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ACTIVITY AND DIVERSITY OF CARABID GROUND BEETLES (COLEOPTERA: CARABIDAE) FOLLOWING PRESCRIBED BURNING IN A MATURE RED AND WHITE PINE STAND IN SOUTHERN MICHIGAN

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ACTIVITY AND DIVERSITY OF CARABID GROUND BEETLES (COLEOPTERA: CARABIDAE) FOLLOWING PRESCRIBED BURNING IN A MATURE RED AND WHITE PINE STAND IN SOUTHERN MICHIGAN

By

David Donald Neumann

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ABSTRACT

ACTIVITY AND DIVERSITY OF CARABID GROUND BEETLES (COLEOPTERA: CARABIDAE) FOLLOWING PRESCRIBED BURNING IN A MATURE RED AND WHITE PINE STAND IN SOUTHERN MICHIGAN

By

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The effects of prescribed burning at 2- and 6-year intervals on Carabid beetle (Coleoptera: Carabidae) populations were investigated in a mature pine stand using pitfall trapping techniques during 1994 and 1995. Hypotheses relating beetle activity to frequency of prescribed burning and vegetation characteristics were tested. Total beetle activity was greater on burned than unburned areas. Differences were significant in 1994 between 6-year burn and unburned plots, but were not in 1995. Carabid species diversity was greater in both years on burned treatments than on unburned plots, as measured by the Shannon, Berger-Parker, Maraglef, Shannon evenness, log normal (λ), and log series (α) indices. Beetle diversity patterns fit the log-series model most closely. I conclude that Carabid diversity was not inversely related to fire frequency in this study. Two-year, 6-year, and unburned plots differed significantly in seedling and sapling density, while percent cover of ground flora differed only between burned and unburned plots. Regression analysis relating Carabid beetle trap catches to vegetation data did not significantly explain beetle activity.

To Marylin Jean Neumann, 9-4-42 to 3-5-96.

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INTRODUCTION

> **I keep six honest serving men**
> **(They taught me all I knew):**
> **Their names are What and Why and When**
> **and How and Where and Who.**
>
> **--Rudyard Kipling, "The Elephant's Child"**

Pine trees and fire have long been natural, synergetic forces shaping northern forest ecosystems. Periodic fires swept through pre-settlement pine forests at intervals of 15 to 50 years in the Lake States region (Burgess and Methven 1977, Bergeron and Brisson 1990, Engstrom and Mann 1991, Maissurow 1941, Pyne 1982, Rouse 1988, Van Wagner 1970). Catfaces can still be seen on the boles of trees in old growth pine forests, attesting to their tolerance of periodic fire (Dickmann 1993). Red pine (*Pinus resinosa* Ait.) and white pine (*Pinus strobus* L.) are two commercially important pine species common to the Lake States region that reproduce vigorously on fire-prepared seed beds and appear resistant to periodic surface fires in mature stands. The natural predisposition of these species to coexist with fire leads to consideration of prescribed underburning as a management option in ecosystems in which they dominate (Dickmann 1993). While demands on woodlands for forest products mount, private and public managers have been pressed to manage forest resources from an ecosystem perspective. Managers must also guide forest product procurement activities toward sustainable rates. Controlled underburning has been suggested as an environmentally benign way of solving some of the problems associated with intensive culture of mature pine stands. Several studies have described the effects of periodic low intensity prescribed fire on mixed red and white pine stands in Michigan (Dickmann, et al. 1987, Henning 1992, Henning and Dickmann 1996). Dickmann (1993) has published a thorough discussion of the multiple use benefits of prescribed burning in pine stands. Yet before prescribed burning can be widely applied, we need to better understand the effects of fire on all components of these ecosystems, including the multitude of invertebrates that inhabit them.

The effects of wildfire or prescribed burning on terrestrial forest arthropods, especially in northern boreal forests, are still poorly understood. The preponderance of research on forest arthropod responses to disturbance in North America has focused on timber harvesting, although some studies have compared fauna communities in stands of different successional stages (Liebherr and Mahar 1979).

Relatively few researchers have investigated changes in terrestrial arthropod fauna following fire, despite the importance of fire as a natural disturbance regime in forested regions and as a management tool. Most fire-related research on insects has focused on changes in soil and litter layer inhabiting micro-fauna following prescribed burning or low to moderate intensity wildfires. (Metz and Farrier 1971, Buffington 1967; Heyward and Tissot 1936;

Ahlgren 1974; Rickard 1969; Moya-Raygoza 1995; Pearse 1943; Johnson 1995; Anderson et al. 1989; Jorgensen and Hodges 1970; Metz and Dindal 1975).

Fire effects on boreal forest Carabid communities has been investigated by only two studies in North America. Holliday (1984), and Richardson and Holliday (1982) investigated Carabid community changes in burned spruce forests in Canada. Viereck and Dyrness (1979) recorded changes in soil arthropod communities following fire in Alaska, briefly noting the response of Carabids.

Other studies of Carabid responses to prescribed burning have been completed in more temperate communities (Harris and Whitcomb 1974; Greenberg and Thomas 1995) or grasslands. Inferences from these studies may not be safely extrapolated to Lake States forest ecosystems.

Effects of Fire on Vegetation

Red and white pine overstories tolerate light understory fires very well, due to the excellent insulating qualities of pine bark (Riefsnyder et al. 1967). This quality is augmented by vigorous resin production that helps stems of these species to recover from moderate cambial wounds (Heinselman 1981). Underburning does not adversely affect overstory tree growth, provided that crown scorch is limited (Alban 1977, Methven and Murray 1974). Red pine can tolerate up to 75% crown damage from fire before dying (Van Wagner 1965, 1970). Lunt observed that 20 years of annual underburning actually increased height and volume growth in red pine stands in Ontario (1950).

Fire has been effective in reducing undesirable hardwood undergrowth in pine stands (Dickmann et al. 1987, Henning 1992, Henning and Dickmann 1996). On better soils or following thinning, red and white pine stands quickly develop a thick community of hardwood species. This proliferation becomes a boon if conversion to hardwood species following final overstory harvest is prescribed; a curse if the pine overstory is to be regenerated. Obtaining adequate regeneration on sites with undesirable hardwood competition is the major problem in red pine management in the Lake States region (Methven and Murray 1974). Periodic underburning kills the emergent portions of most hardwood undergrowth, encouraging low coppice growth in species capable of sprouting. Reduced competition for light also allows herbaceous vegetation to become re-established.

Prescribed burning appears to affect herbaceous species composition more than percent coverage. Red maple (*Acer rubrum*), grasses , and bracken fern (*Pteridium aquilinum*) are common plants under wide-spaced red pine in Michigan (Henning 1992). Burning encourages disturbance-favored species like raspberry (*Rubus* spp.), which reproduce vigorously after fire by sprouting (Ahlgren 1979). During the first three growing seasons following a single burn, vigorous growth of herbs and shrubs can be expected (Ahlgren 1976). Herbaceous vegetation increased in percent coverage with increasing frequency of prescribed burning on sandy sites in New Jersey (Buell and Cantlon 1953). Frequent burning caused the development of a comparatively lush undergrowth of herbs and grasses. Fire stimulates perennial herbs, grasses and forbs to root-sucker and sprout vigorously. Burning can also stimulate flowering of monocots (Trabaud 1987), and increase the nutritional quality of browse and forage in pine stands for wildlife (Dickmann 1993).

Effects of Fire on Insects

The effect of fire on forest invertebrates varies with burn intensity, community type, season, and region. Environmental changes following fire may be more important in determining population dynamics than the direct effects of heat and smoke (Lyon et al. 1978). Micro-climatic and vegetation changes following fire may render conditions unsuitable for surviving species by removing shelter, sources for herbivory and prey. Following a moderate intensity fire in the pine barrens of New Jersey, Buffington (1967) observed a decrease in arthropod abundance caused by a loss of incorporated and unincorporated soil organic matter that served as a food source for soil micro- and mesofauna. Heyward and Tissot (1936) attributed decreases in fauna inhabiting the Ao horizon of burned sites to post-fire xeric soil conditions. Changes in micro-habitat and vegetation structure may expose invertebrates to increased risks of predation (Anderson et al. 1989), while host plant response has been shown to have important effects on the abundance of some species. Several researchers have noted the effects of elevated soil temperatures and grass growth following prairie fires on grasshopper species abundance (Anderson et al. 1964 & 1989, Evans 1984, 1988, Rice 1932, Hurst 1971). Species mobility plays an important role in determining the temporal extent of fire effects. Metz and Farrier (1973) found a 70 percent reduction in the number of acarians inhabiting the upper 7 cm of soil following fire. Populations recovered within 43 months, however. Anderson et al. (1989) noted significantly lower abundance of insect species on sand prairie sites only during the first year after prescribed burning. Rice (1932) found that many species declined in abundance during the fall after burning in prairie lands, but recovered with the spring flush of vegetation.

Some species are attracted and favored by fire disturbance in forests. Bark beetles and wood borers cause considerable damage and economic loss in stands stressed by fire. Pests that home in on trees injured or scorched by fire include the mountain pine beetle (*Dendroctonus ponderosae*), the pine engraver (*Ips pini*), the western pine beetle (*Dendroctonus brevicomis*), the red turpentine beetle (*D. valens*), the Douglas fir tussock moth (*Orgyia psuedotsugata*), and the pandora moth (*Coloradia pandoria*). Low-intensity prescribed burning can sometimes be used to help manage these populations, by destroying litter and woody debris where insects over-winter (Mitchell and Martin 1980, Miller 1978, Simmons et al. 1977).

Frequency of fire disturbance has been shown to be an important factor in determining invertebrate population responses. Grasshoppers occurring on annually burned sites appear to be well adapted to climatic and vegetation changes associated with burning (Evans 1984). Gillon (1972) observed that populations of sun-loving Pentatomidae were maintained by periodic fires in African savannas. Riechert and Reeder (1972) suggest that spider populations in dry prairie sites in Wisconsin are well adapted to fire, noting that periodically burned areas supported stable populations.

The effect of fire on insect abundance and richness has been studied by several researchers using Carabid beetles. Carabid beetle assemblages are convenient for studying the processes of recovery from fire because they are widely abundant, and have a well developed taxonomic nomenclature.

Carabids are generally reduced in abundance for a short period of time following fire. Holliday (1991) observed that most Carabid species become locally extinct during intense forest fires or the extreme habitat changes that follow. Other researchers noted a 60 percent decrease in beetle populations in southern pine stands (Pearse 1943, Heyward and Tissot 1936). Ahlgren (1974) found fewer beetles in prescribed burned jack pine stands in Minnesota.

Rapid colonization by pyrophilous and disturbance-tolerant species occurs following fire (Evans 1984); however, occupation by some species may be transient, lasting less than 2 years in boreal forests (Holliday 1984). Long-term population levels may remain depressed for 10 or more years in some forest stands following intense fires. Fire effects on Carabid beetle assemblages in grasslands may be less severe, partly due to lower fire temperatures. Tester and Marshal (1961) noted increases in both biomass and abundance of beetles on prescribed-burned power line rights-of-way.

The effects of fire on Carabid species diversity are varied. Harris and Whitcomb (1974) noted that annually burned southern pine plantation sites supported lower numbers of individuals and species than sites that had been protected for 10 years. Holliday (1992) noted no differences between species diversity in mature stands and burned sites in two boreal forest types over a 10-year period following wildfire. By contrast, Winter (1980) noted greater numbers of species and individuals in young pine stands for 1 to 3 years after burning in Germany.

The reactions of Carabid fauna to disturbance may reflect the magnitude of the disturbance. During colonization of mining spoils by forests, researchers noted a weak trend toward increasing Carabid species abundance and diversity with increasing successional age in one study in Europe (Neumann 1971), but not in two others (Mader 1986, Hejkal 1985). Increased diversity of Carabid species assemblages on clear-cut relative to uncut forest sites has been noted by several researchers (Niemala et al. 1993, 1993, 1990, Jennings et al. 1986, Lenski 1982).

Important mechanisms governing insect diversity responses to disturbance may include intraspecific competition, size of the potential colonist pool for given sites, and the rate of change in plant species diversity following fire. Holliday (1992) reported estimates of species gain and loss for boreal forest sites in Manitoba on burned and unburned sites following an intense forest fire. Unfortunately, little is known regarding Carabid species colonization and extirpation rates in temperate forest regions.

Goals and Research Hypothesis

The focus for the research project reported in this thesis was to investigate the effects of prescribed burning at different frequencies on Carabid beetle species population diversity and abundance or activity. The study also examined the relationship between beetle observations and vegetation characteristics. The following hypotheses were tested:

Global Hypothesis.

Carabid beetle activity and species diversity in pine plantations are governed indirectly by vegetative responses to fire and not directly by fire frequency.

Corollary Hypotheses.

1. Total Carabid beetle activity increases with the frequency of fire disturbance and diminishes with time since last fire.
2. Total Carabid activity is negatively correlated with density of the woody understory but unrelated to ground (herbaceous) vegetation composition or ground coverage.
3. Carabid species diversity (number and evenness of species) decreases with the frequency of fire and increases with time since the last fire within the two-year burn treatments.

Chapter Two

METHODS

Experiment Site and Design

The study was conducted at the Kellogg Experimental Forest, located in Kalamazoo County in southwest Lower Michigan, T1S R9W (Figure 1). This experiment was established within an on-going prescribed burn study in Compartment 7 of the forest, a 4-ha. mixed plantation of red and white pine. The stand was established in 1932 on an eroding hillside, and had been variably thinned over the years.

The site occupies well drained sandy loam soils of the Kalamazoo and Oshtemo series, derived of glacial till and outwash parent material. The Oshtemo soils are classified as coarse-loamy, mixed, mesic Typic Hapludalfs. Kalamazoo series soils are classified as fine-loamy, mixed, mesic Typic Hapludalfs. Site index varied with slope position, but was higher in block 1 on the Kalamazoo soils.

The burn study was established in 1991 to study the ecological responses to surface fires ignited at different intervals. The plantation was divided into nine plots of about 0.4 ha, and one of three treatments assigned to each: unburned (control), burned every two years, and burned every six years (Figure 2).

Figure 1. Location of the experiment site.

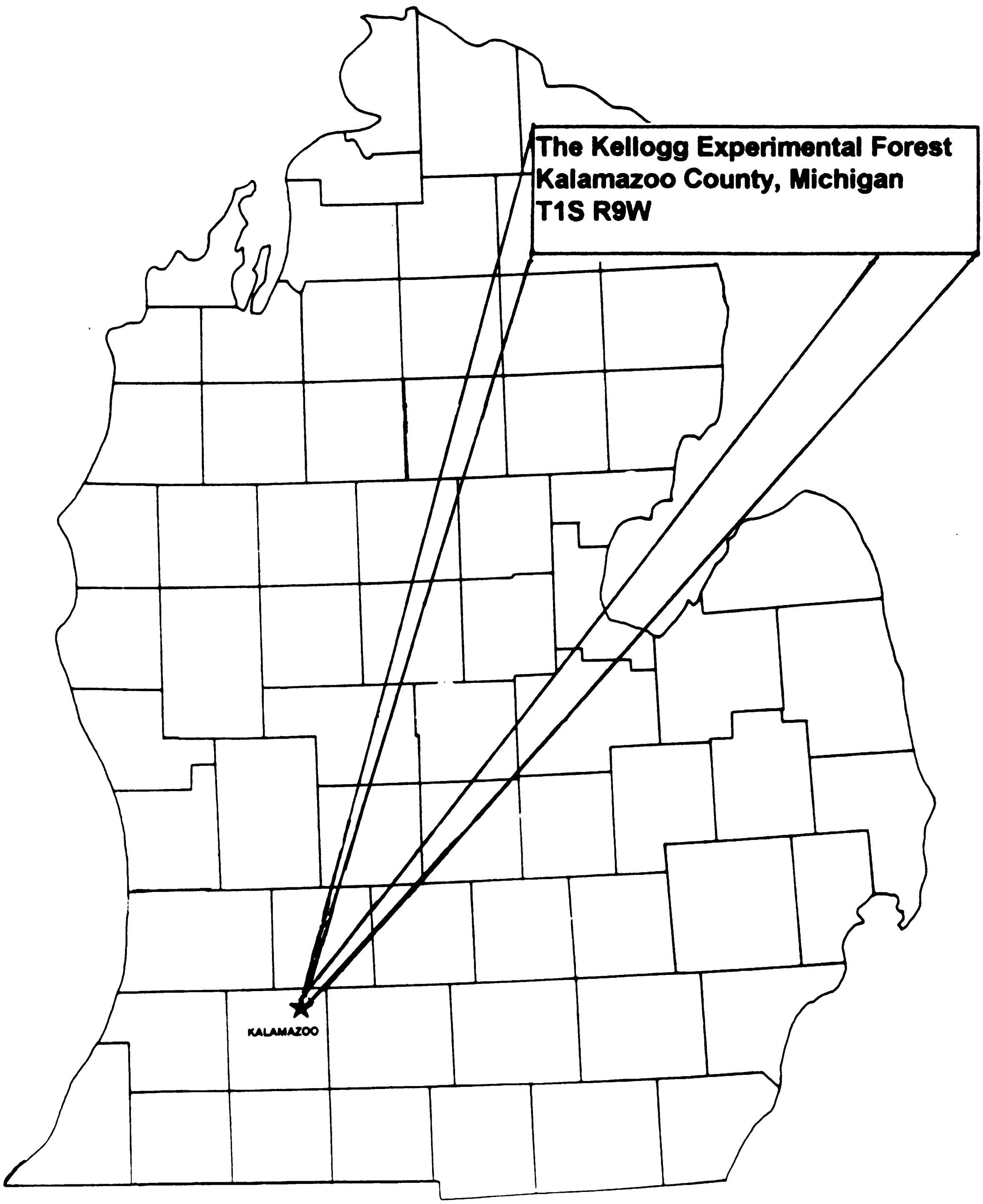
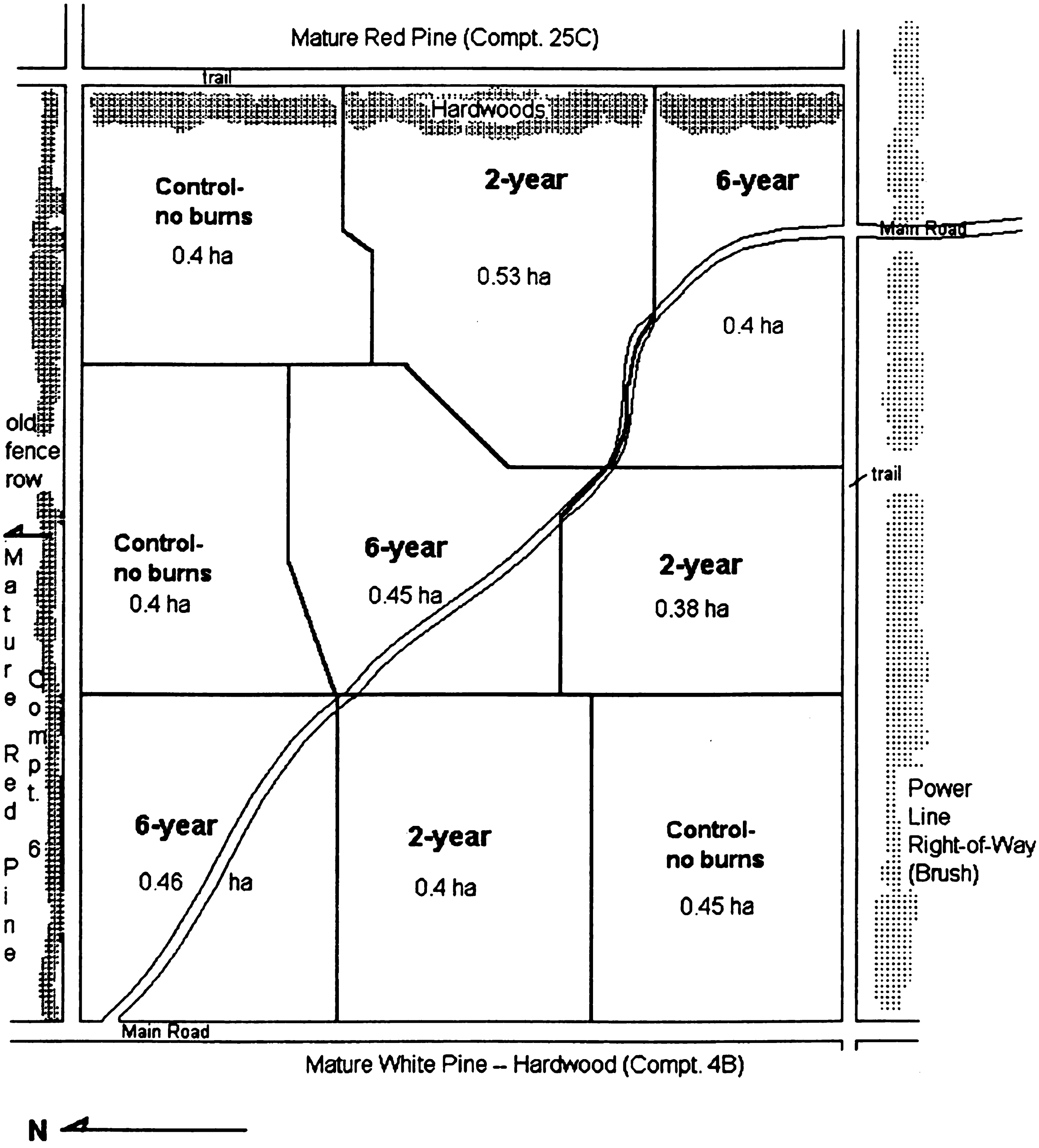


Figure 2. Experiment layout map.



Scale: 1 cm = 15.5 m

Treatments were arranged in a randomized complete block design with three replications. Replicates were assigned to blocks based on slope position (upper, mid, lower). Plots in the two-year-burn treatment had been burned twice with low intensity surface fires at the beginning of my study (May of 1991 and 1993), and were re-burned in May of 1995. Six-year-burn plots had been burned once, in 1991. Fires generally burned within prescription, with flame lengths < 1.5 m and little scorching damage to the crowns of overstory trees, but almost complete topkill of the woody understory (Dickmann, pers. comm. 1995).

To begin to understand invertebrate responses to the prescribed burn treatments, Carabid beetle populations were sampled during 1994 and 1995 using pitfall traps. The use of pitfall traps in population studies has been criticized by researchers (Adis, 1979; Greenslade, 1964) chiefly citing their dependence on population densities and species activity characteristics. Trap catches are biased by the degree to which ground vegetation impedes Carabid movement. Behavior of different species can also reduce the effectiveness of pitfall traps, depending on position of the trap. Traps buried with the rim flush with the mineral soil surface tend to be most effective in trapping terrestrial and litter dwelling species; least effective in collecting arborescent species. Briggs (1961) and Greenslade (1964) deemed the use of pitfall trapping catch data for assessing relative activity of Carabid species within the same habitat acceptable for strictly locomotor activity, however. Niemela et al. (1986, 1990b) recommend use of pitfall trapping mainly for use in comparing relative abundance within species, and in assessing habitat effects on Carabid diversity.

Other researchers found pitfall traps useful for monitoring populations (Luff, 1975) and for assessing relative population levels between habitat types (Baars, 1979; Reeves et al., 1983).

Traps were systematically located on a 15-m grid pattern within each treatment plot. Six traps were located within each plot, for a total of 54. Most trap locations were > 2 m from plot boundaries, however, three traps were within 1 to 2 m of plot edges. Trapping intervals were a compromise between a desire to collect the maximum number of species present on sites, and concerns that the trapping without replacement protocol might deplete local populations. Traps were activated biweekly for a 48-hour period from late May to mid October each year, beginning on May 14 in 1994, and on May 12 in 1995. Sampling in 1994 corresponded to the second post-fire year on biennial burn treatments, and the third year on 6-year-burn plots. Biennial burn treatments were re-burned in May of 1995. Therefore, by sampling the two-year-burn plots during 1995, a complete rotation of this treatment was encompassed. Trap catches were not compared between years, due to concern that the data might reflect two distinctly different causal events. In other words, the burns in the 2-year interval plots in 1993 and in 1995 may not be considered fixed effects.

Pitfall traps consisted of an 8-cm diameter plastic cup (470 ml) and four, 1-m long, 10-cm tall galvanized steel barriers arranged radially at 90° intervals around the collection cup. The cups were buried with the top of the container level with the mineral soil surface. Trapping cups were then covered and left undisturbed for one week prior to activation to avoid the "digging in" phenomena, or temporarily elevated insect activity caused by increased CO_2 levels in the soil following disturbance (Joosse and Kapteijn, 1968). Trap arrays were left in place over the 1994-1995 winter. Traps in the two-year-burn treatment were temporarily removed prior to the burn in May of 1995. Most were returned to their original locations. To correct for spotty burning of the spring 1995 fire, seven traps were relocated to completely burned micro sites within 3 m of their original locations.

Traps were charged with ethylene glycol as a killing solution and preservative. Ethylene glycol was used throughout the 1994 trapping season, and no traps were disturbed during trapping periods. In an effort to mollify public concerns about the toxicity of ethylene glycol, a more benign dilute solution of water mixed with non-scented, clear detergent was employed as a killing agent during the first three trapping dates in 1995. This protocol resulted in the loss of 20 traps to rodents and larger animals, however. Trap losses halted with the resumption of ethylene glycol as a killing agent during the fourth trapping period.

Trap contents were collected at the end of each 48-hour trapping period by removing the inner cup and straining the contents through fine mesh. The contents were washed into a 120 ml collection jar using a solution of 95% ethyl alcohol and 5% glycerin. Specimen jars were labeled with trap number and collection date, then stored for subsequent sorting and identification.

Beetle Sorting

A morpho-classification technique was employed to create a type collection of pinned specimens based on Lindroth's (1969) terminology. The majority of specimens were typed using this collection, then stored in sample vials with a solution of 95% ethyl alcohol and 1% glycerin. Samples were recorded by treatment, trap number, species, number of individuals, and date. The morpho-type collection was tentatively identified using voucher specimens in the Entomology Museum of Michigan State University. The resulting type collection was corrected by Dr. Robert Acciavetti of the USDA Forest Service, Morgantown, West Virginia. Voucher specimens will be lodged at the Carnegie Museum of Natural History by Dr. Acciavetti. The corrected type collection was then used to reclassify morpho-typed samples. Species nomenclature follow the Bousquet and Larochelle (1993).

Vegetation Sampling and Weather

Understory vegetation was sampled every four weeks throughout the trapping seasons to characterize treatment differences. Herbaceous and woody ground flora (<1m tall) species richness and relative ground coverage were sampled on treatment plots using 1 m^2 quadrats located 2 m from trap centers on random azimuths in 1994 (different for each sampling). Species coverage was occularly estimated. During 1995, fixed-location, 1 m^2 quadrats were established within 2 m of each trap center to assess frequency and cover of ground flora. Density of understory woody species (>1 m tall) was sampled using 10 m^2 subplots nested on the 1 m^2 quadrats. This sampling protocol was designed to allow vegetative comparisons among trap sites and among seasonal beetle-catch dates. The basal area of the overstory was determined using a 10-factor prism, with the trap cup as the plot center. Overstory data were expressed as the basal area at each trap. Seedling and sapling data were expressed as the total number of trees per ha in two diameter classes (≤ 1.9 cm dbh, 2.0-5.9 cm dbh).

Weather data were obtained from the Kellogg Experimental Forest. Daily maximum and minimum temperatures, degree day (base 50°F) accumulation, and precipitation data were used to calculate corresponding sampling period variables. Average minimum and maximum temperatures were calculated for the 48-hour sampling period by averaging the corresponding temperatures of the three dates that defined the sampling period. For example, minimum daily temperatures for May 13, May 14, and May 15 were averaged to obtain the average minimum temperature for the first sampling period in 1994. Cumulative precipitation was calculated from January 1 each year through trap closure on each sampling date. Incident precipitation was defined as total rainfall occurring during the two-week trapping period, from trap closure to trap closure. Degree day accretion was calculated as the total number of degree days occurring during the two-week period beginning on the first date after a sampling period and ending on the day of trap closure in the following sampling period; for example, May 16 through May 29. Cumulative degree days were calculated by totaling degree days accumulated from January 1 in each year. Humidity data were not available from the weather station.

Statistical Analysis

All statistical analysis used the SAS System computer statistical software, (Stokes, et al. 1995). A p-value of 0.05 was used to test treatment means for significant differences. Vegetation data were analyzed using standard linear ANOVA techniques to test for differences among the three treatments, after first testing for normality and homogeneity of variance. Data for tree and understory sapling and seedling data were analyzed as a randomized complete block design using the SAS generalized linear model procedure.

Comparison between years using ground flora data was not possible due to the different sampling procedures used. Ground flora data collected for 1994 were collected from plots randomly located at each sampling date; thus comparisons between dates and traps were not possible. These data were summarized as the year-long average percent coverage of woody and herbaceous ground flora in each treatment. The 1995 ground flora data were collected from fixed-location quadrats randomly located at the beginning of the sampling year to allow comparison between traps and treatments by date. Ground flora data were summarized separately as the total percent coverage in woody and herbaceous vegetation classes per quadrat for each sampling date for use in ANOVA split-plot design (plots split for dates) and in regression analysis. Measures of total annual percent coverage, absolute frequency, and relative frequency were calculated by summing across replications within each treatments. Relative frequency was calculated using the sum of absolute frequencies for all ground flora species. Average total annual percent coverage was calculated by dividing the total annual percent coverage for each species by the number of quadrats (n = 18).

Regression analysis was used with data for plot vegetation density and ground flora percent coverage to probe the relationship between vegetation characteristics and beetle activity. Vegetation data were incorporated as continuous variables in the logistic regression models for beetle activity data. In several cases, the resulting models stretched the acceptable limits for the proportional odds assumption that is critical for categorical data analysis using Proc Logistic in SAS. Sparseness of the beetle activity data for some species prevented analysis with vegetation data for some dates. Overstory basal area and data for seedling and sapling density were assumed constant for all trapping dates for this analysis. Ground flora data from the six sampling dates in 1995 were matched with the corresponding beetle trapping dates. Observations for the intervening catch dates were derived by averaging the relevant variables for the two adjacent sampling dates. Thus, the analysis used ground flora values for eleven trapping dates. Regression models were fitted with and without variables for burn treatments, and with woody overstory and ground flora vegetation of variables separately, to test the relative contribution of vegetation data. Models incorporating ground flora data could only be analyzed for 1995 due to collection methods.

Beetle catch data were analyzed using Categorical Data Analysis procedures for the SAS System (Stokes, et al. 1995). Data from pitfall trapping experiments has traditionally been analyzed using ANOVA procedures for linear, continuous, and additive variables, with the aid of an appropriate transformation technique to stabilize the variance (Holliday 1991, Jennings, et. al 1986, Southwood 1978) and occasionally with the aid of data pooling. Data were not pooled and transformed to homogenize variance in this study to avoid the problems of reduced power to detect significant differences, and the inability of traditional transformation techniques to normally distribute the data collected in this study.

Fortunately, pitfall trapping data can also fit alternative distribution models and data classifications. Beetle catch data can be described as categorical, with observations for each trap falling into one or more categories or species. The distribution of such data may fit a binary distribution; observations from traps are either "successes" in the event of positive counts for a particular category, or "failures" when traps do not yield beetles. This characterization of trapping data allows easier analysis of "zero-inflated" data sets by eliminating the need for logarithmic transformations.

Relative abundance of beetles among the treatments was assessed by comparison of the total number of individuals trapped per treatment by date, as well as by species. Comparisons of the abundance of Carabid fauna as a whole between habitats are infrequent in pitfall trapping research, because data derived from pitfall trapping may reflect only the trap's relative efficiency in trapping different species (or the resistance of the ground vegetation to each species movement), rather than absolute population densities (Greenslade 1964). Yet, total Carabid relative abundance may be relevant when used as an index for comparing Carabid activity within the same habitat, across similar habitats, or between years (Mitchell 1963, Niemela et al. 1990. In spite of the differences in ground cover among the treatments, total Carabid activity should serve as an index of the change in beetle activity as a result of prescribed burning. Only species present in sufficient quantity for these analysis (greater than three percent of total annual catch) were analyzed, as determined by trial and error. Separate analyses were conducted for each year, out of concerns that trapping data may reflect the random effects of two different causal events on two-year-burn treatments; the fires in 1993 and in 1995.

Variance was analyzed using logistic regression analysis, with beetle count data treated as the categorical response variables. All but one species specific analysis used only two classes for the response variable; zero beetles, and greater than zero beetles. The analysis for *Pterostichus stygicus* (Casey) used three count classes. Total beetle activity analysis used six classes to characterize count data. Table 1 describes the count data classes used for each of the seven Carabid species. Because of the sparseness of beetle data on some dates, only sampling dates with sufficient observations (2 or more beetles trapped per sample date) to allow analysis were used in regression analysis. Table 2 summarizes the sampling dates used for each species analyzed.

Variance in beetle abundance attributable to time, topography, and other edaphic features were apportioned by including the terms for date, blocking, and seasons in each model. Total relative abundance of Carabids was analyzed using data for all trapping dates, and terms for blocking and seasons. Blocking for seasons was arbitrarily designated after examining plots of trapping date vs.

Table 1. Number of beetles in count data classes used to categorize the relative activity of seven Carabid beetle species for logistic regression analysis.

			Data	Class		
Species	1	2	3	4	5	6
Cyclotrachelus convivus (Leconte)	0	≥1				
C. soldalis (Leconte)	0	≥1				
Carabus goryi Dejean	0	≥1				
Pterostichus mutus (Say)	0	≥1				
P. stygicus (Say)	0	1	>1			
P. tristis (Dejean)	0	≥1				
Trichotichus vulpeculus (Say)	0	≥1				
Total Carabid Species	0	1	2	3-4	5-8	9-15

Table 2. Sampling dates[1,2] used for logistic regression analysis for each of the seven most active Carabid species.

Species	Beetle Sampling Date		
Cyclotrachelus convivus (Leconte)	4	through	8
C. soldalis (Leconte)	4	through	8
Carabus goryi Dejean	1	through	8
Pterostichus mutus (Say)	1	through	3
P. stygicus (Say)	4	through	12
P. tristis (Dejean)	4	through	8
Trichotichus vulpeculus (Say)	4	through	8
Total Carabid Species	1	through	12

[1] Sparseness of count data for some beetle species did not allow use of all sampling dates with logistic regression analysis procedures.

[2] Dates chosen for analysis correspond to the rough season classification outlined in Figure 1, and contain sufficient observations to allow analysis.

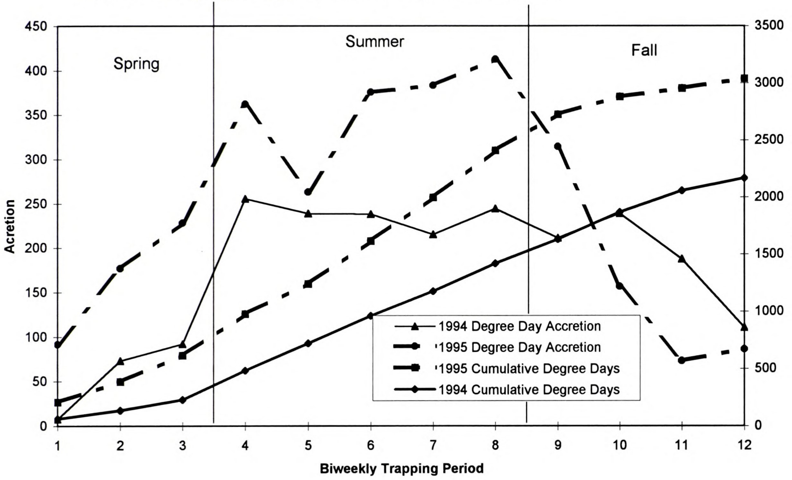
degree day accretion. Seasons were assigned to three periods with roughly equal degree day incidence rate, separated at inflection points indicated on Figure 3.

Individual species activity varied according to date; some species were not present in trap counts until mid-summer, others were present only in spring. Thus, species specific activity data were analyzed using blocking variables for topography, and the dates present.

Species Diversity Analysis

Common diversity indices measuring species richness, abundance, and evenness were calculated, treating each treatment-year combination as a distinct community. This procedure followed suggestions by Magurran (1988) and Southwood (1978) for comparisons of diversity among habitats. Species diversity measures were calculated using the total number of beetles per treatment in each species. Shannon, Simpson, Maraglef, and Berger-Parker diversity indices were calculated for each treatment. The Shannon index was selected because it is widely used and may provide a basis for comparison with other studies. It also has moderate discriminate ability and sensitivity to sample size. Differences in the Shannon H' indices were tested using *t*-tests as described by Hutcheson (1970). The Maraglef index reflects species richness and has good discriminate ability, but it is highly sensitive to bias induced by small sample size. The Berger-Parker index reflects species dominance and has low sensitivity to sample size. The Simpson index also measures species dominance, but it has better discriminate ability. The Shannon evenness index

Figure 3. Demarkation of sampling periods into seasons based on similar rates of degree day accretion and accumulation in 1994 and 1995 (base 50 F). Trapping periods were 48 hours and occurred biweekly May 14-Oct. 16 in 1994 and May 12-Oct. 13 in 1995.



was also calculated; it has poor discriminate ability, but is only moderately sensitive to sample size. The log series α from Williams's nomograph (Williams, 1964; Southwood, 1978) also was calculated. Species abundance models have been fitted for the geometric series, the log series, the log normal series, and the broken stick models. Goodness-of-fit for each abundance model was calculated using the χ^2 test and a p-value of 0.05.

Chapter 3

RESULTS AND DISCUSSION

Overstory and Woody Understory

The mixed pine species overstory in the plantation appears to be relatively homogenous with respect to species density and composition. Average red and white pine densities were 131 and 93 trees per ha, respectively. Average DBH's ranged from 16 to 40 cm for red pine and from 20 to 60 cm for white pine, with the largest trees of both species found on the lower slope positions.

The three treatments also contained similar average basal areas of red and white pine, about 29 and 16 m^2 per ha respectively (Table 3). Results of the one-way analysis of variance for overstory basal area indicate no significant differences in density of the overstory among treatments (Pr F > = 0.81) and blocks ($Pr > \chi^2 = 0.74$) despite a history of variable thinning.

The effects of periodic burning were readily apparent in treated areas within the ground flora, seedling, and sapling vegetation classes. Vegetation on the 2-year burn plots was composed chiefly of low herbaceous and woody ground flora. Only three saplings (2.0-5.9 cm dbh) were observed in eighteen 10 m^2 sample plots; two observations occurred near the edges of treatment

Table 3. Mean overstory basal area (m^2/ha) among burning treatments. Treatment means are followed by their standard deviation.

Burn Interval	Mean	WP[1]	RP[1]
2-year	47.5 ± 11.2	17.8	29.1
6-year	46.7 ± 8.4	15.2	30.1
Control--no burns	48.8 ± 7.9	16.9	29.6

[1] WP = white pine, RP = red pine

areas, and one sapling occurred in an area of the plot where fire did not carry well. These unusual observations were considered outliers and excluded from further analysis. These plots also were virtually devoid of seedling-size woody vegetation (0-1.9 cm at dbh). Nevertheless, ANOVA's for sapling and seedling data were included all burn treatments.

Saplings and seedlings were most dense on the unburned plots. Control treatments were well stocked with advanced regeneration, averaging 3,944 stems per ha in the 2.0 to 5.9 cm dbh class. Saplings were scarce in the once-burned, 6-year treatment plots, with fewer than 400 stems per ha (Table 4). Analysis of variance indicated significant differences in sapling density among treatments ($p = 0.0001$) but not among blocks ($p = 0.34$). Multiple comparison tests indicated that differences were significant at $p= 0.05$ between burned and unburned treatments, but not between burn treatments.

Seedling density on the 6-year-burn plots was roughly half the density of the unburned stand areas (Table 4), with roughly 9,300 and 16,100 seedlings per ha, respectively, while no seedlings were observed during sampling of 2-year burn plots. ANOVA indicated significant differences in seedling density among the treatments ($p = 0.0001$), but not among blocks ($p = 0.08$). Multiple comparison procedures indicated significant differences among all three treatments at $p = 0.05$.

These data are similar to the results of prescribed burn studies in Northern Lower Michigan red pine stands. Henning and Dickmann (1996)

Table 4. Seedling (≤ 1.9 cm at dbh) and sapling (2.0-5.9 cm dbh) density per ha in burned and unburned treatments. Means for each variable are followed by their standard deviation.

Burn Interval	Seedlings	Saplings
2-year	0.0 ± 0.00	166[1] ± 1,130
6-year	9,277 ± 7,870	277 ± 960
Control-no burns	16,111 ± 9,010	3,944 ± 1,860

[1] These estimates reflect data outliers; saplings growing at the edges of plots or in incompletely burned areas.

reported sapling densities of 210, 385, and 4,336 stems per ha for 2-year burns, 5-year burns, and unburned treatments, respectively. They also noted significant differences among these treatments for seedling density, following the same pattern. Niering (1970) and Hodgkins (1958)reported that frequent prescribed burns kill most stems < 10 cm dbh, while larger trees escape relatively unscathed. Prescribed fire effects are short-lived in the absence of repeated burning, as hardwood regrowth may reach heights of up to 1.8 m after only 3 growing seasons (Hodgkins 1958).

The qualitative effects of burning were most evident in the seedling-size class (<1.9 cm dbh). Six-year burn plots contained greater density and a higher percentage composition of disturbance-favored species than the control treatment, including common buckthorn (*Rhamnus cathartica*), sassafras (*Sassafras albidum*), *Viburnum* spp., and tulip poplar (*Liriodendron tulipifera*) (Tables 5, 6, and 7). Control plots contained greater percentages of thin barked species and shrubs, including black cherry (*Prunus serotina*), red maple (*Acer rubrum*), and bush honeysuckle (*Diervilla lonicera*). Several species occurred only on unburned plots: hackberry (*Celtis occidentalis*), flowering dogwood (*Cornus florida*), musclewood (*Carpinus caroliniana*), and prickly ash (*Zanthoxylem americanum*) (Table 6). These plots were dominated by black cherry, honeysuckle, red maple and sugar maple (*Acer saccharum*) seedlings. Prescribed burning apparently did not result in increased oak seedling establishment; control plots contained more red oak (*Quercus rubra*), white oak (*Quercus alba*), and black oak (*Quercus velutina*) than 6-year burn plots.

Table 5. Seedling species composition of 6-year burn and unburned control plots as the percent of total seedling density within each treatment (≤1.9 cm dbh size class).[1]

Burn Interval	BC[2]	BU	EBU	ELD	HON	RM	RO	SAS	SM	VIB	Other spp.	Total
6-year	5%	19%	5%	5%	0%	9%	7%	26%	7%	5%	12%	100%
Control-no burns	20%	6%	5%	3%	8%	22%	4%	3%	7%	0%	22%	100%

[1] Species present at ≥5% in any treatment. No seedlings were recorded in plots burned at 2-year intervals.

[2] Species abbreviations: BC-black cherry, BU-common buckthorn, EBU-European buckthorn, ELD-elderberry, HON-bush honeysuckle, RM-red maple, RO-red oak, SAS-sassafras, SM-sugar maple, VIB-viburnum

Table 6. Mean seedling (≤1.9 cm dbh) species density (per ha) in burned and unburned plots.

Species	Burn Interval[1] 6-year	 Control- no burns
Acer negundo	56	56
Acer rubrum	833	3,611
Acer saccharum	667	1,111
Carpinus caroliniana	0	56
Carya spp.	167	722
Celtis occidentalis	0	111
Cornus florida	0	56
Corylus cornuta	111	167
Diervilla lonicera	0	1,278
Fraxinus americana	111	333
Fraxinus pennsylvanica	0	333
Liriodendron tulipifera	222	0
Morus spp.	56	111
Prunus avium	56	167
Prunus serotina	500	3,167
Quercus alba	389	667
Quercus rubra	667	667
Quercus velutina	0	333
Rhamnus cathartica	1,722	944
Rhamnus frangula	444	778
Sambucus spp.	444	444
Sassafras albidum	2,389	556
Viburnum spp.	444	0
Vitus spp.	0	389
Zanthoxylum americanum	0	56

[1] No seedlings were observed in the 2-year burn interval plots.

Table 7. Species listed in "Other" category (present at <5% of treatment density) in Tables 5 and 8.

Seedlings	Saplings
Acer negundo	*Cornus florida*
Carpinus caroliniana	*Diervilla lonicera*
Carya spp.	*Fraxinus pennsylvanica*
Celtis occidentalis	*Populus tremuloides*
Cornus florida	*Quercus rubra*
Corylus cornuta	*Rhamnus cathartica*
Fraxinus americana	*Rhamnus frangula*
Fraxinus pennsylvanica	
Liriodendron tulipifera	
Morus spp.	
Prunus avium	
Quercus velutina	
Vitus spp.	
Zanthoxylum americanum	

Sapling species composition in the 6-year-burn and control plots also appears to reflects the frequency of disturbance. Six-year-burn plots contained only rapidly growing, intermediate or intolerant shade species including sassafras, hickory (*Carya spp.*), red maple, and black cherry (Tables 8 and 9). Burn plots notably lacked the more tolerant species found in control plots; sugar maple, green ash (*Fraxinus pennsylvanica*), flowering dogwood, and white ash (*Fraxinus americana*).

Sassafras appears to be the most important fire-favored hardwood species on this site. Observations on 2-year burn plots prior to re-burning in May of 1995 suggested that sassafras had very high density in the most frequently burned plots. Although few saplings survived the 1995 spring burn on 2-year plots, root suckers of sassafras quickly re-sprouted and were nearly ubiquitous after only 2 months, although they didn't grow tall enough to be included in the woody understory seedling class. The 6-year burn plots contained nearly 4 times the "seedling" stems per ha as unburned plots. This species has similar responses to those noted for black cherry in a northern Michigan study. Henning and Dickmann (1996) noted that black cherry density was directly related to frequency of burning in red pine stands, possibly owing its success on frequently burned plots to a seed bank strategy. Black cherry has hard coated seeds that are readily disseminated by birds. These seeds undoubtedly survive in the forest floor, germinating quickly following fire. The same response from black cherry was not apparent in my study, probably due to

Table 8. Sapling species composition of 6-year burn and unburned control plots as the percent of total seedling density within each treatment (2-5.9 cm size class).[1]

Burn Interval	BC[2]	HIC	RM	SAS	SM	WA	Other spp.	Total
2-year[3]	33%	0%	0%	0%	67%	0%	0%	100%
6-year	20%	20%	20%	40%	0%	0%	0%	100%
Control-no burns	21%	3%	45%	7%	4%	6%	14%	100%

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[1] Species present at ≥5% in any treatment.

[2] Species abbreviations: BC-black cherry, HIC-hickory, RM-red maple, SAS-sassafras, SM-sugar maple, WA-white ash

[3] These estimates are based on three saplings tallied from (n=18) 10 m^2 plots. These are considered data outliers and have been discarded for ANOVA's and logistic regression analyses.

Table 9. Mean sapling (2.0-5.9 cm dbh) species density (per ha) in burned and unburned plots.

Species	Burn Interval 6-year	Burn Interval Control-no burns
Acer rubrum	56	1,778
Acer saccharum	0	167
Carya spp.	56	111
Cornus florida	0	56
Diervilla lonicera	0	56
Fraxinus americana	0	222
Fraxinus pennsylvanica	0	56
Populus spp.	0	56
Prunus serotina	56	833
Quercus rubra	0	56
Rhamnus cathartica	0	222
Rhamnus frangula	0	56
Sassafras albidum	111	278

differences in site quality and the presence of more rapidly growing competitors at the Kellogg Forest.

Ground Flora

Burned plots contained a rich community of groundflora species, immediately discernible from unburned stand areas. Control plots were relatively depauperate in the diversity and development of understory flora; these areas were characterized by sparse low herbaceous and woody seedling growth. Two-year burn plots contained thick undergrowth that generally averaged less than 1 m in height. Six-year burn plots contained a greater composition of woody ground flora species in 1995, but appeared similar to 2-year plots in 1994; ground flora here averaged 1 to 1.5 m in height.

Coverage by woody and herbaceous ground flora components in 1 m^2 frames was consistently higher on burn treatment plots than on unburned plots in 1994 and 1995 (Tables 10-13). Average percent coverage estimates appear similar for 2-year-burn and 6-year-burn plots in both years. Remarkably, compared to 1994, 1995 coverage and relative frequency of woody ground flora vegetation only decreased slightly (average of 5 percent) on 2-year-burn plots following re-burning of that treatment in May.

Total average coverage also appears similar between years; unburned plots had 27 and 30 percent coverage in 1994 and 1995, respectively. Total coverage for the 6-year burn was nearly the same over the two years. Compared to 1994, total coverage for 1995 two-year burn plots decreased only slightly from 57 to 52 percent, despite extensive consumption of surface litter

Table 10. 1994 woody ground flora species mean percent coverage by burn interval.

Woody Species	2-year	6-year	Control-no burns
Acer spp	0.4	1.6	2.1
Carya spp.	0.4	0.5	0.3
Diervilla lonicera	0.4	0.4	0.6
Fraxinus spp.	0.2	0.3	0.2
Parthenocissus quinquefolia	11.1	12.0	4.9
Pinus spp.	0.3	0.2	0.7
Prunus spp.	0.3	0.4	1.1
Quercus spp.	0.9	1.9	0.5
Rhamnus cathartica	1.5	1.9	0.5
Rhamnus frangula	0.3	0.0	0.0
Rhus spp.	0.2	0.3	0.0
Ribes cynosbati	0.0	0.0	0.1
Rosa spp.	0.0	0.1	0.0
Rubus spp.	16.7	12.7	2.7
Sambucus spp.	0.5	0.0	0.1
Sassafras albidum	4.8	4.8	2.7
Smilax hispida	0.9	0.2	0.9
Tilia americana	0.0	0.1	0.5
Toxicodendron radicans	1.3	1.4	0.7
Vitus spp.	0.4	1.8	1.4
Woody Species Total	**40.7**	**40.6**	**20.0**
s.d.	±37.97	±33.49	±24.11

Table 11. 1994 herbaceous ground flora species mean percent coverage by burn interval.

Herbaceous Species	2-year	6-year	Control-no burns
Apios americana	1.1	1.6	0.3
Apocynum androsaemifolium	0.1	0.8	0.0
Aralia nudicaulis	0.0	0.0	0.0
Arctium minus	0.1	1.0	0.0
Aster spp.	0.1	0.9	0.1
Carex spp.	0.1	0.3	0.0
Circaea quadrisulcata	1.1	0.3	0.6
Cirsium spp.	0.1	0.1	0.0
Fragaria virginiana	0.1	0.2	0.0
Desmodium glutinosum	0.4	0.2	0.0
Floerkea proserpinacoides	0.0	0.0	0.0
Gallium spp.	0.3	0.5	0.4
Geranium maculatum	0.0	0.1	0.0
Hieracium aurantiacum	0.1	0.3	0.0
Hypericum punctatum	0.0	0.0	0.0
Lactuca scariola	0.1	0.1	0.0
Maianthemum canadense	0.0	0.1	0.0
Mitchella repens	0.0	0.3	0.0
Moss	0.0	0.0	0.0
Osmarhiza claytoni	0.1	0.3	0.2
Oxalis acetosella	0.2	0.1	0.0
Phrymu leptostachya	0.2	0.3	0.2
Phytolacca americana	4.8	1.3	0.1
Pilea pumila	0.4	0.0	0.3
Plantago major	0.0	0.0	0.0
Poa spp.	0.2	0.4	0.0
Podophyllum peltatum	0.0	0.2	0.0
Polygonatum biflorum	0.3	0.6	0.3
Potentilla simplex	0.1	0.0	0.0
Pteridium aquilinum	3.2	4.4	2.9
Rumex acetosella	0.1	0.1	0.0
Taraxacum officinale	0.1	0.1	0.0
Trillium spp.	0.1	0.0	0.0
Unknown #10	0.1	0.0	0.0
Unknown #11	0.0	0.0	0.0
Verbascum thapsus	0.0	0.0	0.0
Viola spp.	2.7	0.7	1.7
Herbaceous Species Total	**16.4**	**15.4**	**7.4**
s.d.	±22.44	±20.03	±12.44

Table 12. 1995 woody ground flora species mean percent coverage by burn interval.

Woody species	**2-year**	**6-year**	**Control-no burns**
Acer spp.	0.2	1.5	2.4
Berberis thundbergii	0.0	0.3	0.0
Carya spp.	0.0	0.7	0.0
Celastrus scandens	0.5	0.0	1.8
Diervilla lonicera	0.0	0.6	0.5
Fraxinus spp.	0.0	0.0	0.0
Parthenocissus quinquefolia	0.0	0.0	3.4
Pinus spp.	6.6	13.1	0.7
Prunus spp.	0.1	0.1	1.4
Quercus spp.	0.0	0.8	0.0
Rhamnus cathartica	0.2	1.0	0.1
Rhamnus frangula	0.1	0.8	0.1
Rhus spp.	0.0	0.0	0.0
Ribes cynosbati	0.0	0.0	0.2
Rosa spp.	0.0	0.0	0.0
Rubus spp.	15.6	13.3	4.2
Sambucus spp.	0.9	0.2	0.6
Sassafras albidium	4.7	3.8	0.5
Smilax hispida	0.3	0.0	1.4
Solanum dulcamara	0.0	0.2	0.0
Tilia americana	0.0	0.0	0.0
Toxicodendron radicans	2.5	1.8	1.1
Vitus spp.	0.5	1.6	2.2
Woody Species Total	**32.1**	**39.9**	**20.7**
s.d.	±31.94	±36.52	±25.58

Table 13. 1995 herbaceous ground flora mean percent coverage by burn interval.

Herbaceous Species	2-year	6-year	Control-no burns
Apios americana	0.3	0.9	0.6
Apocynum androsaemifolium	1.0	0.0	0.0
Aralia nudicallis	0.0	1.6	0.0
Arctium minus	0.0	0.2	0.0
Aster spp.	0.1	0.2	0.2
Carex spp.	0.0	0.0	0.0
Circaea quadrisulcata	1.3	0.2	0.8
Cirsium spp.	0.1	0.0	0.0
Fragaria virginiana	0.0	0.3	0.0
Desmodium glutinosum	0.6	0.0	0.0
Floerkea proserpinacoides	0.0	0.0	0.0
Gallium spp.	0.4	0.5	0.7
Geranium maculatum	0.0	0.0	0.0
Hieracium aurantiacum	0.0	0.5	0.0
Hypericum punctatum	0.0	0.0	0.0
Impatiens biflorum	0.0	0.0	0.0
Lactuca scariola	0.1	0.0	0.0
Maianthemum canadense	0.0	0.2	0.1
Mitchella repens	0.0	0.0	0.0
Moss	0.0	0.0	0.2
Osmarhiza claytoni	0.0	0.5	0.3
Oxalis acetosella	0.1	0.1	0.0
Phrymu leptostachya	0.1	0.2	0.3
Phytolacca americana	7.8	1.8	0.0
Pilea pumila	5.0	0.0	0.2
Plantago major	0.0	0.1	0.0
Poa spp.	0.1	0.2	0.0
Podophyllum peltatum	0.0	0.0	0.0
Polygonatum biflorum	0.1	1.0	0.4
Potentilla simplex	0.0	0.0	0.0
Pteridium aquilinum	2.0	7.6	3.0
Rumex acetosella	0.0	0.1	0.0
Taraxacum officinale	0.1	0.1	0.0
Trillium spp.	0.0	0.0	0.0
Unknown #10	0.0	0.0	0.0
Verbascum thapsus	0.0	0.0	0.0
Viola spp.	0.3	1.0	2.6
Herbaceous Species Total	**19.6**	**17.5**	**9.6**
s.d.	±26.8	±24.1	±10.1

and scorching of woody stems by surface fire during re-burning of the plots in May.

Differences in 1995 total coverage means for herbaceous and woody vegetation components were significantly different for treatments (F = 7.46, p = 0.0007) and blocking (F = 11.81, p = 0.0001). Herbaceous ground flora means for 1994 and 1995 were not significantly different between 2-year and 6-year burn treatments in Student-Newman-Keuls and Tukey's HSD ranked means tests (alpha = .05) (Tables 14 and 15). Differences between 2-year and 6-year burn treatment woody ground flora coverage means were not significant in 1994, but significant differences between 2-year burn and 6-year burn means were found using Student-Newman-Keuls tests, but not Tukey's HSD (Table 15.). The Student-Newman-Kuels test has fairly good power to detect differences between means, but does not control the maximum experiment-wise error rate (Einot and Gabriel 1975). Tukey's HSD controls the type I experiment-wise error rate, but has weaker power to detect type II errors (Hayter 1984).

Differences in ground flora species richness were clear in both years between unburned control treatments and 6-year burn plots in both years, but not so with 2-year burn treatments (Table 16). Control treatments contained fewer species in 1994 and 1995 than 6-year burn plots. Two-year burn plots had greater species richness than unburned plots in 1994, but four fewer species in 1995. Following spring burning in 1995, 2-year plots had 11 fewer herbaceous species than in 1994. Given that the 1994 2-year plot vegetation data represented the second year since burning, it is logical to assume that the

Table 14. Ranked means tests for 1994 herbaceous and woody ground flora percent coverage.

		Burn Interval	
Herbaceous	**2-year**	**6-year**	**Control-no burns**
Mean	16.4	15.4	7.4
SNK[1]	a	a	b
Tukey's HSD[1]	a	a	b
Woody	**6-year**	**2-year**	**Control-no burns**
Mean	40.7	40.6	20.0
SNK[2]	a	a	b
Tukey's HSD[2]	a	a	b

[1] means with the same letter are not significantly different (alpha = 0.05, df = 249, n = 90).

[2] means with the same letter are not significantly different (alpha = 0.05, df = 249, n = 90).

Table 15. Ranked means tests for 1994 herbaceous and woody ground flora percent coverage.

Herbaceous	**2-year**	**Burn Interval 6-year**	**Control-no burns**
Mean	19.6	17.5	9.6
SNK[1]	a	a	b
Tukey's HSD[1]	a	a	b
Woody	**6-year**	**2-year**	**Control-no burns**
Mean	39.9	32.1	20.7
SNK[2]	a	b	c
Tukey's HSD[2]	a	a	b

[1] means with the same letter are not significantly different (alpha = 0.05, df = 300, n = 108).
[2] means with the same letter are not significantly different (alpha = 0.05, df = 270, n = 108).

Table 16. Number of ground flora species by year and burn interval.

	1994			1995		
Vegetation Type	2-year	6-year	Control-no burns	2-year	6-year	Control-no burns
Herbaceous	30	32	22	19	26	19
Woody	18	17	18	12	18	16
Totals	48	49	40	31	44	35

1995 fire temporarily reduced species richness on 2-year burn plots; the herbaceous fauna should recover to near 1994 richness by the end of 1996.

Studies by some researchers suggest that ground flora communities exhibit distinct differences in density and species richness following repeated prescribed burning. Henning and Dickmann (1996) found that ground flora coverage on biennially burned treatments in a northern Michigan red pine stand was lower than treatments with longer intervals between fire; plots with 5 and 10 year burn frequencies had the greatest herbaceous coverage. However, species richness did not differ among burn treatments and between burned and unburned plots. By contrast, White (1983) noted that repeated prescribed fires increased overall species richness in a *Quercus ellipsoidalis* community in Minnesota. Lemon (1949) showed that ashes on burned sites stimulate a lush early herb and shrub growth, although survival and increase of herbs are related to life history and form.

Woody species richness differed little among treatments and years (Table 16). Woody species on 2-year plots in 1995 suffered topkill during burning, but the majority of species quickly re-sprouted or germinated from buried seed. The lower overall species richness observed in 1995 was probably due to the difference in plot locations during successive years.

The woody ground flora of control plots contained greater representation of species easily killed by fire or with higher shade tolerance than found on burn plots (Table 12). Control plots had the greatest average percent coverage by maple seedlings, bush honeysuckle, pine species, American basswood (*Tilia*

americana), vine bittersweet (*Celastrus scandens*), wild currant (*Ribes* spp.), greenbriar (*Smilax hispida*), and in 1995, grapevine (*Vitus* spp.).

Two-year burn plots were characterized by fast-growing, disturbance favored species. Although most of the woody stems were killed by the surface fire during 1995 spring burning, these plots were quickly re-vegetated by a dense growth of blackberry (*Rubus* spp.), sassafras, and poison ivy (*Toxicodendron radicans*). By mid-summer, blackberry and sassafras on the freshly burned plots had grown to about 1 m in most areas. Biennially burned plots had greater average coverage by blackberry, sassafras, and elderberry (*Sambucus* spp.) in both years, and the least average coverage in species noted on control plots.

Six-year burn treatments contained the greater average coverage by species that re-sprout after top-kill by fire, i.e. oak and hickory, or that are disturbance-favored but relatively slow growing, i.e. Virginia creeper and barberry (*Berberis thundbergii*). These plots also contained a significant representation by species whose fruit are spread readily by birds and rodents, like common buckthorn, sassafras, and in 1995, black cherry.

Burned treatments contained greater overall coverage by almost all herbaceous species encountered than unburned plots, although mean differences were not statistically tested at the species level. Control treatments contained more moss, bedstraw (*Gallium spp.*), and in 1995, violets (*Viola scandens*), than burn treatments. Herbaceous flora in burned treatments reflect the frequency of disturbance, as well as the degree of shading by woody plant

species. Two-year burn plots in 1995 (season immediately after spring burning) were dominated by pokeweed (*Phytolacca americana*), nettle (*Pilea pumila*), and enchanter's nightshade (*Circaea quadrisulcata*). Species coverage on these plots in the second season after prescribed burning (1994) appeared more like that of the 6-year burn plots, with greatest coverage by pokeweed, bracken fern (*Pteridium aquilinum*), tretick foil (*Desmodium glutinosum*), and violets. The 6-year burn plots contained greater coverage of the following species in both years: fern, common burdock (*Arcticum minus*), wild sarsaparilla (*Aralia nudicallis*), Solomon seal (*Polygonatum biflorum*), groundnut (*Apios americana*), sweet cisely (*Osmarhiza claytoni*), mayapples (*Podophyllum peltatum*), and Aster species.

Weather Effects

Weather conditions during the 1995 were hotter and drier than observed in 1994. Data collected from Kellogg Experimental Forest's weather station also indicate that the winter of 1994 was much colder than 1995. Average minimum temperatures in January and February of 1994 were less than -14 C, with minimum temperatures well below -17 C for more than a week. Temperatures were relatively balmy in early 1995, with minimum readings above -17 C and averages above -7 C. This trend continued throughout the year (Figure 4); average temperatures were 4.5 C (10 F) higher during the 1995 trapping season than in 1994. Minimum temperatures averaged 3 C (8 F) higher during 1995.

Degree day accumulation in 1995 was 150 degree days (base 50 F) ahead of 1994 levels at the start of pitfall trapping in May (Figure 5). Cumulative

degree days averaged 680 days ahead of 1994 throughout the season, reaching 875 degree days by the end of trapping in 1995. The greatest difference in degree day incidence occurred in late June through August sampling dates. Incidence in fall dropped to near or below 1994 levels, when temperatures for the two years were similar.

Overall, 1995 was a slightly drier year than 1994, with the largest differences occurring in snowfall and mid-season rainfall. Pre-trapping season rainfall was similar, with 24.3 and 21.1 cm in 1994 and 1995, respectively. Nearly twice as much snow fell in 1994; 80.6 cm compared to 48.9 cm in 1995. Cumulative precipitation in 1995 lagged 2 to 8 cm behind 1994 levels throughout the trapping season, averaging 6.3 cm less than in 1994 during summer and fall (Figure 6). Rainfall occurred more frequently in 1995 than in 1994. Unusually heavy rainfall occurred during June and August of 1994, with low levels of precipitation during the rest of the year.

Figure 4. Average and minimum temperatures during trapping seasons for 1994 & 1995. Each point represents the average temperatures for the three days that comprise the trapping period, from opening to trap closure.

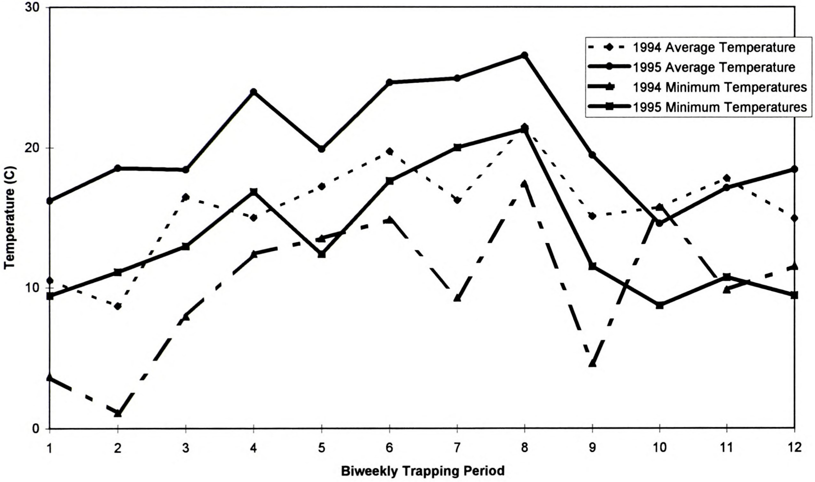


Figure 5. Degree day accretion and accumulation during the trapping season in 1994 and 1995 (base 50 F).

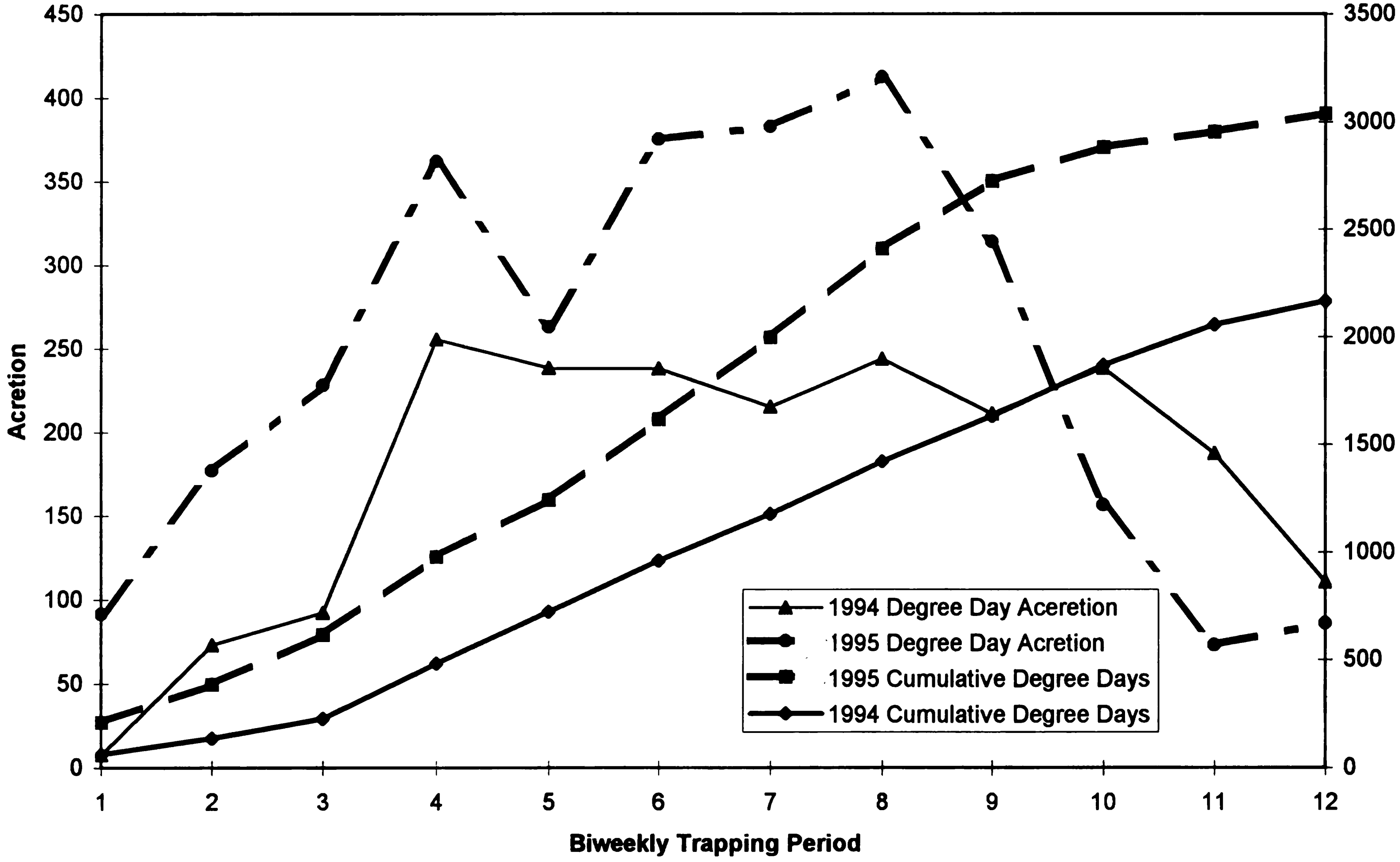
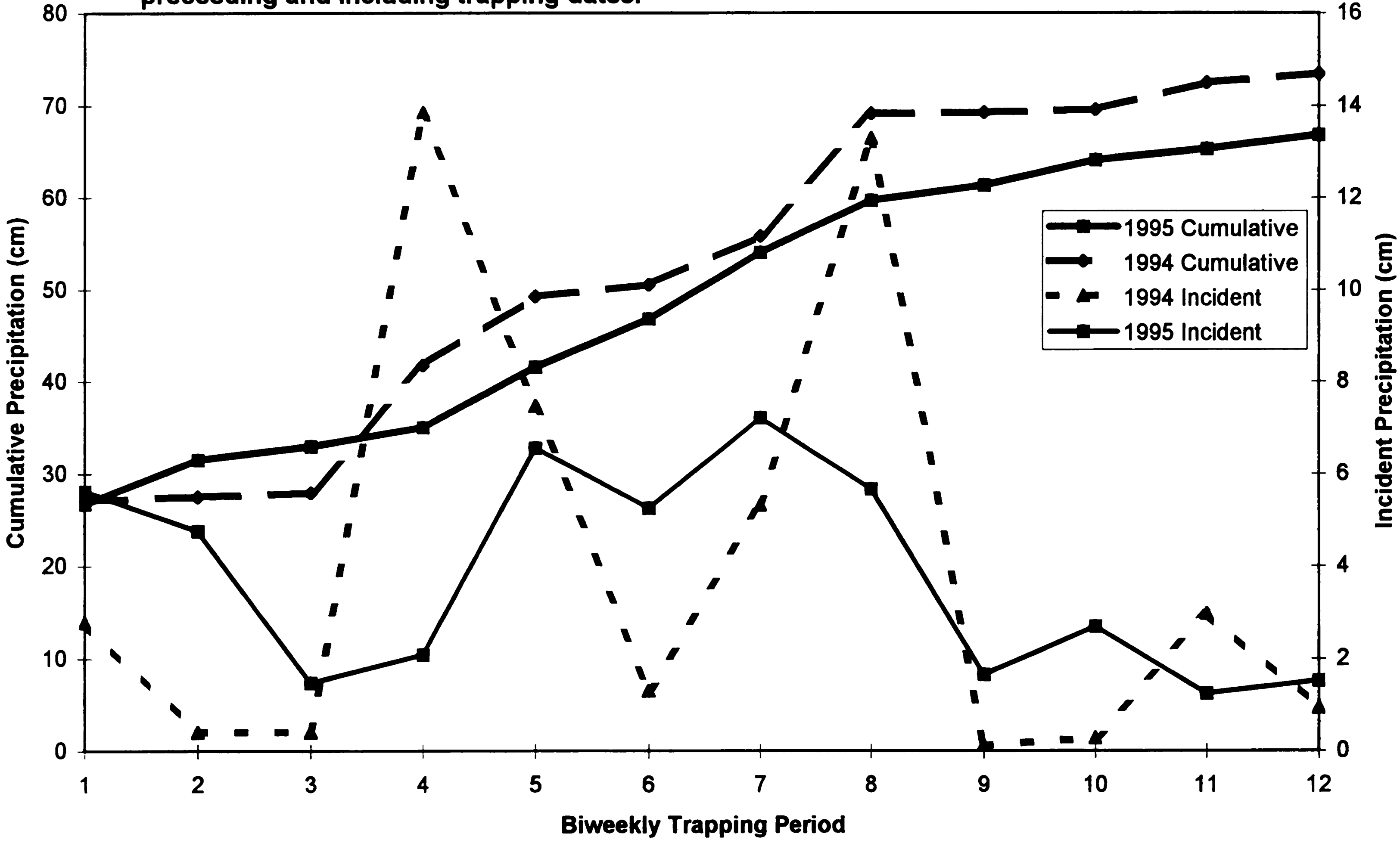


Figure 6. Cumulative and 2-week incident precipitation over the trapping seasons in 1994 and 1995. Each point represents the average of precipitation occuring during the two week period preceeding and including trapping dates.



Carabid Beetle Relative Activity

Pitfall trapping catches indicate that fire and fire frequency have a pronounced effect on beetle activity. Beetles were more active on frequently burned than unburned treatments in both years (Figures 7 and 8). Nearly twice as many Carabids were caught on 2-year burn plots than on unburned plots, 443 beetles in 1994 and 378 in 1995, compared to 233 and 177 for unburned plots, respectively. Traps on six-year burn plots caught more beetles than control plots in 1994, but not in 1995 (Table 17). Total catches over two years clearly show that fires at short intervals had a major effect on beetle activity, whereas fires at 6 year intervals had little effect.

The effect of burn treatment is clearly demonstrated at the species level also (Tables 17 and 18), although the trend varies for each species and for each year. The most commonly trapped species, *Pterostichus stygicus* (Say), was least abundant in traps on the 6-year burn plots in both years. *Synchus impunctatus* (Say) was trapped more often in 6-year burn plots in 1994 than in other treatments. Activity patterns of four species changed in 1995; all showed decreased activity on 6-year burn plots, three showed higher activity on control treatments than 6-year burn plots that year. Three species exhibited activity that seemed directly related to frequency of burning in both years: *Pterostichus mutus* (Say), *Carabus goryi* Dejean, and *Cyclotrachelus soldalis* (Leconte). Similar results have been documented by Harris and Whitcomb (1971), who reported higher abundance among four species of *Pterostichus* (formerly *Evarthrus* : Carabidae) in burned compared to unburned southern pine stands.

Figure 7. Total number of beetles trapped during each trapping period in 1994.

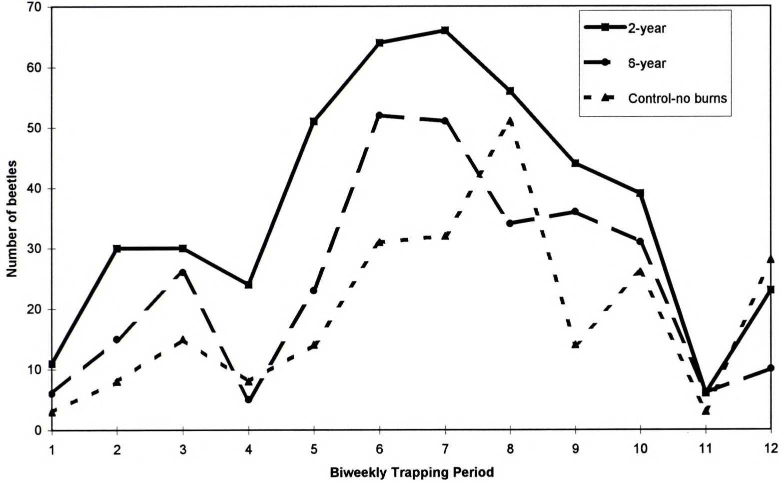


Figure 8. Total number of beetles trapped during each trapping period in 1995.

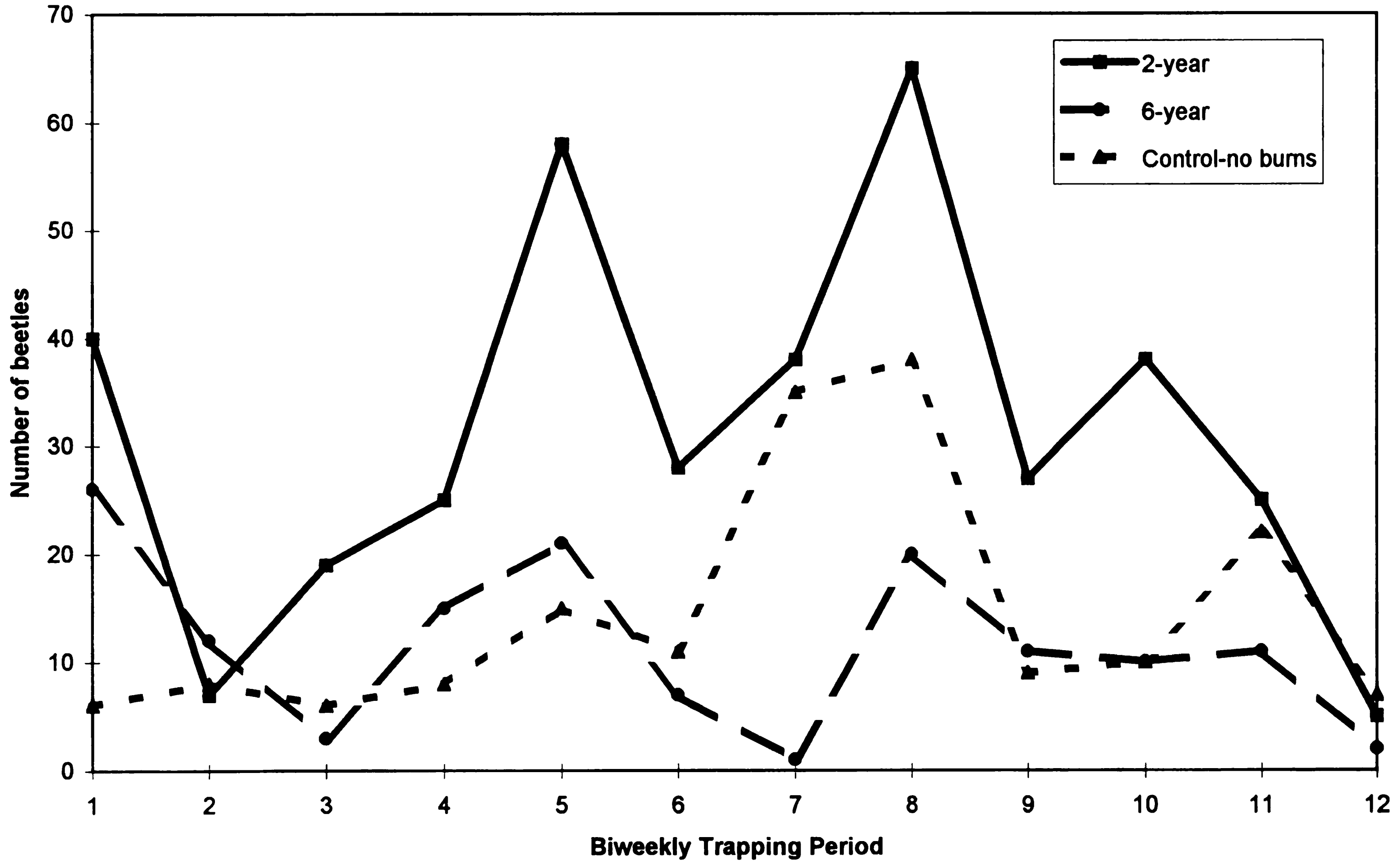


Table 17. Total number of Carabid beetles trapped by species and burn treatment.

	Control		6 year burn		2 year burn	
Species	**1994**	**1995**	**1994**	**1995**	**1994**	**1995**
Sphaeroderus stenostomus lecontei Dejean	19	10	15	4	10	4
Carabus goryi Dejean	5	6	22	21	32	35
Notophilious spp.	0	0	0	1	0	2
Pterostichus femoralis	0	0	0	0	0	2
P. melanarius (Illiger)	1	9	6	0	0	8
P. mutus (Say)	6	2	7	7	62	39
P. pensylvanicus LeConte	10	8	0	5	12	4
P. permundus (Say)	2	0	3	0	2	3
P. stygicus (Say)	110	61	96	32	137	88
P. tristis (Dejean)	16	13	14	8	18	14
Poecilus lucublandis (Say)	1	1	8	1	2	4
Cyclotrachelus convivus (LeConte)	13	15	14	6	34	26
C. soldalis (LeConte)	5	8	7	9	25	30
Calathus gregarius (Say)	0	2	3	3	2	3
Synuchus impunctatus (Say)	23	8	63	8	53	10
Cymindis americanus Dejean	2	0	2	0	1	1
Agonum ferreum Haldeman	0	0	0	1	0	0
A. melanarium Dejean	0	0	0	0	0	1
Platynus hypolithos (Say)	11	13	11	3	7	4
Galerita janus (Fabricius)	0	1	0	2	0	1
Pseudoamara arenaria (LeConte)	0	1	0	4	0	1
Amara familiaris Duftschmid	0	0	0	1	0	2
A. impuncticollis (Say)	0	0	1	0	1	0
Amphasia interstitialis (Say)	0	1	3	1	2	7
Harpalus compar LeConte	1	0	1	0	3	3
H. erythropus Dejean	0	0	0	0	2	1
H. fulvilabris	0	0	0	0	0	1
H. herbivagus Say	0	0	1	0	1	0
H. longicollis LeConte	0	1	1	2	6	21
H. paratus LeConte	0	0	0	0	0	1
H. pensylvanicus (DeGeer)	0	1	2	3	2	0
H. providens Casey	0	0	3	5	3	7
H. puncticepts (Stephens)	0	0	0	1	0	1
H. somulentus Dejean	1	1	0	1	0	0
Anisodactylus nigerriumus (Dejean)	0	0	1	0	0	0
A. rusticus (Say)	0	0	1	0	1	0
Notiobia nitidipennis (LeConte)	1	1	1	3	8	10
Trichotichus dichrous (Dejean)	0	0	0	1	0	1
T. vulpeculus (Say)	6	11	9	6	16	39
Bradycellus badipennis (Haldeman)	0	0	0	0	1	0
Chlaenius tricolor Dejean	0	1	0	0	0	0
Dicaelus elongatus Dejean	0	0	0	0	1	0
Unknown 1	0	1	0	1	0	2
Unknown 2	0	0	0	0	0	1
Unknown 3	0	1	0	0	0	0
teneral spp.	0	0	0	0	0	1
Total per year	233	177	295	140	444	378
Total for 2 years	410		435		882	

Table 18. Mean and total number of Carabids trapped by burn treatment for the nine most active species during 1994 and 1995 seasons. Standard deviation is presented below each treatment mean.

	2 year		6 year		Control-- no burns		Total Carabids	
Species	**1994**	**1995[1]**	**1994**	**1995**	**1994**	**1995**	**1994**	**1995[1]**
Cyclotrachelus convivus	2.9	2.2	1.1	0.5	1.1	1.2	61	47
	11.4	7.2	5.1	3.4	5.0	5.3		
C. soldalis	2.2	2.4	0.5	0.7	0.4	0.7	37	47
	9.5	8.9	3.2	4.0	3.2	3.3		
Carabus goryi	2.7	2.9	1.8	1.8	0.4	0.5	59	62
	9.9	11.5	7.1	9.1	3.6	3.3		
Pterostichus mutus	5.2	3.2	0.5	0.5	0.5	0.2	75	48
	14.7	11.0	3.6	4.7	3.0	1.7		
P. stygicus	11.4	7.4	7.9	2.7	9.2	5.1	343	181
	22.1	17.3	16.3	7.3	21.0	14.5		
P. tristis	1.4	1.2	1.1	0.7	1.3	1.0	48	35
	5.8	4.9	4.8	3.8	4.7	4.5		
Sphaeroderus stenostomus lecontei	0.9	0.3	1.3	0.4	1.6	0.9	44	18
	4.8	2.4	5.2	2.4	5.4	4.0		
Synuchus impunctatus	4.5	0.9	5.2	0.7	2.0	0.7	139	26
	12.8	5.0	15.7	3.8	7.0	4.1		
Trichotichus vulpeculus	1.3	3.2	0.7	0.5	0.5	0.9	31	56
	5.6	11.2	4.7	2.9	6.2	4.2		
Total Carabids	37.1	30.95	24.7	11.5	19.4	15.0	972	695
	43.9	38.8	30.7	18.3	31.1	23.1		

[1] Means for 2-year burn and unburned control treatments reflect the loss of 10 traps in these treatments to varmints.

A weak inverse relationship between activity and burn frequency was demonstrated by one species, *Sphaeroderus stenostomus lecontei* (Dejean); however, this relationship is dubious considering the small sample size, and the large standard deviation for treatment means for this species.

Total catch in my study decreased for all treatments in 1995, possibly due to the effects of weather. As noted in the previous section, 1995 was a hotter, drier year compared to 1994. Insect development cycles are closely related to rates of degree day accumulation; thus it is possible that weather caused some species to become active earlier in 1995 than the previous year. Degree day accumulation was already 150 days ahead of 1994 levels at the start of trapping in mid-May of 1995 ; beetle populations may have been well ahead of 1994 development stages. It is possible that trapping in 1995 began too late to fully represent spring active species whose populations may have reached greatest activity before or soon after the first trapping date. Summer and fall active species were also less active in 1995 according to trap counts, however. Lower overall activity may also have been due to a combination factors: lower moisture conditions, fire induced mortality, or a trapping-out effect.

High sample variance casts doubt on trend predictions, however. Standard deviation for most of the nine most active species trapped were generally twice the mean value. Thus, only the strongest trends are likely to be accurate.

Beetle Categorical Data Analysis

Response variables were modeled by comparison to the control treatment, the third block, and the third season (trapping dates 9-12) or last collection date. The SAS Logistic procedure calculates the contribution of independent variables to the model using Wald chi-square tests. SAS Logistic procedure also calculates maximum likelihood estimates for each variable which represent the probability of obtaining the least ordered response of the dependent variable. Thus, independent variables were tested against control treatments, the third block, and the third season or collection date. Since the least ordered value for beetle count data for these analyses was zero beetles, probabilities reflect the likelihood of trapping fewer beetles than trapped in the control treatment, third block, or last season/trapping date. Odds ratios calculated for the maximum likelihood estimates can be converted to represent the probability of greater catches by inversion. Analyses for several species were possible in only one year due to sparseness of the data in one or more treatments: 1994 only for *C. convivus* and *C. goryi*, 1995 only for *C. soldalis* and *T. vulpeculus*. Trap catch data were pooled across all species for Total Carabid beetle data analyses.

Total Carabid data analysis indicates a highly significant difference for 2-year burn treatments in 1994 ($\Pr > \chi^2 = 0.0001$) and in 1995 ($\Pr > \chi^2 = 0.0001$) compared to control plots (Tables 19). Treatment differences for the 6-year burn plots were significantly different from controls only in 1994 ($\Pr > \chi^2 = 0.026$). Traps in 2-year and 6-year treatments in 1994 were 2.7 and 1.5 times more

Table 19. **Logistic regression analysis results from trap counts of the seven most commonly trapped Carabid species, and total Carabid catch in 1994 and 1995 trapping seasons. Probability values (Pr > χ^2) and odds ratios are listed for independent variables from categorical data analysis.**

	1994							1995						
Species	**2 year**	**Odds ratio**[1]	**6 year**	**Odds ratio**	**2 vs. 6**[2]	**block 1**	**block 2**	**2 year**	**Odds ratio**	**6 year**	**Odds ratio**	**2 vs. 6**	**block 1**	**block 2**
C.convivus[4]	0.14	---[3]	0.4361	---	0.48	0.24	0.10	---	---	---	---	---	---	---
C. soldalis[5]	---	---	---	---	---	---	---	0.02	3.4	0.74	---	0.01	0.95	0.86
C. goryi[6]	0.001	11.7	0.004	9.3	0.56	0.002	0.69	---	---	---	---	---	---	---
P. mutus	0.01	6.9	0.69	---	0.01	0.77	0.20	0.02	6.2	0.79	---	0.03	0.74	0.16
P. stygicus	0.06	1.6	0.70	---	0.12	0.99	0.02	0.02	1.8	0.36	---	0.002	0.26	0.16
P. tristis	0.82	---	0.33	---	0.23	0.001	0.11	0.99	---	0.72	---	0.72	0.49	0.32
T. vulpeculus[7]	---	---	---	---	---	---	---	0.16	---	0.14	---	0.01	0.97	0.83
Total Carabids	0.0001	2.7	0.03	1.5	0.001	0.04	0.04	0.000	2.5	0.25	---	0.0001	0.51	0.21

---

[1] Odds ratios represent the probability that the represented treatment or block will catch more beetles than the last ordered classification variable in the data set; i.e. the probability that 2-year burn plots will catch more beetles than the unburned control treatments, or the probability that block I will trap more beetles than block III.

[2] Results of hypothesis tests H_0: $B_{2\text{-year}} - B_{6\text{-year}} = 0$, reported as (Pr > χ^2).

[3] Odds ratios are reported only for variables that had a significant contribution to the model ($p < 0.10$).

[4] Sparsness of the data for *C. convivus* did not permit analysis of 1995 trap counts.

[5] Sparsness of the data for *C. soldalis* did not permit analysis of 1994 trap counts.

[6] Sparsness of the data for *C. goryi* did not permit analysis of 1995 trap counts.

[7] Sparsness of the data for *T. vulpeculus* did not permit analysis of 1994 trap counts.

likely to catch more beetles than control treatments. Traps in 2-year burn plots in 1995 were 2.5 times more likely to catch beetles than the control. Differences between blocks proved significant in 1994, but not in 1995. Blocks I and II, with totals of 291 and 296 respectively, were not different from each other, but were significantly different from the 385 beetles trapped in block III ($Pr > \chi^2 = 0.041$ and 0.035, respectively) (Table 20). In both years, hypothesis tests indicate that differences between the 2-year and 6-year burn treatments were highly significant ($Pr > \chi^2 = 0.001$).

Not all Carabid species reacted to burn treatments with this pattern. Burn treatment effects were not significant for *Trichotichus vulpeculus. Pterostichus tristis* and *C. convivus* did not show significant differences in activity among treatments; in 1994 for *C. convivus*, both years for *P. tristis*. The effect of blocking was significant for *P.tristis*; this species was twice as likely to be trapped in block I as in block III (Table 20). Data *for C. convivus* were too sparse in the 6-year-burn treatment to allow analysis for 1995, even though the 47 beetles trapped of that species represented 6.8% of the total season catch.

A species closely related to *C. convivus*, *C. soldalis*, showed significant activity differences in 1995 between 2-year burn and unburned treatments($Pr > \chi^2 = 0.02$). Six-year burn treatment activity was not significant from control levels ($Pr > \chi^2 = 0.74$). Burn treatments were significantly different from each other ($Pr > \chi^2 = 0.01$).

Table 20. Block totals for nine common Carabid species and total number of beetles trapped in 1994 and 1995.

	1994			1995		
Species	**Block I**	**Block II**	**Block III**	**Block I**	**Block II**	**Block III**
C.convivus	12	23	26	14	14	19
C. soldalis	8	22	7	11	20	16
C. goryi	4	27	28	1	32	29
P. mutus	23	15	37	17	16	15
P. stygicus	135	88	120	84	48	49
P. tristis	5	17	26	6	14	15
S. stenostomus lecontei	18	11	15	6	5	7
S. impunctatus	14	47	78	2	7	17
T. vulpeculus	19	11	1	31	14	11
Total Carabids	291	296	385	241	222	232

One or more burn treatments had significant effects on *C. goryi*, *P. stygicus*, and *P. mutus*. Traps in 2-year and 6-year burn treatments were 11 and 9 times more likely to catch more *C. goryi* than control treatments ($Pr > \chi^2 = 0.001$ and 0.004), respectively. Six-year burn plot activity was not significantly different from that on 2-year plots ($Pr > \chi^2 = 0.56$), and significant differences occurred between blocks I and III (4 beetles compared to 28).

Pterostichus stygicus had significantly greater activity in 1994 and 1995 on 2-year burn plots than unburned ($Pr > \chi^2 = 0.06$ and 0.02, respectively), but not on 6-year burn plots ($Pr > \chi^2 = 0.70$ and 0.36, respectively). Differences between the two burn treatments were significant in 1994 ($Pr > \chi^2 = 0.002$), but were not in 1995 ($Pr > \chi^2 = 0.12$). Significant differences between blocks occurred only in 1994 for blocks II and III ($Pr > \chi^2 = 0.02$).

Pterostichus mutus also showed significant treatment effects for the 2-year treatment ($Pr > \chi^2 = 0.005$ and 0.02), but not the 6-year burn ($Pr > \chi^2 = 0.77$ and 0.79) in both years. Two year burns were significantly different from 6-year burn plots ($Pr > \chi^2 = 0.01$ and 0.03). Differences between blocks were not significant.

The observation of greater Carabid activity on burned plots vs. unburned treatments in my study is corroborated by a few studies in grasslands and forests. Hansen (1986) collected greater numbers of insects following a 20,000 ha fire on shrub-dominated range sites than on unburned sites. After severe wildfire in Alaskan black spruce stands, total arthropod abundance was higher on burned than similar unburned stand areas (Viereck and Dyrness 1979), although the Coleoptera component of that community was less abundant during the first post-fire year relative to pre-burn activity levels. This decrease was attributed to greater predation success by spiders on burned areas.

In contrast, other studies showed that Carabid activity on burned forest sites is reduced following fire. Holliday (1991) observed that most Carabid species become locally extinct during intense forest fires in northern boreal coniferous forests, or during the extreme habitat changes that follow. In a 10-year study of the same site, Carabid species abundance was generally 34% of unburned control plots (Holliday 1992). Harris and Whitcomb (1971) reported higher abundance among four species of *Evarthrus* (Carabidae) in unburned compared to burned southern pine stands. In a later study, Harris and Whitcomb (1974) noted that annually burned southern pine plantation sites supported consistently lower Carabid beetle populations than sites that had been protected for 10 years. Other researchers noted a 60 percent decrease in beetle populations in southern pine stands following prescribed burning (Pearse 1943, Heyward and Tissot 1936). Ahlgren (1974) found fewer beetles in prescribed burned jack pine stands in Minnesota.

Repeated controlled burning had little effect on beetle abundance in other studies. Researchers in Australia found that two consecutive prescribed fires at a 3-year interval had little effect on total arthropod abundance, although activity of Collembola declined for one year following each fire (Collet et al. 1993). Rickard (1969) found greater abundance of phytophagous beetles on unburned shrub steppe compared to burned sites, but concluded that fire had little effect on the only Carabid studied, *Calosoma luxatum* Say. On sandhill sites in Florida, differences in abundance of common ground dwelling beetle species (Coleoptera: Carabidae and Scarabidae) among plots burned at 1, 2, and 7 year intervals were not significant from unburned sites, although 5-year interval plots were (McCoy 1987). Correlation analysis indicated that the abundance of the four most common beetle species were positively related to time since burning.

Observations of greater beetle activity on 2-year compared to 6-year burn treatments in my study is consistent with the findings of most fire studies in grasslands, but not forest sites. Spider populations in annually burned prairie grass-dominated wetlands were significantly more abundant than populations in unburned sites, consistent with the higher vegetative productivity observed following burning (Johnson 1995). Riechert and Reeder (1972) suggested that spider populations in dry prairie sites in Wisconsin are well adapted to fire, noting that periodically burned areas supported stable populations. The results of these studies may not be directly applicable to forested ecosystems, however.

Gillon (1972) observed that populations of sun-loving Pentatomidae were maintained by periodic fires in African savannas. Metz and Farrier (1973) found that annually burned plots in North Carolina loblolly stands contained significantly lower soil mesofauna abundance than unburned and periodically burned plots. They noted that soil mesofauna recovered to unburned stand population levels after 38 to 46 months, however. In a similar study, Metz and Dindal (1975) observed significantly lower abundance of Collembola in annually burned loblolly stands compared to unburned sites, but no significant differences between periodically burned (every 5 to 8 years) plots and controls.

Vegetation Characteristics of Beetle Activity

The relationship between vegetation characteristics and beetle activity was examined by fitting regression models through categorical data analysis. This procedure used only 1995 ground flora and beetle count data and permitted analysis only for total carabids and five of the common beetle species (Table 21).

Total Carabid Activity Models--When fitted without treatment variables, the 1994 total Carabid activity model incorporating overstory basal area, sapling, and seedling density variables showed significant differences only for sapling density ($Pr > \chi^2 = 0.0003$). Both variables were negatively related to beetle counts, with odds ratios of 0.98 for seedlings and 0.86 for saplings. Using 1995 total Carabid data only, seedling ($Pr > \chi^2 = 0.03$) and season variables were significant ($Pr > \chi^2 = 0.0001$). Again, seedling density was negatively related to Carabid catches, with high density plots 0.98 times as likely to catch beetles as low-density plots. This relationship confirms the overall results of pitfall trapping in both years of the study. More beetles were trapped on the 2-year burn plots than on unburned plots in 1994 and 1995, possibly reflecting the almost complete lack of seedling and sapling size vegetation on these frequently

Table 21. Summary of significant variables in logistic regression models relating vegetation characteristics to beetle activity. Variables included in each model are indicated by entries of NS for not significant, or Pr > χ^2.

Species	2-year burn	6-year burns	Over-story[1]	Saps[2]	Seed[3]	Herb[4]	Wood[5]	Sp[6]	Su[7]
C. soldalis	0.005	0.04	0.05	0.03	0.02	NS	NS	--	--
P. tristis	NS	NS	NS	NS	NS	NS	NS	--	--
T. vulpeculus[8]	--	--	NS	NS	0.04	NS	NS	--	--
P. mutus	NS	NS	NS	NS	NS	NS	NS	--	--
P. stygicus[9]	NS	NS	NS	NS	NS	NS	0.004	--	--
P. stygicus[10]	--	--	NS	0.09	NS	NS	0.007	--	--
Total Carabids[11]	--	--	NS	0.001	NS	--	--	--	--
Total Carabids[11]	--	--	NS	NS	0.03	--	--	0.0001	0.0001
Total Carabids[12]	NS	NS	NS	0.05	NS	--	--	--	--
Total Carabids[13]	0.004	NS	NS	NS	NS	--	--	--	--
Total Carabids[14]	NS	NS	NS	NS	0.07	NS	NS	--	--
Total Carabids[14]	--	--	NS	0.15	0.15	0.09	NS	NS	0.04
Total Carabids[15]	--	--	NS	NS	0.02	NS	NS	NS	0.02

[1] Overstory = basal area at each trap location for trees >5.9 cm dbh.

[2] Saplings = stems per ha 2.0-5.9 cm dbh.

[3] Seedlings = stems per ha at least 1 m tall and 0-1.9 cm dbh.

[4] Herbs = percent ground coverage of herbaceous ground flora in 1 m^2 quadrats.

[5] Woody = percent ground coverage of woody ground flora < 1 m in 1 m^2 quadrats.

[6] Sp = Spring season, or trapping periods 1, 2, and 3.

[7] Su = Summer season, or trapping periods 4, 5, 6, 7, and 8

[8] Only the model fitted without treatment variables attained significance; this model had poor fit.

[9] This model also included variables for seasons; only spring was significant (Pr >χ^2 = 0.001).

[10] Season variables in the model were not significant. Treatment variables were not included.

[11] These models used data for 1994 and 1995.

[12] Model used 1994 data.

[13] Model used 1995 data, but did not include ground flora variables.

[14] Model used 1995 data only.

[15] Model used 1995 data only and included block variables; only block 2 was significant (Pr > χ^2 = 0.09).

disturbed sites.

With the addition of treatment variables, the 1994 model showed significance only for saplings ($Pr > \chi^2 = 0.052$); saplings remained negatively related to beetle activity. Treatment variables were not significant in the combined model ($Pr > \chi^2 = 0.19$ and 0.86 for 2- and 6-year treatments). Seedling density became insignificant for 1995 with the addition of treatment variables ($Pr > \chi^2 = 0.22$). The 1995 model did show a significant 2-year burn treatment effect ($Pr > \chi^2 = 0.004$) but not a 6-year effect ($Pr > \chi^2 = 0.81$).

The addition of ground flora variables to 1995 total Carabid activity models adds little predictive power. Herbaceous ground flora coverage and woody ground flora effects were insignificant. Seedling density had better significance than in the model without ground flora variables ($Pr > \chi^2 = 0.07$) and became weakly positively related to beetle catches. Herbaceous ground flora coverage has greater significance ($Pr > \chi^2 = 0.09$) when treatment variables are removed from the model, while sapling and seedling variables both approach $Pr > \chi^2 = 0.15$. Herbaceous ground flora, seedling, and sapling variables have very low estimates for the regression equations; all three were less than 0.01, translating to odds ratios between 1.0 and .99 for chances of higher catches than low density or coverage plots. Ground flora variables did not have a significant contribution even when run in models with block and season variables ($Pr > \chi^2 = 0.39$ and 0.26). Thus, it is possible to say that ground flora differences among treatments are not significantly related to beetle activity when the variance due to seasons, blocks, saplings, seedlings, and overstory density are removed.

***C. soldalis* models**--Seedling and sapling density were significant ($Pr > \chi^2 = 0.02$ and 0.03) in models incorporating treatments, blocks, dates, and ground flora variables. Overstory basal area differences were marginally significant ($Pr = 0.053$), perhaps reflecting a relationship between crown closure and *C. soldalis* catches. Burn treatment effects were also significant ($Pr > \chi^2 = 0.005$ and 0.04). Sapling, seedling, and overstory basal area variables were directly related to catches, with odds of higher catches on high-density plots of 1.9, 1.1, and 1.05 times the odds on lower density plots, respectively. Seedling and sapling density were not significant in models fitted without treatment variables, whereas basal area differences among traps remained significant ($Pr > \chi^2 = 0.01$). Ground flora variables were not significant in predicting catches ($Pr > \chi^2 = 0.96$ and 0.58).

***P. tristis* models**--All vegetation variables were insignificant at $\alpha = 0.05$ in models for *P. tristis* activity, even when they were fitted separately to the beetle data.

***T. vulpeculus* models**--Seedling density was inversely related to catches ($Pr > \chi^2 = 0.04$) in the model without treatment variables. Ground flora and other vegetation variables were not significant. This model had very poor fit according to the Pearson residual statistic, however ($Pr > \chi^2 = 0.0025$).

***P. mutus* models**--Herbaceous ground flora showed a slight but non-significant relationship to *P. mutus* activity ($Pr > \chi^2 = 0.14$) in models testing solely the effect of ground flora. Models including other variables were not significant. Herbaceous coverage was only weakly and inversely related to higher beetle catches; the probability of catching more beetles on plots with greater coverage were only 0.97.

***P. stygicus* models**--Woody ground flora and seedling density were significantly related to *P. stygicus* activity in models with treatment, block, season, overstory, sapling, seedling, and ground flora variables. Woody ground flora was weakly, but directly, related to catches ($Pr > \chi^2 = 0.004$), while seedling density was not significant ($Pr > \chi^2 = 0.12$). Seedling density was also directly related to beetle activity. These variables had odds of higher catches of 1.02 and 1.04, respectively, on higher density plots.

In models without treatment variables, woody ground flora remained significant ($Pr > \chi^2 = 0.01$), although the attendant odds ratio did not improve. Sapling density was directly related to *P. stygicus* activity ($Pr > \chi^2 = 0.09$), albeit with a low odds ratio of 1.2. This merely reflects treatment effects on sapling density. Seedling density became insignificant with the removal of treatment variables.

Although some vegetation variables appear to be significant in explaining variation in beetle activity, most of the odds ratios are very low, indicating little predictive strength. At the species level, *C. soldalis* was most strongly associated with any vegetation variable. The odds ratio for overstory stocking of

1.93 suggests that microsite variations in basal area may have a significant influence on activity for that species. Sapling density has little effect; the odds ratio for higher catches is nearly zero.

The relationships between the vegetation density or coverage and activity for the individual species tested appear to contradict species totals for the treatments. In this study, this is probably the result of species specific habitat preferences, and sparse data for each species. Twice as many *C. soldalis* were trapped on 2-year burn plots than on the other treatments, yet the regression model predicts greatest activity for this species on sites with higher overstory and sapling density. Estimates for total beetle activity suggest an inverse relationship between herbaceous vegetation and beetle activity; yet nearly twice as many Carabids were trapped on the 2-year burn treatments, which had the highest average and total herbaceous ground flora coverage. This disparity may be partly due to low beetle catches during each trapping period. SAS Logistic procedures require that a majority of the observations in each data class have counts greater than 5 for best performance, yet this condition was not easily met in my study.

Regression models for *P. stygicus* suggest a positive relationship with sapling, seedling and woody ground flora density. The largest number of this individuals of this species were trapped on 2-year burn plots, where herbaceous coverage was highest, and other vegetation variables lowest. Six-year burn plots had the highest average coverage by woody ground flora, but the lowest beetle activity. Simple examination of the data indicate that slightly more than

half of the *P. stygicus* were trapped on plots with woody ground flora coverage greater than 10 percent. Although most of the *P. stygicus* were trapped on 2-year burn plots, 61 beetles were caught in control plots, hence the relationship with seedling and sapling density.

Several explanations are possible. For total Carabid data, the predicted relationship may reflect the habitat preferences of the most active species trapped: *P. stygicus*, *T. vulpeculus*, *C. soldalis*, and *P. mutus*. Regression models for these species all indicated negative relationships between activity and herbaceous vegetation coverage, or stronger relationships with woody vegetation components.

Logically, a great deal of variation in microsite preference should exist for the 45 species trapped. This variation may thwart attempts to associate activity with one or a few common vegetation variables. While *P. stygicus* is described as characteristic of moist forest sites in Lindroth's (1969) classification, it is possible that the species is fairly insensitive to variation in vegetation characteristics, given a uniform overstory. The crudely 3-dimensional measurement of vegetation coverage may not adequately reflect important habitat characteristics.

Habitat suitability for insects is clearly affected by vegetation structure. The availability of suitable microsites for habitation by herbivores may be positively related to floristic heterogeneity, patchiness of vegetation, and plant architecture (Southwood et al. 1979; Schowalter 1986; Lawton 1983; Lawton and Schroder 1977) or may simply be correlated with other relevant habitat variables influencing species abundance. Murdoch (1972) found that Homopteran species diversity was correlated with plant structure and diversity, although others have found no significant correlation with vegetation parameters (Hawkins and Cross 1982). Changes in availability of cover and density of vegetation following fire may provide protection from predation for herbivores and Carabids from predators. McCoy (1987) observed that entomophagous reptile and amphibian abundance was negatively correlated with ground cover density in periodically burned sandhill sites and unburned areas. Abundance of four species of Carabid beetles common to sandhill sites was positively related to density of vegetation cover (>10 cm) and vegetation density at ground level (<10 cm) in the same study. At least one of these four species is known to be consumed by lizards on the site from studies of gut contents. Drastic reductions in vegetation cover and density following more severe burns may expose invertebrates to greater rates of predation (Anderson et al., 1989). Little is known about the rates or factors affecting predation on ground beetles.

Some arthropod species activity may be related to responses of certain key plant species that are favored by fire. Hansen (1986) observed higher abundance of leafhoppers on burned shrub-dominated range sites compared to unburned sites, possibly related to re-growth of preferred browse species. Paradoxically, parasitic wasps including ichneumonids, brachonids, and mutillids were attracted to burn sites in the same study, despite an absence of flower food sources, and presumably, a lack of potential hosts. Changes in the abundance of grass- and forb-eating grasshopper species in burned and unburned prairie sites was related to shifts in the dominance of grass species on prescribed burned areas (Evans 1984, Kucera and Koelling 1964). Other species may be attracted to charred wood and debris created by fire. Richardson and Holliday (1982) noted that *P. adstrictus* occurred most frequently on sites with greater amounts of fallen trees and rotting logs, characteristics most common on burned spruce sites.

Activity of the most abundant species may simply reflect changes in prey density, or changes in nutritional quality of vegetation on burned sites. Holmes et al. (1993) related Carabid beetle distribution to environmental variables including nutrient status, saturation of substrates, altitude, and grazing in a large scale survey of peatlands in England. Higher foliar concentrations of Nitrogen may temporarily result following litter reduction during light burns. Foliar N concentration was positively related to phytophagous insect survival in Minnesota jack pine stands (McCullough and Kulman 1991). A short-term fertilization effect following light burning may have favored higher phytophagous prey populations; yet more severe fires are likely to reduce N availability through volatilization and soil leaching on sandy sites. Light fires may also speed litter breakdown or make conditions more favorable for saprophages and mycophages by virtue of its spotty coverage and partial consumption of large debris. Removal of the dry needle litter and partial consumption of the fermentation layer may result in rapid breakdown of remaining substrates due to greater insolation and surface temperatures. Metz and Dindal (1975) reported that the greatest number of Collembola occurred in the F and H layers of unburned and periodically burned (5- to 8- year intervals) southern pine stands. In turn, this may attract Carabids.

Activity is unlikely to be influenced by changes in the abundance of any single prey species, however. Although Carabids have generally been considered predatory, several authors have suggested phytophagy under certain conditions for many species (Johnson and Cameron 1969, Hengeveld 1980). Loreau (1982) suggested strong polyphagy among small (less than 6 mm) and large (>15 mm) Carabid species and a high degree of adaptability in dietary habits for almost all beetles. Most Carabids are prey on primary consumers, chiefly on myco- and saprophagous species. These include Oligocheta (Lumbricidae and Enchytraeidae), snails and slugs, oribatid mites, Collembola, and nematoceran Diptera (Loreau 1982). Carabids tend to be opportunistic in their dietary habits; Loreau reported that single species formed no more than 15% of any beetle's diet in laboratory studies. Only the medium-sized (6-10 mm) beetles in Loreau's study exhibited a high degree of specialization on Collembola and mites. Larger beetles (>10 mm) formed the majority of the Carabids trapped in this experiment.

Structure and density of vegetation layers may also affect the favorability of habitat microclimate for invertebrates. Thiele (1977) suggested that Carabids are quite sensitive to differences in microclimate between sites. Vegetation structure and density may moderate humidity and temperature extremes in microsites (Gieger 1966, Richardson and Holliday 1982). Neve (1994) found *Carabus* spp. activity positively correlated with mean daily temperature in

European beech-dominated forests. Activity was most closely related to maximum daily temperatures and day/night contrasts in temperature. Humidity also appeared to be positively related to activity (Thiele 1977, Neve 1994) but has been discarded as a variable in other studies (Desender 1983). The complex interaction of edaphic, microclimatc, and vegetation factors make the isolation of specific variables responsible for species distribution difficult (Richardson and Holliday 1982, Holmes et al. 1993).

Species Diversity

Prescribed burning clearly led to increased beetle species diversity on burned plots relative to unburned areas in my study. Burn treatments consistently had greater species richness than control treatments, according to six common diversity indices and formal model fitting (Table 22). Measures differed on ranking the diversity of the two burn treatments, however, according to the diversity element each reflects.

Overall, pitfall trapping produced a total of 45 species over the two years of the study (Table 17). Thirty species were collected in 1994, 39 in 1995. More locally 'rare' species were collected in 1995; 10 species were represented by one individual, whereas single individuals of only four species were collected in 1994. All of the species captured have relatively wide geographic ranges, and are relatively common in the United States, according to Lindroth (1969). Catches also included three "introduced" species from Europe; *Amara familiaris* Duftschmid, *Harpalus puncticepts* (Stephens), *and Pterostichus melanarius* (Illiger). One species trapped, *Amara impuncticollis* (Say), has a holarctic range.

Table 22. Diversity indices by year for burned and unburned treatments.

Diversity Measure	1994			1995		
	Control-no burns	6-year	2-year	Control-no burns	6-year	2-year
Species richness (S)	18	25	27	24	27	35
No. of Individuals	233	295	444	177	140	378
Maraglef	3.2	4.2	4.3	4.4	5.3	5.7
Berger-Parker (N)	2.1	3.1	3.2	2.9	4.4	4.3
Shannon (H')	1.9	2.3	2.4	2.4	2.8	2.7
Shannon evenness (E)	0.68	0.72	0.72	0.76	0.84	0.76
log series (α)	4.6	6.5	6.3	7.5	9.9	9.4
log series α from William's nomograph	5.5	6.0	6.5	8.0	9.5	9.0
log normal (λ)	34.9	50.2	50.1	58.2	68.2	73.6

Burn treatments consistently had greater species richness than unburned plots, as measured by Maraglef's index, which measures the number of species present in a community relative to the total number of individuals sampled. Two-year burn plots were more diverse than 6-year burn plots. This index is highly sensitive to sampling bias, however (Magurran 1988).

The Berger-Parker index (D) shows a higher degree of dominance by the most common species in the control treatments in both years relative to burn treatments. This index also shows higher beetle diversity on burn treatments. Six-year burn treatments had higher species dominance and lower diversity than 2-year burn treatments in 1994; however, the opposite prevailed in 1995. The Berger-Parker index is relatively independent of sample size; however, it can be biased by fluctuations in the abundance of the most common species and this is most likely the case with 1995 six-year burn data.

Species abundance indices also show greater diversity on burned relative to unburned plots, but differ on the relative diversity between burn treatments. Calculations of the log series α indicate greater diversity on 6-year burn treatments in both years, a reflection of the greater number of species with intermediate abundance in that treatment. The log normal λ and Shannon diversity (H') statistics tend to reflect more closely the number of rare species. These measures rated diversity on 6-year burn plots higher than 2-year burn plots in 1994, but lower in 1995.

The Shannon evenness (E) statistic indicates higher diversity on burned compared to unburned treatments due to the equability of species abundance in both years. Differences in burn treatment evenness followed the same pattern described by the log normal λ and Shannon diversity indices.

Pair-wise comparisons of Shannon diversity (H') estimates were conducted using t-tests (Table 23). Differences between estimates for burn treatments and control treatments were highly significant (Pr > .001) in both years. Diversity estimates were not significantly different between burn treatments, however.

Given the similarity of diversity index measurements between 2-year and 6-year burn plots, the safest conclusion would be to reject only part of the third null hypothesis; while burning clearly increased beetle diversity in this study, the diversity measures employed give contradictory results when ranking diversity between frequently and periodically burned treatments. I believe this discrepancy reflects sensitivity of the indexes to small sample sizes on the 6-year burn plots in 1995 and changes in the abundance of the most commonly trapped species, *P. stygicus*. This bias probably obscures diversity patterns between the two treatments; 2-year burn plots contained more rare species and greater absolute species richness than plots burned every six years. In light of these observations, I conclude that Carabid diversity does increase with the frequency of prescribed burning.

The log series had the best fit of the four common species abundance distribution models for all three treatments in 1994 and 1995 ($Pr > \chi^2 > 0.05$) (Table 24). The log normal series also fit treatments well, with the exception of control plots in 1995. Visual inspection of the predicted and observed species

Table 23. T-tests[1] for Shannon diversity index estimates by year and burning treatment.

	1994			1995		
Shannon T-Tests	**Control- no burns**	**6-year**	**2-year**	**Control- no burns**	**6-year**	**2-year**
Shannon (H')	1.9	2.3	2.4	2.4	2.8	2.7
variance	0.007	0.005	0.003	0.007	0.007	0.003
t-statistic	3.09	0.69	4.04	2.92	0.45	2.96
df	492	602	433	314	277	337
	[2]	NS	[3]	[2]	NS	[2]
	A	B	B	A	B	B

[1] means followed by the same letter are not significant at $\alpha = 0.05$;

[2] significant at alpha = 0.01

[3] significant at alpha = 0.001

Table 24. Goodness-of-fit summary ($\alpha = 0.05$) for four common species abundance models.

	1994			1995		
Fit of Models	**Control no burns**	**6-year**	**2-year**	**Control- no burns**	**6-year**	**2-year**
Geometric	no	no	no	no	yes	no
Log series	yes	yes	yes	yes	yes	yes
Truncated Log Normal	yes	yes	yes	no	yes	yes
Broken Stick	no	no	no	no	yes	no

abundance shows that the log normal series predicts more intermediate and highly abundant species than observed on unburned plots in 1995 ($Pr > \chi^2 > 0.05$). Data for the 1995 six-year burn plots fit all four models adequately; this is undoubtedly due to small sample bias (n = 140). The geometric series and broken stick model did not fit the data well.

A good fit for the log series model suggests that relatively few factors dominate the ecology of these communities (Magurran, 1988). These factors could include the frequency of prescribed burning and the amount of sunlight reaching the forest floor. The abundance patterns typical of the log series model have also been interpreted to reflect the occupation of niche hyperspace at random intervals by species migrating into unsaturated habitats (Boswell and Patil 1971, May 1975). This model is generally associated with communities in the early to intermediate stages of succession; those with relatively few species and limiting environmental factors.

Although the log normal model also fit most treatments well, the abundance distribution predicted did not differ significantly from the log series model ($Pr > \chi^2 > 0.05$) for all but the 1995 6-year burn plots. Six-year burn plot estimates in 1995 differed chiefly in the number of species predicted to have the highest abundance. Magurran (1988) recommended that the log normal series be fitted only for continuous data, although it is frequently used for abundance.

The observation of generally higher diversity on frequently burned plots over unburned treatments in my study is consistent with the results of few other studies on prescribed burning. Metz and Dindal (1975) reported increased

diversity of Collembola species on periodically burned plots as calculated by a modified Shannon-Wiener index. Annually burned plots exhibited decreased Collembolan diversity in the L layer of the forest floor but increased diversity in the F + H layers, compared to control plots.

Other researchers found that controlled burns produce little change in insect diversity. Relative to pre-burn levels, consecutive prescribed burns in Australian eucalypt forests produced no significant differences in insect taxa species diversity, richness, and evenness following the first burn (Collet et al. 1993). Species diversity was higher following a second burn conducted 3 years later, primarily due to an increase in species evenness, rather than an increase in species richness. McCoy (1987) noted little difference in Carabid species richness on periodically burned and unburned sandhill plots in Florida. In wildfire studies, several researchers have reported no significant effects on species diversity, evenness, and, in some cases, abundance of Carabid communities following intense burns. Holliday (1992) noted no differences between species evenness and species diversity as measured by α in mature stands and burned sites in two boreal forest types over a 10-year period following wildfire. Greenberg and Thomas (1995) reported no significant differences between diversity, evenness and abundance of Coleopterans in a study comparing effects of high intensity fire and salvage logging to other harvesting disturbances and undisturbed forest sites in Florida sand pine scrub, 5 to 7 years after disturbance. By contrast, Winter (1980) noted greater numbers of species and individuals in young pine stands for 1 to 3 years after wildfire in Germany.

Arthropods inhabiting non-forested ecosystems exhibit varied responses to prescribed burning. Anderson et al. (1989) noted that grasshopper abundance and diversity were unaffected by burning in prairie grass ecosystems, while abundance of other insects were depressed for one year, recovering rapidly to pre-burn levels thereafter. Evans (1988) found that species richness of grasshoppers was greater on infrequently burned or unburned sites than annually or biennially burned prairie grass sites. In addition, grasshopper species richness was found to be positively correlated with local plant species richness and diversity. Bock and Bock (1991) observed a one-year decrease in grasshopper abundance following wildfire in an Arizona grassland. This trend was attributed to direct fire-caused mortality and a reduction in grass cover during the first year following the fire. Johnson (1995) reported greater spider densities and species richness in annually burned vs. unburned wetlands dominated by prairie cordgrass (*Spartina pectina*). Cessation of burning in restored tall grass prairie in Wisconsin caused a reduction in soil arthropod diversity and abundance, however (Lussenhop 1976). Lussenhop suggested that the decline may have been due to reduced root biomass productivity and detritus following cessation of burning.

Beetle diversity changes following prescribed burning may be linked closely to changes in vegetation diversity. Parallel patterns of diversity following disturbance have been observed between insect fauna and flora communities.

Southwood et al. (1979) and Brown and Southwood (1987) noted similar trends in macrofaunal diversity and floral diversity during old-field succession to deciduous forest. Species abundance and richness increased with successional age, while diversity as measured by α rose for one year, then remained stable. The authors attributed initial increases in invertebrate diversity to increasing plant taxonomic diversity, while subsequent stabilization was attributed to increasing spatial diversity of flora, which compensated for the effects of declining plant taxonomic diversity. During colonization of mining spoils by forests, researchers noted a weak trend toward increasing Carabid species abundance and diversity with increasing successional age in one study (Neumann 1971), but not in two others (Mader 1986, Hejkal 1985).

Harvesting disturbances appear to produce opposing patterns of Carabid diversity. Increased diversity of Carabid species assemblages on clear-cut relative to uncut forest sites was noted by several researchers (Niemala et al. 1993, 1990; Jennings et al. 1986). Lenski (1982) reported a significant increase in within-genus species diversity after clearcutting in Appalachian oak-hickory forests. Carabid beetle populations showed greater overall abundance and species richness than undisturbed mature stands in clearcut boreal pine-spruce forests in Canada (Niemala et al. 1993). By contrast, experiments with strip clearcutting in dense spruce-fir stands in Maine showed lower abundance in clearcut strips and uncut dense stands compared to uncut residual strips (Jennings et al. 1986). Species diversity was greater in strip clearcut stands than in dense undisturbed stands, however. Studies in dry site pine stands in

Poland also found greater diversity and dominance in regenerating stands (Szyszko 1987).

Several theories regarding arthropod responses to community disturbance have been advanced to explain changes in species diversity. According to interspecific competition theory, species diversity should decrease in the absence of disturbance, as competitively superior species exclude inferior competitors (Dayton 1971; Sousa 1979). Lenski (1982) and Loreau (1986) consider interspecific competition to be a driving force in the structuring of Carabid beetle assemblages.

A contrasting theory advanced by Liebherr and Mahar (1979) contends that arthropod diversity and abundance are more closely related to vegetation structure and habitat complexity or heterogeneity than to the frequency and magnitude of disturbance. They reported greater beetle diversity and higher abundance in more successionally advanced, structurally diverse stands during a survey in Michigan dry-site oak forests. Species dominance decreased with canopy closure, increased understory development, and floristic diversity. Insect species diversity may be influenced by plant taxa diversity, as well as spatial and architectural complexity in a habitat (Southwood et al. 1979, Schowalter 1986; Lawton 1983).

Important mechanisms governing insect diversity responses to disturbance may include interspecific competition, size of the potential colonist pool for given sites, and the rate of change in plant species diversity following fire. Holliday (1992) reported estimates of species gain and loss for burned and unburned boreal forest sites in Manitoba following an intense forest fire. Lower beetle abundance on burned or early successional stage sites throughout the experiment period were attributed to lower rates of species gain on burned sites. Burned and unburned plots appeared to have similar rates of species loss. Unfortunately, little is known regarding Carabid species colonization and extirpation rates in temperate forest regions.

Qualitative aspects of species diversity

The results of my study do not indicate any dramatic changes in species gain or loss, nor can they be estimated given only two years sampling data. Several new species to the site were encountered in 1995 compared to 1994 collections, but it is not clear whether this represents colonization or merely sampling variability.

Most of the species I captured are typical of dry, sandy environs, and about one third are typical of forests, according to Lindroth's classification (1969). Ten of the species collected in the Tribe Harpalini are customarily found in open, grassy meadow habitats, usually on dry sandy soils. The three *Amara* species collected have been observed by other researchers on dry sandy sites. *Cymindis americanus* is an almost exclusively xerophilous species, occurring on open sandy country with sparse vegetation, but also among dead leaves at the edges of forests. Most of the *Harpalus* spp. sampled were trapped on burn treatments. Habitat preferences of 10 other species included mesic deciduous forests; *Agonum melanarium*, *A. ferreum*, *Chlaenius tricolor tricolor*,and *Platynus hypolithos* were most typical of habitats near streams or water.

Dicaelus elongatus has been found in both dry hillsides and among moist leaves in swamps. Fourteen of the species trapped are typical of forests, only 7 of which inhabit dry woodlands. Unfortunately, little is known about the variation in habitat preferences for these species; descriptions of the ecology for most species is anecdotal. Lindroth's classification (1969) often lists several microsites for each species, sometimes contradictory. The four most abundant species on control plots included *Carabus goryi*, *Pterostichus stygicus*, *Synuchus impunctatus,* and *Platynus hypolithos*, all species typically found in mesic forests or moist microsites. *Pterostichus stygicus*, *S. impunctatus*, *and C. goryi* are also among the most abundant species on 2-year burn plots, along with *P. mutus*, a species typical of xeric open sites.

Although diet habits of Carabids are not well known, most of the species trapped are considered carnivorous, although some tribes of Carabidae are known to be polyphagous. Three large-bodied species, *Dicaelus elongatus*, *Sphaeroderus stenostomus lecontei*, and *Carabus goryi*, are known to prey on large insects, including snails and caterpillars. More *S. stenostomus lecontei* were trapped on control and 6-year burn than on 2-year plots, while *C. goryi* was caught most frequently on burn treatments. Members of the *Notophilious*, *Agonum*, and *Galerita* genera are also decidedly carnivorous.

Under specific conditions, even predaceous genera, including *Carabus* and *Pterosticus*, have been known to search for food and water supply in fresh or rotten fruits, or in green parts of plants (Lindroth 1949, Johnson and Cameron 1969). Johnson and Cameron (1969) observed phytophagous behavior among generally predaceous members of the *Pterostichus* and *Agonum* genera. Species of the Harpalini have generally been considered to have herbivorous or opportunistic predaceous food habits; these were found most frequently on burn plots where herbaceous ground floral coverage was greater. *Harpalus* species are known to alternate from predation to seed eating (Brandmayr 1990). True spermophagus Carabids, belonging to the Amarini, Zabrini, and Harpalini tribes, generally subsist from the small fruits of herbaceous plants, such as are found in the Graminaceae, Umbelliferae, Cruciferae, Labiatae, and Compositae (Brandmayr 1990). Some species, including *Synchus impunctatus* Say (Manley 1971) and *Harpalus pennsylvanicus* (Kirk 1972) are known to store seeds in burrows as adults or larvae. In diet studies, *Harpalus honestus* larvae were reported to exhibit rapid development solely on seeds from *Taraxacum spp.* (Brandmayr 1990). Therefore it seems likely that greater herbaceous plant community development on 2-year burn plots in my study might be related to the observations of higher beetle activity.

Chapter 4

CONCLUSIONS AND SUMMARY

The work reported in my thesis tests a global operating hypothesis that the responses of an insect community, as represented by Carabid beetle fauna, to controlled, low intensity fire can be explained more completely by the fire-induced vegetation characteristics of the site, rather than by fire frequency. This broad concept was examined by focusing on three corollary hypotheses:

1. Total Carabid activity increases with frequency of burning, and diminishes with time since disturbance.
2. Carabid activity is negatively related correlated with the density of woody understory vegetation (saplings and seedlings), but is unrelated to ground flora coverage.
3. Carabid species diversity decreases with the frequency of fire, and increases with the time since disturbance.

Acceptance or rejection of the appropriate null hypothesis for these three theories could provide insight into the causal relationship between insect fauna response to periodic disturbance.

Results of this experiment suggest that Carabid beetle activity, as evidenced by their abundance in traps, does increase with the frequency of prescribed under burning in mixed pine stands. In both years of this study, plots burned every 2 years showed significantly higher activity for beetles than unburned plots. Likewise, higher levels of activity on plots burned every 6 years than on control plots were seen during 1994, but not during the following year. Thus it is possible to conclude that Carabid activity does not decrease with frequency of burning. If anything, these data suggest that activity diminishes with time since disturbance.

The Carabid fauna of burned plots was significantly more diverse than unburned plots in a widely spaced, mixed pine stand. The ranking of diversity between the two burn treatments varied according to which element of diversity each model weighs. T-tests of the Shannon Diversity Index revealed significant differences between burned and unburned sites, but not between 2- and 6-year burn plots. Nevertheless, it is possible to conclude that Carabid species diversity does not decrease with increasing fire frequency in this pine ecosystem.

The evidence neither supports the hypothesis that Carabid diversity is inversely related to time since disturbance, nor rejects it. Diversity estimates were very similar for plots burned at 2- and 6-year intervals. The data suggest that biennially burned plots may have greater abundance and species richness, and in some years lower species dominance. Despite having the lowest activity in 1995, diversity was higher on 6-year burn plots than 2-year plots according to the Berger-Parker, Shannon diversity and evenness, and the log series α. This relationship probably reflects greater evenness of species abundance (lower

species dominance) on the 6-year burn plots in 1995, although the small sample size may have imparted some bias. This problem may be solved only with several more years of sample data, more observations per sample date, or longer trapping periods.

Attempts to explain variation in beetle activity using vegetation characteristics produced marginal results and indicated complex relationships. Total Carabid activity was negatively related to seedling and sapling density, and unrelated to ground flora coverage, albeit with very low probability estimates. Analysis of count data for four common species was not helpful. Activity of *P. stygicus* was positively related to seedling and sapling density, and woody ground flora coverage, although most of these beetles were trapped on 2-year burn plots, where herbaceous coverage was highest, and other vegetation variables lowest. The resulting estimates and predicted relationships have very little predictive weight; probably due to small sample sizes ($N < 150$ for most species). It is also likely that the crudely 3-dimensional measurements used to describe vegetation characteristics, stem density and percent ground coverage by height and dbh class, inadequately characterized habitat elements from an insect's point of view. Some researchers suggest that habitat suitability for insects may be more closely related to vegetation patchiness, floristic heterogeneity, and plant architecture (Southwood et al. 1979, Schowalter 1986, Lawton 1983). Regardless, my results do not clarify how beetle activity is related to vegetation coverage. Unfortunately, this portion of the study was to provide the pivotal evidence for rejection of the global null hypothesis, but this cannot be done. It is clear that vegetation characteristics play an important part in determining beetle activity, but generalizations regarding species-specific activity would be fruitless given the strength of the equations that I have presented.

Many studies have shown detrimental effects on insect fauna from wildfire and prescribed burning. Yet the results of studies involving wildfire may not be accurately compared to the lower-intensity disturbance created by controlled underburning. Earlier prescribed burning experiments cited herein may only reflect the magnitude of disturbance relative to site quality; most of the experiments were conducted in southern U.S. temperate forests on extremely sandy sites. My analysis suggests that controlled low intensity fire, when used for underburning in pine ecosystems on higher-quality sites, may have benign or even positive effects on Carabids and perhaps arthropod communities.

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