Estimating Pre-treatment Variation in the Oak Leaf-chewing Insect Fauna of the Missouri Ozark Forest Ecosystem Project (MOFEP)

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Abstract.—We describe spatial and temporal variation in the insect herbivore communities associated with the MOFEP, prior to application of contrasting cutting regimes. No pre-treatment differences were found in total insect density on either black (*Quercus velutina*) or white oak (*Q. alba*) during 1993-1995. There was great seasonal variation in insect abundance on both host species as well as high variation across years for white oak. White oak on north- and east-facing slopes tended to have more insects than white oak on south- and west-facing slopes. Sites under the auspices of the Missouri Department of Conservation for a longer time had higher insect densities than more recently acquired sites.

The goal of the Missouri Forest Ecosystem Project (MOFEP) is to determine the effects of alternative forest management schemes on long-term forest productivity, genetic structure of plant populations, and biodiversity of the communities under management. Treatments (even-aged versus uneven-aged management, plus controls; see Brookshire *et al.* 1997 for explanation of the MOFEP treatments and design) were begun in 1996. During 1993-1995, sampling was carried out to quantify any differences that might exist among replicates, so that potential true effects produced by the treatments could be distinguished from conditions existing prior to treatment application.

One of the major components of these Ozark forested communities, in terms of their ecological, economic, and conservation role, are the insect herbivores that feed on oaks. The majority of leaf-feeding insects on Missouri oaks are larvae of Lepidoptera (moths and butterflies) (Marquis and Whelan 1994). As herbivores, they have potential growth impact on their hosts. Non-outbreak population levels cause enough damage to reduce growth of saplings (Marquis and Whelan 1994), while outbreak levels can have negative impacts on growth and survivorship of trees (Rexrode 1971, Coffelt *et al.* 1993) and can potentially influence ecosystem processes such as nutrient cycling (Parker and Patton 1975). The resultant economic impact could be substantial because timber harvesting and processing in Missouri generate $3 billion in economic activity annually (T. Robison, personal communication). Oaks are also important as food for wildlife (Brezner 1972, White 1995), but their economic contribution in this form has yet to be estimated.

From a conservation standpoint, Lepidoptera, and butterflies in particular, have come under increasing scrutiny as the abundance of many species declines (e.g., Thomas and Mallorie 1985, Hill 1995, Legge *et al.* 1996). Lepidoptera can be used as indicator species for changes in habitat quality because their populations are intimately tied to the abundance of their host plant, and host plant decimation is often synonomous with habitat destruction (e.g., Eberhardt and Thomas 1991, Sparrow *et al.* 1994). In Missouri, these insects represent a major component of the State's biodiversity and natural heritage: at least 300 species have been documented on oaks in the Eastern United States and 200 on white oak alone in Missouri (Tietz 1972, Covell 1984). Additionally, these insects are important because they serve as hosts for a number of parasitoids, both insects and nematodes. In so doing, they could serve to maintain a reservoir population of parasitoids that might be used to control invading exotic

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insect pests such as the European gypsy moth, *Lymantria dispar.*

The goal of this project was to describe variation in the abundance of the leaf-chewing insect fauna among replicate sites of the MOFEP project during the 3 years before harvesting treatments were applied. Two host plant species were chosen for study, black (*Quercus velutina*) and white (*Q. alba*) oaks. These two species dominate the canopy of most MOFEP upland stands. Limited resources prevented us from sampling more host species. We chose to include all leaf-chewing insect species, and not a subset of that fauna, because preliminary sampling in 1989-1992 suggested that species' abundances of leaf-chewing insects fluctuate unpredictably (RJM, unpublished data). Thus, a study that focused on only common species in one year would have no estimates of abundances of previously rare species that had become common. High diversity of the leaf-chewing guild (at least 200 species) prevented us from sampling other herbivore guilds associated with black and white oak. However, numbers of galling and sap-sucking insects in the MOFEP region, and throughout Missouri, appear to be low (Marquis and Whelan 1994).

Our overall objective here is to describe pre-treatment variation (years 1993-1995) in the abundance of the leaf-chewing insect herbivores associated with *Quercus alba* and *Q. velutina* at the MOFEP sites. In this paper, we first describe the initial sampling undertaken to establish the sample size chosen for the 3 years of pre-treatment sampling. Second, we analyze the pre-treatment data to determine whether sites assigned to different treatments actually demonstrated differences before treatments were applied. Third, we present analysis of the spatial variation in herbivore abundances irrespective of the original sampling design to understand possible sources of background heterogeneity among the study sites, including potential biases inherent in our sampling. Fourth, we discuss whether we are currently undersampling or oversampling in light of the patterns observed. To do so, we use power analysis to predict the minimum difference produced by treatments that we would be able to establish as statistically significant. Finally, we make recommendations about post-treatment sampling. We present results for total insect numbers sampled in the understory and analyze abundances of a subset of species to illustrate the variety of individual species patterns. Results of analyses of herbivore community composition and canopy sampling will be presented separately.

METHODS

General Census Methods

To determine insect abundance, leaves were searched both top and bottom, as were associated branches and the main stem of the tree. Chewing insects encountered were classified to morpho-species. Each census person was given a training period in identification prior to actual sampling, and had a list of descriptions for all morpho-species known to be encountered. At no time were leaves collected. All insects were left intact on the plant unless individuals were unknown. In that case, unknowns were taken back to the laboratory for rearing and photographing. Each unknown was given its own unique sample number and description, and this information was entered into a database. Photographs were taken, and the insect was observed through development until it could be verified as a previously-recognized species or classified as a species new to our inventory. Photos were used in the field to help with identification when necessary.

Preliminary Sampling to Establish Adequate Sample Size

Preliminary sampling was conducted in early September 1992 to determine the sample size necessary to adequately estimate the mean and variance in total numbers of insects per tree per stand and per site, and species composition per site. Ten trees per stand were sampled in site 6 for each of three north-facing slopes and three south-facing slopes for both black and white oak. The mean and variance in total numbers of insects per leaf area per tree were plotted for each stand and across stands for each tree species. The number of new species encountered with increasing number of stands sampled was plotted to determine how the number of insects species found in a site increased with increasing number of stands sampled. The total number of species per site was compared with species accumulation curves for each stand and each host plant. This preliminary sampling then served to determine sample size for all subsequent sampling in years 1993-1995, described below. For this analysis and all subsequent analyses, insect abundance was expressed on a leaf area basis. Average leaf

area per tree species was estimated based on a sample of 200 undamaged, fully expanded leaves per species, with a maximum of five leaves per tree.

1993-1995 Censuses

Overall MOFEP Design

The MOFEP design (see figure 2 in Brookshire *et al.* 1997) includes nine sites of approximately 400 ha each. Each of these sites has been assigned to either a control, even-aged, and uneven-aged treatment. Sites are blocked by geographic proximity and other general characteristics (Sheriff and He 1997).

Tree Attributes

Ground-level censusing (0.5 to 2.5 m) was conducted from a mixture of saplings and low-hanging branches of sub-canopy to canopy trees.

Leaf and Tree Sample Size

When available, we censused a minimum of 3,000 white oak leaves and 1,200 black oak leaves per stand distributed among five white and five black oak trees. More trees were added when necessary to complete the minimum leaf sample. Leaves were counted either in the May (1993 and 1994) or June census (1995).

Stand Sample Size

Sampling was stratified within sites by ecological land type (ELT; see Brookshire *et al.* 1997). From 1993 to 1995, we sampled three stands on south- and west-facing slopes (ELT 17) and three stands on north- and east-facing slopes (ELT 18) per site. The same trees and the same stands were censused each year and across years. Dead individuals were replaced with nearby neighbors to maintain a comparable sample size. Sampled trees were spread over approximately a 0.5- to 1.0-acre area per stand.

Stand Selection

Stands (six per site) were selected randomly from those available in control and uneven-aged sites. To maintain consistency in timing of cutting, stands sampled in even-aged sites were chosen randomly from those likely to be cut in the second round of cutting (year 2006).

Number of Samples

Due to changes in herbivore abundance and composition through the year (Marquis and Whelan 1994), trees were censused four times per year: April-May, late June, late July, and August-September. Each census required 2 weeks to complete. At each census, sites were always censused in the same order for each of the 3 years: 6, 5, 4, 3, 2, 1, 7, 8, 9.

Statistical Analysis

For data collected in years 1993-1995, repeated measures analysis of variance (ANOVA) (Littell *et al.* 1991, p. 130, 282, von Ende 1993) was first used to test for pre-treatment differences among sites as they were assigned to treatments, for block effects as designated in the original design (Brookshire *et al.* 1997), and for the relative importance of ELT, census, and year on insect density (number of insects per leaf area per tree). All but block, treated as a random effect, were considered to be fixed. ELT was considered to be nested within treatment in a split-block design. Separate analyses were run for white oak and black oak. Profile analyses (Littell *et al.* 1991, von Ende 1993) were run to determine during which censuses and years temporal effects were significant. These same analyses were conducted for the five most common herbivore species on white and black oak separately in the May censuses to illustrate individual species patterns.

In a separate repeated measures ANOVA, we tested for initial differences in sites irrespective of the original experimental design described in Brookshire *et al.* 1997. The goal was to determine the degree to which sites were equal replicates. In this analysis, ELT was included to allow statistical comparison of any observed site effect with that of ELT. ELT was considered to be crossed with site, and the effects of both ELT and site were considered to be fixed. An interaction term between ELT and site was included to determine if the effect of ELT was consistent across sites.

Results for both repeated measures models are presented as between subjects effects (effects of treatments across or among trees) and within subjects effects (how treatments interacted with time to influence values obtained for individual trees). Because black oak was not represented in all north- and east-facing slopes sampled,

Type IV SS were used to calculated F- and P-values for effects of ELT on abundances of insects on this tree species. In all other cases, Type III SS were used. A result was considered to be statisticaly significant at P = 0.05 unless otherwise specified.

Possible site effects might occur due to seasonal changes taking place within the course of a census. Because 2 weeks are required to complete an entire census, later censused stands and sites could have different insect numbers than stands and sites visited at the beginning of the spring census. Such seasonal changes occur most rapidly during the April-May census, when there is a change in insect species composition and numbers associated with the completion of leaf expansion (RJM and JL, unpublished data). Accordingly, the April-May censuses were timed by phenology rather than calendar date to take into account the fact that leafing and insect activity vary by years. For both oak species, we tested whether species diversity varied by site for the spring censuses of 1993-1995 using ANOVA on the Shannon-Weiner Diversity Index (Poole 1974).

Finally, we caculated a power analysis (Zar 1984) to determine the minimum detectable difference for each census in insect density given the observed variation. The mean square error for block by treatment term from the ANOVA for each separate census was used, with $\alpha = 0.05$ and power $(1-\beta) = 0.95$.

RESULTS

Preliminary Sampling

Estimates of the mean number of insects per tree per square meter of leaf area and standard deviation of that estimate appear to stabilize at approximately five to six trees at all six stands sampled for both white (fig. 1) and black oak (not shown). For this particular sample, differences in mean values between north- and south-facing slopes were not consistent for either white or black oak (unpublished data).

To determine the number of sampled stands necessary to characterize the variation in insects numbers at a site, the above estimates of the mean number of insects per tree for six trees at each of six stands were used to calculate a mean value per stand. Means and standard deviation values for site 6 appear to stabilize after three to four stands were sampled for

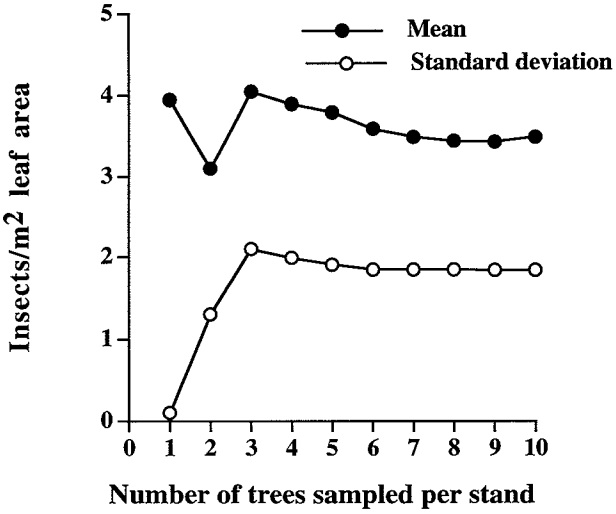


Figure 1.—*One example, chosen randomly from the six patterns available for white oak, showing the relationship between the estimate of the mean and standard deviation of the number of insects per square meter leaf area with increasing number of trees sampled in a stand. Data are from six stands in site 6 collected in September 1992.*

both white and black oak (fig. 2). Finally, number of new species encountered with increasing number of trees sampled per site appears to stabilize at about 30 to 35 trees for each host plant species (fig. 3).

Together, these results suggested that a sample of five trees per species per stand and six stands per site would be adequate to characterize the variation in insect numbers and species composition within a site. Because there was some evidence of differences among stands located on different slope positions, three stands were located on north- and east-facing slopes (ELT 18) and three were located on south- and west-facing slopes (ELT 17).

Sampling 1993-1995

There were no significant main or interaction effects involving treatment and block for number of insects per leaf area on either white or black oak (table 1). ELT had a significant impact (P = 0.001) on insect density on white oak and a significant interaction with year and census (both P = 0.001) (table 1). When differences were significant, there were more insects on trees on north- and east-facing slopes (ELT

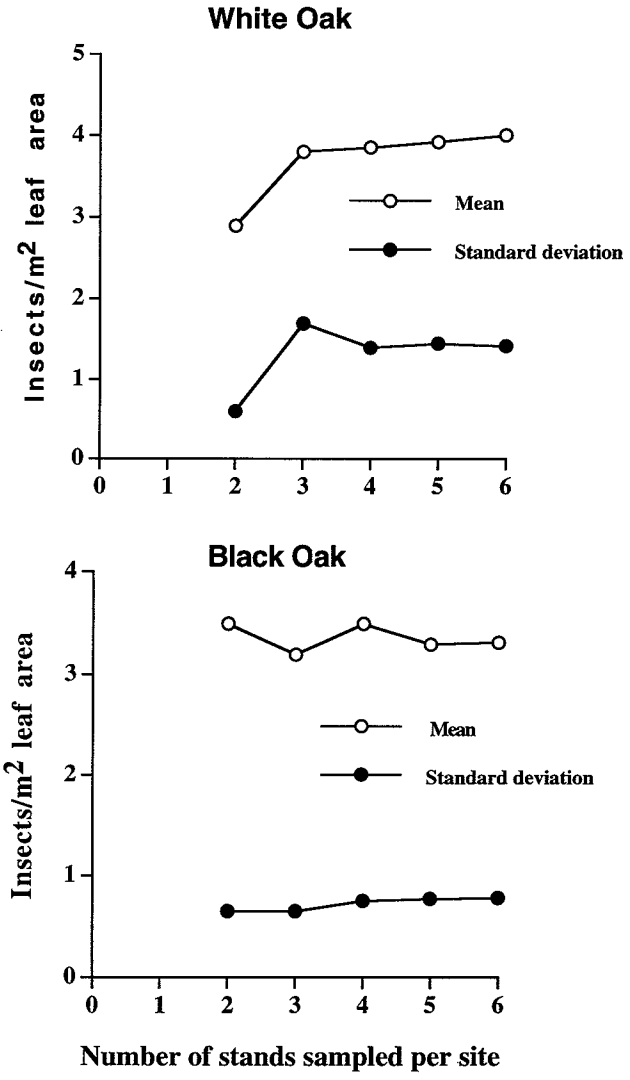


Figure 2.—*The relationship between the estimate of number of insects per tree per stand and its standard deviation and increasing number of stands sampled in site 6 (September 1992) for both white and black oak.*

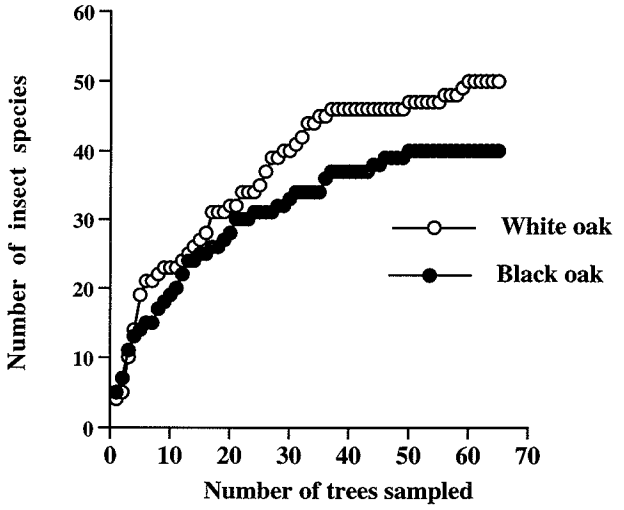


Figure 3.—*The relationship between number of trees sampled and number of species of leaf-chewing insects encountered in site 6 for both white and black oak.*

18) than on trees on south- and west-facing slopes (ELT 17) (fig. 4). Stand as a main effect was a marginally significant predictor of insect abundance in white oak (P = 0.11) but not in black oak (P = 0.31). There was, however, a significant interaction between stand and census for both white and black oak P = 0.012 and 0.013, respectively), demonstrating a stand effect for some censuses in both species, and a significant year by stand interaction (P = 0.014) in black oak (table 1). There were significant interactions of block with census for white oak (P = 0.052) and year for black oak (P = 0.069).

Profile analysis for white oak (table 2) showed that the effect of ELT increased from 1993 to 1994, and then again from 1994 to 1995, irrespective of season (i.e., the interaction effect between ELT and year was significant for both contrasts) (fig. 4). The effect of ELT on insects feeding on white oak was also greater later in the season across all years: its effect increased from June to July (significant ELT effect), and then again from July to August censuses, but not from May to June (table 2, fig. 4).

Insect densities, summed over all sites and all censuses, varied significantly across years (table 1), but more so for white than black oak (fig. 5). For white oak, total numbers of insects found on trees in 1994 and 1995 were twice that in 1993; for black oak, totals in 1995 were 15 percent and 22 percent less than in 1993 and 1994, respectively (fig. 5). Seasonal pattern also varied by year. Seasonal variation in white oak showed two patterns: either high abundance in the spring and fall (1993) or an increase in abundance in spring to fall (1994 and 1995) (fig. 6). In contrast, seasonal pattern of insect abundance on black oak was consistent across years; abundance was highest in the spring (and 50 to 100 percent greater than white oak spring abundances), lowest in the midsummer, then increased again in the fall (fig. 6).

Table 1.—*Repeated measures ANOVA testing possible pre-treatment effects on number of insects per leaf area per tree. F-approximations are based on the Pillai's Trace test statistic. MS_{den} is the denominator used in calculating the F-statistic for the between subjects effects. Ndf and Ddf are numbers of degrees of freedom in the numerator and denominator, respectively, for calculating the F-statistic for within subjects effects. Stand is nested within treatment, block, and ELT.*

Between subjects

		Quercus alba				*Quercus velutina*			
Source	**MS_{den}**	**df**	**MS**	**F**	**P**	**df**	**MS**	**F**	**P**
Treat (T)	MS_{TxB}	2	49.92	0.29	0.762	2	235.8	1.18	0.396
Block (B)	MS_{TxB}	2	453.4	2.68	0.185	2	552.4	2.76	0.176
T X B (whole plot error)		4	169.4			4	399.7		
ELT (E)	MS_{Stand}	1	2,081	14.42	0.001	1	4.46	0.06	0.814
T X E	MS_{Stand}	2	1.67	0.01	0.989	2	61.1	0.77	0.471
Stand	MS_{E}	42	144.4	1.30	0.110	34	79.4	1.11	0.313
Error (subplot)		298	110.9			267			

Within subject

	Quercus alba			*Quercus velutina*		
Source	**Ndf/Ddf**	**F**	**P**	**Ndf/Ddf**	**F**	**P**
Year(Y)	2/297	133.7	0.001	2/266	6.62	0.002
Census (C)	3/296	68.7	0.001	3/265	157.1	0.001
Y X C	6/293	86.1	0.001	6/262	37.17	0.001
Y X T	4/8	0.63	0.656	4/8	1.82	0.190
Y X B	4/8	1.29	0.350	4/58	3.34	0.069
Y X E	2/41	9.14	0.001	2/33	0.145	0.250
Y X Stand	84/596	0.88	0.757	68/534	1.45	0.014
Y X T X E	4/84	1.62	0.178	4/68	0.80	0.527
C X T	6/6	0.64	0.701	6/6	0.39	0.867
C X B	6/6	4.20	0.052	6/6	1.51	0.315
C X E	3/40	8.03	0.001	3/32	1.40	0.262
C X Stand	126/894	1.34	0.012	102/801	1.36	0.013
C X T X E	6/82	0.66	0.677	6/66	1.28	0.279
Y X C X Stand	252/1788	1.16	0.057	204/1602	1.17	0.064
Y X C X T[1]	—	0.51	0.889	—	0.61	0.811
Y X C X B[1]	—	0.85	0.599	—	1.98	0.074
Y X C X E	6/37	0.63	0.703	6/29	0.75	0.613
Y X C X T X E	12/76	0.66	0.785	12/60	0.62	0.817

[1]Insufficient degrees of freedom to calculate values in MANOVA; univariate results are reported.

Analysis of abundance of the five most common species of the May census showed that changes in individual species abundances were not necessarily consistent with those of the entire community (table 3). Like the entire community, all species varied significantly across years (P = 0.001). However, some patterns at the species level contradicted those at the community level. For white oak, for example, there was a "pre-treatment" and ELT effect on abundance of one species, two species varied significantly by block, and three species showed significant variation in abundance by stand. For black oak, one species varied significantly by ELT, two showed significant variation by block, and four of five species varied significantly by stand.

The contribution of geographic scale for insect density differed between white and black oak (table 4). As in the previous analysis (table 1), ELT had a significant effect on overall insect abundance on white oak but not on black oak. However, this second analysis revealed that there was a marginally significant ELT by census interaction (P = 0.08) and a significant census by site by ELT interaction for black oak (P = 0.024). Both suggest a significant ELT effect in black oak, but the effect appears in

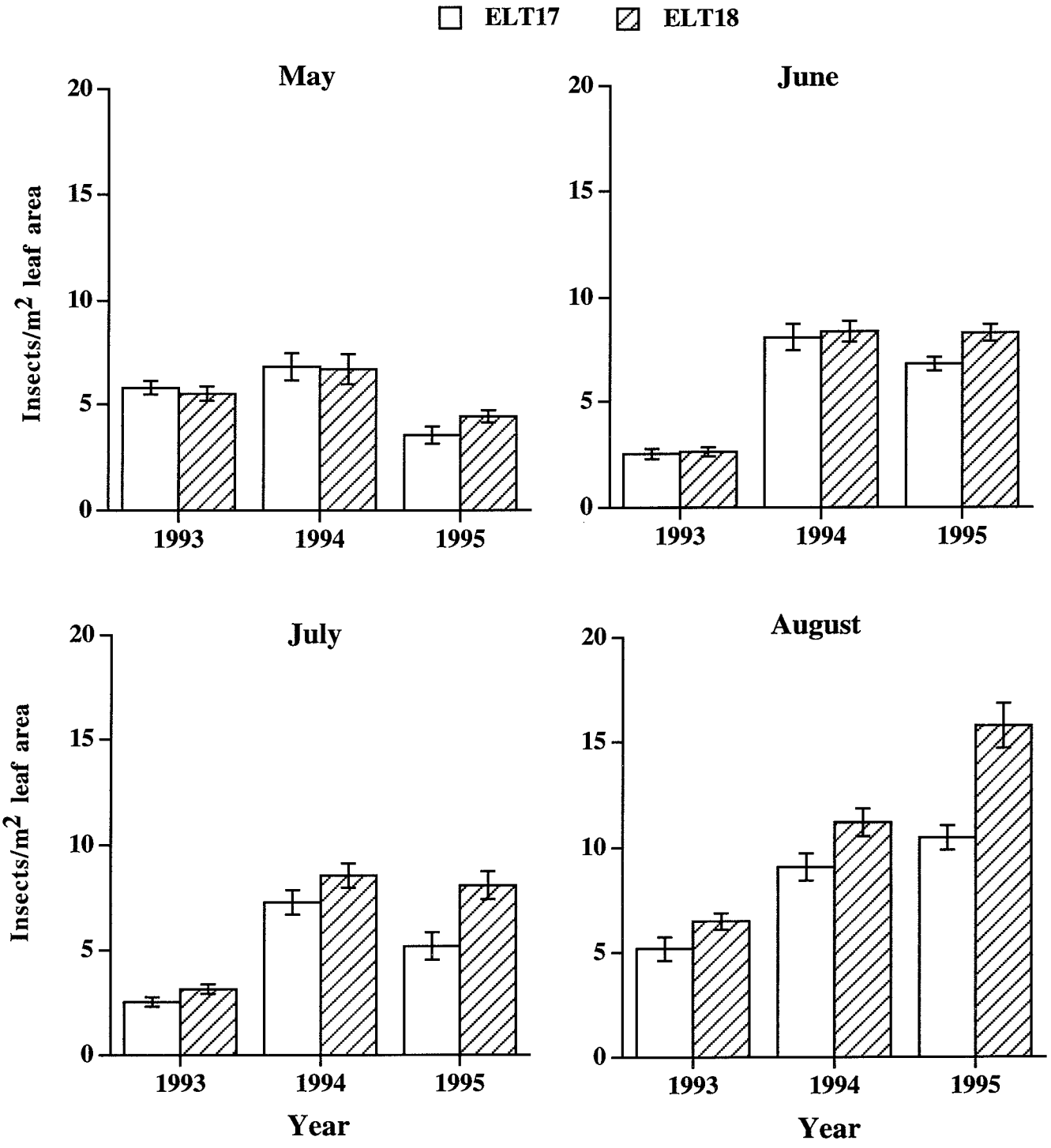


Figure 4.—*Effect of ELT, year, and census on the mean (± SE) number of insects per leaf area on white oak.*

Table 2.—*Profile analysis for* Quercus alba *for the effect of either year or census ("Time") and ELT X Time interaction ("ELT X Time") over the time periods indicated on insect density per tree.*

Source	F	P
Contrast variable: Year 1 - Year 2		
Time	171.6	0.001
ELT X Time	18.4	0.001
Contrast variable: Year 2 - Year 3		
Time	2.4	0.123
ELT X Time	5.4	0.026
Contrast variable: May -June		
Time	14.9	0.001
ELT X Time	1.0	0.323
Contrast variable: June - July		
Time	5.0	0.026
ELT X Time	3.4	0.073
Contrast variable: July - August		
Time	180.5	0.001
ELT X Time	4.5	0.040

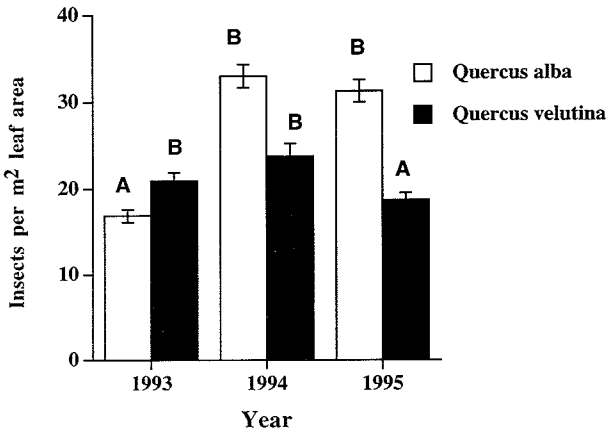
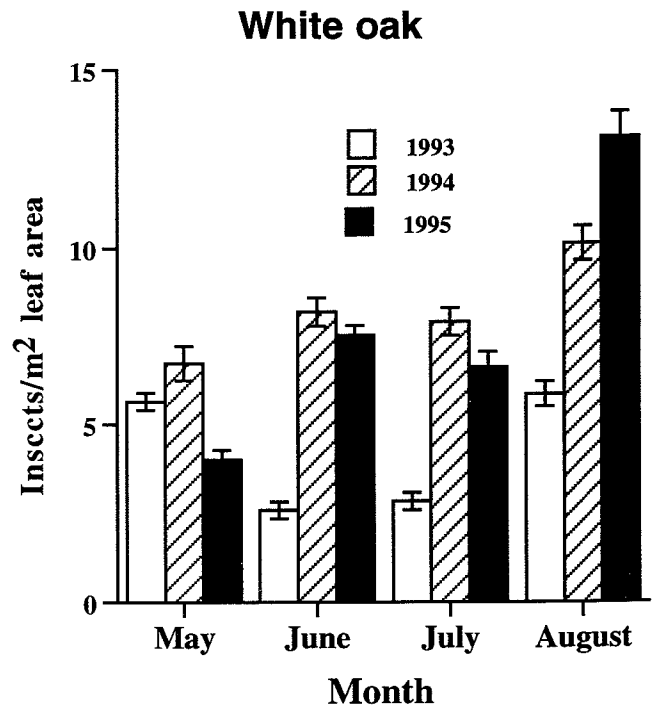


Figure 5.—*Annual variation in the mean (± SE) number of insects per leaf area on white and black oak.*



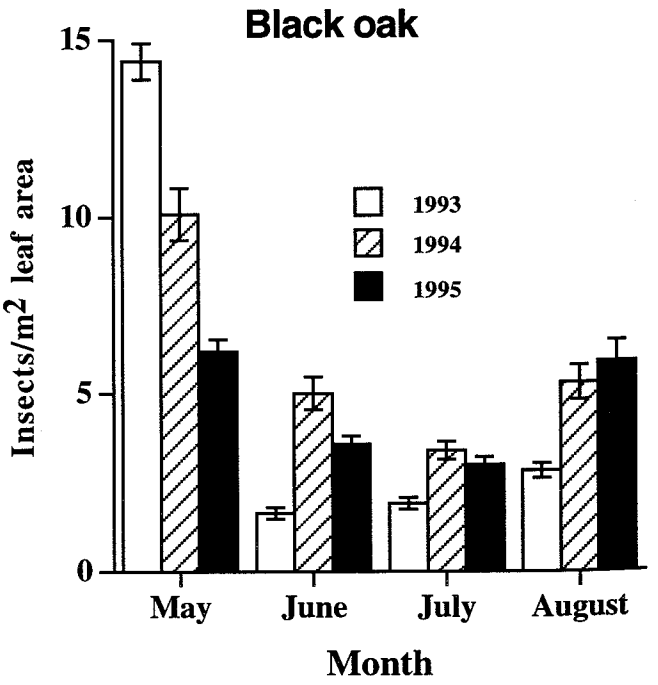


Figure 6.—*Seasonal variation by year in the mean (± SE) number of insects per leaf area in white oak and black oak.*

Table 3.—*Repeated measures ANOVA testing possible pre-treatment effects on numbers of the five most common insect species per leaf area per tree. Analysis is the same as reported in table 1. N.S. = non-significant at P>0.10.*

	Quercus alba				
Factor	***Lithophane antennata***	***Chionodes* sp.**	***Telphusa latifasciella***	***Spargonothis pettitana***	***Dichomeris ligulella***
ELT (E)	N.S.	N.S.	N.S.	N.S.	0.005
Treatment (T)	N.S.	N.S.	N.S.	N.S.	0.017
Block (B)	0.080	N.S.	N.S.	N.S.	0.019
Stand (S)	N.S.	0.061	0.023	N.S.	0.003
T X E	N.S.	N.S.	N.S.	N.S.	N.S.
Year (Y)	0.001	0.001	0.001	0.001	0.001
Y X E	N.S.	N.S.	N.S.	N.S.	0.020
Y X T	N.S.	N.S.	N.S.	N.S.	N.S.
Y X B	N.S.	N.S.	N.S.	N.S.	0.003
Y X S	0.003	0.006	N.S.	N.S.	N.S.
Y X T X E	N.S.	N.S.	0.031	N.S.	N.S.

	Quercus velutina				
Factor	***Chionodes* sp.**	***Telphusa latifasciella***	**unidentified Tortricidae**	***Spargonothis pettitana***	***Dichomeris ligulella***
ELT (E)	0.068	N.S.	N.S.	N.S.	N.S.
Treatment (T)	N.S.	N.S.	N.S.	N.S.	N.S.
Block (B)	N.S.	N.S.	0.078	N.S.	0.054
Stand (S)	0.035	0.006	0.016	N.S.	0.013
T X E	N.S.	N.S.	N.S.	N.S.	N.S.
Year (Y)	0.001	0.001	0.001	0.001	0.001
Y X E	N.S.	N.S.	N.S.	N.S.	N.S.
Y X T	N.S.	N.S.	N.S.	N.S.	N.S.
Y X B	N.S.	0.040	N.S.	N.S.	0.066
Y X S	0.002	0.004	N.S.	N.S.	0.009
Y X T X E	N.S.	N.S.	N.S.	N.S.	N.S.

only some sites for the August-September census. As in white oak, when differences occurred, there were more insects on black oak trees of north- and east-facing slopes (ELT 18) than on trees of south- and west-facing slopes (ELT 17) (25 percent more averaged across all sites in August censuses; not shown).

Site had a significant main effect for black oak (P = 0.005) and a significant site by census interaction for white oak P = 0.002). The site effect in black oak is due in part to consistently higher and lower insect numbers in site 6 and site 2, respectively (fig. 7). The other contributing factor to the site effect is the great range in insect numbers across sites for black oak during the May censuses of 1993 and 1995 (fig. 7, significant year by census by site interaction, patterns by year not shown). The decline in values corresponds to the order in which sites were sampled (sites are listed in sampling order). The significant site by census interaction in white oak is due to a similar pattern: a range in site values occurs only in May, but again corresponds to the order in which sites were sampled (fig. 8). May is when the insect species composition changes most rapidly, and total insect numbers decline over a very short time period as leaves become fully expanded (RJM and JL, unpublished data). However, diversity (Shannon-Weiner index) did not decline as sites were sampled in May for either black or white oak (P > 0.15 for both species and all years). Site differences in insect abundance in May on both black and white oak correspond to the time of acquisition of the sites by the MDC (fig. 9), with those sites under control of the MDC longer having greater insect

Table 4.—*Repeated measures ANOVA for the effect of geographic scale on number of insects per leaf area per tree. F-approximations are based on the Pillai's Trace test statistic. Ndf and Ddf are number of degrees of freedom in the numerator and denominator, respectively, for calculating the F-statistic. Stand is nested within site and ELT.*

Between subjects

	Quercus alba			*Quercus velutina*		
Source	**df**	**F**	**P**	**df**	**F**	**P**
Site (S)	8	1.42	0.221	8	3.70	0.005
ELT (E)	1	14.8	0.001	1	0.08	0.779
S X E	8	0.73	0.666	8	0.88	0.547
Stand	36	1.26	0.151	28	1.10	0.333
Error	298			267		

Within subject

	Quercus alba			*Quercus velutina*		
Source	**Ndf/Ddf**	**F**	**P**	**Ndf/Ddf**	**F**	**P**
Year(Y)	2/297	133.7	0.001	2/266	8.34	0.001
Census(C)	3/296	68.7	0.001	3/265	172.7	0.001
Y X C	6/293	86.1	0.001	6/262	40.22	0.001
Y X S	16/72	1.82	0.045	16/56	2.27	0.012
Y X E	2/35	8.97	0.001	2/27	1.91	0.168
Y X Stand	72/596	0.85	0.796	56/534	1.52	0.012
Y X S X E	16/72	1.17	0.310	16/56	0.80	0.683
C X S	24/108	2.26	0.002	24/84	0.96	0.532
C X E	3/34	8.26	0.001	3/26	2.51	0.081
C X Stand	108/894	1.31	0.023	84/801	1.10	0.253
C X S X E	24/108	0.72	0.818	24/84	1.82	0.024
Y X C X S	48/216	1.53	0.022	48/168	1.58	0.018
Y X C X E	6/31	0.66	0.680	6/23	1.02	0.436
Y X C X Stand	216/1708	1.16	0.060	168/1602	1.14	0.110
Y X C X S X E	48/216	0.64	0.960	48/168	0.86	0.720

numbers (table 5) (r = -0.78 and -0.85, for P = 0.012 and 0.004 for white and black oak, respectively).

Power Analysis

Based on our present estimates of variation, we have enough statistical power to conclude that a twofold to sixfold increase in total insect density would be significant at P = 0.05 (table 6). Power varies by census and year: in some cases a relatively small change (5.7 insects per m^2) would be significant, while in others the differences would have to be much larger (30-50 insects per m^2) to state that a treatment effect had occurred.

DISCUSSION

We found no evidence of differences by treatment for either white or black oak in the total number of insects prior to application of the actual treatments. The lack of treatment effect suggests that there are no pre-treatment differences among sites that later could be misinterpreted as treatment effects (although one of the common species, *Dichomeris ligulella*, shows such a pre-treatment difference on white oak, but not on black oak).

We found no significant main effect of block as proscribed in the original design. However, there were significant interactions of block with census (white oak) and year (black oak). The fact that block does account for some of the variation is support for keeping the block effect (as originally designed) in the model.

Spatial variation in insect numbers existed unrelated to the original blocking. Trees varied in the number of insects depending on the stand, but the stand effect was variable both by year (black oak) and by census (white and black oak). Individual species were more likely to

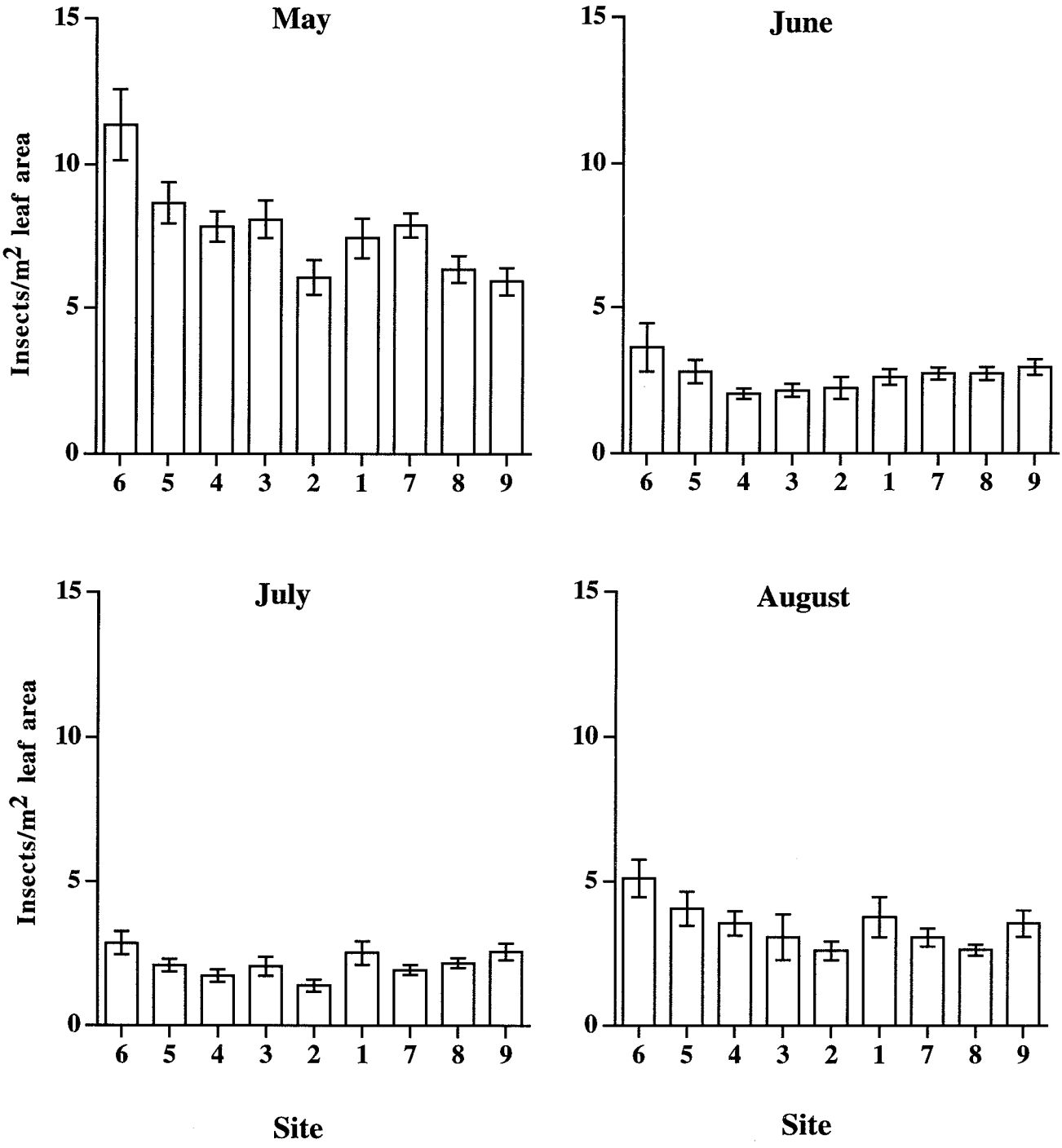


Figure 7.—*Effect of site on estimates in the mean (± SE) number of insects per leaf area for each census across years for black oak. Sites are shown in the order they were sampled.*

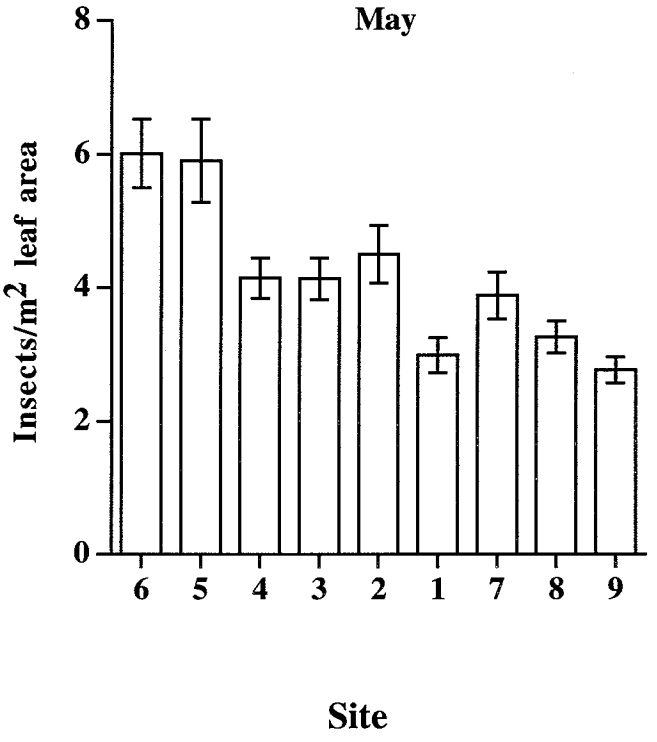


Figure 8.—*Effect of site on estimates in the mean (± SE) number of insects per leaf area for May censuses on white oak. Sites are shown in the order they were sampled.*

vary by stand than did the community as a whole. Stands differed in the number of insects depending on their slope position (ELT), more so for white than black oak. The ELT effect was consistent across sites (no significant ELT by site interaction), and thus appeared to be independent of site, despite the fact that sites vary in soil type (MOFEP unpublished data). Finally, both white oak (for 3 years) and black oak trees (for 2 years) varied in the total numbers of insects in the May census, depending on the site in which they were located. The fact that diversity did not change across sites in the spring censuses suggests that the significant site effect for both oak species is not a sampling artifact due to loss of species (and therefore insect numbers) as the census proceeded. Why the site effect is greatest for the spring census is not clear. Perhaps microsite differences in climate are greatest early in the spring, leading to differences in phenology. For both oak species, there is a strong relation between numbers of insects per site and the time those sites came under the auspices (and protection

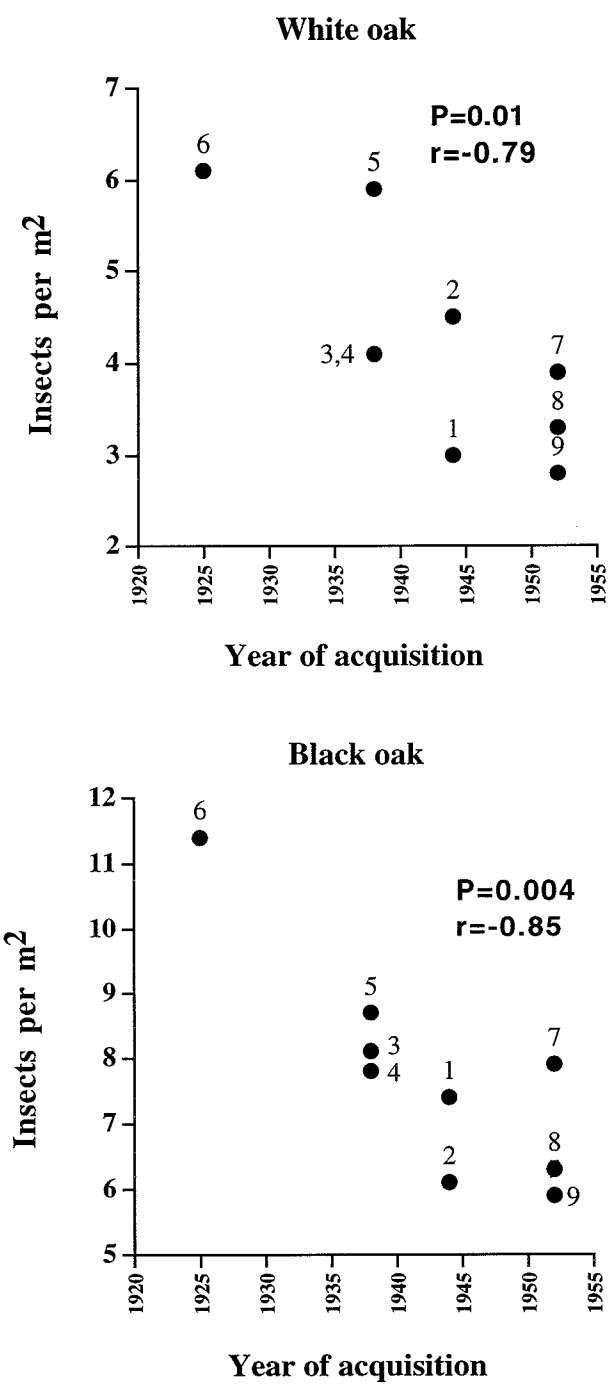


Figure 9.— *The relationship between year of acquisition of a site under the auspices of the Missouri Department of Conservation and the mean density of insects in May censuses (calculated over the years 1993-1995) for both white and black oak. Each point is labeled with its corresponding site number.*

Table 5.—*Relation between year of incorporation of site and the mean number of insects per square meter leaf area (± SE) for white and black oak averaged over the May censuses of 1993-1995.*

Year of acquisition	Site	*Quercus alba*	*Quercus velutina*
1925	6	6.1 ± 0.5	11.4 ± 1.2
1938	5	5.9 ± 0.6	8.7 ± 0.7
1938	4	4.1 ± 0.3	7.8 ± 0.5
1938	3	4.1 ± 0.3	8.1 ± 0.7
1944	2	4.5 ± 0.4	6.1 ± 0.6
1944	1	3.0 ± 0.3	7.4 ± 0.7
1952	7	3.9 ± 0.4	7.9 ± 0.8
1952	9	2.8 ± 0.2	5.9 ± 0.5
1952	8	3.3 ± 0.2	6.3 ± 0.5

from grazing and fire) of the Missouri Department of Conservation. The reason why numbers of insects on black oak are unusually low in site 2 and unusually high in site 6 across censuses and years is unclear (fig. 7). At this time, we also do not know what factors cause the observed stand effects.

Based on our results, we make the following suggestions about future sampling:

1. Present sample size (number of trees per stand or number of stands per site) should be maintained. We now have sufficient statistical power to distinguish "relatively small" treatment effects, but reduction of sample size would jeopardize the power that is available. Increased sampling (more stands per site) should be considered.

2. Because black and white oaks dominate the canopy, we suggest that sampling should continue on both species. Moreover, spatial and temporal variation is different for the two host plants, suggesting that results from one species cannot be extrapolated necessarily to other oak species.

3. The significant effect of ELT suggests that stratified sampling by ELT should continue.

4. Relatively high numbers of insects can occur at any time of the year. In addition, species turnover among the four censuses is relatively high. Taken together, we recommend continued sampling for four times a year.

Table 6.—*Minimum detectable difference (Zar 1984) for each census in the number of chewing insects per square meter leaf area given the observed variation (mean square error for block by treatment term in the ANOVA) for* $\alpha = 0.05$ *and power* $(1-\beta) = 0.95$. *Percent increase in actually observed values that the difference would represent is given in parentheses.*

Census	*Quercus alba*		*Quercus velutina*	
May 1993	13.9	(246)	45.6	(315)
June 1993	8.7	(337)	5.7	(345)
July 1993	7.8	(302)	7.3	(380)
August 1993	5.7	(97)	14.2	(500)
May 1994	37.5	(556)	49.0	(205)
June 1994	8.5	(103)	26.8	(534)
July 1994	30.5	(386)	7.2	(211)
August 1994	28.2	(278)	18.4	(347)
May 1995	12.5	(313)	11.8	(190)
June 1995	10.3	(137)	7.6	(212)
July 1995	31.3	(471)	9.1	(303)
August 1995	41.3	(314)	21.9	(369)

5. Because of the year-to-year variation in total insect numbers and abundance of individual species, we recommend conducting post-treatment sampling every year.

6. Individual insect species exhibit idiosyncratic patterns compared to overall community patterns. Such individual species differences suggest that sampling by insect species should continue, because effects of forestry management on overall insect abundance will entail individual species' responses to the treatments. In addition, a number of our species are known to go through population irruptions (e.g., *Symmerista albifrons, Heterocampa gutivitta, Diapheromera femorata, Lochmaeus manteo, Sabine stimulea, Psilocorsis quercicella, Melanoplus* sp.). Ignoring changes in these particular species for which previous information on their population biology is available might seriously reduce our ability to understand treatment effects.

7. Estimates of amount of leaf area consumption (based on laboratory feeding trials) should be made to translate insect abundance into damage estimates. Given that it is important to know the relative economic impacts of alternative forest managements regimes, estimates of leaf damage will be of more use in estimating treatment effects on tree growth than will estimates of insect numbers. Consumption rates then can be

used to translate estimates of insects numbers from past censuses into leaf damage.

Finally, we make a plea for future integration of sampling and analysis among projects under the MOFEP auspices. As an example of the understanding that might arise from such an integration, we present a path diagram (see Li 1975 and Schemske and Horvitz 1988) in figure 10, which relates herbivorous insect abundance to tree growth, and moderating factors that may directly and indirectly modify this interaction. It is highly likely that many studied taxa and processes will have their own independent, direct effect on tree growth. Thus, in figure 10, insect populations, soil characteristics, tree pathogens, and tree genetic diversity all are shown to have a direct effect on tree growth. However, the impact of insect herbivores on tree growth can be understood thoroughly only by considering the additional indirect effects of the factors listed above (including bird populations) on insect populations. These indirect effects may be as important in determining the relationship among variables as the direct effects. Knowing these indirect effects will require cooperative planning and coordinated sampling for estimation of the path coefficients. Path diagrams like this one could be drawn for each studied taxon and process. In turn, we will want to estimate the coefficients for these path diagrams under each of the treatments to understand how the treatments affect the underlying relationships. Our biggest challenge will be to integrate our efforts so that we can understand the underlying processes that might lead to treatment effects.

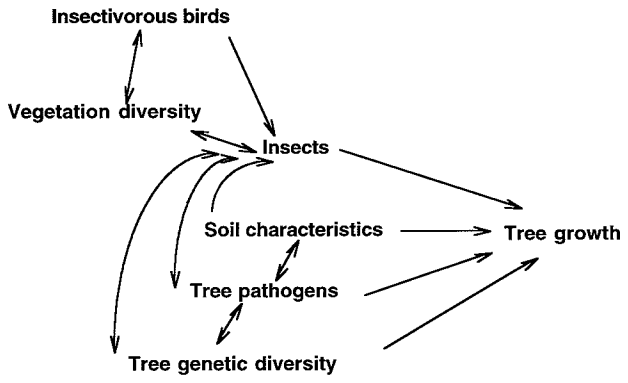


Figure 10.—*Path diagram linking the factors likely to both directly and indirectly affect the impact of herbivorous insects on tree growth in MOFEP.*

ACKNOWLEDGMENTS

We thank Floyd Catchpole, Eric Dahms, Andy Farrell, Katherine Gonzalez, Nancy Greig, Kathy Hayes, Cris Hochwender, Liz Jakse, Damond Kyllo, Diane Lill, John Lill, John McGrath, Kristine Mothershead, Evan Notman, Kirk Stowe, Rick Whitney, and Eric Wold for help with data collection and caterpillar rearing. We are grateful to Steve Passoa, who identified the caterpillars, and to Linda Butler, Jack Schultz, and an anonymous reviewer for comments on a previous draft. We thank the Missouri Department of Conservation staff (particularly Randy Jenson, Terry Robison, and Brian Brookshire) for logistical support and advice in planning. Finally, we thank Victoria Sork and William Connett for lengthy discussions regarding statistical analysis. Financial support came from the Missouri Department of Conservation.

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