

FOREST AGE INFLUENCES OAK INSECT HERBIVORE COMMUNITY STRUCTURE, RICHNESS, AND DENSITY

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Abstract. Plant succession is one of many factors that may affect the composition and structure of herbivorous insect communities. However, few studies have examined the effect of forest age on the diversity and abundance of insect communities. If forest age influences insect diversity, then the schedule of timber harvest rotation may have consequent effects on biodiversity. The insect herbivore community on *Quercus alba* (white oak) in the Missouri Ozarks was sampled in a chronoseries, from recently harvested (2 yr) to old-growth (approximately 313 yr) forests. A total of nine sites and 39 stands within those sites were sampled in May and August 2003. Unique communities of plants and insects were found in the oldest forests (122–313 yr). Density and species richness of herbivores were positively correlated with increasing forest age in August but not in May. August insect density was negatively correlated with heat load index; in addition, insect density and richness increased over the chronoseries, but not on the sunniest slopes. Forest structural diversity (number of size classes) was positively correlated with forest age, but woody plant species richness was not. In sum, richness, density, and community structure of white oak insect herbivores are influenced by variation in forest age, forest structure, relative abundance of plant species, and abiotic conditions. These results suggest that time between harvests of large, long-lived, tree species such as white oak should be longer than current practice in order to maintain insect community diversity.

Key words: chronoseries; community structure; herbivorous insects; Lepidoptera; Missouri; oak; old-growth forest; Ozarks; *Quercus alba*; rotation length; succession; time series.

INTRODUCTION

Forests are subject to natural and anthropogenic disturbances such as fire, wind storms, uprooting and death of individual trees, and timber harvest (Binkley 1999). Although studies of plant succession following these forest disturbances are many (e.g., Lorimer 1980, Hibbs 1983, Reich et al. 1990, Jenkins and Parker 1998, Larsen and MacDonald 1998), there are relatively few studies of animal community responses to plant succession (as noted by Morin 1999). Particularly lacking are replicated studies of changes in insect communities with plant succession. Knowledge of such successional patterns and their underlying causes is important for understanding the forces driving temporal changes in the composition of insect communities. In addition, such knowledge has important implications for forest management. If insect community composition or diversity changes with forest age, short rotation lengths (time between consecutive harvests) may result in the landscape-level loss of unique communities of plants and insects.

Manuscript received 31 March 2005; revised 31 August 2005; accepted 21 September 2005. Corresponding Editor: M. P. Ayres.

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Changes in plant community characteristics driven by architecture or disturbance may influence insect herbivore communities, particularly if herbivores specialize on certain host plant species or on microhabitats provided by a particular plant growth form. Two mechanisms, both related to habitat heterogeneity, suggest that the diversity and abundance of the insect herbivore communities may increase with forest age. First, increasing complexity of plant architecture is associated with higher species diversity of herbivorous insects (Lawton 1983). Older forests may provide more stem diameter size classes and thus, more complex architecture than younger forests. Second, the intermediate disturbance hypothesis predicts that diversity will peak in habitats with intermediate disturbance levels (Connell 1978). Some disturbance types, such as wind damage, may differentially affect older more than younger forests because the risk of wind damage to a tree or a stand increases with age (Oliver and Larson 1996). Tree falls from wind damage in older forests may result in a disturbance regime that is intermediate between that of the most recently cut, very young forests and medium-aged forests, which are less vulnerable to wind damage than older forests. Finally, time since disturbance, disturbance magnitude, and structure may influence plant communities because of plant-specific differences in life span and shade tolerance.

TABLE 1. Site information.

Site	Abbreviation	Description	Latitude north	Longitude west
1	BS	Big Spring Natural Area, Ozark National Scenic Riverway	36°56'38"	90°59'34"
2	CRNA	Current River Natural Area, Pioneer Forest	37°15'13"	91°16'4"
3	D120	Mark Twain National Forest, Doniphan/Eleven Point Ranger District, Compartment 120	36°49'6"	91°4'56"
4	DRE7	Current River Conservation Area, Paint Rock State Forest, Missouri Ozark Forest Ecosystem Project, Site 5	37°10'41"	91°1'58"
5	DR	Current River Conservation Area, Deer Run/Paint Rock State Forest, Missouri Ozark Forest Ecosystem Project, Sites 5 and 6	37°10'9"	91°1'54"
6	P9	Mark Twain National Forest, Potosi Ranger District, Compartment 9	37°59'46"	91°3'27"
7	P13	Mark Twain National Forest, Potosi Ranger District, Compartment 13	37°59'41"	90°57'32"
8	P40	Mark Twain National Forest, Potosi Ranger District, Compartment 40	37°57'14"	91°3'19"
9	SBSP	Sam Baker State Park, Mudlick Mountain Natural Area	37°16'29"	90°31'25"

† Estimated age of sampled stands.

‡ Source of age estimate.

An additional factor that must be taken into account for understanding the effects of forest succession on insect communities are the habitat requirements of the insect taxa under consideration. Previous studies examining forest age and insect diversity have found disparate patterns depending on the requirements of the focal taxa for particular habitats and host plants. Heyborne et al. (2003) and Inoue (2003) found higher insect diversity in younger forests due to relatively large numbers of species specializing on early plant successional stages. Conversely, Grove (2002) and Maeto et al. (2002) found a positive correlation between forest age and beetle diversity, due to the requirements of many specialist species for large trees present only in the later stages of succession. Schowalter (1995), who sampled multiple arthropod trophic levels and feeding guilds on Douglas-fir (*Pseudotsuga menziesii*), found a nonsignificant trend of increasing diversity with forest age.

The objective of the current study was to document characteristics of an herbivorous insect community associated with single deciduous host plant species (*Quercus alba*) over a long time span (300+ year chronoserics) and to relate them to changes in vegetation structure. We sampled insects in multiple stands per forest age, twice during the year and in different microhabitats, allowing us to account for forest age, seasonal effects, and the contribution of slope aspect to the observed patterns. In addition, we related variation in vegetation composition and structure to variation in insect density and species richness. A single previous study (Maeto et al. 2002) has related changes in vegetation structure and species composition as an explanation for the effects of forest age on changing insect communities.

METHODS

Insect surveys were conducted 5–20 May 2003 and 5 August to 5 September 2003. Insects were sampled at

nine sites ranging in age from two years (recently harvested, natural regrowth) to approximately 313 years old in southeastern Missouri, USA (Table 1, Fig. 1; see Plate 1). The nine sites were selected using existing dendrochronological data (stands aged >18 yr) and harvest records (stands aged 2–18 yr) from silviculturalists (Table 1). Slope aspect has been correlated with differences in vegetation (Shifley et al. 2000), insect abundance (Marquis and Le Corff 1997), and wind-throw disturbance (Rebertus and Meier 2001). Therefore, at least four sampling locations from each site were chosen so that two were on north- and east-facing slopes and two were on south- and west-facing slopes. Sampling locations were separated by topographic features, such as ridgetops and ravines, while habitat edges were avoided. At each sampling location, at least six trees were marked (saplings, branches of larger trees) and at least 3000 leaves were sampled. The number of leaves, trees, and sampling locations adequate to assess insect density and richness was established in a previous study (Marquis and Le Corff 1997).

The study host plant, white oak (*Quercus alba*) is a large, long-lived (Burns and Honkala 1990) and abundant tree species in this region, ranking highest in relative density, third highest in relative basal area (Shifley et al. 2000), and highest of five oak species in leaf-chewing insect richness (R. Marquis, *unpublished manuscript*). White oak is an intermediately shade-tolerant tree species present through all stages of Ozark forest succession. It can resprout from stumps after disturbance, persist for up to 90 years in the understory until release by formation of a canopy gap, and often is a dominant canopy tree (Burns and Honkala 1990).

The more than 260 species of leaf-chewing insect herbivores (primarily larval micro-lepidoptera, but also Orthoptera, Coleoptera, larval Hymenoptera, and phas-

TABLE 1. Extended.

Age† (yr)	Source‡	Forest size (ha)	No. stands sampled
122	unpublished tree core data; S. Shifley, <i>personal communication</i>	142	4
313	unpublished tree core data; R. Guyette, <i>personal communication</i>	4	4
18	harvest records, Mark Twain National Forest	64	4
7	harvest records, Missouri Department of Conservation	10	2
49–79	unpublished tree core data; J. Kabrick, <i>personal communication</i>	51	9
111	tree core data, Mark Twain National Forest	59	4
101	tree core data, Mark Twain National Forest	75	4
2	harvest records, Mark Twain National Forest	62	4
223	natural area nomination report (1980), Missouri Department of Natural Resources	283	4

mids) on white oak in Missouri can be identified in situ because researchers have collected, identified, photographed, and reared them for over a decade (Marquis et al. 2006; see Plate 1). Leaf-chewing insects unidentified in the field were individually collected and reared in the lab. During daylight hours, each sapling or tree, the trunk,

associated twigs and branches, and both sides of leaves between ground level and 2.5 m above ground were visually examined. The identity and abundance of all leaf-chewing insects encountered were recorded. Beginning at the base of a selected tree, inspection continued upward 2.5 m until all leaves were examined, or until at

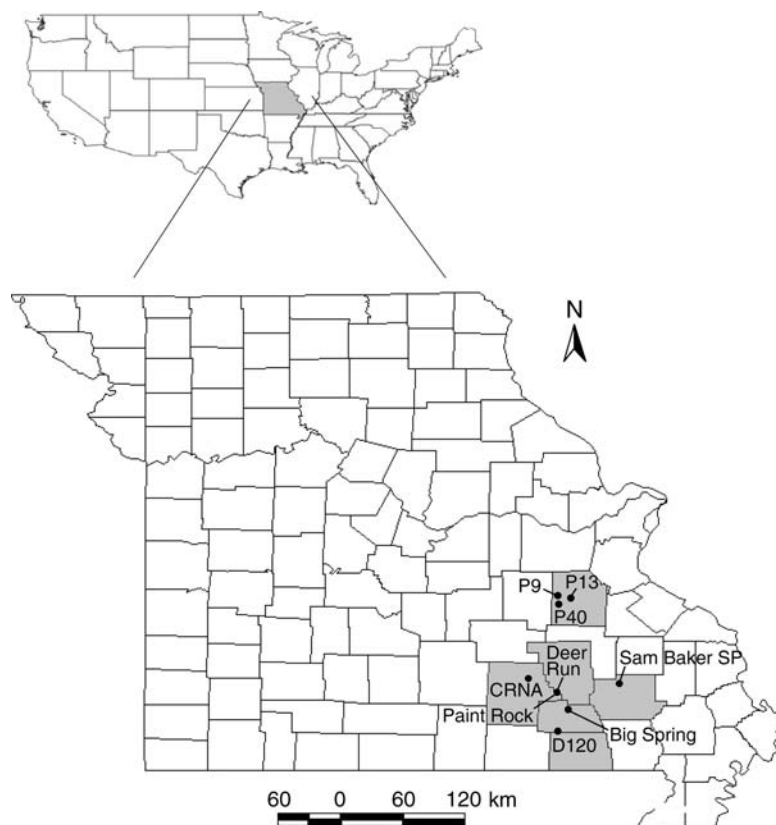


FIG. 1. Study site locations, Missouri, USA. See Table 1 for site coordinates and descriptions.

TABLE 2. Herbivore sampling results.

Location†	Stand, spatial group‡	May 2003		August 2003		Estimated forest age (yr)	Heatload index	Leaf area sampled (m ²)
		Density§	Richness	Density§	Richness			
P40	3, b	2.81	0.72	8.78	0.87	2	0.02	32.00
P40	4, b	4.31	0.64	10.80	0.78	2	0.20	34.55
P40 ave., low htld #		3.56	0.68	9.79	0.83	2	0.11	33.28
P40	2, a	1.73	0.48	5.34	0.70	2	0.65	27.14
P40	1, a	2.26	0.48	5.67	0.68	2	0.80	29.26
P40 ave., high htld #		1.99	0.48	5.51	0.69	2	0.73	28.20
DRE7	DRE36, a	4.77	1.12	3.57	0.77	7	0.01	9.85
DRE7	DRE45, a	4.74	0.85	3.15	0.95	7	0.99	10.55
D120	4, b	3.73	0.98	6.79	1.19	18	0.03	19.31
D120	2, a	3.09	3.09	5.10	0.82	18	0.07	21.98
D120	1, a	7.25	1.36	7.31	0.96	18	0.34	17.66
D120	3, b	3.99	1.20	5.10	0.96	18	0.53	20.78
D120 ave., low htld #		4.52	1.09	6.08	0.98	18	0.24	19.93
DR	DRE31, b	7.05	1.42	8.20	1.43	49	0.00	16.17
DR	DRC30, a	11.09	2.67	2.79	0.48	65	0.07	9.38
DR	DRC23, a	10.97	1.83	4.22	1.01	71	0.60	13.13
DR	DRC6, b	9.50	2.15	2.44	0.95	74	0.11	8.85
DR	DRC14, a	12.73	3.02	3.03	0.95	79	0.20	6.29
DR ave., low htld #		10.27	2.22	4.14	0.96	68	0.19	10.76
DR	DRE27, b	8.02	1.58	5.76	1.60	59	0.76	15.20
DR	DRC50, a	6.52	1.12	4.93	1.13	60	0.89	15.19
DR	DRE43, b	5.13	1.28	4.63	1.25	65	0.76	10.14
DR	DRC61, b	6.60	2.71	2.50	0.77	71	1.00	5.91
DR ave., high htld #		6.57	1.67	4.46	1.19	64	0.86	11.61
P13	3, a	2.47	0.85	5.36	1.20	101	0.11	25.91
P13	1, a	2.39	0.65	5.96	1.01	101	0.19	30.55
P13 ave., low htld #		2.43	0.75	5.66	1.11	101	0.15	28.23
P13	4, b	2.32	0.76	5.59	0.96	101	0.77	30.23
P13	2, b	2.46	0.64	6.37	1.01	101	0.85	29.69
P13 ave., high htld #		2.39	0.70	5.98	0.99	101	0.81	29.96
P9	2, a	3.66	1.14	9.25	1.24	111	0.05	21.84
P9	3, b	1.78	0.57	5.80	0.96	111	0.12	26.40
P9 ave., low htld #		2.72	0.86	7.53	1.08	111	0.09	24.12
P9	1, a	5.31	1.29	3.32	0.96	111	0.96	18.65
P9	4, b	1.94	0.65	2.16	0.86	111	1.00	23.20
P9 ave., high htld #		3.63	0.97	2.74	0.91	111	0.97	20.93
BS	4, b	4.30	0.65	5.78	0.61	122	0.30	30.95
BS	2, a	4.41	0.73	7.28	0.77	122	0.41	24.71
BS	1, a	5.96	0.79	6.66	0.70	122	0.46	31.54
BS	3, b	2.60	0.58	4.77	0.61	122	0.51	34.57
BS ave., low htld #		4.32	0.69	6.12	0.67	122	0.42	30.44
SBSP	1, a	5.76	1.15	8.39	1.47	223	0.04	15.61
SBSP	4, a	4.19	1.74	6.79	1.18	223	0.13	12.66
SBSP ave., low htld #		4.98	1.45	7.59	1.33	223	0.08	14.14
SBSP	3, b	4.26	0.78	4.15	0.88	223	0.84	19.26
SBSP	2, b	4.76	1.24	3.62	1.45	223	0.99	9.67
SBSP ave., high htld #		4.51	1.01	3.89	1.17	223	0.92	14.46
CRNA	4, a	7.43	1.09	9.21	1.39	313	0.00	20.19
CRNA	2, b	6.99	1.04	9.96	1.09	313	0.23	20.18
CRNA	1, a	6.54	1.37	12.19	1.25	313	0.34	16.82
CRNA	3, b	5.73	0.89	9.75	1.08	313	0.54	25.84
CRNA ave., low htld #		6.67	1.10	10.28	1.20	313	0.28	20.76

† Location = site code (Table 1).

‡ Stand = sampling location, shared code = spatial group.

§ Density = no. insects/m² leaf area sampled.|| Richness = no. insect species/m² leaf area sampled.

htld, heat load.

least 600 leaves per tree were sampled. The southernmost sites were sampled before the northern sites for each sampling period. During the second sampling period, all leaves sampled were tallied by tree. The same trees were examined for each sampling period, except for one location at the site Potosi 9 (P91), where a new location was selected because of nearby timber harvest activity.

A vegetation survey for the forest stand surrounding each insect sampling location was conducted 2–29 June 2003. Stem basal area per unit land area was estimated by tree species and by size class using the point-sample Bitterlich method, applied with a 10 basal area factor wedge prism (Husch et al. 1982, Hebert et al. 1988). Slope aspect was determined using a compass, and

percentage of tree canopy cover was estimated using a canopy tube (Grabner 2000) at four locations 10 m from a selected focal tree (one upslope, one downslope, and two at the same elevation as the focal tree but on opposite sides). Vegetation of the sites DRE7 and DR was surveyed between September 2001 and April 2002 (Shifley et al. 2000).

Total leaf area sampled per stand was estimated from the physical count of sampled leaves for each stand multiplied by 58.7 cm², the average understory leaf area (one side) for *Q. alba* in the Missouri Ozarks (Le Corff and Marquis 1999). Three trees from the P40 site, sampling location 1, were excluded from all analyses because the leaf counts greatly exceeded the target of 600 leaves per tree. Heat load index (McCune and Keon 2002) was calculated as $(1 - \cos[\theta - 45])/2$, where θ is the slope aspect (degrees east of north). This equation transforms slope aspect to a number between 0 and 1, with 0 corresponding to the coolest northeast-facing slope and 1 to the warmest southwest-facing slope. Species richness per leaf area sampled was calculated by summing the total number of oak herbivore species encountered in the sampling location, and dividing by the leaf area sampled in that location (Table 2). Herbivore abundance per leaf area sampled (density) was calculated from the total number of individual organisms counted in the sampling location, divided by the leaf area sampled in that location, and ln transformed for normality. These variables thus relate to the insect's food resource and compensate for variability in total leaf area sampled per location. Unidentified insects (118 individuals, May sampling period; 39 individuals, August sampling period) were included in density measures but were excluded from species richness per leaf area.

The relationship between leaf area, forest age, latitude, and slope aspect on the one hand, and herbivore species richness and herbivore density per leaf area on the other was tested with multiple regression at the site level (PROC REG, type II sums of squares [SAS Institute 2004]), separately for lower heat load index (0–0.64) stands (slope aspect 0–151° and 299–360°) and for higher heat load index (0.65–1) southwest-facing stands (slope aspect 152–298°). Possible changes in herbivore community structure with forest age were analyzed with nonmetric multidimensional scaling (NMS; Shepard 1962a, b, Kruskal 1964a, b) using PC-ORD (MjM Software Design, version 4.30, Glenden Beach, Oregon, USA). To reduce potential nonindependence of sampling units (stands) but still retain a sufficient sample size to conduct ordinations, nearest stands within a site were combined into one or two groups (spatial groups), and their values averaged. This resulted in 17 sample units total for all ordinations. The within-site distance between centroids of spatial groups was 587 ± 340 m (mean \pm SE, $n = 8$). Neighboring stands that were averaged to form spatial groups share the same letter following the comma after the stand

designation in Table 2. Insect ordinations were performed separately for May and August herbivore communities, using the Sørensen distance measure and herbivore density for each species, relativized by the maximum average density in each sample unit, to allow comparison among sample units. Rare species were excluded to prevent disproportionate effects on results. As a result, only those species comprising the top 95% of all individuals for each sampling period were included.

Vegetation data also were analyzed with NMS, using the Sørensen distance measure and the basal stem area per unit land area for each plant species, relativized by the maximum average density in each sample unit, to allow comparison among sample units. To include differences in the architecture of the forests, the community was subdivided into size classes (3.8–11.4, 11.4–17.8, and continuing in 10.2-cm increments to 99.1 cm dbh), such that the community matrix consisted of the basal stem area per unit land area covered by each species–size-class combination. Rare species–size-class combinations were excluded, leaving only those combinations that appeared in four or more stands. This analysis was repeated for plant species alone, and for size class alone.

After excluding outlier sample units, optimum dimensionality for plant and insect ordinations was determined through an automated search mode using a random starting configuration, 40 runs with real data, and 50 runs with randomized data. The range of final stress values for all ordinations was 8.8–13.7, stable solutions (instability < 0.00001) were found after 74–110 iterations, and a final solution was found in three dimensions except for the size class ordination where it was found in two dimensions. Randomization tests indicated that low final stress values were not due to chance alone ($P = 0.02$).

Differences among forest age groups (2–18 yr, 49–111 yr, 122–313 yr) in insect and plant communities were tested with multiresponse permutation procedures (MRPP; Mielke 1984, Mielke and Berry 2001) using PC-ORD and Sørensen's distance measure. The step-up Bonferroni procedure (Hochberg 1988) was applied to correct the criteria P value for multiple pairwise comparisons. Insect and plant NMS axes were rotated with respect to forest age, and scores were tested for correlation using multiple regression.

RESULTS

The number of stem diameter size classes present in each site, a measure of structural heterogeneity, increased with forest age (Fig. 2A). Forest age did not explain variation in the number of plant species (49 total sampled) or species–size-class combinations ($P > 0.6$, $r^2 < 0.04$). Basal area of stems taller than 1.4 m (Fig. 2B) increased with forest age, then declined after approximately 200 years. Canopy cover (Fig. 2C) increased sharply in the first 2–18 yr of the chronoserries and changed little thereafter. All three forest age groups had significantly ($P < 0.0001$) dissimilar vegetation com-

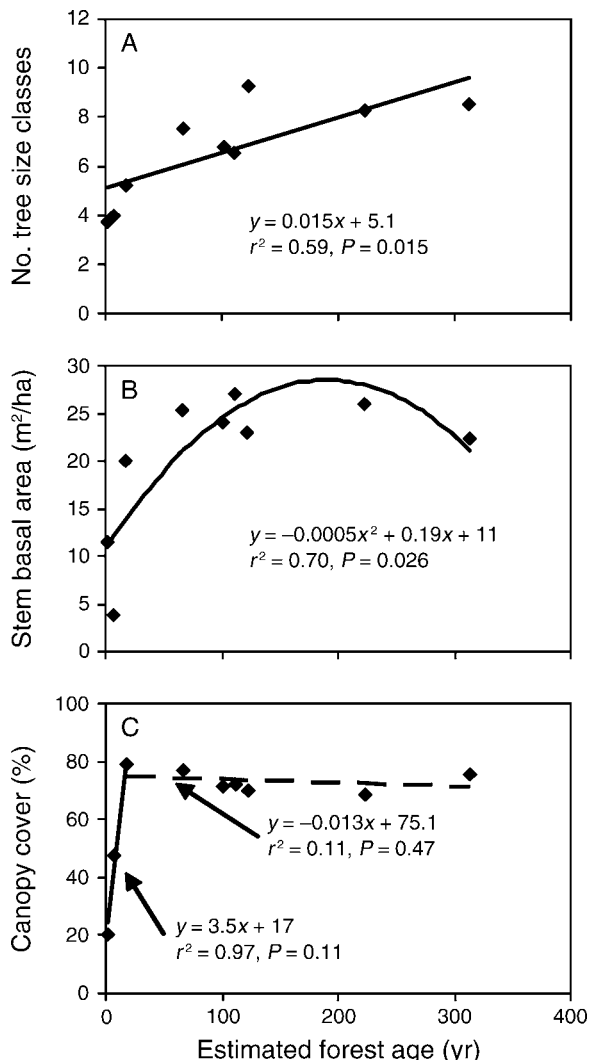


FIG. 2. The effect of forest age on (A) number of size classes, (B) stem basal area/ha, and (C) tree canopy cover.

munities by size class (Fig. 3A) and by combined species–size-class abundance (Table 3). Considering plant species alone, old and young forests were marginally different, while old forests were not significantly different from medium-aged forests (Fig. 3B, Table 3). Old forests were different because of the presence of shade-tolerant (*Acer saccharum*, *Cercis canadensis*) and shade intolerant (*Fraxinus americana*, *Carya tomentosa*) tree species, while young sites were different because of the influence of shade-tolerant (*Morus rubra*, shade-intolerant (*Juglans nigra*, *Pinus echinata*, *Rhamnus caroliniana*), and intermediately shade-tolerant species (*Celtis occidentalis*) (Burns and Honkala 1990). Although the distribution of *Q. alba* among size classes was uneven among sites, with large diameter *Q. alba* weighting older forests (not shown), no age group was weighted by *Q. alba* when considering plant species

alone (Fig. 3B), suggesting similar abundance by basal stem area in all forest age groups.

The total number of herbivore individuals encountered in May was 3216, comprising 79 species; 5007 individuals were recorded in August with 70 species; and 126 species were encountered overall. May insect density correlated negatively with latitude of census site (Tables 4 and 5) for high but not for low heat load index stands. Aside from leaf area sampled, no additional variables

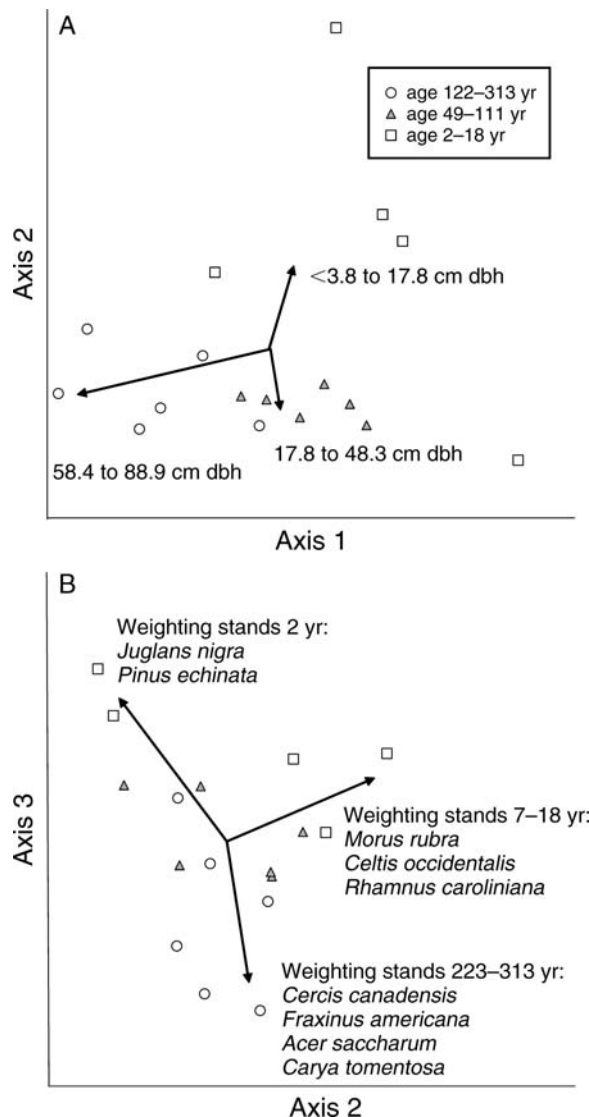


FIG. 3. Nonmetric multidimensional scaling (NMS) scores for vegetation. (A) Ten vegetation size classes of plants taller than 1.4 m, 17 sample units, including size classes occurring in four or more stands. The coefficient of determination for axes 1 and 2 has $r^2 = 0.91$. Differences among age groups are significant ($P = 0.0002$). Vegetation size classes weighting the stand groups are listed. (B) Twenty-seven plant species (of 49 encountered), 17 sample units, including species occurring in four or more stands. The coefficient of determination for axes 2 and 3 was $r^2 = 0.72$. Plant species weighting the stand age groups are listed.

TABLE 3. Multi-response permutation procedures (MRPP) results based on Sørensen distances for herbivore and vegetation communities.

Community	Group, by forest age											
	Old vs. medium			Old vs. young			Medium vs. young			All groups		
	<i>T</i>	<i>A</i>	<i>P</i>	<i>T</i>	<i>A</i>	<i>P</i>	<i>T</i>	<i>A</i>	<i>P</i>	<i>T</i>	<i>A</i>	<i>P</i>
Herbivores												
May	-1.68	0.039	0.063†	-2.98	0.078	0.010*	-2.05	0.051	0.036†	-3.48	0.071	0.002*
August	-3.12	0.070	0.005*	-2.73	0.071	0.011*	-1.52	0.032	0.075†	-3.60	0.072	0.001*
Vegetation												
Species–size class	-2.9	0.048	0.006*	-4.09	0.066	0.0006*	-2.35	0.044	0.016*	-4.73	0.067	<0.0001*
Species only	-1.72	0.035	0.058	-2.45	0.055	0.019†	-0.12	0.004	0.376	-2.01	0.041	0.037*
Size class only	-4.11	0.135	0.003*	-4.13	0.155	0.003*	-4.34	0.174	0.003*	-6.41	0.192	<0.0001*

Notes: Key for column headings: *T*, separation test statistic; *A*, chance-corrected within group agreement.

* Statistically significant at $\alpha = 0.05$; † Statistically significant at $\alpha = 0.10$ (multiple comparisons were evaluated by Hochberg [1988] step-up Bonferroni correction).

were significant predictors of May insect species richness or density. After accounting for variation in leaf area sampled, August herbivore species richness and density correlated positively with forest age (Fig. 4A and B, Tables 4 and 5), and August herbivore density correlated negatively with heat load index for high heat load index sites (Fig. 4C, Tables 4 and 5).

The herbivore communities differed by forest age groups for May (Fig. 5A) and August (Fig. 5B, Table 3). After rotating NMS scores with respect to forest age, insect and plant scores were correlated, with plant species and size class scores explaining 22–62% of the variation in May and August insect community structure ($P = 0.07$ maximum, Tables 6 and 7). Plant species and plant size class scores were also significantly correlated with each other (Tables 6 and 7).

DISCUSSION

Increasing forest age resulted in higher density and species richness of white oak herbivores for low heat load index stands in the August 2003 census. Previously, Marquis and Le Corff (1997) and Marquis et al. (2000) had found similar results for insect communities on *Q. alba* and *Q. velutina* in medium-aged forests that varied by 25 years in age. The results of the current study

extend these earlier findings to both older and younger forests. Similar results have been found in two other systems: insect species richness and abundance positively correlated with forest age for saproxylic beetles in Australian tropical rainforest (Grove 2002) and longicorn beetles in Japanese temperate forests (Maeto et al. 2002). However, these insects have specific habitat requirements better fulfilled by forests with very large trees, as compared to the present study of oak herbivores, in which the host plant was abundant in all stands sampled. Schowalter (1995) found slightly higher diversity of temperate conifer canopy arthropods with increasing forest age of non-plantation Douglas-fir forests from 150 years to 400 years old, although the trend was not significant.

The positive correlation of insect species richness with forest age is consistent with two related hypotheses: (1) increasing complexity of plant architecture with forest age (Lawton 1983) and (2) changing disturbance regimes with forest age (Connell 1978). First, forest age groups differed significantly in plant architecture as indicated by the ordination of tree size classes and the positive correlation of number of size classes with forest age. Specifically, oldest forests were less dense (stem basal area/ha) than medium-aged forests and contained structural components (two classes of the largest diameter trees) not present in medium-aged forests. The heterogeneous architecture present in older forests may positively influence insect herbivore richness, as there is a well-established relationship between plant architecture and insect herbivore diversity (Strong et al. 1984 and references therein).

Second, the intermediate disturbance hypothesis (Connell 1978) proposes that ecosystems at equilibrium are less diverse than those of intermediate age, while recently highly disturbed ecosystems have lower species richness because few species have accumulated in the short time available for colonization. The plant and insect communities in the young forests of this study are recovering from recent timber harvest (clear-cutting),

TABLE 4. Multiple regression models for herbivore species richness and density.

Model	r^2	<i>P</i>
Low heat load index stands, by site, $n = 9$		
Richness August 2003 = $0.85 + 0.001(\text{age})$	0.45	0.048
$\ln(\text{density Aug 2003}) = 1.04 + 0.03(\text{lfm}^2) + 0.002(\text{age})$	0.66	0.040
High heat load index stands, by site, $n = 6$		
$\ln(\text{density May 2003}) = 8.44 - 0.04(\text{lfm}^2) - 0.17(\text{lat})$	0.91	0.032
$\ln(\text{density Aug 2003}) = 3.91 - 2.85(\text{htld})$	0.83	0.011

Note: Abbreviations are: Age, forest age; lfm^2 , total leaf area sampled; htld, heat load; lat, latitude.

TABLE 5. Multiple regression partial r^2 and P values for herbivore species richness and density.

Variable	Low heat load index stands, by site				High heat load index stands, by site			
	August 2003 richness		August 2003 density		May 2003 density		August 2003 density	
	r^2	P	r^2	P	r^2	P	r^2	P
Total leaf area sampled		NS	0.61	0.038	0.75	0.096		NS
Forest age	0.45	0.048	0.15	0.064		NS		NS
Heat load index		NS		NS		NS	0.83	0.011
Latitude		NS		NS	0.19	0.004		NS

Note: NS, not significant (not included in model).

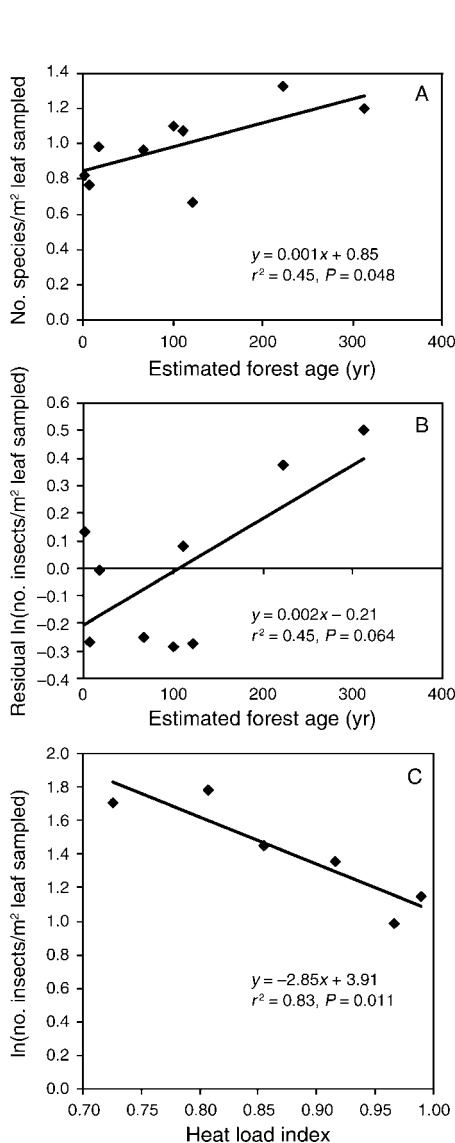


FIG. 4. Significant multiple regression variables in the August 2003 herbivore census: (A) species richness of herbivorous insects increases with forest age for low heat load index stands; (B) density of herbivorous insects increases with forest age for low heat load stands, after controlling for total leaf area; (C) density of herbivorous insects decreases with heat load index (heat load index: 0 = most shaded northeast aspect, 1 = sunniest southwest aspect) for high heat load index stands.

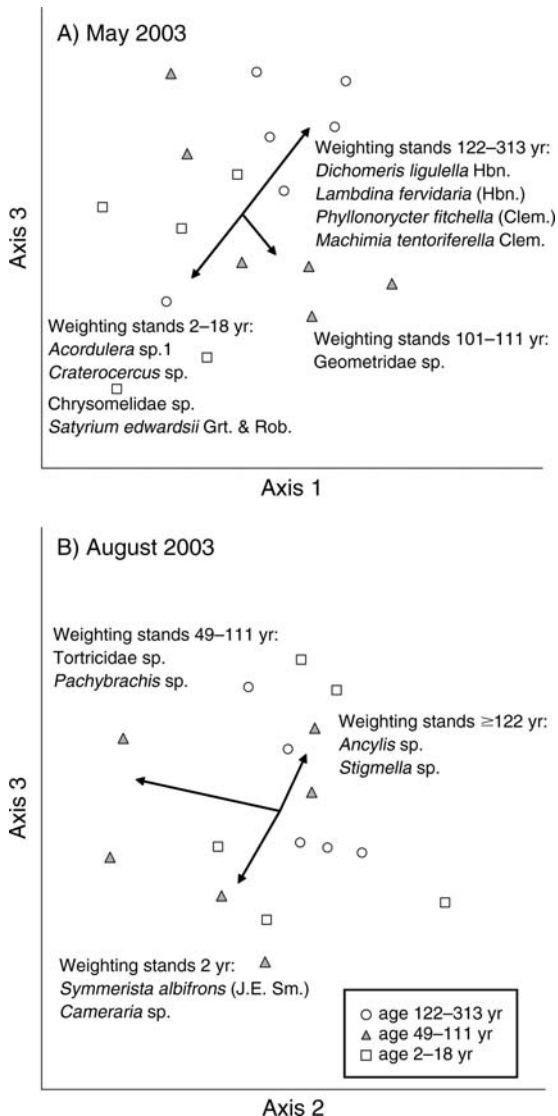


FIG. 5. Nonmetric multidimensional scaling (NMS) scores for insects. (A) Thirty-two May herbivore species (of 70 May species), 17 sample units. The coefficient of determination for axes 1 and 3 has $r^2 = 0.58$. Herbivore species weighting the stand groups are listed. (B) Twenty-six August herbivore species (of 79 August species), 16 sample units (one outlier, SBSPb, was removed). The coefficient of determination for axes 2 and 3 has $r^2 = 0.59$. Herbivore species weighting the stand age groups are listed.

TABLE 6. Multiple regression models for plant and herbivore NMS scores, after rotating axes with respect to forest age.

Model	r^2	P
May herbivores axis 1 = $-0.08 + 0.54(\text{vegsize1})$	0.34	0.018
May herbivores axis 2 = $-0.08 - 0.28(\text{vegsize2})$	0.22	0.070
May herbivores axis 3 = $0.02 - 0.49(\text{vegsp1}) + 0.42(\text{vegsp3})$	0.62	0.002
Aug herbivores axis 1 = $-0.04 + 0.87(\text{vegsp1})$	0.51	0.002
Aug herbivores axis 2 = $-0.006 + 0.42(\text{vegsize2})$	0.30	0.0275
Aug herbivores axis 3 = $-0.01 - 0.48(\text{vegsp3})$	0.40	0.009
Veg size axis 1 = $0.0005 + 0.94(\text{vegsp2}) - 0.47(\text{vegsp3})$	0.62	0.002
Veg size axis 2 = $0.0003 - 0.63(\text{vegsp3})$	0.37	0.013

Note: The variable vegsp2 (axis 2 for plant species composition) was not significantly correlated with insect scores, but was correlated with vegsize variables (vegetation size class categories).

and might be expected to have lower oak herbivore species richness. As the forest ages, colonizers arrive, and richness increases. Comparison of disturbance regimes of medium-age (49–111 yr) and older (122–313 yr) forests could lead to two outcomes for insect species richness. If the original timber harvest is the only important disturbance, then older forests would be expected to have lower richness than medium-aged forests because more time has elapsed since the disturbance, promoting equilibrium through interactions such as competition, where the best competitors may eventually fill the available niche space. However, if smaller, patchy disturbances (Pickett 1976), such as fire, treefalls, or insect outbreaks occur more frequently in older than in medium-aged forests, then higher species richness could be supported in older forests. These older forests would consist of an array of microhabitats that vary in structural complexity and disturbances that prevent competitive exclusion.

A disturbance that might differentially affect old and medium-aged forests is damage from wind. The oldest trees offer more resistance to wind because of their large crowns, resulting in higher risk of wind damage to a tree or a stand with increasing age (Oliver and Larson 1996). And when wind damage does occur, treefalls in northern hardwood old-growth forests generate gap areas over four times larger than those created by treefalls in medium-aged forests (Dahir and Lorimer 1996). Furthermore, slope aspect patterns of windthrow may interact with increasing forest age. In a study of medium-aged (50–100-yr-old) Ozark forests, Rebertus and Meier (2001) found treefall gaps unevenly distributed with respect to slope aspect, with fewer on south-facing slopes than on others. In the present study, total basal stem area declined after approximately 200 years (Fig. 2B) suggesting that tree mortality is present in the old-growth sites, which could result in patchy disturbances. Thus, if wind-induced treefalls in older forests represent an intermediate disturbance regime, then old forests could be expected to have higher insect diversity than both younger and medium-aged forests.

It is difficult to determine the relative contribution of the architecture and disturbance hypotheses considered here. This is due in part to the fact that the variety of structures, both large and small, available in the oldest forests is due to the presence of the large size, long-lived trees as well as small trees in gaps generated by windfall of canopy trees. Plant species composition and forest architecture change with forest age, and the two contribute approximately equally to differences in insect community structure (Tables 6 and 7). Other potential mechanisms for the observed patterns of diversity and abundance might include gap and predator dynamics, and changes in plant chemistry with forest age, which represent avenues for future research.

There was a significant, positive correlation between forest age and insect density but only in August on slopes with low heat load indices (Tables 4 and 5). Maeto et al. (2002) tested the effect of slope aspect on species richness, and found no slope effect, but the

TABLE 7. Multiple regression partial r^2 and P values for plant and herbivore NMS scores, after rotating axes with respect to forest age.

Variable	Vegetation species						Vegetation size class			
	Axis 1		Axis 2		Axis 3		Axis 1		Axis 2	
	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P
May herbivores axis 1		NS		NS		NS	0.34	0.018		NS
May herbivores axis 2		NS		NS		NS		NS	0.22	0.07
May herbivores axis 3	0.21	0.02		NS	0.31	0.01		NS		NS
August herbivores axis 1	0.51	0.02		NS		NS		NS		NS
August herbivores axis 2		NS		NS		NS		NS	0.30	0.028
August herbivores axis 3		NS		NS	0.40	0.01		NS		NS
Veg size axis 1		NS	0.46	0.002	0.25	0.01				
Veg size axis 2		NS		NS	0.37	0.01				

Note: NS, not significant, $P > 0.05$.

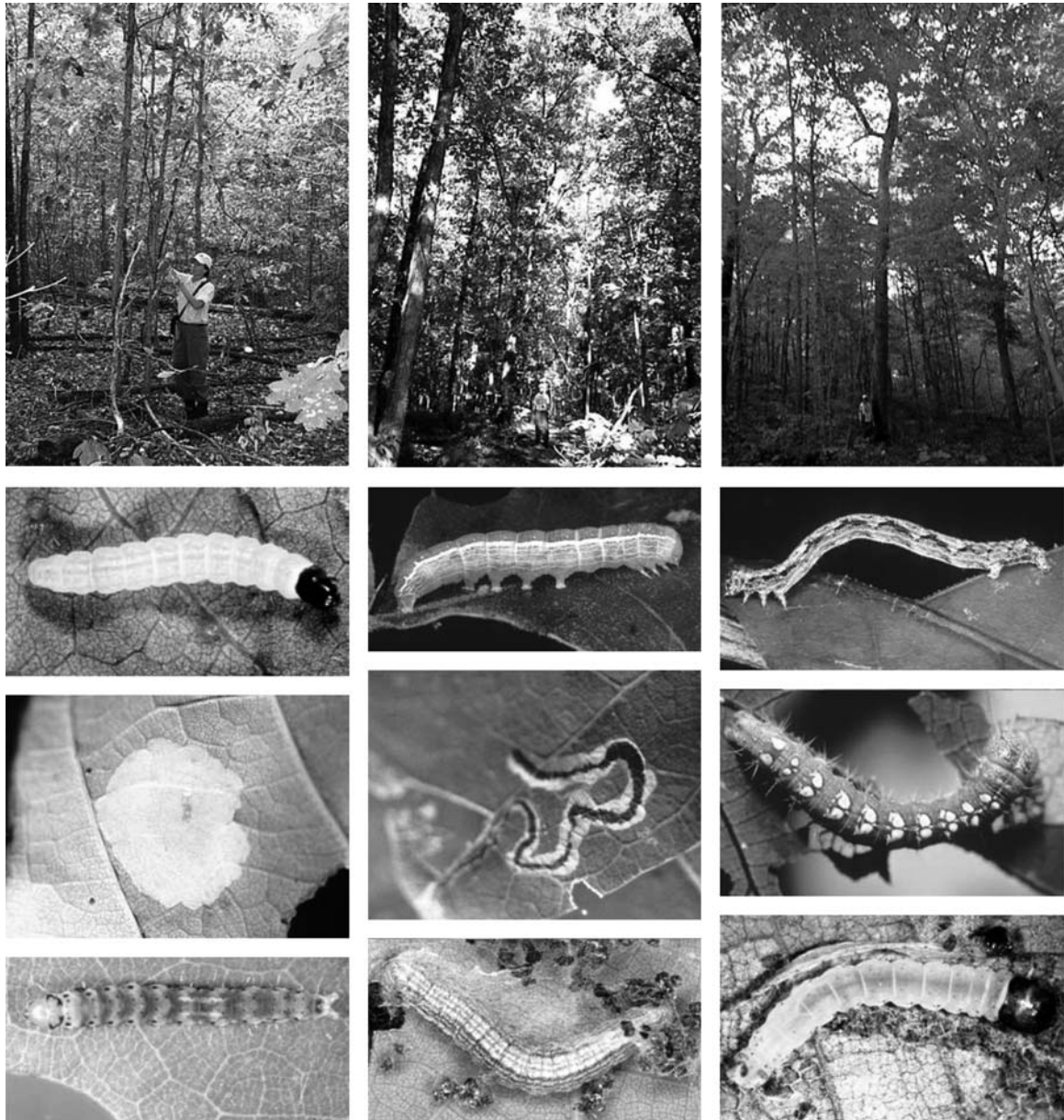


PLATE 1. Oak forests and a selection of the most abundant herbivores. Forests, top row, left to right: D120 (18 yr old), P13 (101 yr), CRNA (313 yr). May 2003 herbivores, second row and first panel in third row; August 2003 herbivores, last five panels. Insects, (left to right in rows 2–4): *Chionodes adamas* Hodges, *Himella intractata* (Morr.), *Lambdina fervidaria* (Hbn.), *Phyllonorycter fitchella* (Clem.), *Aconicta increta* (Morr.), *Stigmella* sp., *Pseudotelphusa* sp., *Pococera expandens* Walker, *Psilocorsis reflexella* (Pack.). Photo credits: top row, Matt Jeffries; insects, R. J. Marquis.

wood- and bark-feeding insects they studied may have been better protected from heat stress than the more exposed leaf-chewing insects of the present study. Marquis and Le Corff (1997) showed that slope aspect affects oak herbivore insect abundance in Ozark forests, with fewer insects on sunny south- and west-facing slopes than on shaded north- and east-facing slopes. The current study confirms that result, with declining abundance (Tables 4 and 5, Fig. 4C) correlated with increasing heat load index (sunny slopes). Abiotic

conditions can influence herbivore survival directly through stressful temperatures and humidity. Herbivore sensitivity to abiotic conditions is demonstrated by the relatively low densities of insects on sunny slopes in August but not in May when temperatures would be cooler (Tables 4 and 5). The structure of the oldest forests may ameliorate stressful abiotic conditions by offering stable microclimates that favor herbivore success, compared to younger forests. Chen et al. (1995) found microclimatic gradients from clear-cut

edges into old-growth Douglas-fir forests, with more stable conditions within the old-growth forest than in the clear-cut edges. Differences in microclimate among forests could be important late in the season when herbivores may experience stress from high temperatures, compared to milder early season conditions. Variation in temperature and relative humidity can affect oviposition and egg development of insect herbivores (Tisdale and Wagner 1990), which may affect their abundance. Insects also could be affected indirectly through changes in plant quality. Jacquart et al. (1992) found increasing plant water stress at edges of an old-growth deciduous forest, while declining leaf quality over the season (Feeny 1970, Forkner et al. 2004) and on sunny slopes (Forkner and Marquis 2004) represents a biotic gradient to oak herbivore insects. How this biotic gradient relates to forest age was not determined, but could contribute to the overall seasonal patterns of species richness and density found here.

The results of this study have implications for timing between timber harvests and for conservation planning. Adequate conservation of the insect fauna in forests of long-lived trees such as white oak may require longer time periods between timber harvests at the same location (extended rotation time) for some portion of the total forested landscape than is prescribed by current silvicultural practice. Rotation times are partially based on maximizing the economic gains from timber harvest (Smith 1996) by limiting timber losses due to age and accident. Current practice in Ozark forests is to harvest every 80–100 years (Brookshire et al. 1997). The present study indicates that oak herbivore species richness and density continue to increase for 200 years beyond the current rotation period, and that unique communities exist in older forests (122–313 yr) compared to medium-aged (49–111 yr) and young (2–18 yr) forests. The same is true for salamander density in this system (Herbeck and Larsen 1999). However, modern harvest practices differ greatly from those used when medium-aged forests were last cut (Guyette and Larsen 2000): instead of entire landscapes being harvested, now smaller areas are cut at any one time. These harvest techniques leave a forest mosaic of differing ages, which may positively influence the recovery rate of recently harvested forests. The evidence presented here suggests that the highest levels of insect richness and density, along with unique assemblages of plants and oak herbivore insects, occur in older forests. If so, core areas of old growth, with attention given to site-specific slope aspects, should be preserved within this mosaic in order to maintain the biodiversity of the system.

ACKNOWLEDGMENTS

We thank R. Jensen for assistance in planning and carrying out this project, and the agencies and personnel at each of the research sites for their cooperation and assistance: Pioneer Forest, Missouri Department of Natural Resources, National Park Service, Mark Twain National Forest, and the Missouri Department of Conservation. S. Shifley and J. Kabrick

provided advice and assistance in planning this project. We thank the following for help in the field: K. Knox, A. Loayza, N. Moorehouse, L. Lihou, J. Floyd, L. Hirst, M. Jeffries, T. Boshart, and B. Baker. This manuscript was improved with comments and suggestions by A. Masís, R. Ríos, K. Boege, B. Baker, L. Abdala, P. Van Zandt, N. Barber, M. Ogburn, H. Dutra, R. Ricklefs, P. Stevens, and T. Knight. This work was supported in part by USDA Cooperative Lands, Prevention and Suppression Grant 02 DG 1124225 430, and the Missouri Department of Conservation.

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