other insect groups (Panzer et al. 1995). Insect species and individuals are patchily distributed within and among prairie sites (references above). Herbivores, predators, and parasitoids are present and range from extreme specialists to extreme generalists in their choice of host plants, prey, or hosts. Prairie insects that are dependent on vertebrates, such as dung-feeding scarabs, tenebrionids that use animal burrows as shelters, and vertebrate ectoparasites, are often absent from small prairie remnants; their conservation is of special interest (Opler 1981).

The Combustion Phase

Some arthropod species come to burns because they are attracted to smoke or heat. Buprestids (wood-boring beetles) and cerambycids (long-horn beetles) are most often reported (Evans 1971, Hansen 1986), but some spider species (Reichert and Reeder 1970), silphids (carrion beetles) (Evans 1971, Hansen 1986), and tabanids, empidids, and platypezids (all Diptera or fly families) (Evans 1971) have also been reported from fires.

Mortality and population reduction rates during the combustion phase vary greatly among arthropod taxa. Individuals of many taxa die during the combustion phase, including the stem-boring larvae of the gall wasp *Anistrophus silphii* Gillette (Fay and Samenus 1993), spider species that were active on the surface at the time of the burn (Reichert and Reeder 1970), ambush bugs (*Phymata* spp.) (Dana 1991), tenebrionids, carabids, spider "cocoon," and cutworm larvae (Rice 1932); adult and nymphal grasshoppers are killed, especially flightless species (Bock and Bock 1991). Very few insects were collected in malaise traps for 2 weeks following a Utah range fire (Hansen 1986).

Other taxa have been reported to survive the combustion phase. For example, ants, gryllacridids, carabids, and tenebrionids survived the combustion phase of a range fire in Utah sagebrush (Hansen 1986). Spiders in burrows, sacs under rocks, and clumps of dense vegetation survived a

Wisconsin prairie burn (Reichert and Reeder 1970), and crab spiders in Minnesota survived an early spring burn (Dana 1991).

Burn tolerance may depend on burn season: for example, *Hesperia dacotae* and *H. ottoe*, prairie skippers (Lepidoptera: Hesperidae), showed low larval mortality in a test burn early in the season when the larvae were in burrows; later fires caused higher mortality because the larvae had moved to surface shelters (Dana 1991).

Burns are usually patchy; only part of a site is burned. Savannas and woodlands, and areas of heterogeneous topography, generally have more unburned patches than more uniform sites such as prairie restorations on former agricultural fields (Schwarzmeier 1994). Unburned patches sometimes allow survival of arthropods such as larvae of Karner blue butterfly (*Lycaeides melissa samuelis*) (Swengel 1995), chinch bugs, cutworm larvae, and centipedes (Rice 1932).

The Shock Phase

During the shock phase following a burn, soil temperatures are increased, soil moisture is reduced, and litter is reduced or eliminated (Glenn-Lewin et al. 1990). Diapausing arthropods emerge earlier on burned areas: these include spiders (Reichert and Reeder 1970) and grasshoppers (Evans 1984). Adult insects that survive the combustion phase may remain on the area and survive or die, or they may leave the site in search of food, prey, or cover. For example, rove beetles, flower beetles, and chinch bugs left an Illinois site following a burn (Rice 1932). Spiders with high moisture requirements and those needing structural support for webs sought unburned areas (Reichert and Reeder 1970). Bock and Bock (1991) found that while most grasshopper species declined temporarily following a wildfire in ungrazed Arizona grassland, a few species that preferred bare ground and/or herbaceous foods increased immediately after the fire.

Shock phase population changes influence species interactions such as predator-prey relationships; these have not been well studied, although Dana (1991) noted that prairie skippers may benefit from the ab-

sence of one of their predators, *Phymata* sp., following a burn.

The Recovery Phase

Relative to unburned areas, forbs and grasses develop and flower earlier in the season during the first growing season following a spring burn, and vegetation productivity increases (Hulbert 1986). Generalist and specialist plant-feeding insects are attracted to the new growth to feed on leaves, sap, or nectar, or for oviposition on plants that are their larval food (Cancelado and Yonke 1970, Nagel 1973, Halvorsen and Anderson 1980, Van Amburg et al. 1981, Hansen 1986).

In general, insect biomass, numbers, and relative representation of orders and families on small burned sites adjacent to unburned areas return to levels similar to those of unburned areas by the middle or end of the summer following a spring burn (Tester and Marshall 1961, Cancelado and Yonke 1970, Halvorsen and Anderson 1980, Van Amburg et al. 1981, Hansen 1986, Dunwiddie 1991). Studies with longer follow-up and studies of specific taxa reveal more complex patterns.

Studies of the effects of a single burn on arthropod groups for a single season sometimes differ in their results, but many spider taxa (Araneae) have been found to leave the burned area (Rice 1932, Bulan and Barrett 1971, Nagel 1973, Halvorsen and Anderson 1980, Dunwiddie 1991). Millipedes (Chilopoda) tend to be more numerous on burned areas compared to unburned controls during the recovery phase (Rice 1932, Nagel 1973, Van Amburg et al. 1981, Seastedt et al. 1986). Hemiptera and Homoptera are reduced in population numbers during the combustion and shock phases but tend to invade recently burned areas where the vegetation is regrowing (Cancelado and Yonke 1970, Nagel 1973, Halvorsen and Anderson 1980, Van Amburg et al. 1981, Seastedt et al. 1986, Anderson et al. 1989, Dunwiddie 1991). Coleoptera, Lepidoptera, Orthoptera, and Diptera vary among taxa in their responses to burning. Ants (Hymenoptera: Formicidae) tend to survive burning well (Warren et al. 1987). Few

statistically significant observations have been made on other insect groups.

Arthropod Responses to Postburn Successional Stages

Controlled burns initiate successional processes rather than produce stable plant and animal populations. The arthropod community of a site at any stage of the post-burn succession includes taxa that survived the burn on the site and taxa that invaded the burn site from other areas (some species may do both, depending on the timing and completeness of the burn). As the plant community changes over the growing seasons following a burn (the postburn succession), the arthropod community changes also. If burning is repeated, a successional cycle of plant and arthropod species composition and abundance occurs.

Swengel (1996) observed butterflies on prairie sites of varying length-of-time-elapsed-since-last-burn. Overall, sites that had been burned since the last growing season had 42% of the individual butterflies, although only 22% was expected based on the observation time spent on these sites. The increase in individuals was based on large populations of monarchs (*Danaus plexippus*), which did not reproduce on the site. Eleven of thirty-three species were proportionally more common on the recently burned sites than on all sites combined, including red admiral (*Vanessa atalanta*), cabbage white (*Pieris rapae*), and coral hairstreak (*Satyrium titus*). In contrast, 22 species were less common on recently burned sites than on all sites combined. The Poweshiek skipperling (*Oarisma poweshiek*), Ottoo skipper (*Hesperia ottoe*), arogos skipper (*Atrytone arogos*), and silver-bordered fritillary (*Boloria selene*) showed especially low representation on recently burned sites. When sites were classified by years since last burn, monarch, painted lady (*Vanessa cardui*), and coral hairstreak were relatively most common on sites burned since the last growing season (compared to sites unburned for 1 or more years), arogos skipper was most highly represented on sites unburned for 4 or more years, ottoo skipper and silver-bordered fritillary were relatively most common on sites last burned

3 years earlier, and Poweshiek skipperling was most common on sites last burned 2 years earlier. The common wood-nymph (*Cercyonis pegala*), cabbage white, and orange sulphur (*Colias eurytheme*) showed little preference for any successional stage.

Differences in insect populations at different stages of the postburn succession also were observed among grasshoppers on the Konza prairie in Kansas, which has a long history of annual burning. Sites that had been protected from fire for 4 years or more showed higher grasshopper and forb species richness than sites burned annually or biennially. Following a burn, grasses and grass-feeding grasshoppers were most numerous; later, forbs and forb-feeding grasshoppers increased, and grass feeders decreased (Evans 1984, 1988a, 1988b).

Unpublished data from studies now in progress suggest that some prairie specialist leafhopper species reach their highest populations the second year after a fire (R.H. Henderson, terrestrial ecologist, Wisconsin Department of Natural Resources, Monona, pers. com.), while carabid beetles on prairie sites in Iowa are most abundant the summer following a burn (Larsen 1996). In both cases, species differed in their response to burning.

Colonization or recolonization of a site by a species depends on two factors: the ability of a species to invade (reach the site), and its ability to become established once it arrives. Insect species are more likely to invade new sites if they have populations close to the site to be colonized, if their populations are large, and if their mobility is high; thus the composition of the colonizers for a site will depend on the species present in surrounding areas (Dempster 1991). These principles have clear implications for planning of burning programs but need validation for prairie species. Very little is known about what factors determine the ability of prairie arthropod species to colonize or recolonize sites, or even about how far they are able to move. As prairie fragmentation continues, populations of prairie specialist insects may be too far apart to allow recolonization to occur, and repeated local extinctions will lead to species extinctions.

Responses of Arthropod Communities to Frequent Burning or Fire Suppression

Frequent burning of wooded sites in prairie areas causes prairie plants to increase and woody plants to decrease; on prairie sites, grasses, especially C4 grasses, increase with frequent burning. Aboveground plant biomass appears to reach its maximum in about 6 years if no burn occurs, and fire reduces litter depth for up to 5 years in the northern tallgrass prairie (Ehrenreich and Aikman 1963). Timing of burns (spring, summer, or fall) strongly influences forb species presence and blooming (Glenn-Lewin et al. 1990). These habitat changes, as well as the different fire tolerances of arthropod species, allow different taxa to become established on frequently burned sites than on sites protected from burning. For example, in Missouri and Illinois "the litter-inhabiting cryptic species and twig-, stem-, and acorn-nesting species which make up a large portion of the woodland ant fauna are virtually lacking in regularly burned prairies, while the prairie is much richer than the woodlands in mound-building and subterranean root-aphid tending species" (Trager 1990: 104). Prairie ants, which are all soil-dwelling, are unaffected by burning frequency, as long as the open, native-dominated character of the vegetation is maintained (Trager 1990).

The relative abundance of grass-feeding grasshoppers as a group increased with increasing fire frequency and consequent increase in grass biomass on the Konza prairie (Evans 1984, 1988a, 1988b). Forb-feeding grasshopper species, as well as the forbs they eat, are more susceptible to fire than are grass-feeding grasshoppers. Within these groups, relative abundance of individual grasshopper species was related to burn frequency. For example, *Orphulella speciosa* was most abundant on sites burned every year, while *Phoetaliotes nebrascensis* was most abundant on unburned sites. Both species are grass feeders.

Ballard and Greenlee (1994) studied orthopteran abundance and species diversity on 30 Missouri sites including prairies and glades. Microhabitat features such as the

presence of rock outcrops were required for certain species, while other species required tall grasses. Annually burned prairies showed consistently higher orthopteran abundance and diversity than comparable unmanaged sites. The annually burned sites also had more diverse and healthier grasses and forbs, and lacked a heavy thatch layer. Unexpectedly, species of Orthoptera that were potentially susceptible to fire damage due to flightlessness or aboveground oviposition, among other factors, were more diverse in fire-managed sites than in unburned sites. The authors concluded that there is no evidence that frequent or even annual burning poses a threat to orthopteran species in Missouri habitats. Faunal composition and diversity were highly divergent among tracts with different fire history and site quality, even among the same community type.

Johnson (1995) found that annually burned and long-term unburned *Spartina pectinata* wetlands contained similar spider species. Annually burned wetlands had greater spider species richness and higher spider density than the unburned sites; these observations are consistent with the greater productivity of the burned areas.

PREDICTING THE EFFECTS OF BURNS

To predict the effect of a burn on a single arthropod species one needs to understand that species' basic biology, including (1) its burn tolerance or sensitivity during the season when the burn is done; (2) its population dynamics on the postburn site—that is, the potential for the population to increase or decline, and the speed at which the change will occur; (3) its colonization potential—What other populations of the species exist, how far away are they, and how rapidly can they spread onto the burn site?; and (4) its response to all phases of the postburn succession.

These factors vary in importance depending on the site and its surroundings as well as on the species; interactions among factors may occur. Insect species whose populations are reduced by burns, but that also require postburn successional habitats, may be especially difficult to conserve, especially if their mobility is low. These spe-

cies include insects whose larval food plants respond positively to fires, such as the Karner blue (Andow et al. 1994) and some prairie specialist Lepidoptera (Swengel 1996). Among prairie Orthoptera species in Missouri, the advantages of the postburn habitat appear to outweigh the dangers of burning even for species with low mobility and aboveground oviposition (Ballard and Greenlee 1994).

The effects of a single burn or a series of burns on the insect community of a prairie site can be predicted if one knows (1) what species are initially present on the site, and whether they are reproducing on the site or colonizing the site from adjacent areas; (2) what insect species will invade and colonize the site, both immediately after the burn and during various stages of vegetation regrowth (this depends on what species are present in the surrounding areas and on their mobility, as well as their attraction to various postburn successional stages); (3) the interactions of surviving species with invading species; and (4) what other changes will occur in the habitat, especially in the plant community, with or without further burning.

The following is a general description of burn effects derived from the studies cited above. Further research will be needed to validate this model. Sites and communities vary, but in general, following a burn, populations of burn-sensitive species are reduced or eliminated during the combustion phase. Burn-tolerant species are not affected immediately. Thus sites with a high proportion of burn-sensitive species decline in arthropod species richness immediately following a single burn; these are sites where fire has been suppressed for at least a few seasons. Sites with a high proportion of burn-tolerant species show little change in insect species richness or composition following a single burn; this occurs on sites burned regularly in the past, as noted above for grasshoppers (Evans 1984).

As regrowth of the vegetation begins, burn-tolerant species persist and species attracted by fire or by the immediate postburn habitat invade. Widespread, mobile species invade also. If the site is not burned

again, burn-sensitive arthropod species that are dependent on postburn successional plant species colonize the site if they are present nearby or if they have survived in unburned patches. This may be the time of highest insect species richness.

If no further burn occurs, burn-sensitive plants and arthropods colonize the site and the burn-tolerant species decline. If the site remains unburned, and if no drought occurs, over the course of years or decades, woody plants invade, prairie plant species decline, burn-sensitive arthropod and plant species invade, and arthropod species that are dependent on the postburn habitat decline as the prairie becomes forest.

The highest arthropod species richness will occur in landscapes containing sites at different successional stages and sites varying in burn frequency. On the landscape scale, the tallgrass prairie may be maintained as a patchwork of areas including parts that are burned every year, parts burned every few years, and parts burned rarely, so that the whole range of species—from the most to least burn tolerant—is maintained in the landscape. Burn-sensitive species can recolonize burned areas from their populations on other sites.

On isolated prairie sites that are burned at intervals, insect species richness and insect community composition follow a successional cycle. Managers attempt to maximize arthropod species richness by burning every few years to allow a mix of burn-sensitive and burn-tolerant insect species to persist. Unburned areas are left to allow survival of burn-sensitive species on parts of each site, permitting internal recolonization of burned areas (Moffat and McPhillips 1993).

IMPLICATIONS FOR MANAGEMENT AND RESEARCH

The studies cited here provide ample evidence that burning has a major influence on the presence and persistence of arthropod species on prairie sites. The effects of burning vary among species and among sites, and differ depending on the season of the burn and its completeness, and with

the length of the interval between burns. The delicate balance among insect and plant population responses to the burn and postburn phases, based on insect population increases and decreases on the site as well as on colonization, make each year different, especially for insect species that are dependent on successional plant species and whose populations are influenced by the burn. Past management practices may be maintained to allow whatever insect species are currently present on a site to survive (presumably they are adapted to this management, although they may be threatened by habitat change).

Biological features must be considered in connection with the goals and scale of prairie management. The goal of arthropod management on prairie sites may be to protect individual species, to maintain a typical prairie insect community, to maximize biodiversity, or some combination of these. No site can be managed for all species simultaneously. The scale of management may be small (a single site) or large (a whole landscape).

Much more research is needed to describe prairie insect communities and the factors that influence them, and to devise management strategies that can be applied to the prairie sites that are now being protected and restored. Many taxa have received very little study. It would be especially valuable to know whether certain sites support high species richness of all insect groups, or whether sites rich in some groups are poor in others. (For example, Orthoptera appear to be relatively burn tolerant, and Lepidoptera relatively burn sensitive: Can we see high diversity of both on one site?). This information would help identify possible trade-offs in management for different groups, and would aid in determining whether any species exist that can be used as indicators of the health and diversity of the prairie arthropod community.

Other important questions include the following: At what time during the postburn succession is species richness highest? How long does the whole successional process take? Which arthropod species require or benefit from burns, and how rapidly are

they lost from unburned sites? How can burn-sensitive species be maintained on sites where external recolonization is unlikely? For single sites, what is the role of burn survival compared to postburn recolonization? All factors related to colonization and recolonization need more study. Do generalist invaders influence the survival and growth of prairie obligate species, and if so can buffer zones be created around prairie sites? Studies of mutualisms, such as those between specialist bees and their flowers, or among parasitoids and their hosts, and of the effects of timing and extent of burns on interactions will interest ecologists and managers alike. In particular, studies of several insect groups on the same site are required. Monitoring of insect responses to management is essential, and study sites must be replicated.

The successional nature of the prairie habitat in the northern tallgrass region, and the dynamic and patchy nature of insect populations, make prairie insect conservation a continuing challenge for managers and an exciting area for researchers.

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