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Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium: Post-treatment Results of the Landscape Experiment

Stephen R. Shifley and John M. Kabrick, Editors



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**Proceedings of the Second Missouri
Ozark Forest Ecosystem Project
Symposium: Post-treatment Results
of the Landscape Experiment**

Held in
St. Louis, Missouri

October 17-18, 2000

Edited by Stephen R. Shifley and John M. Kabrick

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FOREWORD

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a centuries-long experiment to examine the impacts of alternative forest management practices on a wide array of ecosystem attributes. MOFEP includes an integrated program of research studies conducted by dozens of scientists and technicians. The studies are replicated on nine forest compartments that are the experiment sites. Between 1990 and 1996, all MOFEP sites were monitored to collect pre-treatment baseline data. The pre-treatment conditions are thoroughly documented in two previous MOFEP publications:

Brookshire, Brian L.; Shifley, Stephen R., eds. 1997. Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: an experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 378 p.

Shifley, Stephen R.; Brookshire, Brian L., eds. 2000. Missouri Ozark Forest Ecosystem Project: Site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. Gen. Tech. Rep. NC-208. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 314 p.

This publication complements the first MOFEP Proceedings (Brookshire and Shifley 1997). This second proceedings reports findings 2 to 3 years after implementation of the even-aged, uneven-aged, and no-harvest management treatments. The introductory paper by Sheriff describes the experiment and sets the stage. The remaining papers describe the treatment effects for many different ecosystems attributes.

In combination, the papers quantitatively and qualitatively describe the response of the forest ecosystem. Most papers describe treatment effects (or their absence) at the landscape scale. Many papers also present information on responses measured at finer spatial scales (e.g., due to variation within a treatment unit). The papers in this volume provide a detailed summary of short-term forest changes that result from operational forest management. Over time, as the MOFEP experiment continues, long-term treatment responses will be documented.

We thank the authors of the 15 papers included in this volume. They put great energy into data collection, analysis, manuscript preparation, and revision. Each paper received two statistical reviews, a review by one or more subject matter specialists, and two rounds of editorial review. Steven Sheriff (Missouri Department of Conservation) and Carl Mize (Iowa State University, Natural Resource Ecology and Management Department) reviewed all manuscripts with a particular eye toward statistical details. The many reviewers from other disciplines are listed on the following page. They have our thanks, as do several others who chose to remain anonymous. We also thank B.J. Gorlinsky for creating the detailed site maps showing all study locations. Finally, we thank Lucy Burde and Mary Peterson for their unerring editorial guidance and skill in preparing the printed document.

Stephen R. Shifley

John M. Kabrick



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Missouri Ozark Forest Ecosystem Project: The Experiment

Steven L. Sheriff¹

Abstract.—The Missouri Ozark Forest Ecosystem Project (MOFEP) is a unique experiment to learn about the impacts of management practices on a forest system. Three forest management practices (uneven-aged management, even-aged management, and no-harvest management) as practiced by the Missouri Department of Conservation were randomly assigned to nine forest management sites using a randomized complete block design. Unique features of the MOFEP experimental design include collection of pre-treatment information, use of replicate forest management units, and the long-term nature of the project. In the case of MOFEP, pre-treatment data were collected up to 5 years before the harvest treatments were applied in 1996-1997. The design of MOFEP also allows for three complete rotations of harvest treatments with each site. Since the periods between the application of even-aged and uneven-aged harvest practices will be 10 to 15 years and the rotation length will be about 100 years, we expect the life of MOFEP to be at least 300 years. Throughout this project, results will provide information valuable to understanding and designing forest management practices that will benefit forest ecosystem health. Through MOFEP's example, lessons can be learned about the application of large-scale (spatially and temporally) experiments in natural resources management. The MOFEP experience has demonstrated that learning about the impacts of management on natural ecosystems can be accomplished on a scale relevant to managers and researchers.

Forest management, as well as most other natural resources management, has moved into an era in which decisions must be based on sound science that correctly predicts the outcome of the chosen practice. In Missouri, the public demands science-based forest management decisions (Missouri Department of Conservation 1996, Palmer 1996). Conducting research for making sound predictions requires going beyond developing hypotheses. Research that tests hypotheses and theory is required before predictions can be made with any certainty.

During the mid-1980s, the impact of forest management on neotropical migrant songbirds caught the attention of ornithologists and the public alike. Monitoring of bird communities in forest systems led to hypotheses of how these

communities might be affected by forest management (Annard and Thompson 1997; Robbins *et al.* 1989; Robinson *et al.* 1995; Thompson *et al.* 1992, 1993). These hypotheses, however, had not been rigorously tested to develop information useful in predicting implications for forest management decisions. Short-term data from these studies provided the foundation for sound hypotheses and helped establish theories that decision makers could consider. However, these hypotheses and theories about the effects of forest management on the bird communities and the entire forest ecosystem needed testing.

Romesburg (1981) called for natural resources management and research to go beyond hypothesis development to hypothesis testing. In a decision process, if only untested hypotheses are used, then "educated guesses" as to the viability of each hypothesis are required. The decision maker must rely upon his or her own experiences and perceptions in predicting the outcome of management alternatives. The uncertainty in hypotheses and predictions is not

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easily evaluated in the informal atmosphere that often accompanies the natural resource decision making process (Walters 1986). Even though in most cases the decision maker may understand and "mentally" evaluate the impacts of a management decision, the information gained is not often or easily transmitted to the next generation of decision makers. In other words, lessons learned through experience are often lost. To "learn" while managing requires a more formal framework for the decision process. Walters (1993) advocated the use of large-scale field experiments in impact assessment and management. Romesburg (1981) advocated the use of hypothetico-deduction when testing hypotheses. By combining the hypothetico-deductive process with the management by experiment idea, experiments are designed to determine cause-and-effect relationships among management alternatives. Through this paradigm and the desire to confront forest management decisions based on data, the Missouri Ozark Forest Ecosystem Project (MOFEP) was designed and implemented.

Designing MOFEP was a difficult task that required much thought and cooperation over several years (Kurzejeski *et al.* 1993), but there was a tremendous desire to implement a project that would provide an opportunity to learn about impacts of different forest management practices at a landscape scale typically used by managers in the Missouri Ozark forests. The development of this unique project in the late 1980s required a herculean effort by many individuals (Brookshire *et al.* 1997, Kurzejeski *et al.* 1993).

Objectives of this paper are: (1) to provide a review of the design of MOFEP, (2) to supply background information on the forest management treatments, and (3) to critique MOFEP so that others might learn from our experiences when designing similar projects in other ecosystems. Our goal is to provide information about things that we have done right and those that we have done wrong.

THE MOFEP DESIGN

MOFEP was initiated in 1989 to investigate forest management effects on the forest and wildlife community of the Missouri Ozarks (Brookshire *et al.* 1997). In designing MOFEP,

we used experimental design techniques emphasizing the manipulative or hypothetico-deductive approach for hypothesis testing (Sheriff and He 1997). The manipulative experimental approach employed in MOFEP allows for cause-and-effect relationships to be inferred (Eberhardt and Thomas 1991, Green 1979, James and McCulloch 1985, Romesburg 1981, White and Garrott 1990).

To be successful, an experiment must have five major components (Hurlbert 1984): (1) the hypothesis, (2) experimental design, (3) experiment execution, (4) statistical analysis, and (5) interpretation of results. If one of these elements is missing or completed poorly, doubt and suspicion can cloud the usefulness of the results in the decision process and compromise the value of the experiment.

The Hypothesis of MOFEP

MOFEP's null hypothesis is that no effects on ecosystem components, such as vegetative and animal communities, will be found due to the forest management practices used (Sheriff and He 1997). This hypothesis is a testable statistical hypothesis. It is reasonable and desirable to determine if forest management practices affect different components of the forest ecosystem. This null hypothesis, however, is also a nonsensical hypothesis, because we know that it is false from the beginning (Johnson 1999). By merely harvesting a single tree within a forested area, we affect the forest in some way. The challenge is to measure the impact and magnitude of this manipulation. The question also needs to be asked: does this manipulation create a significant biological difference even if a statistical difference can be found (Steidl *et al.* 1997)?

To defend the stated hypothesis of MOFEP, it is important to understand that it is testable and allows us the opportunity to learn about the uncertainties associated with forest management. By testing this hypothesis, we can learn about the magnitude of differences, the temporal aspect of effects, the ways in which different forest management practices diverge and converge through time, and their similarities and differences. The time series of data derived from each experimental unit is important in our understanding of how the null hypothesis is shown to be false during the statistical analysis phase of the experiment (more on this topic in the experimental design section).

The Experimental Design of MOFEP

The experimental unit chosen for MOFEP is the site (Brookshire *et al.* 1997). Each site is a large forested area typically managed as a unique administrative unit. Nine sites were defined for use in MOFEP in Carter, Reynolds, and Shannon Counties in the southeast Missouri Ozarks. This part of Missouri is approximately 84 percent forested. The area has not been glaciated and most soils have been exposed for more than 250 million years. Physical site characteristics are presented in detail by Meinert *et al.* (1997) and Kabrick *et al.* (2000). Selected sites had to be: (1) at least 600 acres in size; (2) in contiguous tracts with minimal edge; (3) largely free from manipulation for at least 40 years and preferably longer (i.e., less than 5% of area disturbed); (4) owned by the Missouri Department of Conservation (MDC); (5) located in the southeast Missouri Ozarks; and (6) in close proximity to each other. Sites were selected following a search of MDC inventory records, discussions with local site managers, and numerous aerial and field evaluations (Kurzejeski *et al.* 1993). Additional description of the study area is provided by Brookshire *et al.* (1997), Brookshire and Hauser (1993), Brookshire and Shifley (1997), and Shifley and Brookshire (2000) (fig. 1). MOFEP experimental sites are analogous to forest compartments and each includes between 41 and 70 forest stands.

Three forest management practices were defined as treatments (Brookshire *et al.* 1997): uneven-aged management, even-aged management, and no-harvest management. The nine sites were visually inspected to determine if like sites could be blocked to aid in the efficiency of the experimental design. Through these observations, three blocks containing three sites each were made. A randomized complete block design (Steel and Torrie 1980:196-197) was used to assign treatments to sites within each block (Sheriff and He 1997).

To strengthen the design and increase the "learning power" from MOFEP, data were collected in the 5 years before treatments were begun. These pre-treatment data are critical to understanding the impacts of the three forest management practices (Sheriff and He 1997). For example, if information from MOFEP resembled that shown in figure 2A, then we would conclude that forest management practice 2 had an impact. If data resembled those shown in figure 2B, then we would conclude that forest

management did not have an impact. If only post-treatment data were available, figure 2B would appear to indicate practice 2 had an impact. If results resembled those shown in figure 2C, then we might conclude that there was a confounding of effects due to the treatments or there was some broader ecological impact occurring at the time treatments were applied. Without the pre-treatment data, we might not even be aware of the phenomenon demonstrated in figure 2C.

The Execution of MOFEP

Treatments

The three forest management treatments compared in the MOFEP experiment are even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) (fig. 3). These treatments represent the range of silviculture practices applied on private and public lands in Missouri. Treatments are briefly described below; additional detail is available in Brookshire and Hauser (1993) and Brookshire *et al.* (1997).

Even-aged Management

Even-aged management followed MDC Forest Land Management Guidelines (1986), with a cutting rotation of 100 years. Under this management, approximately 10 percent of each site (i.e., each compartment) is left as old growth and reserved from harvest in perpetuity. In the remainder of the site, the desirable tree size class distribution is 10 percent seedlings, 20 percent small trees (2.5 to 5.5 in. or 6 to 14 cm diameter at breast height (d.b.h.)), 30 percent poles (5.6 to 11.5 in. or 14 to 29 cm d.b.h.) and 40 percent sawtimber (>11.5 in. or 29 cm d.b.h.). To achieve this size distribution, regulated harvests of 10-12 percent of the area per entry are done on a 10- to 15-year re-entry period. Harvest prescriptions follow Roach and Gingrich (1968). For MOFEP's first entry into even-aged managed sites, clearcutting was used to regenerate stands scheduled for harvesting. With clearcutting, nearly all trees are cut down except for some snags or den trees left to provide wildlife shelter and for some shortleaf pine (*Pinus echinata* Mill.) left to provide seed for pine regeneration. Non-merchantable trees that were not harvested are cut down during slashing operations following commercial harvesting.

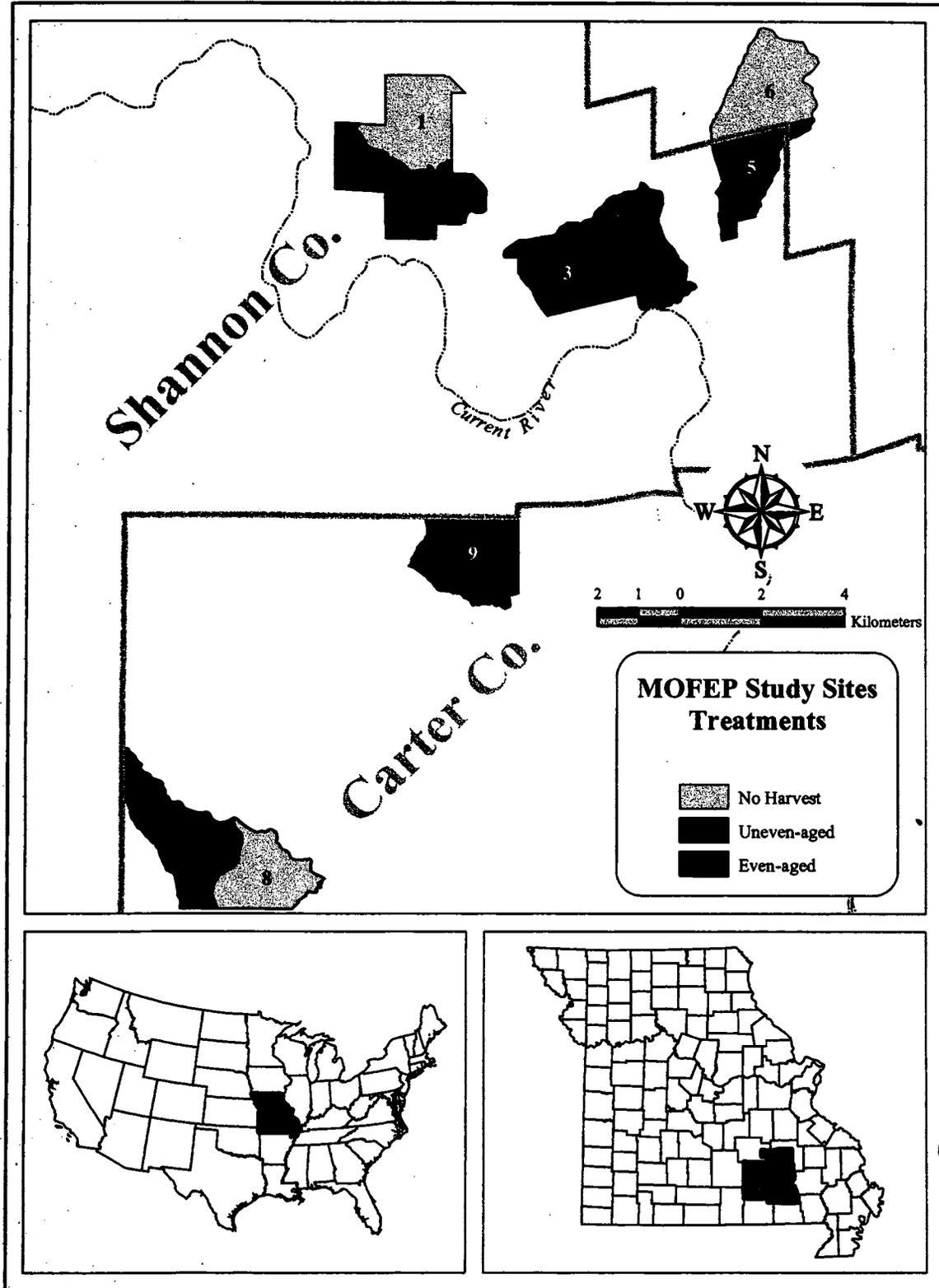


Figure 1.—Location of the nine MOFEP experimental sites (compartments) and their assigned treatments. See figure 3 for additional detail about each site.

Post Treatment Results of the Landscape Experiment

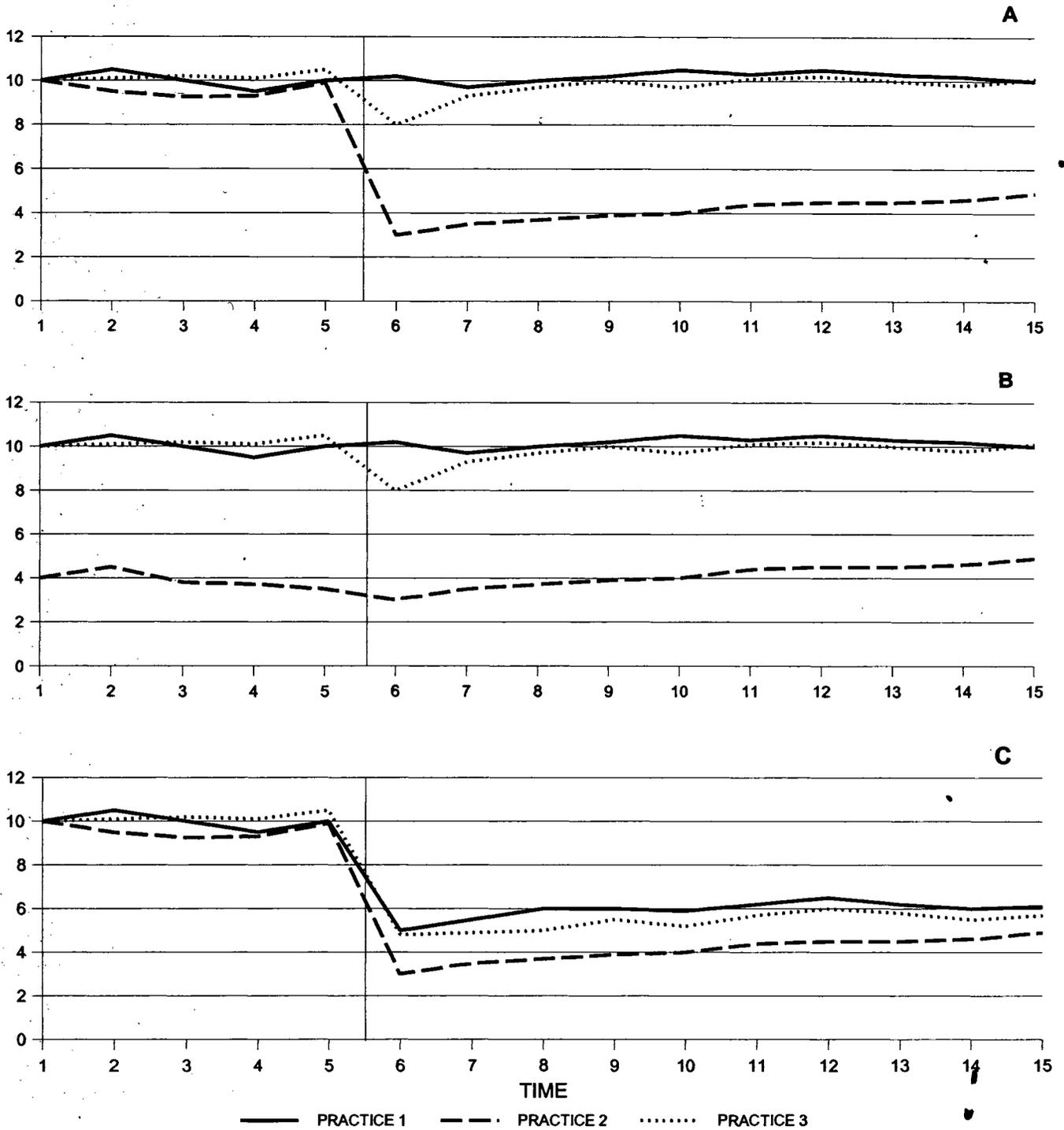


Figure 2.—Illustration of results from three experimental studies showing importance of pre-treatment data. Illustration A shows a treatment effect for practice 2, whereas illustration B has no treatment effect. Illustration C shows a possible confounding of treatments or a broad ecological effect at the time of treatment. Vertical line between period 5 and 6 shows when treatment was applied.



Data Collection Location Legend

- *Permanent Weather Station* (Chen et al., 1997¹)
- *Sampled Soil Profile* (Meinert, 2001²)
- × *Soil Nutrient Sample* (Spratt)
- ⊕ *Soil Nutrient Sample, Watershed Study* (Spratt)
- ▼ *Litter Invertebrate Sample* (Weaver and Heyman, 1997¹)
- ◇ *Canopy Invertebrate Sample* (Marquis et al.)
- *Genetic Sample* (Apsit et al.; Guyette and Kabrick)
- *Hard Mast Sample Plot* (Vangilder, 1997¹)
- *Vegetation Plot With Armillaria Sampling*
(Bruhn et al.; Grabner and Zenner; Kabrick et al.; Dey and Jensen;
Jensen and Kabrick; Guyette and Kabrick)
- *Vegetation Plot*
(Dey and Jensen; Grabner and Zenner; Jensen and Kabrick; Kabrick et al.;
Guyette and Kabrick)
- ▲ *Herpetofaunal Array* (Renken and Fantz; Guyette and Kabrick)
- ∩ *Bird Transect* (Clawson et al.; Guyette and Kabrick)
- *Small Mammal Sample Grid* (Fantz and Renken)
- *Uneven-aged Management Stands* (Sheriff)
- *Even-aged Management - Clear Cut Stands* (Sheriff)
- *Even-aged Management - Intermediate Cut Stands* (Sheriff)

¹ See Brookshire, Brian L.; Shifley, Stephen R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: An Experimental Approach to Landscape Research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station

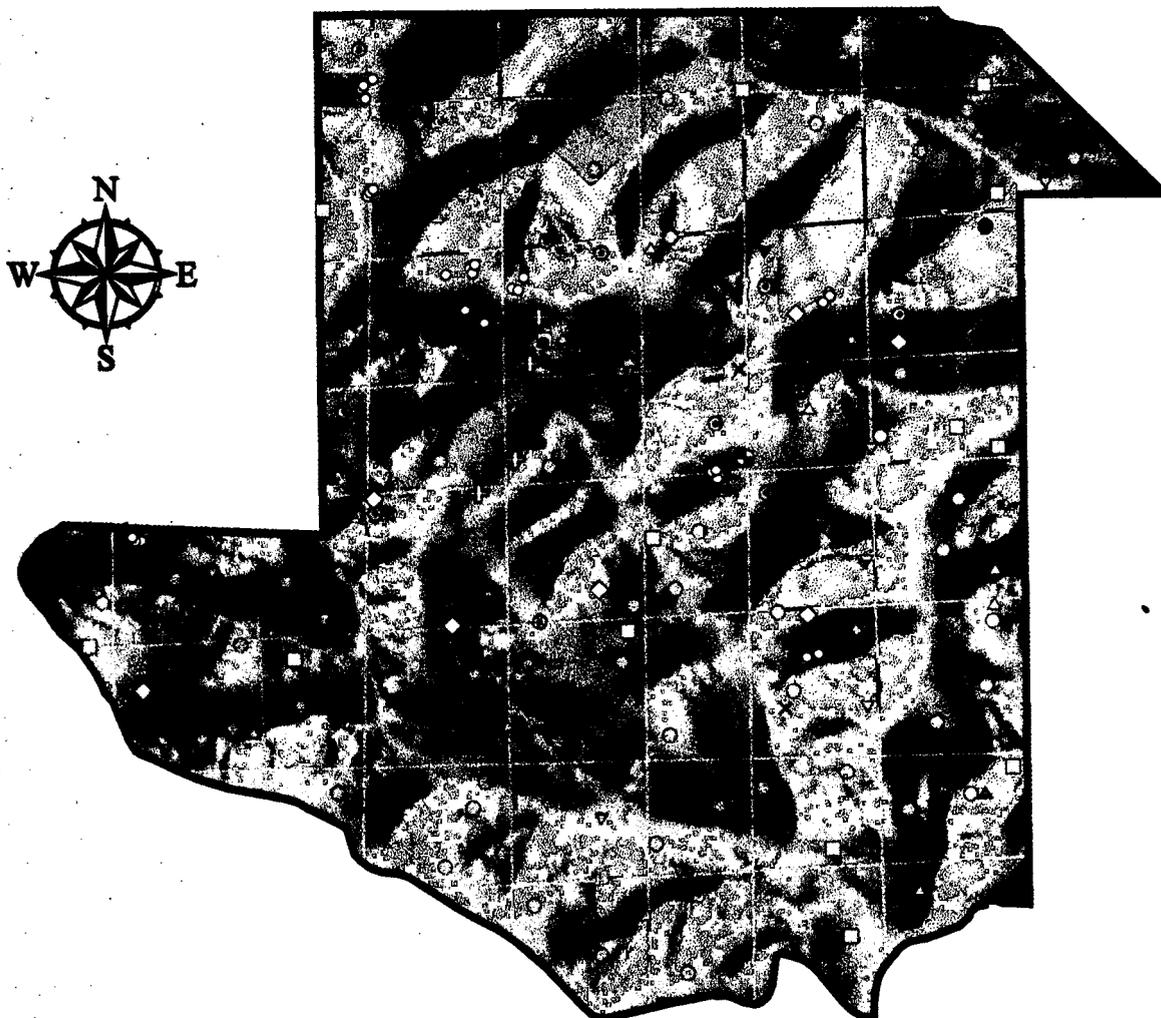
² Meinert, D.M. 2001. Soils-Geo-Landform Relationships and the Missouri Ozark Forest Ecosystem Project. Missouri Department of Conservation Publication.

Figure 3.—The nine MOFEP sites (nine maps plus a legend) showing the areas treated by clearcutting or intermediate thinning (even-aged treatment) and by individual-tree selection or group selection (uneven-aged treatment). Sampling locations for all the associated MOFEP studies are also shown. The legend indicates sources of more information about methods and results for the various studies. When the legend lists an author without a publication date, the reference is to another paper included in this proceedings. See figure 1 for the general location of each site, and see table 1 for a summary of harvested volumes and areas.

Site 1

Data Collection Locations

(Block 1 - No Harvest Management - 389 ha)

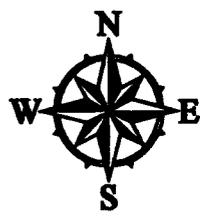
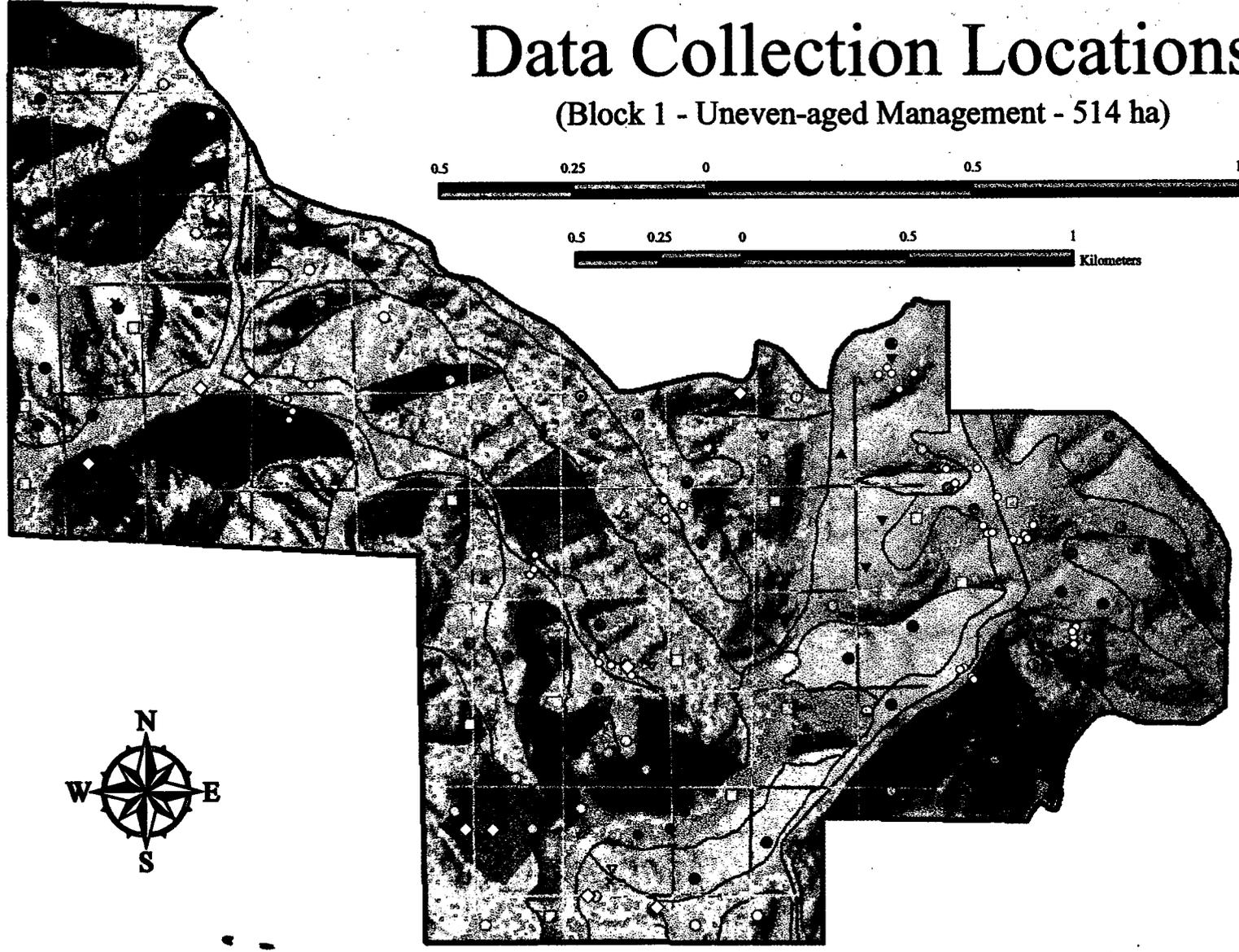




Site 2

Data Collection Locations

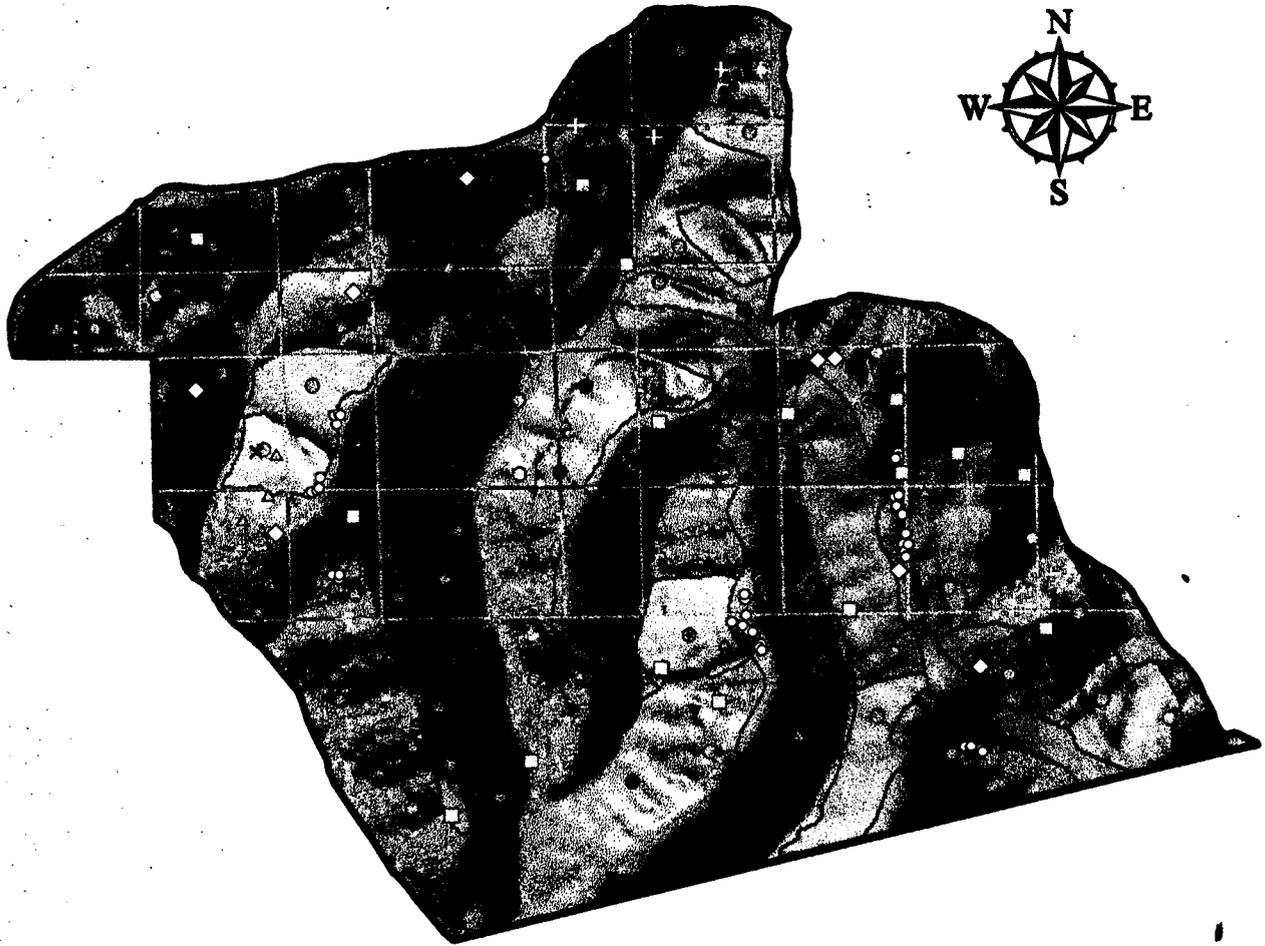
(Block 1 - Uneven-aged Management - 514 ha)



Site 3

Data Collection Locations

(Block 1 - Even-aged Management - 360 ha)

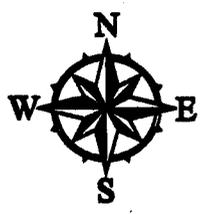




Site 4

Data Collection Locations

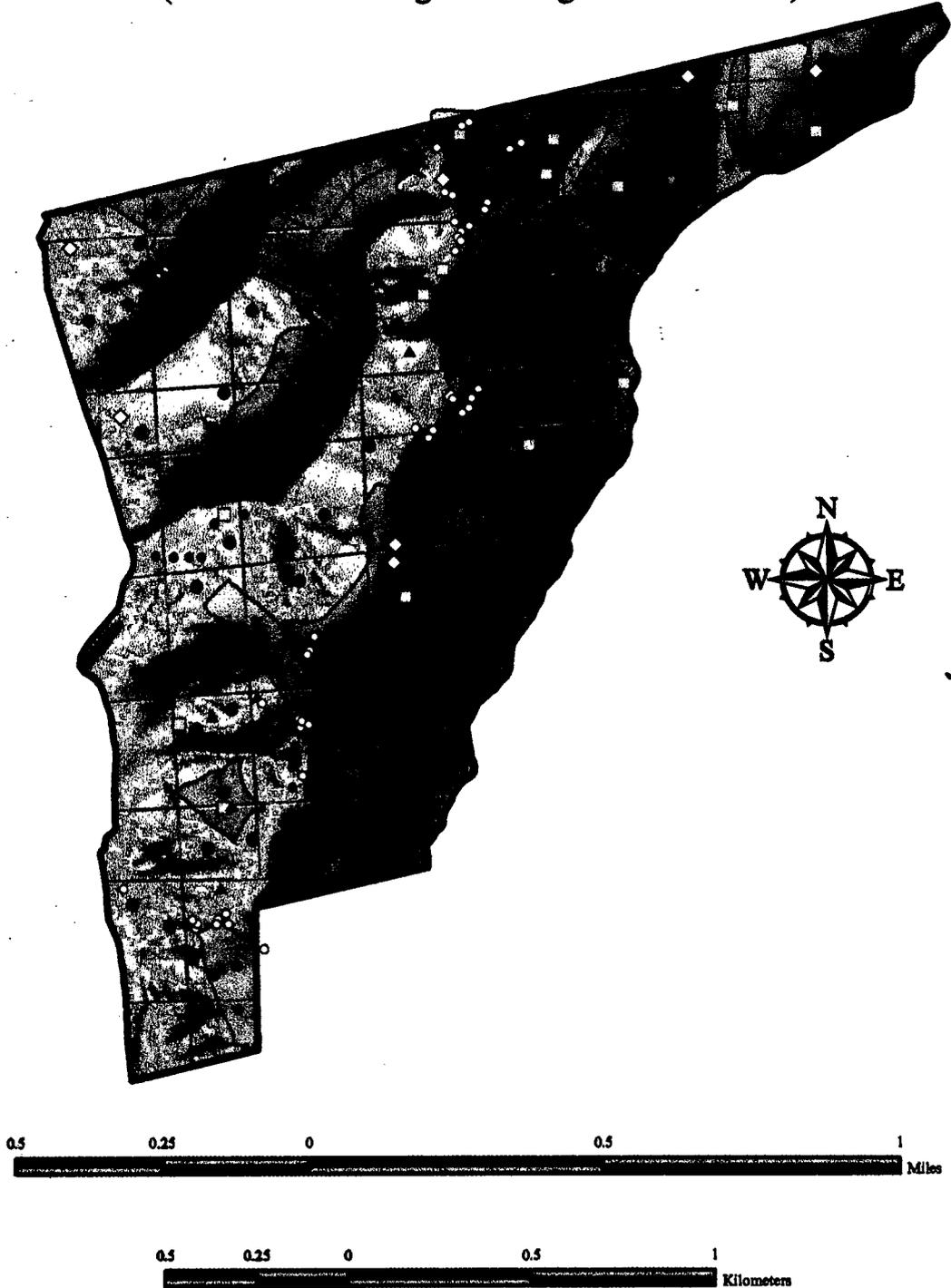
(Block 2 - Uneven-aged Management - 479 ha)



Site 5

Data Collection Locations

(Block 2 - Even-aged Management - 312 ha)

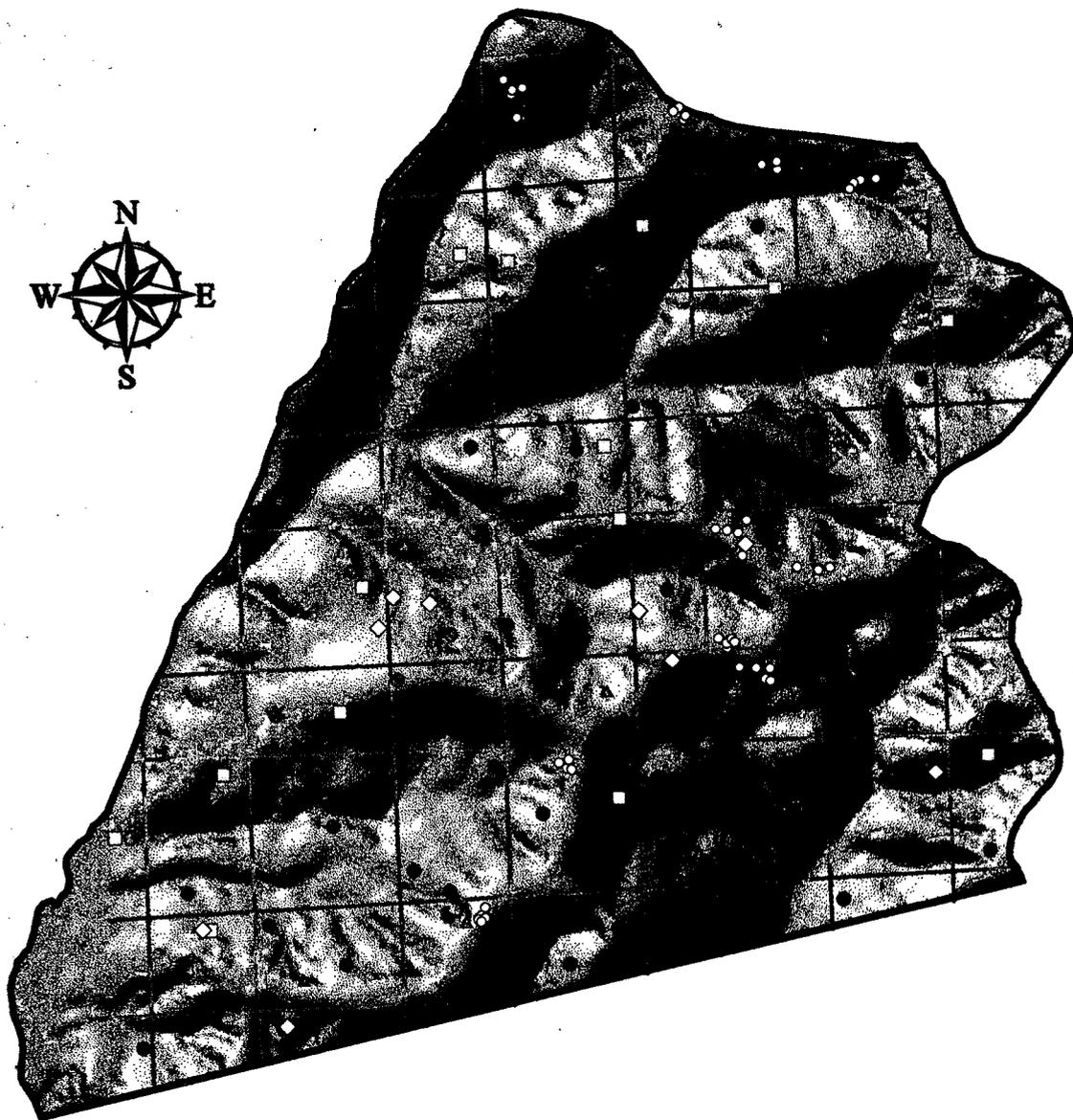




Site 6

Data Collection Locations

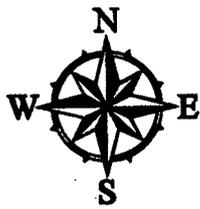
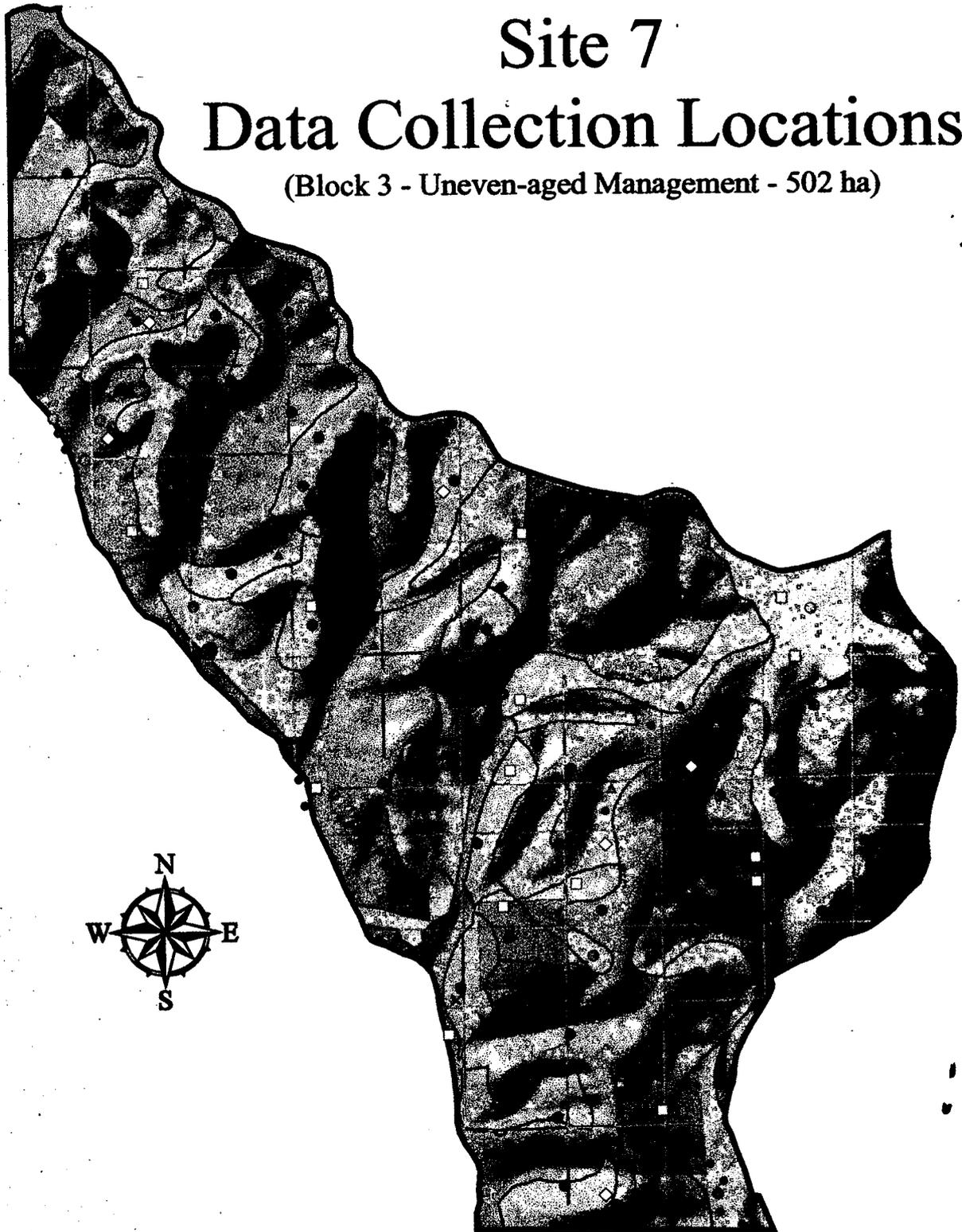
(Block 2 - No Harvest Management - 440 ha)



Site 7

Data Collection Locations

(Block 3 - Uneven-aged Management - 502 ha)

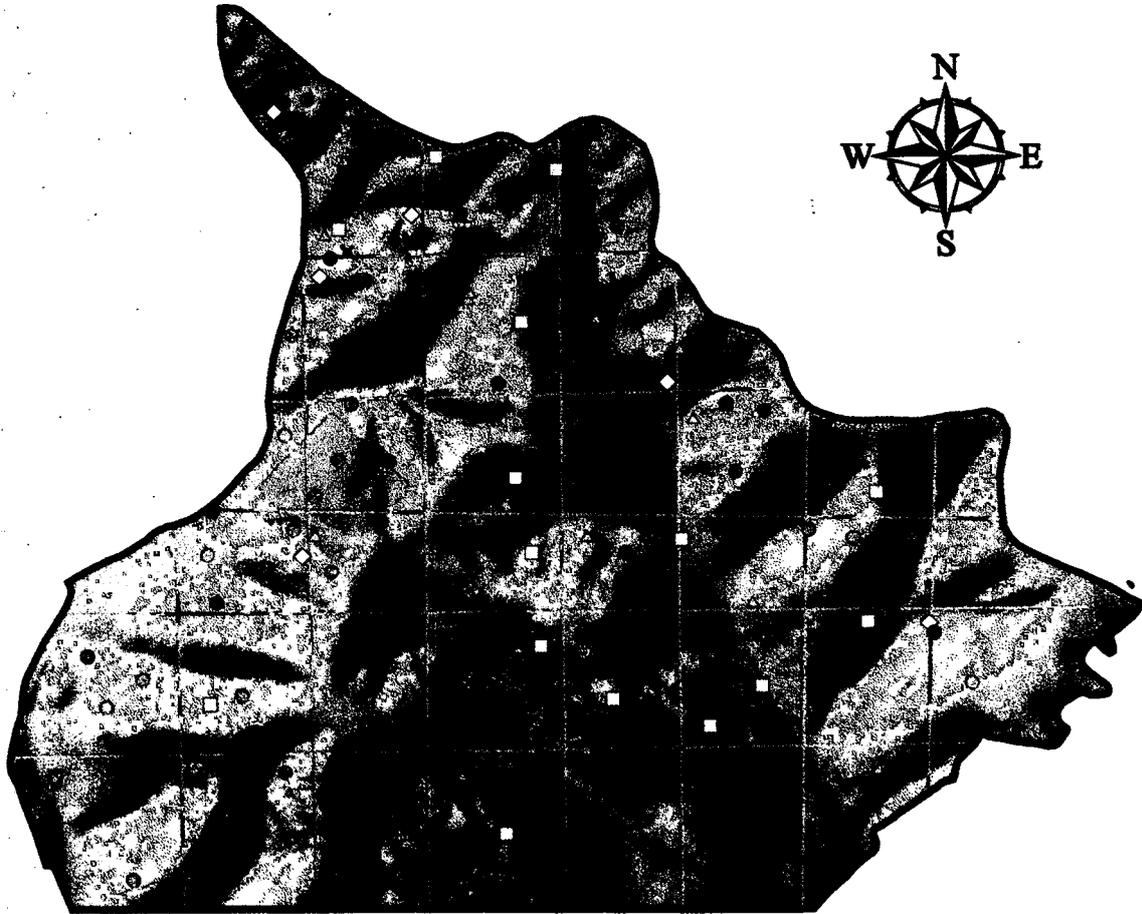




Site 8

Data Collection Locations

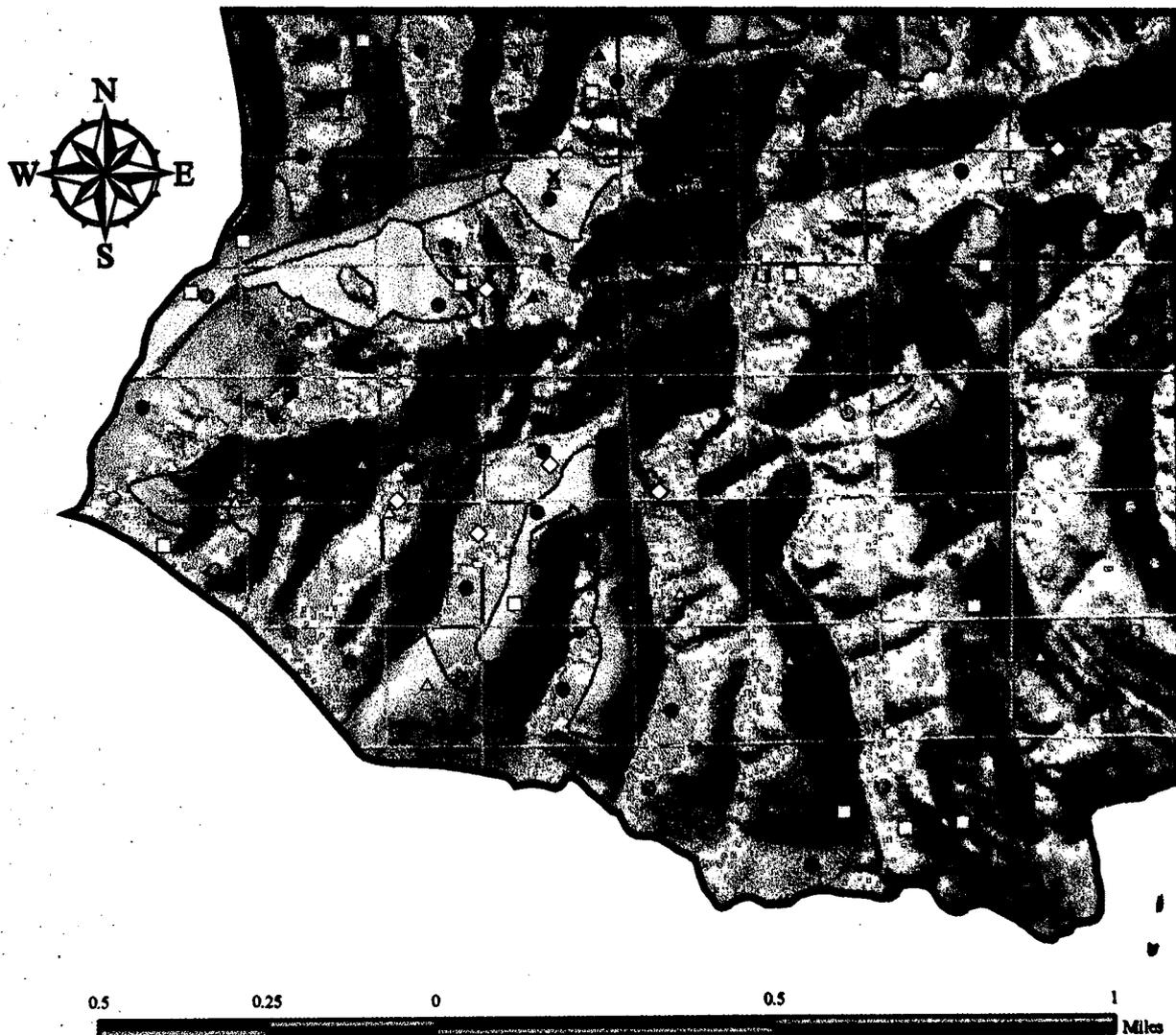
(Block 3 - No Harvest Management - 340 ha)



Site 9

Data Collection Locations

(Block 3 - Even-aged Management - 462 ha)





At MOFEP sites, stands with trees least likely to survive until the next re-entry in 10-15 years were selected first for harvest. Remaining stands needing regeneration were deferred to the next entry. Selected stands with site index > 55 (base age 50 years) were treated with intermediate harvesting (also called thinning) according to Roach and Gingrich (1968). These stands had high stocking rates and were made up of predominately immature sawtimber or poletimber that would benefit from thinning. Removals focused on mature trees and undesirable immature sawtimber and poles. Mature tree size class varies by site. The mature size class for red oaks was usually within the range of 18 to 22 in. (46 to 56 cm) d.b.h. while mature white oaks were usually between 20 and 24 in. (51 and 61 cm) d.b.h. The mature size class for each stand was determined during the inventory process. Stands treated with intermediate cutting in this first cutting cycle will be clearcut in later re-entry periods during this first 100-year rotation. Glades, food plots, ponds, and other amenities were managed according to the 1986 MDC Forest Land Management Guidelines (Missouri Department of Conservation 1986).

Uneven-aged Management

Uneven-aged management was also implemented using MDC Forest Land Management Guidelines (1986) with stand treatments following Law and Lorimer (1989). Approximately 10 percent of each site was designated as old growth in perpetuity, and the remaining 90 percent was managed using uneven-aged silviculture. Each UAM site was divided into management units of 20 to 80 ac (8 to 32 ha), and management objectives were set for largest diameter tree (LDT), residual basal area (RBA), and q-value. The LDT objective was equal to the desired sawtimber size objective for an identical stand under EAM. An overall RBA equivalent to B-level stocking was chosen, with adjustments made to anticipate for logging damage (Roach and Gingrich 1968). Q-value objectives for 2-in. diameter size class ranged from 1.3 to 1.7 (Law and Lorimer 1989). The target tree size class distribution for UAM was identical to the composite size class distribution across the EAM sites. Treatments on UAM sites are timed to coincide with treatments on EAM sites.

Uneven-aged management on MOFEP includes both single-tree selection and group selection for timber harvest and regeneration (Law and

Lorimer 1989). Single-tree selection is used to improve stand quality and to regulate tree size distribution. Group selection is included because canopy gaps created with single-tree selection are usually not large enough to regenerate tree species that are intolerant or intermediate in shade tolerance such as most oaks (*Quercus* spp.) and shortleaf pine (Law and Lorimer 1989). With group selection, small openings are created. The guidelines we use at MOFEP recommend creating group openings 70 ft (21 m) in diameter (i.e., approximately one tree height) on south-facing slopes, 105 ft (32 m) in diameter on level areas, and 140 ft (43 m) in diameter on north-facing slopes (Law and Lorimer 1989). The total area of group openings on MOFEP sites was to be approximately 5 percent of the total area harvested during the first entry.

No-Harvest Management

Sites under no-harvest management are not manipulated. Natural catastrophic events, including tornadoes, fires, insects, or disease, will be treated as if on any other State-owned forest land, except that salvage harvests will not occur. Wildfires will be suppressed and areas will not be exempted from control measures applied to surrounding areas in the event of a large-scale damaging insect outbreak. This treatment serves as an experimental control treatment in this project (Sheriff and He 1997).

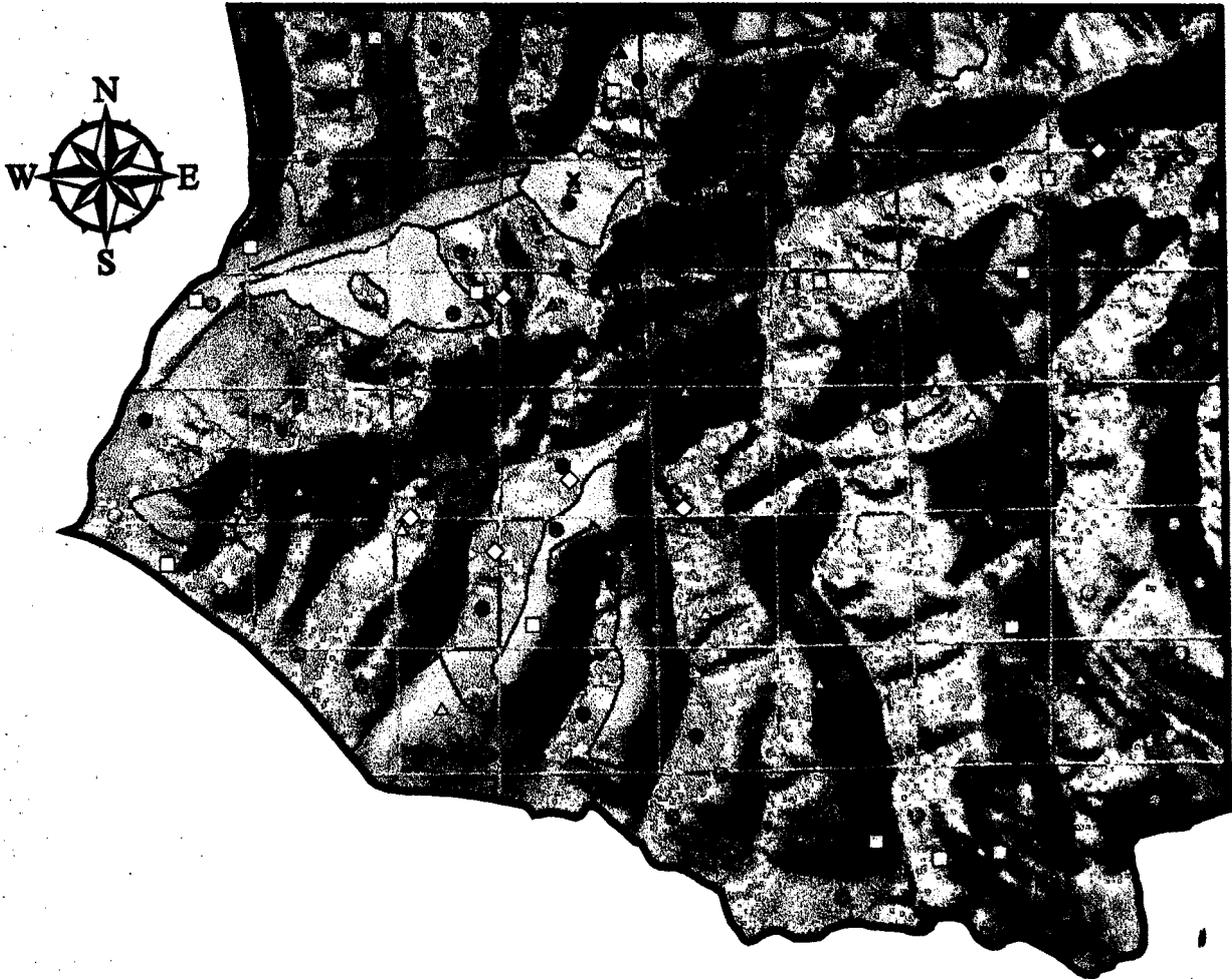
Implementation

The best experiment can be designed to answer a hypothesis, but if the experiment is not conducted the hypothesis will remain untested. During the summer of 1991, pre-treatment data collection began for many of the ecosystem component studies, and it continued until May 1996. From May to October 1996, commercial timber harvest was done on the even-aged management and uneven-aged management treatment sites. Removal of non-merchantable stems marked for slashing according to the silvicultural prescriptions occurred during or after commercial harvesting and was finished in May 1997 (Brookshire *et al.* 1997). For site 7 on Peck Ranch, slashing was done concurrent with the commercial timber harvest. Due to safety concerns during the harvesting operation, many principal investigators did not collect data during this period. Data collection resumed in

Site 9

Data Collection Locations

(Block 3 - Even-aged Management - 462 ha)



May 1997. Nearly 5,896,000 board feet of commercial timber were removed from these six sites during this 1-year period (table 1).

A unique feature of MOFEP concerns the protocols for the even-aged management and uneven-aged management treatments. Forest managers were allowed to prescribe treatments within broad definitions using state-of-the-art practices at the time of harvest. Brookshire *et al.* (1997) described the process for developing these prescriptions for the 1996/1997 harvest period. As we learn from MOFEP studies, forest managers will be allowed to adjust their thinking and prescriptions within the broad definitions of even-aged management and uneven-aged management. The experimental design allows for this flexibility as long as harvesting of timber from each of the six sites assigned to these two treatments occurs simultaneously during the same year and period of time (Sheriff and He 1997). Natural catastrophic events, including fires, insects, disease, or tornadoes, will be treated on MOFEP sites as on any other MDC-owned forest land, but no salvage harvests will occur on the no-harvest treatment sites (Brookshire *et al.* 1997:19).

During the pre-treatment phase, 28 individual studies were associated with MOFEP (Brookshire *et al.* 1997:23) (fig. 3). It is through these studies that knowledge about the impact of forest management will be gained.

The Statistical Analysis of Data from MOFEP

Many of the independent ecological studies conducted during the pre-treatment phase of MOFEP used the randomized complete block design as a basis for their statistical analyses (Brookshire and Shifley 1997). A common analytical approach for the pre-treatment data was to use the basic two-way analysis of variance presented by Sheriff and He (1997:29-32). For data collected after the treatments were completed in 1997, Sheriff and He (1997) recommended several approaches for the analysis of post-treatment data conditional on pre-treatment information. The simplest approach is to pool the pre-treatment data within each site and to pool data from the post-treatment period, find the difference between the post-treatment and pre-treatment means by site, and use these resulting estimates in the two-way or split-plot analysis of variance approaches (Sheriff and He 1997:30-31). Sheriff and He (1997) also advocated an indexing approach for adjusting each year's post-treatment data by the pre-treatment responses, and then using a profile analysis of repeated measures (von Ende 1993). If pre-treatment data are not available, then the post-treatment data would not be adjusted in relation to pre-treatment conditions.

These approaches recommended by Sheriff and He (1997) do not take advantage of the complexity in the full data set, especially when post-treatment data are being analyzed without adjusting for pre-treatment conditions. The full

Table 1.—Acres within each MOFEP site, assigned forest management practice, acres harvested, and tree volume (in thousands of board feet) taken from each MOFEP management unit

Site	Acres in site	Forest management practice	Acres harvested	Volume of timber harvested in 1996/1997
1	960	No-harvest	0	0
2	1,275	Uneven-aged	876	1,146
3	892	Even-aged	304	754
4	1,186	Uneven-aged	735	952
5	775	Even-aged	256	927
6	1,086	No-harvest	0	0
7	1,242	Uneven-aged	513	1,344
8	839	No-harvest	0	0
9	1,141	Even-aged	172	773
Total	9,397		2,856	5,896



repeated measures design across the boundary between pre-treatment and post-treatment cannot be taken advantage of due to the "pseudo-treatment" effects in the pre-treatment data (Sheriff and He 1997:31). Therefore, further statistical development must occur to incorporate this complexity in the full data set.

Fortunately, work is occurring in this area, and Reiczigel (1999) showed that this problem may have a potential solution. This approach breaks the analysis into two steps. In the first step, the repeated measures from individual sites are examined. The time series coverage for a site is examined to determine the baseline length, the minimum or maximum value, and the time to this value. This is done using moving averages. In the second step, standard statistical methods are used to compare differences among groups or treatments. At this time the method of Reiczigel (1999) has not been fully explored to ensure that it is directly applicable to the MOFEP case, but it is encouraging to see such developments. Future statistical development will need to occur throughout the life of MOFEP to provide more information that is more useful to natural resource managers.

Beyond the null hypothesis testing approach, methods of statistical estimation and statistical modeling can also be quite useful. Vangilder (1997) used both hypothesis testing and statistical estimation in examining acorn information from MOFEP. Through the estimation approach, estimates of precision for parameter estimates can be determined by site. Using statistical modeling with these data, one can explore ecological theory to determine factors influencing these estimates (Shenk and Franklin 2001). Information-theoretical methods may be particularly useful for model selection and in data exploration for hypothesized relationships (Burnham and Anderson 1998). Models that show relevant hypothesized relationships are the basis for further research and experimentation.

The Interpretation of Results from MOFEP

Depending upon the researcher's desires, the proper statistical analysis should lead to proper interpretation of results for the intended audience. Sheriff and He (1997:33) addressed the issue of whether blocks were fixed or random effects (Littell *et al.* 1996) when interpreting results for decision making that would affect

forests in the Missouri Ozarks (Xu *et al.* 1997). This issue is important to the usefulness of results.

The interpretation is also restricted by the temporal nature of MOFEP. Because MOFEP may have a life of 300 or more years, data and results interpreted during this first phase should not be considered the definitive answers to forest management issues. In fact, these results may not be good long-term predictors of impacts that the three forest management practices might have upon forest ecosystems. Temporal variation due to abiotic and biotic factors during this relatively short period in the life of MOFEP may be unusual and have only immediate impact. Therefore, the commitment to MOFEP and its long-term nature should be emphasized for gaining reliable knowledge about long-term effects.

If we keep the long-term nature of MOFEP in mind, short-term results and interpretation can help us develop predictions that can facilitate learning in the future. Results from hypotheses tested as well as results from statistical estimation and modeling can be used to develop sound predictions for forest managers. These predictions can also be used as hypotheses or models for development of theory that can be tested during the life of MOFEP. Forest managers should use these predictions in their planning for each re-entry (future harvest). Models can be built based upon this information to test different adjustments to silvicultural prescriptions within the even-aged management and uneven-aged management protocols. As forest managers focus on a specific objective for their management, they can use adaptive management procedures (Walters 1986).

LESSONS LEARNED FROM MOFEP

MOFEP has already taught us many lessons. Our decision to design MOFEP as an experiment has proven to be a vital one. By developing MOFEP as an experiment as opposed to an observational study, we are able to test hypotheses instead of confirming or developing hypotheses. Through hypothesis testing we are able to learn much more rapidly than through a succession of observational studies and model-based predictions. In a forest ecosystem where the generation time is long, observational studies and model-based predictions require

significantly more time to gain knowledge about the impact of forest management. The experimental approach allows us to determine cause-and-effect relationships.

Because of randomization and replication in assigning forest management practices to landscape scales typically used by forest managers (i.e., MOFEP sites or compartments), the inferential basis for individual studies is applicable at a scale usable by and familiar to forest managers. Studies that focus on timber stands within a forest management unit, such as soil compaction studies (Ponder 1997), the DEMO project with 420 ac (180 ha) for each replication of six treatments (Franklin *et al.* 1999), and the study of environmental effects at the stand level in Arkansas (Baker 1994), are limited in their scope and meaning to forest managers. These smaller scale studies can provide data only at a limited spatial scale, which may not be applicable at larger ecological scales. MOFEP's broader scope allows forest managers and wildlife scientists to learn about how larger forest communities react to operational forest practices at a scale relevant to the forest community and management. Replication of forest management practices allows comparisons across a wider range of forest conditions. Randomization ensures that biases occur by chance.

Lessons learned by mistakes are often memorable and important in helping others. In designing MOFEP, we made many memorable errors that may be valuable lessons for others. Not enough time seems to go into planning any project or study, which usually is evident to investigators after a study is implemented and a field season or two has passed. At that point, it is not easy to go back and redesign the study, but one must go on with the established protocol and make recommendations to future researchers. This is also true for MOFEP, but we are fortunate to be able to offer some wisdom now.

Several problems have become evident. The first of our problems concerns the selection of experimental units. In the late-1980s, most forest management units (administrative compartments) were under active forest management. Few sites were available that met our criteria for selection as satisfactory experimental units (Brookshire *et al.* 1997:2). Therefore, the number of replicates to which we could

apply treatments was limited. MOFEP probably consists of the last nine or so sites that met our criteria for selection in the southeastern Missouri Ozarks. The lesson learned was the value of having large areas where active natural resource management is not conducted, except under a designed experiment or adaptive resources management process (Walters 1986, 1993).

Another lesson we have learned concerns the selection of studies conducted on MOFEP sites. Rigorous planning for the integration of information derived from different ecosystem component studies was not done before pre-treatment data collection began. Therefore, the task of data integration from different MOFEP studies has not been easy (Gram *et al.* 1997). Our failure was in the selection of sampling scale and coordination of sampling plots among individual studies. Several of the studies required that researchers restrict their sampling to limited locations within a site so that it would be practical to accomplish their work at a reasonable cost (e.g., Marquis and Le Corff 1997, Renken 1997, Weaver and Heyman 1997). As MOFEP progresses, we also see a need for additional studies that were not begun during the pre-treatment phase. The MOFEP steering committee has identified several of these studies—for example, on nutrient cycling (Missouri Department of Conservation 1999).

To avoid these problems of sampling scale, coordination of sampling plots, and the need for additional studies, a modeling approach might have been developed during MOFEP's planning phase. Ecological models could have been developed to examine ecosystem components, such as vegetation, animals, and abiotic factors (e.g., microclimate and soil nutrients), that might be sensitive to different forest management practices. Interactions of ecosystem components could have been built into these models to examine how a single component affects other components. These models could have been developed based on knowledge derived from the literature and through principal investigators developing hypothesized ecosystem linkages from ecological theory. During these modeling exercises, important ecosystem components could have been identified to ensure that critical components would be studied to decrease our uncertainty of their value in the forest ecosystem complex. GIS-ecosystem modeling could also have been used

their prescriptions of uneven-aged management and even-aged management, and to compare outcomes from these practices with those of the no-harvest management option. The results and lessons from MOFEP can be used by other researchers and managers to design similar management experiments. The key is commitment to doing long-term management and research so that learning can occur as rapidly as possible. This commitment requires many resources, such as available landscapes for conducting these studies, financial support, and enthusiasm to learn and apply the knowledge gained.

The lessons we have learned from MOFEP can readily be applied to any ecological study of management practices (Resetarits and Bernado 1998). These issues are not unique to MOFEP, but they are common to all large-scale experimental research projects (Brown 1998). The shortcomings, such as heterogeneity within blocks, low statistical power, brevity of our pre-treatment data collection period, lack of temporal variation, and potential problems with integration of studies, that we have experienced with MOFEP do not detract from the overall benefits of conducting this large-scale experiment. MOFEP provides an extremely valuable examination of hypotheses concerning the impact of management practices in the Missouri Ozark forests. Cause-and-effect relationships are being determined—relationships that could only be hypothesized through observational studies. Instead of guessing that forest management has a certain impact, we will be able to demonstrate it or show that it did not occur across replicated sites. This knowledge will aid forest and wildlife managers in the future as they perpetuate the Missouri Ozark forests in a sustainable state.

SUMMARY

MOFEP is a unique ecological study. It is designed as an experiment to evaluate changes in ecosystem components as impacted by different forest management practices. The experimental treatments are three different forest management practices advocated for sustaining an oak-hickory forest in the southeastern Missouri Ozarks: (1) even-aged management, (2) uneven-aged management, and (3) no-harvest management. The experiment is occurring at a large landscape scale typically used as administrative units in managing forests under the ownership

of the Missouri Department of Conservation. These forest management units, which are used as experimental units in this project, are normally over 600 ac (242 ha) in size. For MOFEP, we are using nine of these sites, which are all over 772 ac (312 ha). These sites were placed into three homogeneous blocks. The randomized complete block design was used to assign treatments within blocks.

Another unique feature of MOFEP is that forest managers can adjust their state-of-the-art application of the three treatments as they learn from this project or through other sources. Therefore, the even-aged and uneven-aged management practices will reflect state-of-the-art application at the time of re-entry for timber harvest. This feature is necessary to allow forest managers to learn from their experiences and adjust their practices. Therefore, results from MOFEP will be a record of how changes in forest management practices as applied by MDC have impacted the ecosystem components being studied.

The necessary ingredient to maintain MOFEP as a successful long-term management-experiment is commitment. Investigators, administrators, and forest managers must maintain their long-term commitment of resources (financial support and land) and interest in this project. Otherwise, if MOFEP is stopped because of the lack of commitment, the investment in understanding the impact of the three management practices on Missouri Ozark forests will be lost. MOFEP has a theoretical life of three full rotations of each management treatment. If a rotational period is considered to be 100 years for the oak-hickory forest, then the life of MOFEP could extend 300 years. This length of time is mind-boggling, but the knowledge gained through this long-term experiment will be extremely valuable throughout the life of MOFEP. Therefore, this information will be invaluable to wildlife and forest managers for generations yet to come.

Lessons learned from our experiences with MOFEP will help others as they implement large-scale experiments in other ecosystems. One of the key lessons we learned was that adequate planning helps avoid many shortcomings and problems. Planning these types of studies requires a team effort to ensure that all aspects of a project like MOFEP are taken into account (Resetarits and Bernardo 1998). The most important lessons learned from MOFEP



concern the value of the experimental approach for gaining knowledge for management. Determining the cause-and-effect relationships of management actions to response in ecosystem components provides information about the impact of an action without continuously guessing about the hypothesized impact. Planning and use of the experimental design methods will ensure that ecosystem projects will succeed and that knowledge will be gained from all aspects of these projects.

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The Legacy and Continuity of Forest Disturbance, Succession, and Species at the MOFEP Sites

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Abstract.—Information about the scale, frequency, and legacy of disturbance regimes and their relation to the distribution of forest species is sparse in Ozark ecosystems. Knowledge of these relationships is valuable for understanding present-day forest ecosystem species composition and structure and for predicting how Missouri's forests will respond to management. Here, we generate a correlation matrix of diverse variables to evaluate the hypothesis that plant and animal species abundances at MOFEP are closely linked to historic disturbance regimes induced by long-term interactions between humans and topographic roughness. Abrupt ring-width reductions in shortleaf pine, fire frequency, and historical data were used to determine the frequency of disturbance. Disturbance variables are correlated with topographic roughness, forest bird territory density, lizard and skink captures, blueberry fruit abundance, *Armillaria* spp. abundance, and three indices of forest succession derived from overstory tree species, oak overstory species, and tree species ground flora. Disturbance history, species distributions, and tree species diversity at the MOFEP sites support the argument that long-term disturbance regimes and successional sequences are major factors affecting species and structure in Ozarks forests.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term study initiated to quantify the effects of standard forest management practices on forest flora and fauna (Brookshire *et al.* 1997, Brookshire and Hauser 1993, Kurzejeski *et al.* 1993). As such, MOFEP is focused on how the contemporary Ozark forest responds to silvicultural disturbances. Considerable effort has been devoted to quantifying contemporary plant and animal species distributions and ecosystem processes (cf. Brookshire and Shifley 1997). However, our understanding of the contemporary Ozark forests may be incomplete without knowledge of the natural and anthropogenic disturbances

that created these forests. For example, extensive timber harvests during the late 1800s and early 1900s followed by wildfire and overgrazing removed most of the native shortleaf pine (*Pinus echinata*) in the Ozarks (Cunningham and Hauser 1989, Galloway 1961, Krusekopf *et al.* 1921). Guyette and Dey (1997) estimated that the contemporary forests at MOFEP site 8 contain 66 percent less shortleaf pine than the pre-European forests. Moreover, there is evidence that natural and anthropogenic fire was an important disturbance of the pre-European forests in the MOFEP study sites (Guyette and Cutter 1997). These fires certainly affected forest composition, structure, and ecosystem function long before Europeans settled this region.

In addition to ecological significance, the scale, frequency, and legacy of disturbance regimes and their effects on the distribution of forest species also have important management, policy, and political implications. Debates about clearcutting versus selective cutting often hinge on what is "natural," or what was the pre-European disturbance regime. Managers and policy makers are often interested in mimicking

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natural disturbance regimes with silvicultural prescriptions to foster native plant and animal species diversity (Loucks 1970). Unfortunately, there is little quantitative knowledge about the scale, frequency, and spatial distribution of historic forest disturbance regimes and their legacy on the forest ecosystems of the Ozark Highlands.

The primary objective of this research is to quantify long-term forest disturbance regimes in the Current River Hills Subsection (Nigh *et al.* 2000) of the Ozark Highlands and to relate them to forest succession and plant and animal species associations at the MOFEP study sites. Specific objectives are to 1) quantify disturbance legacy using abrupt growth reductions in shortleaf pine, fire frequency based on a model by Guyette and Dey (2000), historical forest density, and historical grazing protection; 2) relate disturbance legacy to plant successional states; and 3) identify interrelations between disturbance legacy, successional state, and present-day plant and animal species abundance. The central hypothesis is that anthropogenic disturbance and topography have been major factors affecting disturbance frequency at the MOFEP sites and that historic disturbance regimes have a legacy that continues to affect contemporary plant and animal distributions today. Specifically, the roughness of the topography around a site mitigates the propagation of disturbance related factors (fire and logging) and increases the abundance of late-successional plant and animal species.

METHODS

The MOFEP study is described by Brookshire and Hauser 1993, Brookshire *et al.* 1997, and Kurzejeski *et al.* 1993. MOFEP experimental design is described by Sheriff and He (1997) and experimental treatments are described by Brookshire *et al.* (1997).

Quantifying Disturbance

We quantified four measures of disturbance for our analysis: shortleaf pine abrupt growth reduction intervals, mean fire intervals, an 1820 forest "openness" index, and a grazing protection index. Shortleaf pine abrupt growth reduction intervals were estimated using ring-width measurements of 14,801 annual rings from 98 trees on MOFEP sites. Abrupt growth reductions are defined as sudden ring-width reductions that are at least 15 percent of previous growth and that last for 7 or more years. Abrupt growth reduction return intervals are calculated as the number of growth reductions per years of tree growth. The years of record (number of years of growth) for each site (table 1) are the sum of the number of annual growth rings measured on each study site tree. The degree of each growth reduction was calculated by dividing the mean ring-width during the growth reduction by the mean ring-width before the growth reduction and multiplying by 100.

Table 1.—Data and statistics (means and standard deviations) that describe the frequency, degree, and duration of abrupt radial growth reductions in shortleaf pine. Standard deviations are given in parentheses.

MOFEP site number	Number trees	Years of record	Number growth reductions ^a	Reduction return interval (yrs)	Reduction degree (% growth)	Reduction duration (yrs)
1	5	855	2	427	62 (11)	11 (3)
2	13	1,960	6	327	53 (12)	20 (16)
3	13	2,174	8	272	52 (20)	19 (8)
4	9	1,318	4	329	50 (16)	16 (9)
6	9	1,137	5	227	41 (8)	25 (16)
7	11	1,785	21	85	58 (15)	26 (18)
8	4	596	7	85	52 (17)	16 (8)
9	11	1,619	8	202	57 (12)	24 (24)

^a Abrupt growth reductions are sudden ring-width reductions that are at least 15 percent of previous growth for at least 7 years.



Mean fire frequency was estimated with regressions developed from fire scar chronologies at 26 sites in the Current River watershed (Guyette and Cutter 1997, Guyette and Dey 2000) and fire frequency data derived from the MOFEP sites. Regression predictions of fire frequency are used since they are derived from a much larger set of data (26 sites) and a larger range of conditions than individual MOFEP site fire histories, some of which have limited fire scar data or are as yet incomplete. The regression used to predict past fire frequency at the MOFEP sites for this study is:

$$MFI = -442.1 + (449.9 \times \text{topo}) - (0.001 \times \text{pop}), \quad (1)$$

where: MFI = mean fire interval,
 topo = index of topographic roughness for a 5-km radius circle,
 pop = natural log of human population density times distance upstream,
 n = 78 (three time periods, 29 sites),
 R² = 0.51, variable and intercept significant at P<0.01.

All MFI estimates in this study are for the period of maximum variation in fire frequency between sites, which occurred during three early periods (1700-1780, 1781-1820, 1821-1850). Site-specific fire data from eight of the MOFEP sites are used to show topographic and fire frequency relationships at the MOFEP sites and in the correlation analysis with topographic roughness.

An index of forest openness in 1820—Openness Index (1820)—was constructed as a proxy for the frequency of disturbances that delayed forest succession at the MOFEP sites before European settlement. The index is based upon data compiled from Public Land Survey notes (Batek *et al.* 1999). The index uses two variables: the distance class to bearing trees and the number of survey lines described as open or with few trees. We normalized (divided by the mean) and averaged these variables to develop this index.

We estimated protection from disturbances caused by domestic livestock by calculating the percent of each MOFEP site that has been fenced. The length of fenced portion of the site perimeter was divided by the length of the total site perimeter and multiplied by 100. This index is called the Grazing Protection Index.

Topographic Roughness

The highly dissected topography of the Current River watershed has been shown to affect the spread and frequency of fires during periods of low human population density when anthropogenic ignitions were limited in number (Guyette and Dey 2000). Indices of topographic roughness were developed from the surface area measurements at two different scales (Krstansky and Nigh 1998). Land surface area of 30-m squares within circles of 900 and 5,000 m in radius was calculated and then indexed (divided) by the planimetric surface area of circles of 900 and 5,000 m in radius. The ratios of the actual surface area to the planimetric surface area are the indices of Topographic roughness. Thus, high index values mean the topography is hilly. There is about an 87-percent overlap of the 5,000-m radius circles at MOFEP sites that are adjacent to one another and no overlap of 900-m radius circles. Thus, the spatial data are not completely independent for the larger measure (5,000 m) and the p-values of the correlation coefficients may be biased.

Successional Indices

Successional indices for all overstory tree species (Overstory Successional Index) and for oaks (Oak Successional Index) were developed based on the shade tolerance of species. Data for developing these indices are from Kabrick *et al.* 1997. Indices of forest succession were created by summing the number of trees per hectare of shade tolerant (tolerant to intermediate), late-successional species and subtracting the numbers of trees per hectare of shade intolerant (intolerant to very intolerant), early-successional species (table 2). Many characteristics such as fire tolerance, seed size, and life history might be used to classify tree species into early- and late-successional classes, but are very difficult to quantify. Information on shade tolerance is both available (Abrams 1998, Burns and Honkala 1990, Kramer and Kozlowski 1979) and unbiased (at least with respect to this study), and shade tolerance is important in the succession of plant species under conditions of changing light levels. In addition, shade tolerance is inversely related to the compensation points and dark respiration among tree species. Shade intolerant species show the greatest plasticity in growth response

Table 2.—Successional indices based on the shade tolerance (Burns and Honkala 1990) of overstory tree species are the number of early-successional (right side of table) individuals (trees > 11.4 cm) subtracted from the number of late-successional individuals (left side of table).

OAK SUCCESSIONAL INDEX			
LATE SUCCESSION		EARLY SUCCESSION	
Species	Shade tolerance	Species	Shade tolerance
<i>Q. alba</i>	intermediate	<i>Q. coccinea</i>	very intolerant
<i>Q. rubra</i>	intermediate	<i>Q. stellata</i>	intolerant
<i>Q. velutina</i>	intermediate	<i>Q. marilandica</i>	intolerant

OVERSTORY SUCCESSIONAL INDEX (oaks+others)			
LATE SUCCESSION		EARLY SUCCESSION	
<i>Acer saccharum</i>	very tolerant	<i>Juniperus virginiana</i>	very intolerant
<i>Acer rubrum</i>	tolerant	<i>Pinus echinata</i>	intolerant
<i>Carya glabra</i>	intermediate	<i>Carya tomentosa</i>	intolerant
<i>Nyssa sylvatica</i>	tolerant	<i>Carya texana</i>	intolerant

to light (Kozlowski *et al.* 1991). Thus, because of their higher potential growth rates, shade intolerant species are more adaptive to early-successional stages in high disturbance environments. Competitive exclusion, reproductive strategies, and size-related fire effects on mortality favor their numbers during early-successional stages.

The Seedling Successional Index was developed for tree species under 1 m in height, using the data of Grabner *et al.* (1997). The frequency of plots with shade tolerant (and intermediate) versus shade intolerant tree species was differenced by subtraction. The sum of the number of plots at each MOFEP site that had shade intolerant species (*Quercus stellata*, *Quercus marilandica*, *Ulmus alata*) was subtracted from the sum of the number of plots with shade tolerant species (*Acer saccharum*, *Carya glabra*, *Ulmus rubra*, *Viburnum rufidulum*) to develop the Seedling Successional Index.

Many factors associated with disturbance, succession, and fire may affect the ecology and distribution of *Armillaria* spp. (Kile *et al.* 1991). We hypothesize that the spatial distributions of long-lived species such as *Armillaria* spp. (Bruhn *et al.* 2000) may reflect their adaptations for different host tree species, for live or dead woody substrate, and for certain fire effects, such as the removal of woody debris by burn-

ing. An *Armillaria* successional index was constructed by subtracting the percent of sites where *Armillaria mellea* was detected from the percent of sites where *Armillaria gallica* was detected. *Armillaria* data from Bruhn *et al.* (1997) were used to calculate the *Armillaria* Successional Index for the MOFEP sites.

Composite Successional Indices were constructed from MOFEP data based on normalized values of disturbance and species variables. Two composite indices were developed based on disturbance variables, species abundances, and characteristics. All variables were scaled so that the highest index values indicated the most advanced successional stages or had the longest mean disturbance-free interval. These indices are relative values with a mean of one. The disturbance-free interval index was calculated as the mean of normalized growth reduction return intervals, the normalized fire return intervals, the standardized protection from open range grazing, and standardized Government Land Office note data on forest openness (Batek *et al.* 1999). The Species Successional Index was calculated as the mean of the standardized values of the Overstory Successional Index, the Seedling Successional Index, the *Armillaria* spp. Successional Index, a standardized measure of five forest bird species nesting territories, a standardized measure of the abundance of five lizard species, and standardized blueberry fruit abundance.



Species Associations

Two years of blueberry abundance data at the study plots (Fantz and Hamilton 1997) were used to illustrate the effects of disturbance and succession on soft mass. Low bush blueberry (*Vaccinium vacillans*) data were used because of the abundance of this species across sites and the lack of an association between the abundance of this species and sitewide substrate.

Data of Clawson *et al.* (1997) on the abundances of five forest dwelling bird species (ovenbird, *Seriurus aurocapillus*; worm-eating warbler, *Helmitheros vermivorus*; Kentucky warbler, *Oporornis formosus*; wood thrush, *Hylocichla mustelina*; Acadian flycatcher, *Empidonax virescens*) were used in the correlation analysis. The total number of nesting territories of the five birds species was also used in the correlation analysis.

Data on reptile and amphibian captures from Renken (1997) were used in the correlation analysis. The total numbers of captures of four skinks (broadhead skink, *Eumeces laticeps*; coal skink, *Eumeces anthracinus*; five-lined skink, *Eumeces fasciatus*; ground skink, *Scincella lateralis*) and one lizard species (fence lizard, *Sceloporus undulatus*) commonly found at the MOFEP sites were also used in the correlation analysis.

Genetic data on the inbreeding of two tree species (*Quercus alba*, *Sassafras albidum*) was used in the correlation analysis (Sork *et al.* 1997). We include data on these tree species and our analysis of them based on the hypothesis presented by these authors, that differences in genetic inbreeding and diversity may be related to the environmental history of the MOFEP sites.

Statistical Analyses

Correlation analysis was used to evaluate relationships among disturbance variables, successional indices, and plant and animal abundances. Correlation coefficients and their corresponding significance levels were calculated using SAS programming and statistical procedures (SAS 1989). We used site-level data, so all correlations and associations have a maximum of nine observations. The small sample size made it impossible to determine if variables were normally distributed, which is a

requirement for hypothesis testing in correlation analysis. Therefore, caution is needed when interpreting significance of correlations. Despite this limitation, the correlation analysis has strength in its simplicity for evaluating associations among many diverse variables measured in many different ways.

Independence of observations is also a requirement of hypothesis testing. Significance levels in correlation analysis can be biased when observations of a population are statistically dependent in space or time. Spatial and serial data are often autocorrelated. We examined the autocorrelation function of the Species Successional Index to assess the independence of our variables. We used the Species Successional Index because this index incorporates many species, it is at the heart of our general hypothesis, and its use would overcome many of the problems involved in estimating autocorrelation functions for individual species from data sets with few observations at the regional level. An autocorrelation function was calculated by correlating the distance between all possible pairs of MOFEP sites with the difference between the index values at each site pair. Correlations were calculated for five distance classes of 4.8 km (3 mi) each. The autocorrelation functions for the Species Successional indices showed no significant autocorrelation at any of the five distance lags. A function of diminishing correlation with distance, which was expected, was not found. The lack of significance and pattern in the spatial autocorrelation function indicates that observations are independent and that most of the data and significance levels are unbiased. If there is an underlying population autocorrelation function, it was not apparent in the sample data. The lack of significant autocorrelation may in part be due to the small number of site comparisons (36) and their distribution with distance. However, even when we grouped distance into two classes (<12, >12 km), there was no significant correlation among single variable differences and distance between sites.

We performed several analyses on a studywide basis. The first was to compare the number of significant versus the number of non-significant correlations we found to the number of significant and non-significant correlations that would be expected by chance alone. Significance for this test was based on the rejection of the null hypothesis for tests of individual biological hypotheses. The 38 significance levels of the

correlations for all individual species with the Disturbance Interval Index (made up of non-species data) were classed ($p < 0.05$, $p < 0.1$, non-significant) and counted. The percentages of significant versus non-significant correlations were calculated and compared with the percentage of significant correlations that would be expected by chance alone. The second test was a sequential Bonferroni test (Rice 1989, Holm 1979) designed for simultaneous testing of a number of variables. This test was performed on the correlation matrix among 11 disturbance, successional, and species groups (table 4) to adjust for the increased probability of not

rejecting a true null hypothesis when a number of variables are tested simultaneously. Third, a group (table 3) of several correlations addressing the same question (is topographic roughness associated with all disturbance and species variables as a group) was evaluated as a common null hypothesis by the use of canonical correlation analysis and CANCORR statistical software (SAS 1989). Variables were combined by averaging into two groups, historic and current (table 3), to use measurements of both the present and past conditions at the sites and to increase the degrees of freedom in the canonical correlation analysis.

Table 3.—Correlation coefficients among topographic roughness and disturbance variables, successional indices, fruit production, species abundances, and inbreeding at the MOFEP sites. This table illustrates the numerous associations of topographic roughness with many very different, but disturbance-related variables within the ecosystem. P-values are given in parentheses for tests of individual hypotheses. Simultaneous hypothesis testing with a sequential Bonferroni (Rice 1988) test yields no significant ($\alpha = 0.05$) correlations for variables in the first 11 rows. Emphasis is placed, however, on the significance level of the multivariate analysis of canonical variables (see text) with topographic roughness (last row) for the nine MOFEP sites. This analysis correlates all variables (first 11 rows) in two groups (first column) with topographic roughness at two scales.

Group	Variable	Topographic Roughness Index ^a (900 m radius)	Topographic Roughness Index (5,000 m radius)
Historic	Growth reduction interval	0.70 (0.03)	0.86 (0.01)
Historic	Mean fire interval (1700-1850)	0.43 (0.25)	0.80 (0.01)
Historic	Openness Index (1820) ^b	-0.72 (0.03)	-0.79 (0.01)
Historic	Overstory Succession (1820)	0.59 (0.10)	0.66 (0.05)
Current	Overstory Successional Index ^c	0.77 (0.02)	0.81 (0.01)
Current	Seedling Successional Index ^d	0.77 (0.02)	0.76 (0.02)
Current	<i>Armillaria</i> Successional Index ^e	0.57 (0.11)	0.53 (0.14)
Current	Blueberry fruit density ^f	-0.68 (0.04)	-0.79 (0.01)
Current	Forest bird territories ^g	0.52 (0.15)	0.48 (0.18)
Current	Lizards ^h	-0.43 (0.25)	-0.54 (0.14)
Current	Sassafras inbreeding ⁱ	-0.51 (0.16)	-0.74 (0.02)
All	Canonical variables (2 groups)	0.82 (0.04)	0.85 (0.02)

^a Data: Krstansky and Nigh (1999).

^b Batek *et al.* (1999).

^c Data: Kabrick *et al.* (1997).

^d Data: Grabner *et al.* (1997).

^e Data: Bruhn *et al.* (1997).

^f Fantz and Hamilton (1997).

^g Data: Clawson *et al.* (1997).

^h Data: Renken (1997).

ⁱ Data: Sork *et al.* (1997).



Table 4.—Correlation coefficients for disturbance, successional, and species variables for the nine MOFEP sites. Significance levels for individual hypothesis testing ($\alpha < 0.05$) are in parentheses while those for simultaneous hypothesis testing (Rice 1989) at $\alpha < 0.05$ are denoted by an *.

	Mean fire interval	Openness Index (1820) ^a	Overstory Index (1820)	Overstory Succession Index ^b	Seedling Succession Index ^c	Armillaria Succession Index ^d	Blueberry fruit density ^e	Forest bird territories ^f	Skink and lizard captures ^g	Sagebrush Inbreeding ^h
Mean abrupt growth reduction interval	0.98* (0.0001)	-0.82 (0.001)	0.82 (0.006)	0.71 (0.05)	0.83 (0.01)	0.77 (0.016)	-0.83 (0.005)	0.64 (0.07)	-0.67 (0.05)	-0.1 (0.1)
Mean fire interval		-0.86 (0.003)	0.79 (0.01)	0.77 (0.02)	0.83 (0.01)	0.72 (0.023)	-0.84 (0.004)	0.68 (0.047)	-0.68 (0.04)	-0.1 (0.1)
Openness Index (1820)			-0.85 (0.004)	-0.85 (0.006)	-0.87 (0.002)	-0.78 (0.01)	0.94* (0.0003)	-0.80 (0.01)	0.57 (0.11)	0.4 (0.1)
Overstory Succession Index (1820)				0.76 (0.02)	0.92* (0.0005)	0.93* (0.0003)	-0.87 (0.002)	0.92* (0.0005)	-0.80 (0.01)	-0.1 (0.1)
Overstory Succession Index					0.93* (0.0003)	0.74 (0.02)	-0.71 (0.032)	0.76 (0.009)	-0.59 (0.10)	-0.1 (0.1)
Seedling Succession Index						0.92* (0.0004)	-0.82 (0.007)	0.92* (0.0004)	-0.73 (0.03)	-0.1 (0.1)
Armillaria Successional Index							-0.76 (0.018)	0.97* (0.0001)	-0.77 (0.01)	-0.1 (0.1)
Blueberry fruit density								-0.78 (0.013)	0.57 (0.112)	0.4 (0.1)
Forest bird territories									-0.65 (0.056)	-0.1 (0.1)
Skink and lizard captures										0.7 (0.1)

^a Batek *et al.* 1999.
^b Kabrick *et al.* 1997.
^c Grabner *et al.* 1997.
^d Bruhn *et al.* 1997.
^e Fantz *et al.* 1997.
^f Clawson *et al.* 1997.
^g Renken 1997.
^h Sork *et al.* 1997.

RESULTS

Topographic Roughness and Disturbance

Many of the disturbance variables and indices were highly associated with topographic roughness (table 3) and indicate that increasing topographic roughness around a site decreases the frequency of disturbance. Canonical correlation analysis of the two groups of 11 variables (historic versus current variables, table 3) with topographic roughness showed significant correlation between topographic roughness and the canonical variable for the two groups. The mean fire interval (modeled with topographic roughness), the growth reduction return intervals, and the Openness Index (1820) were all significantly correlated with each other (table 4). Significant correlations among topographic roughness, growth reductions, fire frequency, and other measures of disturbance suggest that topographic roughness is a strong factor mitigating the frequency of disturbance and fire.

Disturbance, Successional Indices, and Species Associations

Tests of the significance of correlations on a studywide basis yielded results that indicate the rate of significant correlation among study variables is much more than would be expected by chance alone. Significant correlations among individual species and the Disturbance Interval Index occurred eight times more often than is expected by chance alone at the 0.05 level and five times more often than expected by chance at the 0.1 level (table 5). A sequential Bonferonni analysis, based on the assumption of simultaneous testing as opposed to the

testing of individual, ecologically generated, hypotheses, yielded nine significant correlations from the correlation matrix (table 4).

Study site means of abrupt growth reductions ranged from 41 to 62 percent and had mean durations that ranged from 11 to 26 years (table 1). Growth reduction return intervals in shortleaf pine were significantly correlated with many variables (table 4), such as fire frequency, the Overstory Successional Index, the Oak Successional Index, the Seedling Successional Index, inbreeding coefficients of sassafras (Sork *et al.* 1997), and the sign of correlation was consistent ecology theory. Specifically, early successional species were more abundant at sites where pines had short mean growth reduction intervals while late successional species were more abundant at sites with long mean growth reduction intervals.

The frequency of historic growth reductions in shortleaf pine was significantly correlated with the abundance of several wildlife species. The combined density of five forest birds territories was correlated with growth reduction return intervals (table 4). The historic (1700-1850) mean fire intervals were correlated with the modern frequency of two (worm-eating warbler (*Helmitheros vermivorus*), $r=0.75$, $p=0.02$; Acadian flycatcher (*Empidonax virescens*), $r=0.85$, $p=0.004$) of five forest bird population densities measured by Clawson *et al.* (1997). The frequency of historic growth reductions in shortleaf pine was significantly correlated (table 4) with the sum of the abundance estimates of five lizards (*Eumeces laticeps*, *Eumeces anthracinus*, *Sceloporus undulatus*, *Eumeces fasciatus*, *Scincella lateralis*) measured at the MOFEP sites by Renken (1997). The broad

Table 5.—The number and percent of individual species variables that are significantly and non-significantly correlated with the Disturbance Interval Index at two levels of probability. Percent values are given in parentheses.

	Significant correlations with disturbance	Non-significant correlations with disturbance	Total number of species correlations	Significant correlations expected by chance alone
Number correlations ($\alpha = 0.05$)	16 (42%)	22 (58%)	38 (100%)	1.9 (5%)
Number correlations ($\alpha = 0.10$)	20 (53%)	18 (47%)	38 (100%)	3.8 (10%)



headed skink was the lizard species most highly correlated ($r=0.74$, $p=0.02$) with the growth reduction return intervals. The historic (1700-1850) mean fire intervals were also significantly correlated with the present-day abundance estimates of the sum of five lizards. Two reptile species, the copperhead (*Agkistrodon contortrix*) and the three-toed box turtle (*Terrapene carolina*), were correlated ($r=0.75$, $p=0.02$; $r=0.77$, $p=0.01$) with growth reduction return intervals. No amphibians (*Notophthalmus viridescens*, *Ambystoma opacum*, *Plethodon serratus*, *Plethodon glutinosus*, *Ambystoma maculatum*, *Bufo americanus*, *Rana clamitans*, *Rana palustris*, *Rana utricularia*, *Pseudacris crucifer*) were significantly correlated with growth reduction intervals.

Successional indices, based on the shade tolerance of tree species were related to a number of variables in addition to their correlation with growth reduction variables. Two of the succession indices (Overstory Tree Species and Oak) are not independent, however, since the same oaks comprise the majority of the number of individual trees counted in both indices. Successional indices of both oak and all overstory species were highly correlated with the mean fire interval (fig. 1) at the nine MOFEP sites. A significant correlation was found among the mean number of tree species per plot at the MOFEP sites and the Overstory Successional Index ($r=0.68$, $p=0.04$). The Oak Successional Index, although not significantly correlated ($r=0.56$, $p=0.11$) with the number of tree species per plot, had a similar pattern. The Seedling Succession Index, made up of sugar maple, winged elm, slippery elm, black haw, post oak, and blackjack oak was significantly correlated with the Oak and Overstory Tree Species successional indices.

Successional indices were correlated with both forest birds and lizards (table 4). Successional indices were significantly correlated with the sum of five forest bird territories and strongly correlated with the number of territories of Acadian flycatchers (*Empidonax vireescens*) ($r=0.88$, $p=0.0015$) and worm-eating warblers (*Helmitheros vermivorus*) ($r=0.92$, $p=0.0005$). Not all individual forest bird species were significantly correlated with the Overstory Successional Index. Ovenbirds (*Seiurus aurocapillus*) were not significantly correlated with the all species successional index (0.55, $p=0.12$) but were significantly correlated with

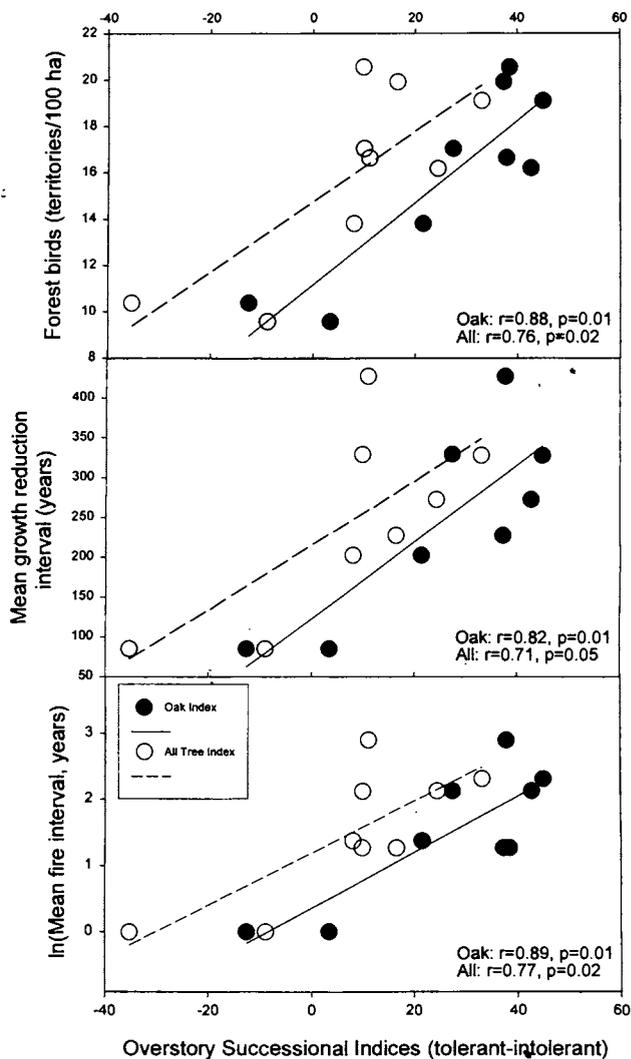


Figure 1.—Relationships between the Overstory Successional Indices (all tree species and oak tree species) and the mean fire return interval, the mean growth reduction return interval, and the density of forest bird territories. The Oak Successional Index is best related to disturbance and species variables. This figure indicates the associations among the successional status of the overstory, disturbance, and species variables.

the Oak Successional Index (0.70, $p=0.04$). Kentucky warblers (*Oporornis formosus*) were not significantly correlated with the all species successional index (0.59, $p=0.10$) or the Oak Successional Index (0.46, $p=0.21$). Wood thrush (*Hylocichla mustelina*) territories were not significantly correlated with the Overstory Successional Index (0.22, $p=0.57$) or the Oak Successional Index (0.38, $p=0.21$). In general,

forest bird species were more highly correlated with the Oak Successional Index than they were with the Overstory Successional Index (fig. 1). All forest bird species were positively correlated with the successional indices.

Successional indices were significantly correlated with the mean number of captures of one lizard (*Sceloporus undulatus*) and four skinks at the MOFEP sites (table 4). Not all lizard species were significantly correlated with the successional indices. The coal skink was most highly correlated ($r=-0.71$, $p<0.03$) with the three successional indices, while the broad headed skink had the lowest correlations ($r=0.45$, $p<0.25$) with the successional indices. All lizard species were negatively correlated with all the successional indices (table 4). Snakes and the three-toed box turtle (*Agkistrodon contortrix*, *Storeria occipitomaculata*, *Diadophis punctatus*, *Terrapene carolina*) were generally positively but not significantly correlated with the successional indices. No amphibians (*Notophthalmus viridescens*, *Ambystoma opacum*, *Plethodon serratus*, *Plethodon glutinosus*, *Ambystoma maculatum*, *Bufo americanus*, *Rana clamitans*, *Rana palustris*, *Rana utricularia*, *Pseudacris crucifer*) were significantly correlated with any of the successional indices.

The abundance of *Armillaria* species was significantly correlated (table 4) with indices of disturbance, species abundance, and succession. *Armillaria gallica* abundance was significant and positively correlated with the time between disturbance events such as the mean fire interval ($r=0.76$, $p=0.02$) and growth reduction return interval ($r=0.81$, $p=0.01$). Forest bird nesting territories ($r=0.96$, $p=0.001$) and all successional indices ($r=0.71$ to 0.91) were also highly correlated with the abundance of *Armillaria gallica*. In contrast, *Armillaria mellea* was negatively correlated with the length of disturbance intervals, successional indices, and forest bird territories ($r=-0.71$, $p=0.03$). Thus, *A. mellea* was more abundant on sites with a high frequency of disturbance while *A. gallica* was less abundant. In contrast, *A. gallica* was more abundant on late-successional sites with less frequent disturbances than was *A. mellea*. The *Armillaria* Successional Index, which incorporated the ratio of the *Armillaria* species (*A. gallica*/*A. mellea*), was positively correlated with disturbance, successional, and species indices (table 4).

The density of blueberry fruit on the MOFEP sites was highly correlated with disturbance variables, successional indices, and species abundances (table 4). Fire frequency and growth reduction return intervals were significantly correlated with blueberry abundance. Successional indices of *Armillaria* species, tree species, oak species, and tree seedlings were significantly correlated with the density of blueberry fruit. Species and species groups that were significantly correlated with blueberry fruit abundance were *Armillaria gallica*, forest birds, lizards, and skinks.

The inbreeding coefficients of sassafras were significantly correlated with the mean fire interval, the growth reduction return interval, and the combined abundance of skink and lizard captures but not significantly correlated with the seven other variables in the correlation matrix (table 4). The inbreeding coefficients of white oak were not significantly correlated with any of the variables in table 4.

Composite Disturbance and Successional Indices

Composite index values were constructed from disturbance variables and species variables (table 6). The Disturbance Interval Index reflects the relative duration between disturbances at each MOFEP site. The Species Successional Index reflects the abundance and successional characteristics of 30 species (10 animal and 20 plant). The Species Successional and Disturbance Interval Indices are significantly correlated ($r=0.89$, $p=0.001$). A logarithmic transformation of the Disturbance Interval Index improved the strength of this relationship ($r=0.93$, $p=0.001$). The Disturbance Interval Index is composed of measurements that are unconstrained by species abundances. On the other hand, the Species Successional Index is based solely on measurements and successional configurations of species abundances. These indices may be of future use in evaluating different types of variables and the responses to MOFEP treatments.



Table 6.—Two indices derived from MOFEP site data that are based on disturbance variables, species characteristics, and abundances. The highest index values indicate the most advanced successional stages or have had the longest mean disturbance interval. The indices are relative values with a mean of one. The Disturbance Interval Index is derived from four disturbance indicators: growth reduction frequency, fire frequency, grazing protection, and pre-European forest structure. The Species Successional Index is derived from standardized values of the Overstory Successional Index, the Seedling Successional Index, the *Armillaria* spp. Successional Index, forest bird nesting territories, lizard abundance, and blueberry fruit abundance.

	Disturbance Interval Index (physical Indicators)	Species Successional Index (species indicators)
SITE 1	1.24	1.14
SITE 2	1.04	1.30
SITE 3	0.95	1.16
SITE 4	1.01	1.19
SITE 5	0.76	1.18
SITE 6	1.12	1.17
SITE 7	0.20	0.47
SITE 8	0.25	0.53
SITE 9	0.77	0.87

DISCUSSION

Disturbance and Topographic Roughness

There is little inherent evidence that accompanies most individual growth reductions in pine trees to indicate the cause. The strength of correlation between growth reduction variables and fire frequency (table 4) indicates that fire is probably the most important cause of most abrupt growth reductions. Some growth reductions begin in the same year that a fire scar is formed or in a year when other trees at a site show fire scars. Many growth reductions, however, are not associated with fire scars and are often found on trees with no fire scars. Growth reductions could include a number of disturbances that affect the growth of shortleaf pine trees such as weather (drought, wind, ice),

insects, *Armillaria* spp., or other pathogens. The inverse relationship between topographic roughness and growth reductions may in part be explained by the impediments to the spread of fire caused by topographic roughness.

Evidence suggests that most growth reductions in shortleaf pine are the result not of low intensity surface fires, but moderate to high intensity wildfires occurring during extreme fire weather, and thus, represent much more severe disturbances that have been recorded on rare survivor trees. Several lines of reasoning point to more severe disturbances as the cause of most growth reductions. The first is that fire intensity and size are exponentially related to frequency (Guyette 1995). Thus, it is reasonable to consider that with an exponential distribution, a mean fire interval of approximately 5 years, and a growth reduction return interval of 85 years, 1 out of every 17 fires might be expected to result in the crown scorch (and a mean radial growth reduction of about 52 percent) of even mature shortleaf pine. The sample trees used to reconstruct growth reduction intervals had an average age of more than 152 years. The average age of a pine tree when a reduction occurred was more than 85 years. Thus, growth reductions were occurring in mature trees with foliage well off the forest floor. Second, since we can only sample what were survivor trees, our estimation of the severity of fires is biased by trees that survived low and high intensity fires. Third, the degree of drought in years in which abrupt growth reductions began indicates severe rather than low intensity fires. Growth reduction events occurred in years with an average Palmer Hydrologic Drought Index value (PHDI=-1.32). That value was well below normal between 1700 and 1850 (Cleavland and Stahle 1997). At least 10 extensive fires occurred in the Current River watershed during years of extreme drought (Guyette 1995) in the 1700s indicating that intense fire, if not common, probably did follow an exponential distribution based on very frequent fires. Fourth, stand replacement events have been documented from pith dates at several sites in the Ozarks (Cutter and Guyette 1994, Guyette 1993). In short, it is difficult to imagine a drought prone ecosystem with abundant anthropogenic ignitions such as in the Ozarks (Guyette and Cutter 1997), in which intense fires occurred less frequently than growth reduction return intervals reported in table 1.

The strong negative correlations between the Openness Index (1820) and growth reduction interval, mean fire frequency, and topographic roughness suggest that fire, mitigated by local topography, played a primary role in reducing the density of the pre-European forest. This is consistent with the findings of Batek *et al.* (1999), who show for Missouri's Current River region that areas of greater tree densities, as determined from witness tree distances in Public Land Survey notes, were found where the landscape is more dissected. Areas having low topographic roughness (i.e., less dissection) have fewer natural fire breaks and consequently have a greater fire frequency and/or greater fire intensity than areas having greater topographic roughness.

The effects of topographic roughness on the ecosystems of the Current River watershed have not been limited to fire-related disturbances. Topographic roughness has been and still is an important factor affecting anthropogenic disturbances to forested environments. Logging and transportation have always been inhibited by high degrees of topographic roughness. For example, remnants of intense logging disturbance are much greater at MOFEP sites 7 and 8 than at the other MOFEP sites. Clearcutting of these sites in about 1900 is evident from the fact that few, if any, trees on these sites are older than 100 years. Clearcutting here was made economical by the much gentler slopes and valleys of these sites. MOFEP sites high in topographic roughness such as sites 3 and 4 show evidence, via their tree-age structure, of being selectively logged over a period of many years. In general, the relationship of topographic roughness to disturbance is that the effects of any phenomena propagated via the land surface will be mitigated by topographic roughness. This would include such diverse phenomena as wildland fire, logging tracks, grazing, road construction, seed dispersal, and aquatic and terrestrial species movements. Table 3 suggests that in addition to the associations of vegetation with the soils and geology (Meinert *et al.* 1997), topographic roughness and successional sequences should be considered in characterizing biotic associations.

Disturbance, Succession, and Species Associations

The significant correlations among disturbance measures, successional indices, and species associations support our central hypothesis that historic disturbance regimes have a legacy that is apparent in contemporary plant and animal distributions at MOFEP sites. The tree species successional indices are one dimensional in nature, that is, based only on shade tolerance and not on the fire-related characteristics of each species. Despite some inherent limitations, these indices indicate autogenic succession in a forest ecosystem in which shade intolerant species are replaced by shade tolerant species as a growth limiting factor (light) changes.

A recent study that reconstructs early 19th century vegetation (Batek *et al.* 1999) supports the hypothesis that fire-related disturbances had a strong effect on tree species distributions over a much broader range in the Current River watershed than the range of the MOFEP study sites. The spatial distribution of shortleaf pine, red oaks, eastern redcedar, sugar maple, and red maple in 1820 is related to the frequency of fire reconstructed from fire scar chronologies.

Armillaria spp. are long lived (Bruhn *et al.* 2000) and as such may persist in the continuum of a long-term disturbance regime. Differences in the abundance and pathogenicity of *Armillaria* species may be linked to factors such as the abundance of woody debris and the frequency of tree stress (Kile *et al.* 1991). These factors are mitigated and controlled by fire frequency and succession. We propose the hypothesis that *Armillaria* species at the study sites are distributed with respect to disturbance regimes created by the long-term effects of fire and logging and the subsequent patterns of forest succession.

The abundance of blueberry fruit at the MOFEP sites lies along a successional gradient as indicated by its correlation with successional indices. This is true even though the occurrence of blueberry plants is not significantly correlated with any of the successional indices or disturbance variables. The abundance of blueberry fruit probably reflects more light energy near the ground surface at early-successional sites.

If the successional indices indicate a degree of forest succession at the MOFEP sites, then it follows that there might be an observable relationship between species diversity and successional stage. This is perhaps the most interesting corollary and prediction of our hypothesis that the long-term interactions of fire, topography, and anthropogenic disturbance have resulted in a successional gradient among the MOFEP sites. Thus, succession, in addition to soils, substrates, and land forms, may be a factor controlling species diversity within forest successional stages. Until the development of the successional indices presented here, judgments about Ozark forest succession were largely qualitative. The successional indices allow for the quantitative testing of successional corollaries. Herein lies an important new tool for understanding ecosystem dynamics in the Ozarks.

There are many theories concerning how diversity changes within a successional sere (Hunter 1990, Loucks 1970), but data on diversity and the succession of macrospecies suggest that mid-successional stages have the highest species diversity because these transitional stages have species adapted to both early- and late-successional stages (Loucks 1970). On the other hand, early- and late-successional stages have the least diversity because of the limitations imposed by vegetation and the physical environment. At the MOFEP sites, the mean number of overstory tree species is significantly correlated with the Overstory Successional Index. The linear relationship between the Overstory Successional Index and the number of tree species per plot can be interpreted in at least two ways. One interpretation is that species diversity reaches its peak during late-successional stages (Odum 1969) at the MOFEP sites. A second interpretation is that peak diversity is reached at mid-successional stages but that none of the forests at the study sites have reached late-successional stages. Both of these interpretations may have merit at the MOFEP sites, but certainly, none of these sites have been free of disturbance (fire and logging) for more than 60 years.

Another indication that diversity is affected by disturbance regimes and succession is the relationship between genetic diversity of a species and disturbance as proposed by Sork *et al.* (1997). These investigators hypothesized that

“the year of acquisition” was a proxy disturbance variable and was related to trends in the inbreeding coefficients of sassafras at the MOFEP sites. The correlation of genetic inbreeding coefficients and disturbance and successional variables (table 4) supports the hypothesis that historic and long-term disturbance regimes may have an effect on genetic diversity of some tree species.

Another corollary of our successional hypothesis is that animal species, which are often adapted to various stages of forest succession, should be distributed along a gradient as quantified by the successional indices. Avian nesting populations have been related to stages of forest succession (Thompson and Dessecker 1997). Forest bird nesting populations at the MOFEP sites, as defined by Clawson *et al.* (1997), are adapted to late-successional forest habitats. In general, the positive relationships between forest bird species and the successional indices support the hypothesis that the forests at the MOFEP sites are in various stages of succession. In contrast to forest bird species, the negative correlations between successional indices, disturbance variables, and (table 4) lizard species indicate that lizard species are in general early-successional species whose abundance diminishes as overstory succession progresses.

Although none of the five salamander species were significantly correlated with any of the disturbance or successional variables or indices, there may be several reasons why this is not an indication that no change in their abundance might occur with a forest disturbance. There could, for example, be spatially limiting factors in their abundance, such as breeding habitat or coarse woody debris, that limit their abundance at the MOFEP sites. Schurbon (2000) found no negative effects of prescribed fire on amphibians but did find that Ambystomid salamanders were more common in forests that had not burned within 3 years. Also, the low power (only nine observations) of the test data may not be enough to detect weaker relationships. For example, the abundance of southern redback salamanders (*Plethodon serratus*) is correlated ($r=0.59$, $p=0.10$) with the length of the growth reduction return intervals, suggesting a possible relationship with disturbance.

Disturbance Frequency and Species Longevity

The strength of correlation between the Disturbance Interval Index and the abundance of tree species was related to their potential longevity (fig. 2). The absolute value of r (for the Disturbance Interval Index versus tree species abundance) was related to the mean maximum longevity of 16 common tree species at the MOFEP sites. This implies that a legacy of the long-term disturbance regime persists on the MOFEP sites to the greatest extent in organisms

that are long lived. This is to be expected since they take up more resources for longer periods, reach reproductive age later, and have longer periods of reproduction. Tree species provide an excellent example of this relationship because of the considerable variability in longevity of different tree species and because the documentation of their ages in both the literature (Burns and Honkala 1990) and in the study region. Tree species longevity accounts for about 73 percent of the variance in the correlation strength (absolute r value) between the Disturbance Interval Index and their abundance

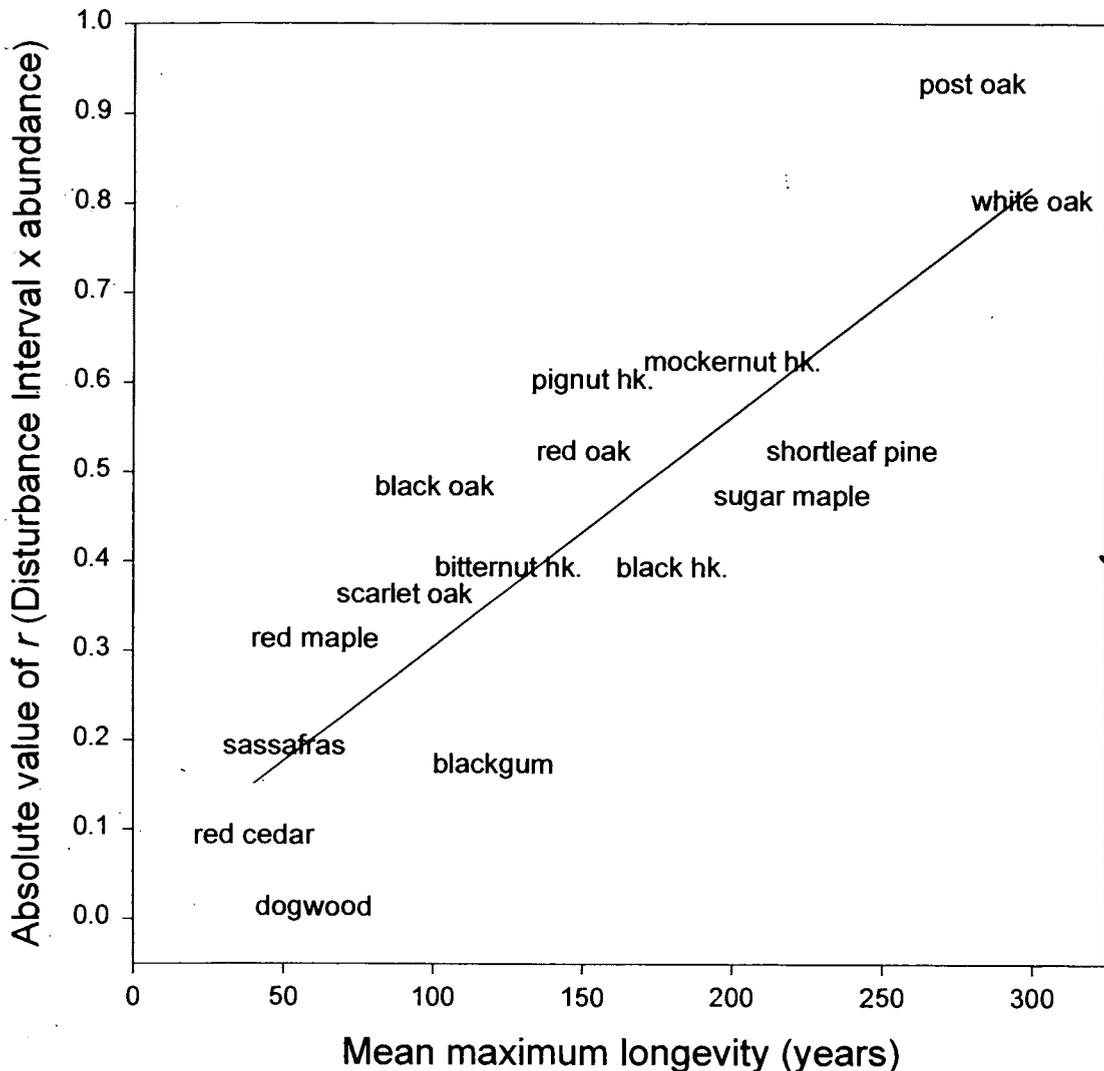


Figure 2.—Long-lived species are more strongly related to differences in long-term disturbance regimes. Tree species longevity accounts for about 73 percent of the variance in the strength of correlation (absolute value of r) between the Disturbance Interval Index and a tree species abundance. For instance, post oak, a long-lived species, is strongly and negatively correlated with a high frequency of disturbance, while white oak, also a long-lived species, is strongly and positively correlated with a low frequency of disturbance. Both these species are thus good indicators of the long-term disturbance frequency. In contrast, the abundance of sassafras, a short-lived species, is weakly correlated with disturbance frequency, high or low.



(fig. 2). Thus, the long-term legacy of disturbance is best reflected on a site by the relative abundance of long-lived species. Another example of the relationship between species longevity and disturbance frequency can be found in the distribution of *Armillaria* spp., which are among the longest lived (Shaw and Kile 1991) species in many forests. Among the different organisms at the study sites, *Armillaria* spp. are one of the most strongly correlated with the disturbance and successional correlation matrix (table 4). In summary, long-lived tree and fungal species have more ecological persistence and best reflect the long-term gradient in ecosystem stability that has occurred at the MOFEP sites.

Implications for MOFEP

Many factors will influence the rate of change at the MOFEP sites in the years to come. The extent to which the frequency of disturbance (treatments) at the MOFEP sites compares with that over the last centuries will be a major factor affecting change. Limited comparisons can be made between historic disturbance regimes and MOFEP treatments using fire history reconstructions (Guyette 1995, Guyette and Cutter 1997, Guyette and Dey 2000). Fire frequency and fire area per year in the Current River watershed can be compared with MOFEP treatments (fig. 3). A treatment with a 10-year re-entry and 10-percent overstory removal is similar to what is reconstructed for the historic fire regime. Not all fires, however, were stand

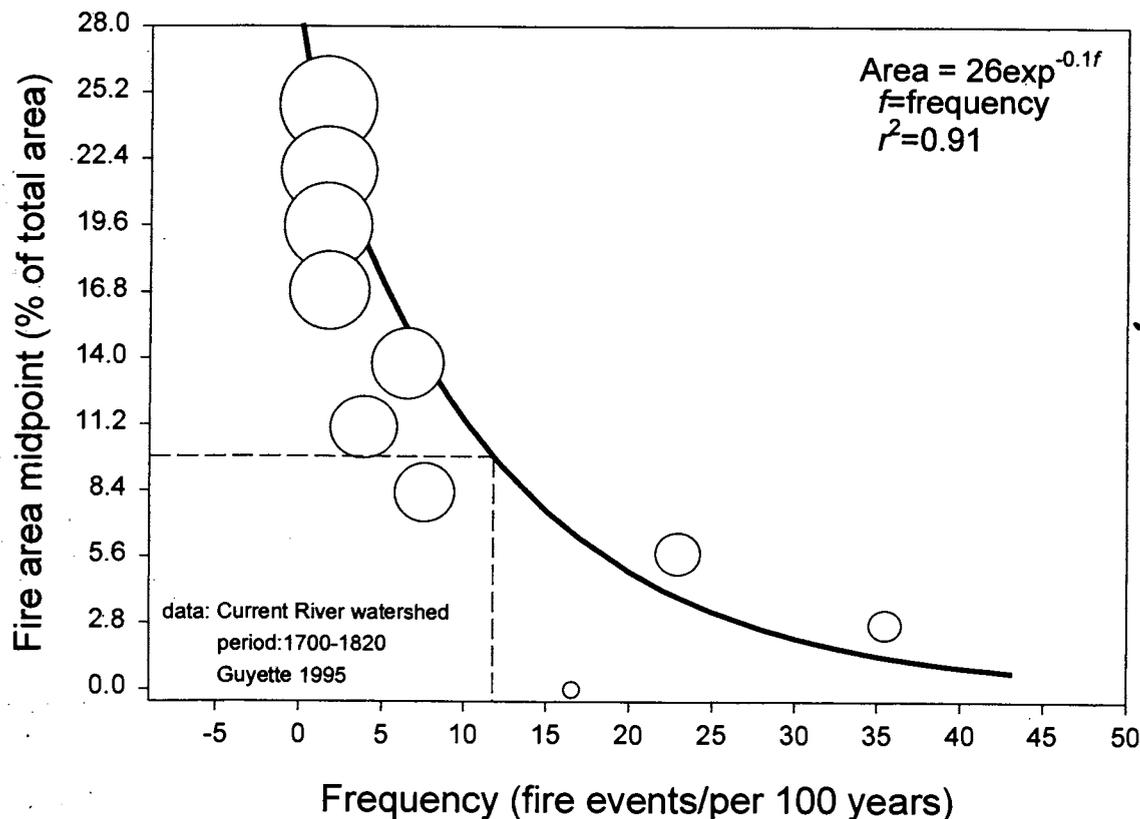


Figure 3.—Relationship between fire frequency and fire area per year in the Current River watershed and how this historic fire regime compares with MOFEP even-aged treatments. The dotted lines represent treatment intervals and areas that approximate MOFEP treatments. The regression line is based on the 10 midpoints and the frequency data. The areas of the circles are roughly proportional to the area class of the midpoint. This figure indicates that the disturbance frequency created by the MOFEP even-aged treatments is similar to the long-term disturbance frequency in the region. This does not imply that even-aged treatments are qualitatively similar to stand replacement by fire.

replacement events. Indeed, the vast majority of fires were low intensity surface fires. Fire intensity and stand replacement were probably much greater for those years in which large areas burned. For example, four large fires (2 largest data points, fig. 3) occurred in 120 years. These events are estimated to have burned up to a quarter million acres in a single year. These fires alone burned an area equivalent to the whole Current River watershed in 120 years. Thus, if 10 percent of the area burned in these fires was of sufficient intensity to initiate stand replacement, then an average of about 12 percent of the forests were replaced every 120 years. Differences in scale and intensity limit the implications of these comparisons, but even-aged treatments and rotations may not differ from historic disturbance regimes.

Our findings provide a means for predicting how MOFEP sites will respond to silvicultural treatments based on the historic and present successional stages of the MOFEP sites and the nature of treatments applied. Species composition is expected to change at both sites with infrequent historical disturbances (high disturbance-free indices) and at sites with frequent historical disturbances (low disturbance-free indices). Even-aged treatments are more likely to enhance early-successional species than uneven-aged treatments. No-harvest treatments will enhance late-successional species. However, these trends will be mitigated by the present status and direction of succession at the sites. Disturbance and species successional indices (table 6) and no-harvest treatment suggest that species abundance and distributions in control sites 1 and 6 will change very little because of their late-successional status and no-harvest treatment. The continued protection from fire at these sites may contribute to limited changes in vegetation, however. Sites 1 and 6 may provide the best late-successional controls. Even-aged site 9 will also change very little because of its early-successional state and even-aged treatment. Site 2 is difficult to predict because of its uneven-aged treatment and mixed index values (table 6). Early-successional stages will be maintained to some degree at MOFEP site 7 by uneven-aged treatments, which will continue to set back the successional development as both natural and anthropogenic disturbances have for centuries. Similarly, early-successional stages will be maintained at site 5 through the use of even-aged treatments. Site 4 will change

more than sites 1, 6, 7, and 9 because of its late-successional state and uneven-aged treatment. Control site 8 will change more than sites 1, 6, 7, 9, and 4 in species abundances and distributions because of its early-successional stage, protection from fire and logging disturbance, and its no-harvest treatment. Finally, site 3 may change the most due to the combined effects of its relatively infrequent historic disturbances and its even-aged treatment.

SUMMARY

A correlation matrix of species distributions and species characteristics support the hypothesis that the interactions of fire, topographic roughness, and disturbance have resulted in varied successional stages among the MOFEP sites. A continuum of anthropogenic disturbance patterns, from wildfire to logging, spans the historic period (1700-1850) and the 20th century. This continuum is caused by the effects of topographic roughness on the propagation of fire and human activities across the landscape. The successional construct offers much in terms of interpreting pre-treatment data at the MOFEP sites and will offer even more in interpreting and predicting MOFEP experimental results. Disturbance frequency and succession have and will continue to change the distribution of species at the MOFEP sites. The successional indices presented here have many potential uses in ecology, forestry, and wildlife management. Biologically based successional indices could be created for other classes and guilds of species and could present new ways of interpreting complex ecological data. A rule of thumb relating topographic roughness to disturbance is that the effects of any phenomena propagated via the land surface will be mitigated by topographic roughness.

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Plant Distribution and Diversity Across an Ozark Landscape

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Abstract.—The distribution, abundance, and diversity of plant species in a landscape are related to factors such as disturbance history, landform, and climate. In examining the potential effects of landscape structure on the distribution of plant species of the southeast Missouri Ozarks, we sampled a 10,000-m transect in a south-north direction. In September 1997, two 1 x 1 m plots were placed every 10 m along the transect to tally canopy cover, overstory type, coverage of all understory species, and micro-topographic features. We calculated Shannon and Simpson's diversity and species richness for all plots and used correlation and wavelet analyses to examine changes in these variables with elevation across different scales. Of the 332 species recorded along the transect, 104 species occurred only once. *Desmodium nudiflorum* and *Parthenocissus quinquefolia* were the two most frequent species (48.8 percent and 37.0 percent of plots, respectively), while 323 of the 332 species occurred within < 10 percent of the plots. Seventy-one plots contained no species and another 71 plots had only one species. Most plots contained one to seven species. Over 95 percent of the total species were found in < 10 percent of the quadrats. Species richness, Shannon diversity, and Simpson's diversity all correlated negatively with elevation. Distribution of plant species in the landscape was significantly related to position in the landscape, measured by relative elevation ($R^2 = 0.78$). Plots near riparian areas contained more species (> 30 species/plot) than any other plots along the transect. The patterns of patches of elevation and species diversity were most visible at the 1,800-m scale, but the spatial relationship between these patterns was best revealed at scales between 1,340 and 1,400 m. Changes in wavelet variance suggested that multiple scales should be examined when exploring potential influences of landscape structure on plant species.

Understanding organisms and their distributions within ecosystems or landscapes is the first step in any applied or basic ecological research. Such information is critical not only for explaining the processes (e.g., extinction and invasion) and dynamics of the system, but also

for developing strategic plans to preserve biological diversity within the scope of natural resource management objectives (Vogt *et al.* 1996). Because the current crisis in loss of global biodiversity is mostly related to human activities, one of the greatest challenges is to adjust current management practices so that human impacts on species are minimized[†] (Frankel *et al.* 1995). The Missouri Ozark Forest Ecosystem Project (MOFEP), initiated in 1991 by the Missouri Department of Conservation, was a landscape-scale experiment undertaken with such an ecosystem management or sustainable management philosophy (Larsen *et al.* 1997). As one of >20 research projects associated with MOFEP, this study has focused on plant distributions across the Ozark landscape.

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The MOFEP sites are located in the Ozark Highlands Section and dominated by deciduous



forests. Although the soils in the Ozarks are extremely heterogeneous (Hammer 1997), the overall landscape structure characterized by current vegetation is simple, with 73 percent of the landscape defined by the overstory as oak-hickory upland forests (Xu *et al.* 1997). The original forests were cleared in the 1800s to meet the demand for timber. As timber and pulp and paper industries declined early in the 20th century, the vegetation developed into a relatively homogeneous, mixed oak-hickory forest. Suppression of fires in the latter half of the 20th century may have also contributed to the homogeneity of forest patterns across this landscape (Guyette and Dey 1997). Other minor elements of the landscape include dense streams (density $\approx 971 \text{ m.km}^{-2}$, Chen *et al.* 1999a,b) and roads (density $\approx 1950 \text{ m.km}^{-2}$), bottomland forests and wetland (5%), and shrub or young forests (9%). About 87 percent of the land has slopes <25 percent; and 91.9 percent of the land area is between 150 and 300 m in elevation (Xu *et al.* 1997). With these landscape characteristics, it seemed logical that plant distribution may be strongly influenced by physiological features such as elevation and slope.

Ecologists have long asserted that species distributions are tightly related to their habitats (e.g., Brown and Lomolino 1998). While new studies continue to find examples of unexpected relationships between structure (i.e., habitat) and species distribution, current management and conservation efforts are often made based on local or fine-scale habitat attributes instead of broad-scale landscape perspectives (Franklin 1993). The northern spotted owl (*Strix occidentalis caurina*) provides an example of this mismatch between conservation initiatives and habitat requirements in the Pacific Northwest (PNW). Although the northern spotted owl has traditionally been considered an old-growth species (Bart and Forsman 1992, Carey *et al.* 1992), it can also be found in young plantations. Thus, both environmental groups and industries have tended to use this species to advance opposing protocols for management of old-growth forests in the PNW. The real issue is not the dependency of the species on the old-growth forest but, more importantly, its need for multiple habitats, including old-growth forest in a landscape context, i.e., landscape complementation (Burnett *et al.* 1998, Dunning *et al.* 1992). This example highlights some of the strengths of MOFEP, but also the difficulties associated with data interpretation. All nine

experimental sites in the MOFEP study had a similar overstory structure, allowing examination of the effects of silvicultural treatments on various ecological properties, including distributions of flora and fauna, within a somewhat controlled field setting. This similarity in overstory structure, however, may confound the results, and the data may not reflect the overall dynamics of the species across the landscape. To address this issue, one of the initial goals of our study was to provide baseline information for exploring the differences between data collected within (Grabner *et al.* 1997) and outside of the MOFEP experimental units.

A number of studies have suggested that spatial distribution and temporal dynamics of species in a landscape are scale dependent (Rosenzweig 1995, Wiens 1989). For example, Brosnokske *et al.* (1999) found that, across the homogeneous pine-barrens in northern Wisconsin, plant species clustered differently depending on scales used in analysis. A habitat patch can be species-poor at smaller scales, but this patch may be nested within a species-rich landscape at broader scales. Many avian species perceive not only the local-scale structure as traditionally studied (e.g., MacArthur and MacArthur 1961) but also the landscape-level structure of their environment (e.g., Hansen and Urban 1992, McGarigal and McComb 1995, Storch 1997); persistence of avian populations is often dependent not only on habitat structure within focal patches, but also on resources within patches in the surrounding landscape (Whitcomb *et al.* 1977). The communities of neotropical migrants parasitized by brown-headed cowbirds (*Molothus ater*) in the Midwest U.S. change regionally (Hahn and Hatfield 1995), and, consequently, reproductive success and population stability of these species depend on habitat characteristics at the landscape scale (Donovan *et al.* 1995, Robinson *et al.* 1995). Similarly, the foraging behavior of ungulates has been shown to depend on factors such as forage quality, plant species composition, and position in the landscape that will vary in scale from meters to thousands of hectares (Turner *et al.* 1997). Previous simulation studies have also demonstrated the importance of landscape composition and arrangement at multiple scales in determining the dispersal patterns of organisms (Gustafson and Gardner 1996). Thus, landscape-level examinations of habitat-species relationships can link traditional, local microscale studies with information on regional distributions (Dunning *et al.* 1992).

The objective of this study was to explore the spatial relationships between plant species distribution and diversity with position in the landscape (e.g., high or low elevation) at multiple spatial scales in the southeastern Missouri Ozarks. Specifically, we aimed to: (1) explore the changes in understory vegetation with physiography of the landscape using relative elevation as a proxy measurement; (2) examine the importance of scale in quantifying community composition; and (3) discuss research needs for understanding species distributions in the Ozark landscape and priorities for adaptive landscape management. A central hypothesis of this study was that landscape structure, defined by both biotic and abiotic variables, determines the spatial distribution of plant species and, therefore, the species diversity and abundance can be predicted from various, multi-scale measurements of landscape structure. In the southeastern Missouri Ozarks, mature, homogeneous oak-hickory and oak-pine forests cover the majority of the landscape. Physiographical features (e.g., elevation, slope, and aspect) are the dominant structural features affecting species distribution, in addition to characteristics induced by human disturbances.

METHODS

Our study area is located in the southeast Missouri Ozarks (36°15'N and 90°33') where nine sites had been identified for a large, comprehensive scientific study known as the Missouri Ozark Forest Ecosystem Project (MOFEP) (Brookshire and Shifley 1997). The area is characterized by a humid continental climate, with hot, humid summers and cool winters. Average annual precipitation is 112 cm with the majority of rain falling in spring and summer (Chen *et al.* 1999b). Dolomitic limestone embedded with large quantities of chert dominate the watershed. The soil is clay to clay loams, with extremely variable depths and content across the landscape (Hammer 1997). Due to the clearing of almost all the forest in the 1800s, the landscape is covered by mature, relatively unfragmented southern hardwoods (Guyette and Dey 1997).

In 1995, we used a digital compass to lay out 3,940 m of transect southward and 6,060 m of transect northward (total 10,000 m) from a permanent climatic station installed in the

center of site 1 (Chen *et al.* 1997). A global positioning system (GPS) unit was used to precisely measure the geographic location of the transect, including elevation, every 10 m (Xu *et al.* 2000). With differential correction, GPS locations could be determined within 1.3 m in the horizontal plane and within 28 m in elevation. Vegetation was sampled every 10 m in a 1 x 1 m quadrat on each side of the transect, resulting in a rectangular sample area of 2 m² within 1,001 plots along the 10,000 m transect. To avoid biases that may be caused by seasonal dynamics of vegetation, we collected vegetation data between September 2 and September 20, 1997. The Shannon-Wiener diversity index (H') (natural log), Simpson's diversity index (D) (natural log), and species richness (N) (Magurran 1988) were calculated. For each species, growth form (e.g., forbs vs. grass), longevity (annual, biennial, and perennial), seed dispersal mechanism (e.g., wind vs. animal), nitrogen fixation capability (actinomycetes vs. *Rhizobium*), and origin (i.e., native vs. exotic) were identified from existing literature and databases (Gleason and Cronquist 1991, Grabner *et al.* 1997, Wherry 1995). The frequency of species occurring along the transect, species richness by plot, and average cover of each species by plot were also calculated. The cumulative number of species was used to generate a species-area curve starting at the southern end of the transect and incorporating new species encountered moving northward.

Our initial analysis indicated a gradual increasing trend in elevation along the transect (fig. 1a). Since our primary interest was to examine how position in the landscape affects plant distribution, we calculated the relative elevation (RE) by subtracting the linear trend of elevation changes (based on a linear regression model) from the actual elevation and scaling its minimum value to be sure to avoid possible computation problems (e.g., log-transformation) later in the analysis. The following equation was used to calculate RE:

$$\text{Relative Elevation (RE)} = -0.3 \cdot (188.72 + 0.01007 \cdot \text{Distance-Elevation}) + 20$$

The RE removed the trend while keeping the information on the relative position of each point in the landscape (fig. 1b). The average, minimum, and maximum values for RE along the transect were 19.9, 2, and 35.4 m, respectively (table 1).

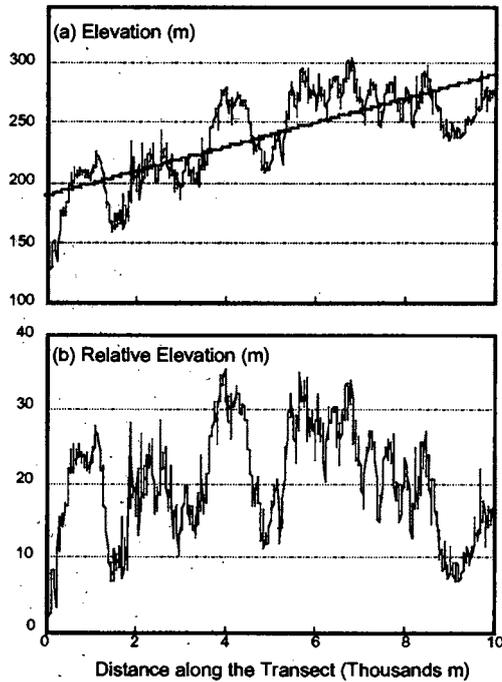


Figure 1.—The trend of increasing elevation (m) along the 10-km transect (a) was measured using a sub-meter global positioning system (GPS). A linear model (see text) was subtracted and scaled to generate the relative elevation (m; b) for analyzing the importance of elevation in controlling species distribution.

To examine the effects of scale on plant distribution, plant diversity, and position in the landscape, we used wavelet analysis as the primary statistical tool to explore the spatial changes of RE, richness, and diversity indices along the transect at scales between 10 and 3,500 m (see Bradshaw and Spies 1992, Brosofske *et al.* 1999, Gao and Li 1993, and Saunders *et al.* 1998 for methodology, application details, and interpretations). Wavelet analysis quantifies the pattern within a data series as a function of scale and location along a transect and indicates the dominant scales of pattern in a data set (Bradshaw 1991, Graps 1995). We calculated wavelet transforms for RE, H', D, and N along the transects as:

$$W(a, b) = \frac{1}{a} \sum f(x) * g\left(\frac{x-b}{a}\right)$$

where the shape (i.e., the dimension of the window of analysis) of the analyzing wavelet, $g(x)$, changes with scale, a , and the analyzing wavelet moves along the data series, $f(x)$, centered at each point, b , along the transect (Bradshaw and Spies 1992, Li and Loehle 1995). The wavelet transform was calculated across scales of $a = 10, 20, \dots, 3500$ in $a \leq b \leq n-a$. We used the wavelet variance, $V(a)$:

$$V(a) = \frac{1}{n} \sum W^2(a, b)$$

Table 1.—Summary statistics of plant species richness and diversity, and of elevation along a 10-km transect in the southeast Missouri Ozarks

	Average	Minimum	Maximum
Total number of species	332		
Accurately identified	302		
Elevation (m)	239	129.3	303.1
Relative elevation (m)	19.9	2	35.4
No. species/plot	6.54	0	43
Shannon H'	0.88	0	2.13
Simpson's D	0.77	0	2.93

to capture the dominant scales of patch patterns. Use of this technique ensured that our analysis of patterns and relationships across the landscape need not be restricted to data sets with stationary statistical properties (i.e., properties such as mean and variance that are similar regardless of location along the transect) as with related techniques such as Fourier analysis (Bradshaw 1991). Because information on location along the transect is retained for the wavelet transform, we were able to examine our data *post hoc* for features in the landscape that might have influenced patterns in species distribution. A program developed by Li and Loehle (1995) was used to calculate both Mexican hat wavelet transform and wavelet variance. The Pearson correlation coefficient (r) was used to examine the relationship between wavelet transforms of relative elevation and species diversity and thus to identify the most prominent scales for species "hot spots" in the landscape.

RESULTS

We encountered 332 plant species (302 were identified to the species level) in the 1,001 plots along the 10-km transect, with average, minimum, and maximum richness of 6.5, 0, and 43 species per plot, respectively (table 1). Because many plots had fewer than two species, the Shannon H' and Simpson's D indices varied from 0 to 0.88 and 0.77, respectively (table 1). All 332 of 332 species occurred within <10 percent of the plots, and 72 species were encountered only once along the transect. *Desmodium nudiflorum* and *Parthenocissus quinquefolia* were the two most frequently encountered species (48.8 and 37.0 percent of plots, respectively). Only two plots had no species, and 197 and 114 plots had one and two species, respectively. Two-thirds of the plots (67.8%) contained < seven species (fig. 2).

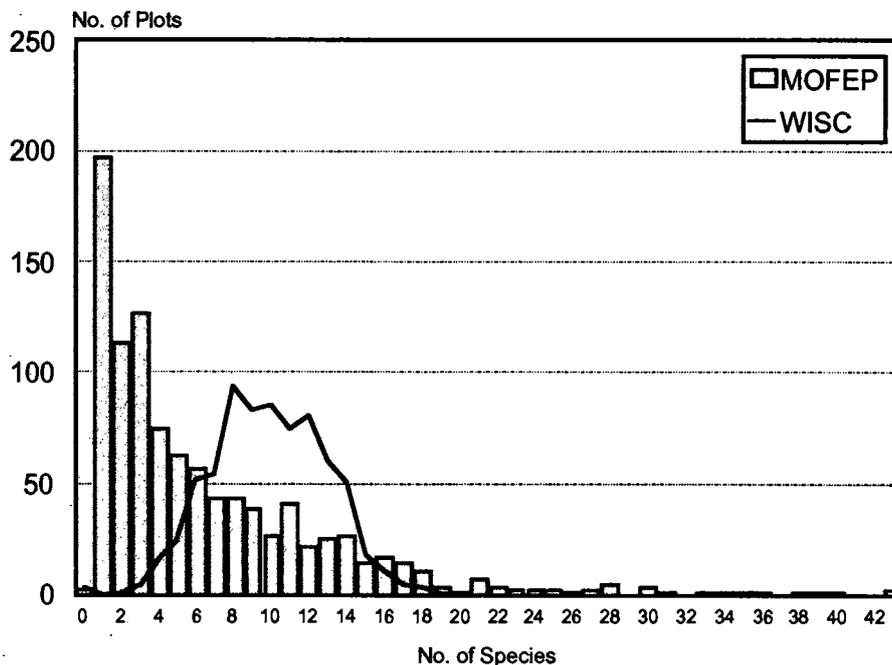


Figure 2.—Frequency distribution of sampling plots by the number of species per plot along the 10-km transect oriented south-north in the Missouri Ozarks. Most plots contained fewer than six species.



Most species (193 of 302, 63.9%) were forbs, excluding 23 legume species (table 2). Regarding lifespan, 251 (83.1%) of the species were perennial and only 5 species were biennial. Eighteen of 302 species were nitrogen fixers. When we examined the seed dispersal mechanisms of these plants from existing publications, most (246 of 302, 81.4%) had mixed dispersal mechanisms such as by both wind and animal. No plant was found to be solely dependent on wind or water for its seed dispersal. Twenty-three species were identified as being solely dispersed by animals. Ten exotic species were encountered (appendix 1).

Table 2.—Distribution of plant species within different functional groups. This table includes only plants that were identified to species.

Category	Species Number
Plant Form	
Forbs (1)	193
Shrub (2)	30
Grass (3)	27
Sedge (4)	16
Fern (5)	8
Legume (6)	23
Tree (7)	5
Longevity	
Annual (1)	39
Biennial (2)	11
Perennial (3)	252
Seed Dispersal	
Wind (1)	0
Animal (2)	23
Water (3)	0
Mix (4)	244
Wind/Water (5)	35
N-fixation	
N-Fixation (1)	18
No. N-fixation (2)	284
Origin	
Native (1)	292
Exotic (2)	10
Total	302

The cumulative number of species we encountered moving away from a point along the transect (i.e., β -diversity) suggested that new species added to the total pool tended to occur when RE changed (fig. 3). This suggested that heterogeneity of landform in the landscape was a key determinant of the overall, regional diversity (i.e., γ -diversity). Along the transect, we detected several jumps in β -diversity at 900-1,000 m, 4,800-5,000, and 8,900-9,100 m. It was clear that many sampling plots within a wide range of the landscape were needed to obtain a thorough species list for the Ozarks (fig. 3). With 600 1 x 1 m plots at 3,000 m from the south end of the transect, we encountered only 278 of 332 species (83.7%). Excluding the 30 new species added to the pool where a north-facing slope dropped to a bottomland at about 9,000 m near the north end of the transect, we collected 92.1 percent of the total species encountered within the first 3,000 m of the transect. The plots at around 5,000 and 9,200 m on the transect were near small streams and contained more species (>30/plot) than any other plots along the transect. Overall, uplands (3,800 to 10,000 m), generally had 5 species/plot while plots in the Current River Valley (i.e., 0 to 3,800 m) contained 10-15 species (see fig. 3). Small differences existed between lowlands and uplands in the Current River Valley (<3,800 m) where species diversity was similar to that of low elevation areas in the uplands. It was apparent that three quantitative measurements (i.e., H', D, and N) provided different information on the effects of landforms on plant distributions.

Changes in species abundances were strongly associated with RE, as evident from the two most frequent species (fig. 4). Generally, north-facing slopes and the bottomlands appeared to be preferred habitats for new species. The lowland areas at 1,500, 5,000, and 9,000-10,000 m along the transect were obviously the "hot spots" for both species richness and abundance. However, the relationship varied among species, and the correlation between species abundance and elevation was dependent on location. For example, both *Desmodium nudiflorum* and *Parthenocissus quinquefolia* were abundant at a bottomland between 4,200 and 5,600 m along the transect, but not at other bottomlands (fig. 4). In general, measures of species richness correlated negatively with relative elevation, although there were very weak correlations between diversity measurements and relative elevation (fig. 5).

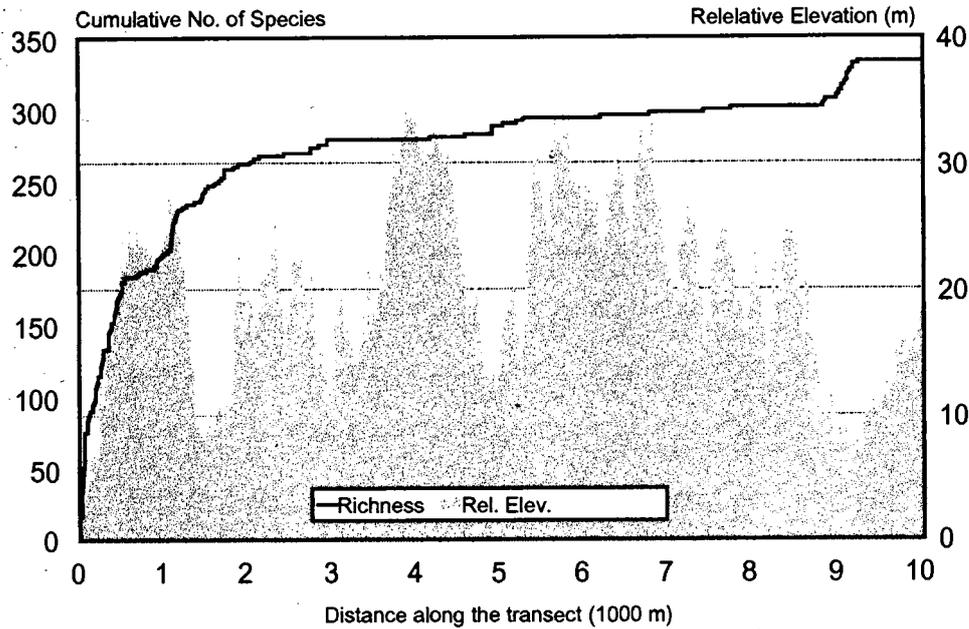


Figure 3.—Changes in cumulative number of plant species, overlaid on relative elevation, along the 10-km transect in the southeast Missouri Ozarks. It appears that at least 300 1x2 m² plots (i.e., 600 m²) spread across at least 3,000 m are needed to encounter most (278 of 332 species, 83.7%) of the total species in the landscape.

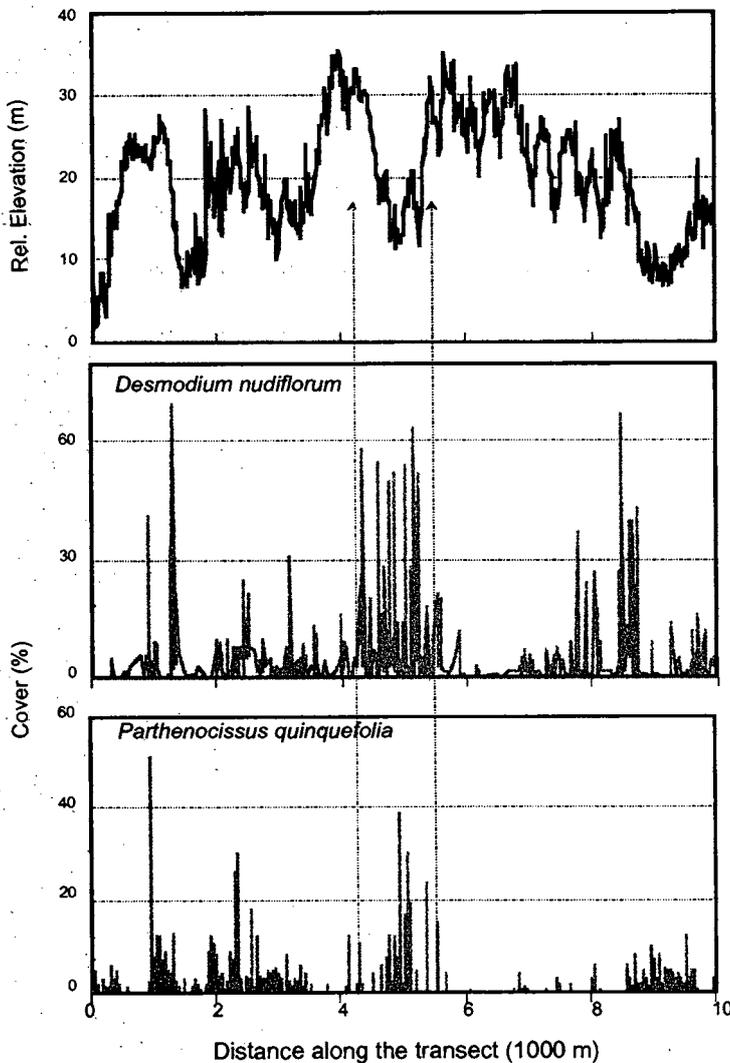


Figure 4.—Changes with elevation (a) in species cover of the two most frequent species (b and c) along the 10-km transect in the southeast Missouri Ozarks. There is a clear negative correlation with relative elevation, i.e., the two selected species are more abundant in areas with low relative elevation.

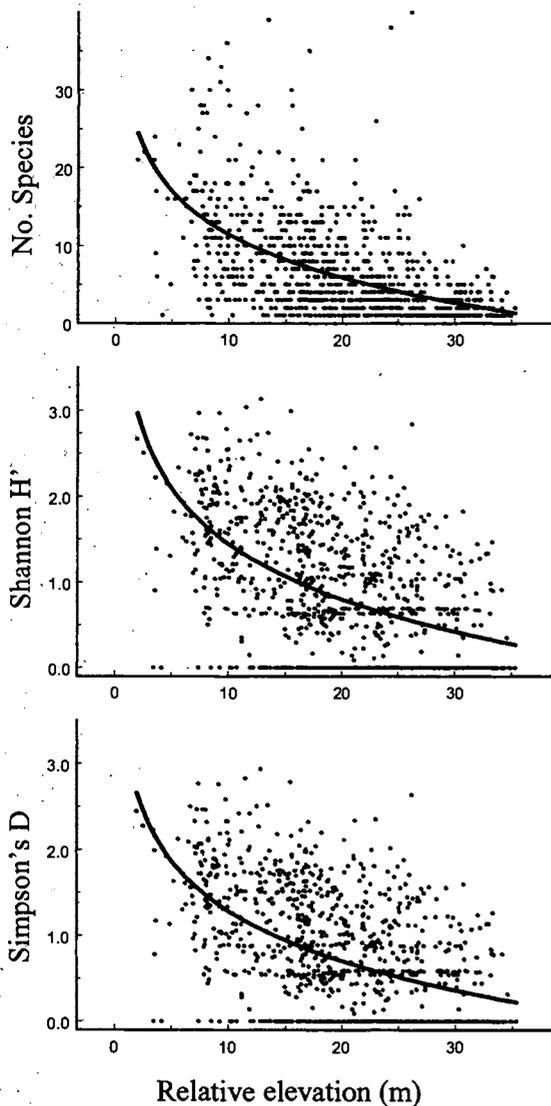


Figure 5.—Relationships between three measurements of species diversity and relative elevation along the 10-km transect in the southeast Missouri Ozarks. The solid lines are logarithm regression models showing the general trends for each of the three diversity measurements.

The changes in wavelet transforms of relative elevation, species richness, Shannon diversity, and Simpson diversity suggested that scale had an important effect on underlying patterns in diversity (fig. 6). Patterns were scale-dependent. For example, a low-diversity patch at about 4,000 m on the transect was visible only at scales of 1,800-2,300 m, while another similar patch at 900 m could only be detected at analysis scales of 300-1,700 m. Finally, it seemed that the patch patterns of relative elevation were similar to those of diversity measurements.

The correlation between diversity and relative elevation also showed a strong dependency on scale, with a peak at 1,340 -1,400 m (fig. 7a) for all three diversity measurements. However, the changes in wavelet variance (an indicator of dominant patch size) with scale (fig. 7b) suggested that even broader scales are necessary when diversity measures are independently analyzed. For example, wavelet variance of diversity measures peaked at a scale of 1,720 m, while for relative elevation most of the variation in patterns based on wavelet variance occurred at 1,850 m. This suggests that 1,400 m is the most appropriate scale to use in identifying "diversity patches," but smaller scales between 1,340 and 1,400 m are more appropriate to examine the spatial relationships between diversity measurements and elevation. The above differences in determining the right scales for patch delineation and spatial correlations were likely caused by distance lags (i.e., about 500-m differences) between the elevation patch and diversity patch.

DISCUSSION

One significant characteristic of the Ozarks landscape is its high plant richness, although the landscape structure (defined as overstory vegetation) along the transect is relatively simple and homogeneous. Associated with the MOFEP treatment sites, Grabner *et al.* (1997) reported that 530 vascular species in 85 families were identified, including 25 exotic species. We encountered 332 species within a 2,000 m² sampling area; Brososke *et al.* (1999) found fewer than 150 species in a similar study in northern Wisconsin. This high γ -diversity is not associated with total number of species per plot (α -diversity), but with high species variation among the plots (i.e., the β -diversity). In the

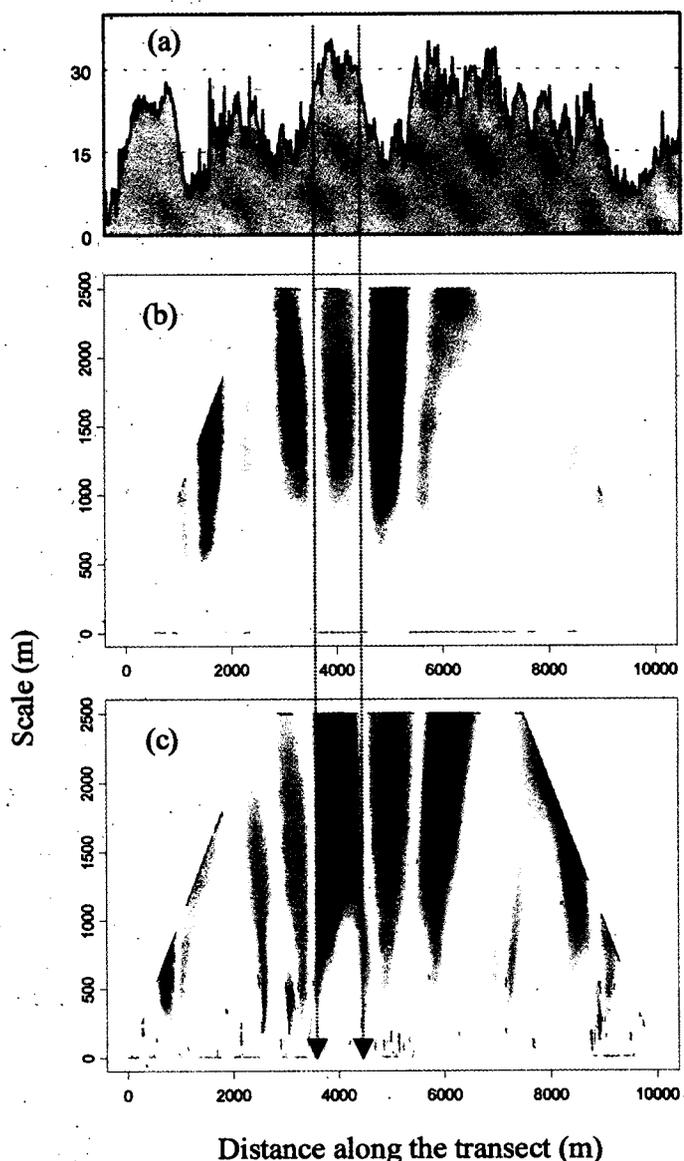


Figure 6.—Relative elevation (a) and wavelet transforms of relative elevation (b) and the Shannon diversity index (H') (c) along the 10-km transect in the southeast Missouri Ozarks. The negative correlation between relative elevation and plant diversity is clearer with increasing scale. Changes from green to red indicate a decrease in wavelet transform.

Ozark landscape, there was a J-shaped frequency distribution of plots by category of number of species (fig. 2), but in northern Wisconsin, there was a bell-shaped frequency (Brosofske *et al.* 1999). One possible explanation for the high γ -diversity in the Ozarks is that species contained in each plot differ from each other. The high species turnover among plots in the Ozark landscape contrasts with other regions such as northern Wisconsin. In Wisconsin, where intense and frequent disturbances (e.g., fires and harvesting) have occurred since the 19th century, high average numbers of species per plot were also observed. However, species composition was similar among plots. In

the two previous case studies, it is apparent that the warm, humid climate is responsible for the high total number of species (Brown and Lomolino 1998) in Missouri, but it cannot explain the high variation among the plots. Although time since disturbance, initial cutting practices, and post-harvest silvicultural management could lead to high levels of variation in plant diversity at the scale observed in Wisconsin (e.g., see Rubio *et al.* 1999), these factors are unlikely to produce the finer scale variation observed among plots in Missouri. We suggest that the terrain and heterogeneous soils (Hammer 1997) are probably responsible for the high β -diversity in the Ozarks.

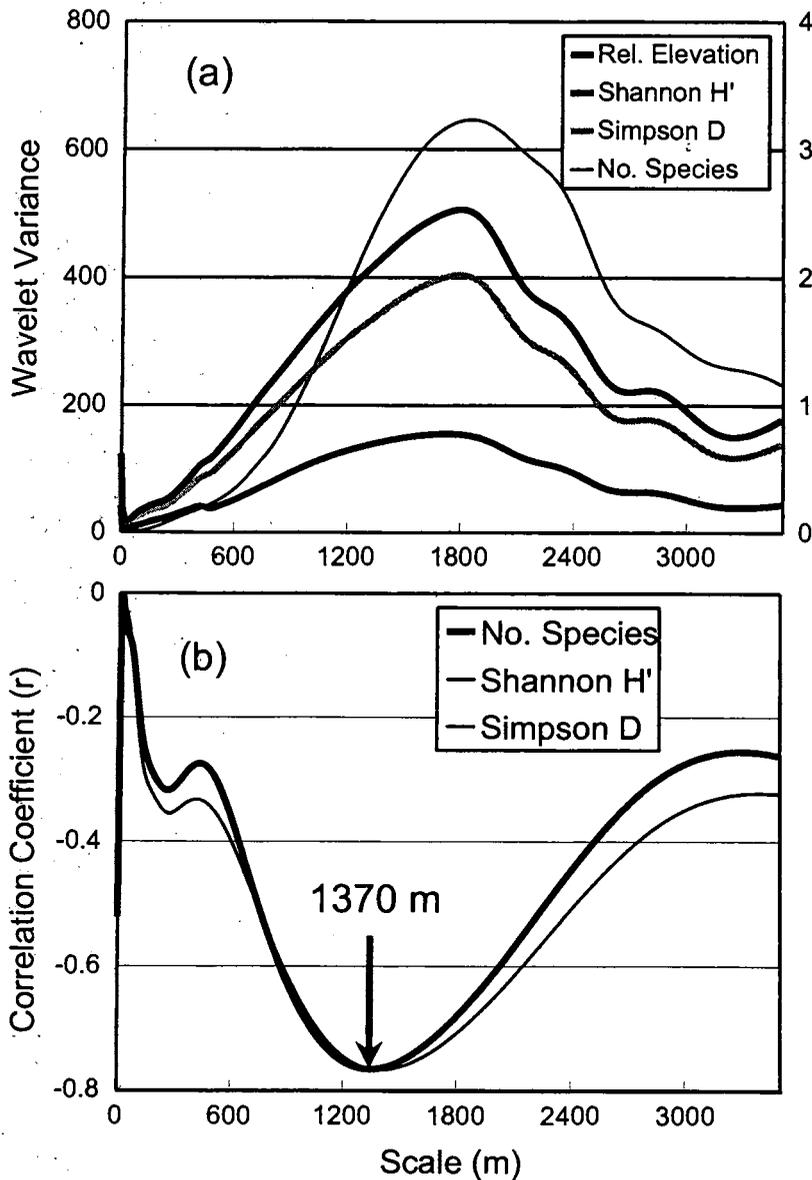


Figure 7.—Wavelet variance peaks (i.e., patterns are strongest) for the three diversity measurements and relative elevation at scales between 1,500 m and 2,100 m (a). However, the correlations between the wavelet transforms of relative elevation and species diversity are strongest at a scale of 1,370 m (b). The two lines representing Shannon and Simpson indices are almost identical and the differences cannot be visually detected in (b).

We found that spatial distributions of plants were dependent upon their relative position in the landscape. For the southeastern Missouri Ozarks, where vegetation is relatively homogeneous, landscape structure such as soils and RE are likely the dominant structural features affecting ecological characteristics across the landscape. Current and future management attention should be directed to the bottomlands in the Ozarks, because they provide habitats for a large number of understory species. However, based on our results that the correlation between species abundance and elevation is location dependent, it suggests that conservation planning may have to be undertaken on a site-specific (fine-scale) basis. The determinants of understory richness and distributions of certain species may vary among geographic

locations (Huebner *et al.* 1995, McKenzie and Halpern 1999). This research provides further support for the use of ecological land types not only in understanding vegetation patterns but also in predicting vegetation types using physiography (Barnes *et al.* 1982, Cleland *et al.* 1994).

Wavelet analysis was used recently in landscape ecology to explore the changes in patterns and their relationships with landscape processes across scales (Bradshaw *et al.* 1992, Dale and Mah 1998, Saunders *et al.* 1998). Although our spatial data were collected along a single transect, due to limitations of time and labor requirements in the field, we would expect the results from the wavelet variance to be similar along additional transects at similar or different

orientations within this landscape. The wavelet variances indicated that the patch patterns of relative elevation and diversity measurements could be best described at a scale of about 1,800 m (fig. 7), while the best scale for examining their spatial relationships was 1,400 m. At scales between 1,370 and 1,400 m, the wavelet transforms of diversity and elevation exhibited clear and strong negative correlations (fig. 6). These results supported recent theories that "choosing the right scale" (Holling 1992) and "exploring the pattern-process relationship at multiple scales" (Levin 1992) are both important. Indeed, we propose that the "right" scale or scale "range" may vary with locations across the landscape, suggesting that different "right" scales could be applied for the same landscape. Analysis of determinants of understory plant distributions in the Pacific Northwest similarly demonstrated that the best predictive models changed with both scale and geographic location. Response patterns of species to elevation, slope, moisture, and overstory cover at one scale may not parallel responses at other ecological levels (McKenzie and Halpern 1999). Further, although species distributions may have some common causes across scales, finer scale floristic variation may be only weakly related to larger scale patterns and be primarily the product of causes that are relatively unimportant at broad scales (Palmer 1990).

It appeared that the peaks in wavelets variance at 1,340-1,400 m scales reflect the topographical settings of the Ozarks. More importantly, RE alone can explain a large proportion of the variance in the distribution of plant species across the landscape ($R = 0.78$). However, correlation analysis suggested only weak correlations between diversity measurements and relative elevation (fig. 5). We believe that scale might be the explanation for these low correlations. When examined at appropriate and multiple scales, these correlations should be strengthened. With further information on overstory vegetation, soils, roads, and both human and natural disturbances, we are confident that one could develop a highly predictive model to explain the distribution of plants across scales in the Ozarks landscape.

Landscape structure can be quantified using different variables, such as vegetation or physical conditions. We are exploring how plant distributions are affected or related at multiple

scales to ecological landtype, canopy coverage, amount of coarse woody debris (CWD), leaf area (e.g., NDVI), and microclimate along the transect. We expect a comprehensive image will be developed to predict the effects of various land management activities and/or changes in landscape structure on plant species. For example, ecological indicators of change in forest conditions at specific scales and in the scale- and location-specific associations between plant diversity and landform may be identified by examining the influence of reproductive biology and life history traits we recorded (e.g., see Dibble *et al.* 1999). If such patterns exist, this information could be useful in predicting the establishment, spread, and persistence of plant species in particular habitats and disturbance regimes. The latter may be especially useful in predicting the potential impact of invasive exotic species and the potential loss or recovery of threatened species in a given landscape.

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Post Treatment Results of the Landscape Experiment

Appendix I.—Species characteristics and their frequency and coverage encountered along a 10-km transect in the southeast Missouri Ozark landscape. See table 2 for their forms, life spans, origins, N-fixation, and seed dispersal mechanisms. The species noted with * were not found in the MOFEP database (Grabner et al. 1997).

Scientific name	Common name	Life span	Origin	N-fixation	Dispersal mechanism	Cover (%)	Max cover (%)	Relative freq (%)	Frequency
<i>Desmodium nuttallii</i>	Nuttall's trefoil	2	1	1	2	2.7	23.6	47.5	475
<i>Parthenocissus quinquefolia</i>	Virginia creeper	2	1	1	4	1.8	37.5	37.0	370
<i>Amphicarpa bracteata</i>	Hog peanut	2	1	2	4	1.7	18.5	29.2	292
<i>Vitis aestivalis</i>	Summer grape	2	1	1	4	1.3	21.8	23.8	238
<i>Vaccinium vacillans</i>	Low blueberry	2	1	1	4	1.5	13.9	21.2	212
<i>Carex nigromarginata</i>	Black-edged sedge	2	1	1	4	0.3	3.0	17.5	175
<i>Panicum boscii</i>	Bosc's panic grass	2	1	1	4	0.4	2.0	16.7	167
<i>Viola sororia</i>	Hairy wood violet	1	1	1	4	0.6	10.5	13.0	130
<i>Potentilla simplex</i>	Common cinquefoil	2	1	1	4	0.8	12.5	12.3	123
<i>Pteridium aquilinum</i>	Bracken fern	2	1	1	4	1.2	11.5	12.3	123
<i>Solidago ulmifolia</i>	Elm-leaved goldenrod	2	1	1	1,3	0.6	4.5	10.0	100
<i>Desmodium glutinosum</i>	Pointed tick trefoil	2	1	1	2	1.5	16.5	8.5	85
<i>Toxicodendron radicans</i>	Poison ivy	2	1	1	1,3	2.2	17.3	7.4	74
<i>Aristolochia serpentaria</i>	Virginia snakeroot	2	1	1	4	0.2	0.5	7.2	72
<i>Dioscorea quatemata</i>	Four-leaf yam	2	1	1	4	0.9	3.0	7.1	71
<i>Vaccinium stamineum</i>	Deerberry	2	1	1	4	1.2	7.0	7.1	71
<i>Carex</i> spp.	Sedge					0.3	6.5	7.0	70
<i>Galium circaezans</i>	Wild licorice	2	1	1	4	0.2	1.0	6.9	69
<i>Panicum dichotomiflorum</i>	Knee grass	1	1	1	4	0.3	2.0	6.9	69
<i>Smilacina racemosa</i>	F. False Solomon's seal	2	1	1	4	0.6	2.9	6.2	62
<i>Brachyelytrum erectum</i>	Long-awned grass	2	1	1	4	1.2	10.0	5.8	58
<i>Phryma leptostachya</i>	Lopseed	2	1	1	4	0.4	2.9	5.8	58
<i>Sanicula</i> spp.	Snakeroot					0.6	13.1	5.6	56
<i>Viola triloba</i>	Three-leaved violet	1	1	1	4	0.2	1.3	4.9	49
<i>Cunila organoides</i>	Dittany	2	1	1	4	0.6	2.8	4.9	49
<i>Vitis</i> spp.	Grape					0.1	0.7	4.8	48
<i>Panicum commutatum</i>	Panic grass	2	1	1	4	0.3	2.6	4.7	47
<i>Carex blanda</i>	Wood sedge	2	1	2	4	0.6	4.0	4.6	46
<i>Acalypha virginica</i>	Virginia mercury	2	1	1	4	0.3	1.3	4.6	46
<i>Bromus purgans</i>	Woodland brome	2	2	1	4	0.6	10.0	4.6	46
<i>Monarda russeliana</i>	Bradbury beebalm	2	1	1	4	0.6	4.9	4.5	45
<i>Helianthus strumosus</i>	Pale-leaved sunflower	2	1	1	4	0.5	2.1	4.4	44
<i>Danthonia spicata</i>	Poverty oat grass	2	1	1	4	0.4	2.5	4.3	43
<i>Galium concinnum</i>	Shining bedstraw	2	1	1	4	0.4	2.0	4.3	43
<i>Rubus enslenii</i>	Southern dewberry	2	1	1	4	1.3	7.5	4.1	41
<i>Galium arkansanum</i>	Arkansas bedstraw	2	1	1	4	0.2	1.0	4.0	40
<i>Geranium maculatum</i>	Wild geranium	1	1	1	4	0.6	2.5	4.0	40
<i>Uvularia grandiflora</i>	Bellwort	2	1	1	4	0.7	4.5	3.9	39
<i>Geum canadense</i>	White avens	2	1	1	4	0.9	2.6	3.7	37
<i>Aster anomalus</i>	Blue aster	2	1	1	1,3	0.5	2.0	3.7	37
<i>Desmodium dillenii</i>	Tall tick clover	2	1	1	2	1.0	9.1	3.7	37
<i>Aster patens</i>	Spreading aster	2	1	1	1,3	0.4	1.5	3.6	36
<i>Silphium asteriscus</i>	Starry rosinweed	2	1	1	4	0.5	2.3	3.6	36
<i>Uniola latifolia</i>	Spike grass	2	1	1	4	0.8	3.5	3.5	35
<i>Symphoricarpos orbiculatus</i>	Corallberry	2	1	1	4	1.5	7.0	3.5	35

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(Appendix continued)

Scientific name	Common name	Life span	Origin	N-fixation	Dispersal mechanism	Cover (%)	Max cover (%)	Relative freq (%)	Frequency
<i>Asplenium platyneuron</i>	Ebony spleenwort	2	1	1	4	0.4	3.3	3.4	34
<i>Viola</i> spp.	Violet					0.1	0.4	3.4	34
<i>Rubus pensilvanicus</i>	Yankee blackberry	2	1	1	4	2.0	20.0	3.4	34
<i>Euphorbia corollata</i>	Flowering spurge	1	1	1	1,3	0.3	2.5	3.3	33
<i>Carex umbellata</i>	Umbel - like sedge	2	1	1	4	0.2	0.9	3.2	32
<i>Helianthus hirsutus</i>	Oblong sunflower	2	1	1	4	0.8	3.5	3.1	31
<i>Phlox divaricata</i>	Blue phlox	2	1	1	4	0.3	1.4	3.1	31
<i>Dioscorea villosa</i>	Wild yam	2	1	1	4	0.7	2.1	3.0	30
<i>Parthenium integrifolium</i>	Wild quinine	2	1	1	4	0.6	2.5	3.0	30
<i>Antennaria plantaginifolia</i>	Pussy's toes	2	1	1	4	0.3	1.1	2.9	29
<i>Vitis vulpina</i>	Frost grape	2	1	1	4	1.1	7.0	2.9	29
<i>Cimicifuga racemosa</i>	Black cohosh	2	1	1	4	2.6	7.0	2.8	28
<i>Elymus villosus</i>	Silky wild rye	2	1	2	4	1.3	4.8	2.8	28
<i>Pilea pumila</i>	Clearweed	1	1	1	4	3.9	18.5	2.8	28
<i>Sanicula canadensis</i>	Canadian black snakeroot	3	2	1	4	0.6	6.5	2.8	28
<i>Carex complanata hirsuta</i>	Hirsute sedge	2	1	1	4	0.8	9.0	2.8	28
Unknown						0.5	6.5	2.7	27
<i>Solidago hispida</i>	White goldenrod	2	1	1	1,3	0.6	2.6	2.7	27
<i>Lespedeza repens</i>	Creeping bush clover	2	1	1	2	0.3	1.6	2.7	27
<i>Verbesina alternifolia</i>	Yellow ironweed	2	1	1	4	0.8	3.0	2.6	26
<i>Panicum lanuginosum</i>	Woolly panic grass	2	1	1	4	0.3	0.6	2.6	26
<i>Ipomoea pandurata</i>	Wild sweet potato	2	1	1	4	0.6	1.8	2.5	25
<i>Solidago flexicaulis</i>	Broad-leaved goldenrod	2	1	1	1,3	0.8	3.1	2.4	24
<i>Krigia biflora</i>	False dandelion	1	1	1	4	0.3	1.5	2.4	24
<i>Panicum linearifolium</i>	Slender-leaved panic grass	2	1	1	4	0.5	4.3	2.4	24
<i>Lespedeza procumbens</i>	Trailing bush clover	2	1	1	2	1.5	11.5	2.4	24
<i>Verbesina helianthoides</i>	Wing-stem	2	1	1	4	1.5	13.0	2.2	22
<i>Galium triflorum</i>	Sweet-scented bedstraw	2	1	1	4	0.8	6.5	2.2	22
<i>Polygonum scandens</i>	Climbing false buckwheat	2	1	1	4	0.4	1.0	2.2	22
<i>Clitoria mariana</i>	Butterfly pea	2	1	2	4	0.6	2.0	2.2	22
<i>Lysimachia lanceolata</i>	Lance-leaved loosestrife	2	1	1	4	0.4	1.0	2.2	22
<i>Lespedeza hirta</i>	Hairy bush clover	2	1	1	2	0.8	5.0	2.1	21
<i>Solidago</i> spp.	Goldenrod					0.3	0.8	2.1	21
<i>Eupatorium rugosum</i>	White snakeroot	2	1	1	4	0.7	1.6	2.0	20
<i>Carex cephalophora</i>	Woodbank sedge	2	1	1	4	0.4	1.3	2.0	20
<i>Scutellaria elliptica</i>	Hairy skullcap	2	1	1	4	0.6	3.5	2.0	20
<i>Festuca subverticillata</i>	Fescue					0.3	0.8	2.0	20
<i>Erechtites hieracifolia</i>	Fireweed	1	1	1	4	1.2	5.0	2.0	20
<i>Viola striata</i>	Cream violet	1	1	1	4	1.6	8.0	2.0	20
<i>Muhlenbergia sobolifera</i>	Rock satin grass	2	1	1	4	0.5	2.0	1.9	19
<i>Geum</i> spp.	Avens					0.7	6.4	1.9	19
<i>Panicum sphaerocarpon</i>	Round-fruited panic grass	2	1	2	4	0.1	0.3	1.8	18
<i>Carex retroflexa</i>	Reflexed sedge	2	1	1	4	1.5	20.0	1.8	18

(Appendix continued on next page)

Post Treatment Results of the Landscape Experiment

(Appendix continued)

Scientific name	Common name	Life span	Origin	N-fixation	Dispersal mechanism	Cover (%)	Max cover (%)	Relative freq (%)	Frequency
<i>Polygonum virginianum</i>	Virginia knotweed	2	1	1	4	1.3	3.6	1.8	18
<i>Solidago nemoralis</i>	Old-field goldenrod	2	1	1	1,3	0.4	2.0	1.8	18
<i>Desmodium laevigatum</i>	Smooth tick trefoil	2	1	1	2	0.8	4.0	1.7	17
<i>Rubus</i> spp.	Blackberry/raspberry					1.1	5.6	1.7	17
<i>Hydrangea arborescens</i>	Wild hydrangea	2	1	1	4	3.8	14.9	1.7	17
<i>Botrychium virginianum</i>	Rattlesnake fern	2	1	1	4	0.3	0.8	1.7	17
<i>Heiracium gronovii</i>	Hairy hawkweed	2	1	1	4	0.3	1.0	1.7	17
<i>Ranunculus hispidus</i>	Hispid buttercup	2	1	1	4	0.4	1.1	1.7	17
<i>Smilax bona-nox</i>	Saw greenbriar	2	2	1	4	0.8	4.1	1.6	16
<i>Rubus allegheniensis</i>	Common blackberry	2	1	1	4	2.6	12.1	1.6	16
<i>Rosa carolina</i>	Pasture rose	2	1	1	1,3	0.5	2.4	1.6	16
<i>Desmodium nudiflorum</i>	Bare trefoil	2	1	1	2	2.3	7.8	1.6	16
<i>Passiflora lutea</i>	Yellow passion flower	2	1	1	4	0.3	1.0	1.5	15
<i>Desmodium rotundifolium</i>	Round-leaved trefoil	2	1	1	2	0.7	2.3	1.5	15
<i>Lonicera flava</i>	Yellow honeysuckle	2	1	1	4	0.9	4.1	1.5	15
<i>Desmodium paniculatum</i>	Panicled trefoil	2	1	1	2	0.5	0.8	1.5	15
<i>Agrimonia pubescens</i>	Soft agrimony	2	1	1	4	0.4	1.3	1.5	15
<i>Oxalis dillenii</i>	Yellow wood sorrel	2	1	1	4	0.3	0.8	1.5	15
<i>Lespedeza intermedia</i>	Wandlike bush clover	2	1	1	2	0.3	1.4	1.5	15
<i>Galium pilosum</i>	Hairy bedstraw	2	1	1	4	0.2	0.5	1.5	15
<i>Specularia perfoliata</i>	Venus' looking glass	1	1	1	4	0.4	1.0	1.4	14
<i>Ambrosia artemisiifolia</i>	Common ragweed	2	1	1	1,3	0.2	0.5	1.4	14
<i>Sanicula gregaria</i>	Black snakeroot	2	1	1	4	5.8	25.0	1.4	14
<i>Ceanothus americanus</i>	New Jersey tea	2	1	1	4	0.3	1.3	1.4	14
<i>Lespedeza virginica</i>	Bush clover	2	1	1	2	0.3	0.5	1.4	14
<i>Smilax herbacea lasionuera</i>	Carrion flower	2	1	1	4	0.9	6.0	1.4	14
<i>Smilax tamnoides hispida</i>	Bristly greenbriar	1	2	1	4	0.4	1.5	1.4	14
<i>Silene stellata</i>	Starry campion	2	1	1	4	0.4	1.5	1.4	14
<i>Polystichum acrostichoides</i>	Christmas fern	2	1	1	4	0.5	2.0	1.3	13
<i>Hypericum hypercoides</i>	St. Andrew's cross	2	1	1	4	0.5	1.3	1.3	13
<i>Oxalis</i> spp.	Wood sorrel					0.3	1.9	1.3	13
<i>Laportea canadensis</i>	Wood nettle	2	1	1	4	4.6	13.0	1.3	13
<i>Asclepias quadrifolia</i>	Four-leaved milkweed	2	1	2	2,4	0.2	0.8	1.3	13
<i>Panicum clandestinum</i>	Deer tongue grass	2	1	1	4	0.6	1.8	1.2	12
<i>Hepatica nobilis obtusa</i>	Round-lobed hepatica	2	1	1	4	0.7	3.0	1.2	12
<i>Galactia volubilis</i>	Milk pea	2	1	1	4	0.4	1.5	1.2	12
<i>Cacalia atriplicifolia</i>	Plain Indian plantain	2	1	1	4	1.0	5.9	1.1	11
<i>Lespedeza violacea</i>	Violet bush clover	2	1	1	2	0.5	1.3	1.1	11
<i>Cassia nictitans</i>	Wild sensitive plant	1	1	1	4	0.2	0.3	1.1	11
<i>Leersia virginica</i>	White grass	2	1	1	4	0.3	1.0	1.1	11
<i>Salvia lyrata</i>	Lyre-leaved sedge	2	1	1	4	0.5	1.0	1.0	10
<i>Rubus occidentalis</i>	Black raspberry	2	1	1	4	4.6	25.0	1.0	10
<i>Tephrosia virginiana</i>	Goat's rue	2	1	2	2	0.5	2.1	1.0	10
<i>Gillenia stipulata</i>	Indian physic	2	1	1	4	0.4	0.8	0.9	9
<i>Andropogon scoparius</i>	Little bluestem	2	1	2	4	0.5	2.5	0.9	9
<i>Aster turbinellus</i>	Prairie aster	2	1	1	1,3	0.4	1.0	0.9	9
<i>Gerardia flava</i>	Smooth false foxglove	2	1	1	4	0.7	2.6	0.9	9
<i>Aster sagittifolius</i>	Arrow-leaved aster	2	1	1	1,3	0.5	1.0	0.8	8
<i>Veronicastrum virginicum</i>	Culver's root	2	1	1	4	1.6	3.3	0.8	8
<i>Andropogon gerardi</i>	Big bluestem	2	1	2	4	0.7	4.5	0.8	8

(Appendix continued on next page)



(Appendix continued)

Scientific name	Common name	Life span	Origin	N-fixation	Dispersal mechanism	Cover (%)	Max cover (%)	Relative freq (%)	Frequency
<i>Lobelia inflata</i>	Indian tobacco	1	1	1	1,3	1.1	6.0	0.8	8
<i>Carex digitalis</i>	Slender wood sedge	2	1	1	4	0.3	0.5	0.8	8
<i>Prenanthes altissima</i>	Tall white lettuce	2	1	1	4	0.5	1.8	0.8	8
<i>Phytolacca americana</i>	Pokeweed	2	1	1	4	0.6	1.6	0.8	8
<i>Carex oligocarpa</i>	Few-fruited sedge	2	1	1	4	0.5	1.1	0.8	8
<i>Poa sylvestris</i>	Woodland blue grass	2	1	2	4	0.3	0.6	0.8	8
<i>Menispermum canadense</i>	Moonseed	1	1	1	4	1.2	2.5	0.8	8
<i>Plantago pusilla</i>	Slender plantain	1	1	1	4	1.0	4.4	0.7	7
<i>Tridens flavus</i>	False redtop	2	1	2	4	0.4	1.5	0.7	7
<i>Panicum laxiflorum</i>	Lax-flowered panic grass	2	1	1	4	0.7	1.5	0.7	7
<i>Rudbeckia lacinata</i>	Wild golden glow	3 or 2	1	1	1,3	2.1	7.5	0.7	7
<i>Agrimonia rostellata</i>	Beaked agrimony	2	1	1	4	1.2	5.5	0.7	7
<i>Ligusticum canadense</i>	Angelico	2	1	1	4	0.8	2.0	0.7	7
<i>Lespedeza striata</i>	Japanese bush clover	1	2	1	2	0.2	0.3	0.7	7
<i>Lacuta canadensis</i>	Wild lettuce	1	1	1	4	0.4	1.0	0.6	6
<i>Zizia</i> spp.	Golden Alexanders					0.4	0.9	0.6	6
<i>Perilla frutescens</i>	Beefsteak plant	1	2	1	4	0.4	1.0	0.6	6
<i>Rubus flagellaris</i>	Common dewberry	2	1	1	4	2.9	7.5	0.6	6
<i>Desmodium cuspidatum</i>	Bracted tick trefoil	2	1	1	2	1.1	2.5	0.6	6
<i>Anemone virginiana</i>	Tall anemone	2	1	1	4	0.5	1.5	0.6	6
<i>Lespedeza cuneata</i>	Silky bush clover	2	1	1	2	0.4	0.7	0.6	6
<i>Liatris aspera</i>	Rough blazing star	2	1	1	4	0.3	0.5	0.6	6
<i>Carex glaucoidea</i>	Blue sedge	2	1	1	4	0.2	0.5	0.6	6
<i>Ranunculus recurvatus</i>	Hooked buttercup	2	1	1	4	0.3	0.5	0.6	6
<i>Apocynum cannabinum</i>	Prairie dogbane	2	1	2	4	0.4	0.5	0.6	6
<i>Scutellaria ovata</i>	Heart-leaved skullcap	2	1	1	4	1.3	4.1	0.6	6
<i>Silene virginica</i>	Fire pink	2	1	1	4	0.3	0.4	0.5	5
<i>Cryptotaenia canadensis</i>	Honewort	2	1	1	4	0.8	1.0	0.5	5
<i>Scleria triglomerata</i>	Tall nut rush	2	1	1	4	0.4	0.5	0.5	5
<i>Scleria</i> spp.	Nut rush					0.1	0.1	0.5	5
<i>Carex artitecta</i>	Bellows-beaked sedge	2	1	1	4	0.8	2.9	0.5	5
<i>Cassia fasciculata</i>	Partridge pea	1	1	1	4	0.2	0.4	0.5	5
<i>Carex convoluta</i>	Stellate sedge	2	1	1	4	1.2	4.0	0.5	5
<i>Rosa multiflora</i>	Multiflora rose	2	1	1	1,3	2.3	6.5	0.5	5
<i>Cirsium altissimum</i>	Tall thistle	3	1	1	1,3	1.3	3.5	0.5	5
<i>Schrankia uncinata</i>	Sensitive briar	2	1	1	2	0.8	1.5	0.5	5
<i>Scrophularia marilandica</i>	Late figwort	2	1	1	4	1.4	5.3	0.5	5
<i>Euphorbia dentata</i>	Toothed spurge	1	1	1	1,3	0.2	0.3	0.5	5
<i>Anemonella thalictroides</i>	Rue anemone	2	1	1	4	0.2	0.5	0.5	5
<i>Rudbeckia hirta</i>	Black-eyed susan	3 or 2	1	1	1,3	0.5	1.3	0.5	5
<i>Hypericum</i> spp.	St. John's wort					0.5	1.5	0.4	4
<i>Aralia racemosa</i>	Spikenard	2	1	1	4	0.2	0.3	0.4	4
<i>Corylus americana</i>	American hazelnut	2	1	1	4	1.8	6.3	0.4	4
<i>Ambrosia trifida</i>	Horseweed	2	1	1	1,3	0.5	1.0	0.4	4
<i>Juncus tenuis</i>	Roadside rush	2	1	1	4	0.3	0.7	0.4	4
<i>Aster cordiformis</i>	Heart-leaved aster	2	1	1	1,3	0.2	0.5	0.4	4
<i>Rudbeckia subtomentosa</i>	Sweet black-eyed Susan	3 or 2	1	1	1,3	0.7	1.4	0.4	4
<i>Erigeron canadensis</i>	Daisy fleabane	1	1	1	4	0.3	0.3	0.4	4

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Post Treatment Results of the Landscape Experiment

(Appendix continued)

Scientific name	Common name	Life span	Origin	N-fixation	Dispersal mechanism	Cover (%)	Max cover (%)	Relative freq (%)	Frequency
<i>Baptisa leucophaea</i>	Cream wild indigo	2	1	1	2	0.1	0.3	0.4	4
<i>Lespedeza</i> spp.	Lespedeza					0.2	0.3	0.4	4
<i>Chenopodium album</i>	Lamb's quarters	1	1	1	4	0.6	1.8	0.4	4
<i>Smilax pulverulenta</i>	Carrion flower	2	1	1	4	0.6	1.8	0.4	4
<i>Poa</i> spp.	Kentucky bluegrass					0.1	0.3	0.4	4
<i>Triosteum aurantiacum</i>	Horse gentian	2	1	1	4	0.4	0.5	0.4	4
<i>Campanula americana</i>	Tall bellflower	2	1	1	4	1.2	3.3	0.4	4
<i>Thaspium trifoliatum flavum</i>	Meadow parsnip	3	1	1	4	0.3	0.5	0.4	4
<i>Heliopsis helianthoides</i>	False sunflower	2	1	1	4	0.3	0.5	0.4	4
<i>Lacuta floridana</i>	Blue lettuce	2	1	1	4	0.3	1.0	0.4	4
<i>Elymus virginicus</i>	Virginia wild rye	2	1	2	4	0.2	0.3	0.4	4
<i>Coreopsis tripteris</i>	Tall coreopsis	2	1	1	4	0.3	0.5	0.4	4
<i>Physalis heterophylla</i>	Clammy ground cherry	2	1	1	4	2.3	6.3	0.3	3
<i>Asarum canadense</i>	Wild ginger	2	1	1	4	1.1	2.0	0.3	3
<i>Smilax rotundifolia</i>	Horsebriar	2	1	1	4	1.0	2.3	0.3	3
<i>Erigeron annuus</i>	Daisy fleabane	1	1	1	4	0.9	2.0	0.3	3
<i>Vicia caroliniana</i>	Wood vetch	2	1	1	2	0.5	1.0	0.3	3
<i>Hedeoma pulegioides</i>	American pennyroyal	1	1	1	4	0.9	1.8	0.3	3
<i>Teucrium canadense</i>	Germander	1	1	1	4	1.7	4.0	0.3	3
<i>Hamamelis virginiana</i>	Witch hazel	2	1	1	4	0.5	1.1	0.3	3
<i>Ruellia humilis</i>	Hairy ruellia	2	1	1	4	0.2	0.3	0.3	3
<i>Elephantopus carolinianus</i>	Elephant's foot	2	1	1	4	0.5	0.8	0.3	3
<i>Viburnum rufidulum</i>	Southern black haw	2	1	1	4	0.4	0.8	0.3	3
<i>Cyperus strigosus</i>	Straw-colored flatsedge	2	1	1	4	0.6	1.4	0.3	3
<i>Lobelia spicata</i>	Pale spiked lobelia	1	1	1	1,3	0.4	0.8	0.3	3
<i>Senecio obovatus</i>	Round-leaved ragwort	2	1	1	4	0.3	0.5	0.3	3
<i>Aster azurens</i>	Azure aster	2	1	1	1,3	0.5	0.9	0.3	3
<i>Celtis occidentalis</i>	Hackberry	2	1	1	4	0.2	0.3	0.3	3
<i>Asclepias verticillata</i>	Whorled milkweed	2	1	2	2,4	0.4	0.5	0.3	3
<i>Viola pedata</i>	Bird's foot violet	1	1	1	4	0.4	0.5	0.3	3
<i>Coreopsis palmata</i>	Prairie coreopsis	2	1	1	4	0.1	0.3	0.3	3
<i>Luzula bulbosa</i>	Wood rush	2	1	1	4	0.2	0.3	0.3	3
<i>Cocculus carolinianus</i>	Carolina snailseed	2	1	1	4	0.3	0.3	0.3	3
<i>Sisyrinchium bermudiana</i>	Pointed blue-eyed grass	2	1	1	4	0.3	0.3	0.3	3
<i>Physalis virginiana</i>	Lance-leaved ground cherry	2	1	1	4	0.3	0.5	0.3	3
<i>Sporobolus clandestinus</i>	Rough rush grass	2	1	2	4	0.7	1.0	0.3	3
<i>Penstemon pallidus</i>	Pale beard tongue	2	1	1	4	0.1	0.3	0.3	3
<i>Commelina virginica</i>	Virginia dayflower	2	1	1	4	0.1	0.3	0.3	3
<i>Solidago caesia</i>	Blue-stemmed goldenrod	2	1	1	1,3	0.7	1.0	0.2	2
<i>Matelea decipiens</i>	Climbing milkweed	2	1	1	4	2.3	4.5	0.2	2
<i>Rhus radicans</i>	Poison ivy	2	1	1	1,3	1.6	2.0	0.2	2
<i>Stylosanthes biflora</i>	Pencil flower	2	1	1	4	0.5	0.8	0.2	2
<i>Achillea millefolium</i>	Yarrow	2	1	2	4	0.5	0.8	0.2	2
<i>Carex jamesii</i>	Grass sedge	2	1	1	4	0.9	1.5	0.2	2
<i>Hybanthus concolor</i>	Green violet	2	1	1	4	0.6	0.8	0.2	2
<i>Rhus copallina latifolia</i>	Shining sumac	2	1	1	4	1.7	2.5	0.2	2
<i>Prunus mexicana</i>	Mexican plum	2	1	1	4	1.3	1.9	0.2	2

(Appendix continued on next page)



(Appendix continued)

Scientific name	Common name	Life span	Origin	N-fixation	Dispersal mechanism	Cover (%)	Max cover (%)	Relative freq (%)	Frequency
<i>Kuhnia eupatorioides</i>	False boneset	2	1	1	4	0.1	0.1	0.2	2
<i>Prunella vulgaris lanceolata</i>	Heal-all	2	1	1	4	0.1	0.1	0.2	2
<i>Physostegia virginiana</i>	Dragonhead mint	2	1	1	4	0.3	0.3	0.2	2
<i>Carex meadii</i>	Mead's sedge	2	1	1	4	0.3	0.3	0.2	2
<i>Ranunculus abortivus</i>	Small-flowered crowfoot	2	1	1	4	0.1	0.1	0.2	2
<i>Carex rosea</i>	Stellate sedge	2	1	1	4	0.1	0.1	0.2	2
<i>Plantago major</i>	Common plantain	1	1	1	4	0.1	0.1	0.2	2
<i>Sphenopholis intermedia</i>		2	1	1	4	0.2	0.3	0.2	2
<i>Paronychia fastigiata</i>	Chickweed	1	2	1	4	0.3	0.4	0.2	2
<i>Gerardia grandiflora</i>	Big-flowered gerardia	2	1	1	4	0.2	0.3	0.2	2
<i>Paronychia canadensis</i>	Forked chickweed	1	2	1	4	0.4	0.5	0.2	2
<i>Oxalis stricta</i>	Common wood sorrel	2	1	1	4	0.3	0.4	0.2	2
<i>Oxalis violacea</i>	Violet wood sorrel	2	1	1	4	0.2	0.3	0.2	2
<i>Impatiens capensis</i>	Touch-me-not	1	1	1	4	1.0	1.0	0.2	2
<i>Bidens frondosa</i>	Common beggar's ticks	1	1	1	4	0.3	0.3	0.2	2
<i>Gallinea stipulata</i>						0.3	0.4	0.2	2
<i>Cinna arudinaceae</i>		2	1	1	4	0.4	0.5	0.2	2
<i>Desmodium marilandicum</i>	Small-leaved tick trefoil	2	1	1	2	0.4	0.5	0.2	2
<i>Eryngium yuccifolium</i>	Rattlesnake master	1	1	1	4	0.1	0.1	0.2	2
<i>Erigeron strigosus</i>	Daisy fleabane	1	1	1	4	0.6	0.6	0.1	1
<i>Rumex obtusifolius</i>	Bitter dock	1	1	1	4	0.4	0.4	0.1	1
<i>Vernonia crinita</i>	Great ironweed	2	1	1	1,3	0.5	0.5	0.1	1
<i>Verbesina virginica</i>	White crownbeard	2	1	1	4	0.8	0.8	0.1	1
<i>Ruellia strepens</i>	Smooth ruellia	2	1	1	4	0.5	0.5	0.1	1
<i>Cornus florida</i>	Flowering dogwood	2	1	1	4	0.1	0.1	0.1	1
<i>Polytaenia nuttallii</i>	Prairie parsley	2	1	1	4	0.1	0.1	0.1	1
<i>Lysimachia nummularia</i>	Moneywort	2	1	1	4	0.1	0.1	0.1	1
<i>Verbena urticifolia</i>	White vervain	2	1	1	1,3	0.6	0.6	0.1	1
<i>Verbena stricta</i>	Hoary vervain	2	1	1	1,3	0.3	0.3	0.1	1
<i>Verbascum thapsus</i>	Common mullien	3	1	1	4	0.9	0.9	0.1	1
<i>Smilax ecirrhata</i>	Carrion flower	2	1	1	4	0.5	0.5	0.1	1
<i>Polygala senega</i>	Seneca snakeroot	2	1	1	4	0.1	0.1	0.1	1
<i>Thaspium barbinode</i>	Hairy meadow parsnip	2	1	1	4	0.1	0.1	0.1	1
<i>Liparis liliifolia</i>	Purple twayblade	1	1	1	4	0.1	0.1	0.1	1
<i>Panicum spp.</i>	Panic grass					0.5	0.5	0.1	1
<i>Fragaria virginiana</i>	Wild strawberry	2	1	1	4	0.1	0.1	0.1	1
<i>Cystopteris fragilis</i>	Fragile fern	1	1	1	4	0.3	0.3	0.1	1
<i>Coreopsis lanceolata</i>	Sand coreopsis	2	1	1	4	0.1	0.1	0.1	1
<i>Lindera benzoin</i>	Spicebush	2	1	1	4	0.3	0.3	0.1	1
<i>Sorghastrum nutans</i>	Indian grass	2	1	2	4	0.8	0.8	0.1	1
<i>Carex vulpinoidea</i>	Fox sedge	2	1	1	4	0.1	0.1	0.1	1
<i>Carex albursina</i>	White bear sedge	2	1	1	4	0.1	0.1	0.1	1
<i>Liatris cylindracea</i>	Cylindrical blazing star	2	1	1	4	0.1	0.1	0.1	1
<i>Cypripedium reginae</i>	Showy lady's slipper	2	1	1	4	0.4	0.4	0.1	1
<i>Hypericum punctatum</i>	Spotted St. John's wort	2	1	1	1,3	0.4	0.4	0.1	1
<i>Eupatorium perfoliatum</i>	Common boneset	2	1	1	4	0.3	0.3	0.1	1
<i>Orchis spectabilis</i>	Snowy orchis	1	1	1	4	0.3	0.3	0.1	1
<i>Houstonia longifolia</i>	Long-leaved bluets	2	1	1	4	0.3	0.3	0.1	1
<i>Melica nitens</i>	Tall melic grass	2	1	1	4	0.1	0.1	0.1	1
<i>Psoralea psoralioides</i>	Sampson's snakeroot	2	1	1	2	1.5	1.5	0.1	1

(Appendix continued on next page)

Post Treatment Results of the Landscape Experiment

(Appendix continued)

Scientific name	Common name	Life span	Origin	N-fixation	Dispersal mechanism	Cover (%)	Max cover (%)	Relative freq (%)	Frequency
<i>Mirabilis albida</i>	Pale umbrellawort	2	1	1	4	0.3	0.3	0.1	1
<i>Elaeagnus umbellata</i>	Autumn olive	2	1	1	4	0.6	0.6	0.1	1
<i>Heliotropium tenellum</i>	Glade heliotrope	1	1	1	4	0.1	0.1	0.1	1
<i>Helenium autumnale</i>	Sneezeweed	1	1	1	4	1.0	1.0	0.1	1
<i>Quercus alba</i>	White oak	2	1	1	2	6.5	6.5	0.1	1
<i>Monarda fistulosa</i>	Wild bergamot	2	1	1	4	0.3	0.3	0.1	1
<i>Podophyllum peltatum</i>	May apple	2	1	1	4	3.5	3.5	0.1	1
<i>Pyrrhopappus carolinianus</i>	False dandelion	1,3	1	1	4	0.5	0.5	0.1	1
<i>Elymus</i> sp.	Wild rye					0.1	0.1	0.1	1
<i>Rudbeckia triloba</i>	Brown-eyed Susan	3 or 2	1	1	1,3	0.5	0.5	0.1	1
<i>Panicum virgatum</i>	Switch grass	2	1	2	4	0.1	0.1	0.1	1
<i>Thaspium</i> spp.	Meadow parsnip					0.1	0.1	0.1	1
<i>Diarrhena americana</i>		2	1	1	4	0.5	0.5	0.1	1
<i>Pycnanthemum tenuifolium</i>	Slender mountain mint	2	1	1	4	0.4	0.4	0.1	1
<i>Rosa setigera</i>	Prairie rose	2	1	1	1,3	0.5	0.5	0.1	1
<i>Galium obtusum</i>	Wild madder	2	1	1	4	0.1	0.1	0.1	1
<i>Pellaea atropurpurea</i>	Purple cliff break	2	1	1	4	0.4	0.4	0.1	1
<i>Crataegus intricata</i>	Thicket hawthorn	2	1	1	4	0.1	0.1	0.1	1
<i>Blephilia hirsuta</i>	Wood mint	2	1	1	4	0.1	0.1	0.1	1
<i>Blephilia ciliata</i>	Ohio horse mint	2	1	1	4	0.4	0.4	0.1	1
<i>Boehmeria cylindrica</i>	False nettle	2	1	1	4	1.0	1.0	0.1	1
<i>Muhlenbergia tenuiflora</i>	Muhly grass	2	1	1	4	0.3	0.3	0.1	1
<i>Triosteum perfoliatum</i>	Late horse gentian	2	1	1	4	1.0	1.0	0.1	1
<i>Polygonum punctatum</i>	Smartweed	1,2	1	1	4	0.3	0.3	0.1	1
<i>Iris cristata</i>	Crested iris	2	1	1	4	0.1	0.1	0.1	1
<i>Acaphylla rhomboides</i>	Rhombic	2	1	2	4	0.3	0.3	0.1	1
<i>Triosteum angustifolium</i>	Yellow-flowered horse gentian	2	1	1	4	0.3	0.3	0.1	1
<i>Corallorrhiza odontorrhiza</i>	Late coral root	3	1	1	4	0.6	0.6	0.1	1
<i>Daucus carota</i>	Queen Anne's lace	2	1	1	4	0.1	0.1	0.1	1
<i>Hypericum spathulatum</i>	Shrubby St. John's Wort	2	1	1	1,3	0.1	0.1	0.1	1
<i>Amelanchier arborea</i>	Shadbush	2	1	1	4	0.1	0.1	0.1	1
<i>Solanum carolinense</i>	Horse nettle	2	1	1	4	3.5	3.5	0.1	1
<i>Phaseolus polystachios</i>	Wild bean	2	1	1	4	0.4	0.4	0.1	1
<i>Rudbeckia fulgida umbrosa</i>	Coneflower	3 or 2	1	1	3	0.1	0.1	0.1	1
<i>Ciracea quadrisulcata canadensis</i>	Enchanter's nightshade	2	1	1	4	0.3	0.3	0.1	1

Changes in Ground Layer Vegetation Following Timber Harvests on the Missouri Ozark Forest Ecosystem Project

Jennifer K. Grabner¹ and Eric K. Zenner²

Abstract.—The Missouri Ozark Forest Ecosystem Project (MOFEP) is a landscape-scale experiment to test for effects of the following three common forest management practices on upland forests: 1) even-aged management (EAM), 2) uneven-aged management (UAM), and 3) no-harvest management (NHM). The first round of harvesting treatments was applied on the nine MOFEP sites in 1996. One forest component evaluated on MOFEP is the ground layer vegetation. Pre-treatment ground flora data were collected from permanent sample plots during the summers of 1994 and 1995; post-treatment data were gathered in 1999 and 2000. We evaluated differences between pre- and post-treatment values for ground flora parameters including species richness, percent ground cover, and relative abundances of several functional plant groups. Tests for treatment effects for each parameter were performed using analysis of variance on the difference between pre- and post-treatment means on each site. Significant treatment effects were observed for species richness, percent ground cover, and the relative abundance of annual/biennial species, woody vines, and legumes. Mean species richness per plot decreased significantly on all control (NHM) sites and increased slightly on both EAM and UAM sites. Total percent ground cover increased on all sites; harvested sites increased more than NHM sites. Annual/biennial species increased slightly on all sites, but most consistently on EAM sites. Woody vines increased on all sites, but most noticeably and consistently on EAM and UAM sites. The relative abundance of legumes decreased significantly on harvested sites and increased slightly on NHM sites.

To better understand the treatment effects described above, we also analyzed ground flora data at the plot level to determine if the treatments affected uncut as well as cut plots within harvested sites. Overall, patterns observed among uncut plots on harvested sites mirrored those observed for the NHM, or control, sites. Specifically, species richness declined, percent cover remained unchanged, and there were no noticeable changes in the relative abundances of most plant groups. Conversely, plots directly impacted by the harvests mirrored the results seen for treated sites: species richness increased, cover increased dramatically, annuals/biennials and woody vines increased in abundance, and legumes decreased noticeably in abundance. Our results provide no evidence that the harvests have impacted areas other than those locations that were actually cut.

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Increasingly, public forest land managers are being required to scientifically defend management practices and to identify potential impacts of those practices on multiple ecosystem components and processes. The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, large-scale experiment designed to evaluate effects of three standard forest management practices currently practiced on Missouri's public and private lands (Brookshire and Hauser 1993, Brookshire and Shifley 1997, Kurzejeski *et al.* 1993). The three practices, or treatments, being evaluated include: 1) even-aged management (EAM), 2) uneven-aged management (UAM), and 3) no-harvest management (NHM). Typically on Missouri's State-owned forests, forest inventories and management prescriptions are implemented on a 10- to 15-year re-entry cycle for each compartment (MOFEP experimental sites average 423 ha in size and are equivalent to compartments). The first round of harvesting treatments was implemented on MOFEP sites from May 1996 through May 1997. This paper documents initial changes in ground layer vegetation (both woody and herbaceous) following this first round of harvesting treatments on the MOFEP sites.

Ground layer vegetation is an important component of any forested landscape. The composition and structure of the ground flora contributes greatly to overall forest biodiversity, to wildlife habitat quality, and to the character of future forest stands. Understory plant species have been successfully used as indicators of potential site productivity, soil moisture status, and disturbance history (Cajander 1926, Daubenmire 1976, Rowe 1956). Very few studies of ground flora response to timber harvesting have been conducted in Missouri. Earlier projects typically focused either on wildlife forage and cover values, or on woody regeneration (Crawford 1971, 1976; Crawford and Harrison 1971; Murphy and Crawford 1970). One recent project, conducted in southern Missouri, compared clearcut stands of various ages, but did not have the benefit of pre-treatment data (Unger 1994).

MOFEP provides one of the first opportunities in Missouri to experimentally test for effects of forest management practices at a landscape scale on the ground layer vegetation of upland

Ozark forests. Information about the MOFEP ground flora will serve not only to address vegetation questions, but will also aid in the interpretation of many of the other MOFEP studies, both at the landscape (among-site) and local (within-site) scales.

METHODS

Study Area

There are nine MOFEP experimental units or compartments, hereafter referred to as sites in this paper. All nine MOFEP sites are in the Current River Hills Subsection of the Ozark Highlands, located in Carter, Reynolds, and Shannon Counties of southeastern Missouri (see figure 1 in Sheriff, this proceedings). The sites range in size from 314 to 516 ha (776 to 1,275 ac). The Current River Hills Subsection can be characterized as a deeply dissected landscape with broad to narrow ridges, steep sideslopes, and narrow valleys associated with the Current, Jacks Fork, Eleven-Point, and Black Rivers (Nigh *et al.* 2000). The MOFEP study sites are all within the Current River watershed and primarily encompass upland landscape positions; they do not include landform features associated with large creeks or rivers. Local relief within the MOFEP sites ranges from 46 to 137 m (150 to 450 ft). MOFEP sites include landscape positions of all aspects and have slopes ranging from 0 to >60 percent.

Bedrock geology of the MOFEP sites includes Ordovician sandstones, cherts, and dolomites from the Roubidoux and Gasconade formations, as well as Cambrian cherts and dolomites from the Eminence formation (Kabrick *et al.* 2000, Meinert *et al.* 1997). Soils of the MOFEP sites are fairly typical of the Current River Hills Subsection, with patterns in parent materials, texture, base saturation, and depth to bedrock strongly associated with the geology and landforms on which they occur (Kabrick *et al.* 2000; Meinert 1998, 2001; Meinert *et al.* 1997). Multiple soil parent materials are common and are characterized by mode of deposition or by type of bedrock if weathered in place. Dominant parent materials in the upland MOFEP sites are hillslope sediments, loess, and residuum (Meinert 1998, 2001; Meinert *et al.* 1997).

Experimental Design and Treatment Implementation

MOFEP is unique in being a true field experiment with nine large landscape-scale experimental units arranged in a randomized complete block design. The three silvicultural treatments being tested (even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM)) form a gradient from complete canopy removal to partial removal to no canopy removal. Even-aged management, as conducted by the Missouri Department of Conservation, involves clearcutting and intermediate thinnings, and it has been practiced on publicly owned forest lands in Missouri for more than 30 years (Missouri Department of Conservation 1986). MOFEP sites 3, 5, and 9 were designated as EAM sites. Uneven-aged management involves combinations of single-tree removals with scattered small group openings throughout the sites and is a relatively new technique for public land management in Missouri. MOFEP sites 2, 4, and 7 were selected as UAM sites, and the harvests were implemented following prescription guidelines presented in Law and Lorimer (1989). As the name implies, no timber harvesting will occur on the no-harvest management sites (1, 6, and 8) for the duration of the project. The NHM sites will serve as control replicates for the experiment and will provide valuable information on changes that occur over time in mature upland Ozark forests in the absence of active management.

MOFEP was designed as a long-term study (>100 years), with harvests to be conducted every 10 to 15 years. The nine MOFEP sites, or experimental units, were grouped into three replication blocks. Treatments were randomly assigned within blocks so that each block contains one EAM site, one UAM site, and one NHM site (figs. 1 and 2 in Sheriff, this proceedings; Sheriff and He 1997). The first round of harvesting treatments was implemented on MOFEP study sites from May 1996 through May 1997 (Brookshire *et al.* 1997). For a more detailed description and discussion of the strengths and weaknesses of the MOFEP experimental design, see Brookshire *et al.* (1997), Sheriff and He (1997), and Sheriff (this proceedings). For more complete descriptions of the first round of harvesting treatments as well as the volume, density, and composition of woody vegetation removed, see Kabrick *et al.* (this proceedings) and Sheriff (this proceedings).

Ground Flora Data Collection

MOFEP ground flora data were collected on the same 645 0.2-ha (0.5 ac) permanent circular plots used for the woody vegetation projects (Brookshire and Dey 2000, Kabrick *et al.* 1997 and this proceedings, Shifley *et al.* 1997). Vegetation plots were initially located in a stratified random manner, ensuring 1 plot per stand, for a range of 70 to 74 plots per site (table 1). For the ground flora data collection, 16 permanently marked 1-m² quadrats were sampled within each 0.2-ha (0.5 ac) plot. For a

Table 1.—Number of MOFEP vegetation plots according to the management they received as a result of the 1996 harvest treatment implementation. Site-level treatments refer to the three treatments being experimentally tested: even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM).

Block	Site	Site-level Treatments	Clearcut Plots	Plots in Group Openings	Plots with intermediate selection cuts	Plots with Multiple Treatments	Uncut Plots	Total Number of Plots
1	1	NHM	-	-	-	-	73	73
1	2	UAM	-	16	33	0	24	73
1	3	EAM	7	-	16	1	48	72
2	4	UAM	-	21	25	0	28	74
2	5	EAM	8	-	13	9	40	70
2	6	NHM	-	-	-	-	71	71
3	7	UAM	-	8	21	0	42	71
3	8	NHM	-	-	-	-	70	70
3	9	EAM	7	-	4	1	59	71
Totals:	9 sites	3 treatments	22	45	112	3	458	645

diagram of the MOFEP vegetation plot design, see figure 1 in Kabrick *et al.* (this proceedings).

Within each 1-m² quadrat, all herbaceous plants, and all woody plants with live foliage less than 1 m above the ground, were identified to species and assigned estimates of percent live foliar coverage. Plants not identifiable to the species level were labeled to genera when possible, or to the next most precise taxonomic level known (e.g., family, functional group, monocot or dicot, etc.). Nomenclature follows that of Steyermark (1963). Our sample included individuals rooted within the quadrat frame as well as those not rooted in but with live foliage hanging over the frame. Numbers of stems less than 1 m tall were recorded for all tree species; total percent ground cover (vegetation <1 m tall) was recorded for each quadrat. Although not summarized for this report, estimates of percent cover were also recorded for features such as rock, bare ground, leaf litter, dead wood, non-vascular species, and canopy closure. For a more detailed description of methods used to collect MOFEP ground flora data, see Grabner (2000).

Pre-treatment data used for this report were collected during the summers (June 1 through August 25) of 1994 and 1995; post-treatment data were gathered from June through August of 1999 and 2000. MOFEP sites were sampled in the same order and, as a result, during the same basic period each year to avoid potentially confounding seasonal effects. Immediate post-harvest data were collected in 1997 but were incomplete and were not used for this report. Ground flora data were not collected in 1998 due to budget constraints.

Numerical Analyses

Calculations and Plant Groups

Species richness per plot was calculated as the total number of species identified on the 16-m² quadrat samples within each 0.2-ha (0.5 ac) plot. Mean total percent ground cover per plot was calculated by summing the total coverages for each quadrat and then dividing by 16. Percent relative cover was calculated by summing the coverage of each individual species (or species group) on each plot, dividing by the sum of all species coverages on that plot, and then multiplying by 100. For all analyses, pre-treatment means were calculated as the average

of 1994 and 1995 values, and post-treatments means were calculated as the average of 1999 and 2000 values.

Functional plant groups used for this report were 1) exotic species (all life forms), 2) native annual and/or biennial species, 3) native non-leguminous forbs, herbaceous vines, and ferns, 4) native grasses, sedges, and rushes, 5) native legumes, 6) native shrubs, 7) native trees, 8) native woody vines, and 9) unknowns.

Analysis of Variance and Confidence Limits

Analyses for this report were conducted at two levels: among sites and within sites. Analysis of variance (ANOVA) was used to test for treatment effects among sites. Response variables were plotted and checked for adherence to the assumptions of the analysis of variance (particularly the equal variance assumption). Our analysis indicated transformations were not needed, so we proceeded with untransformed response variables. Variables tested included mean plot richness, mean percent ground cover per plot, and the percent relative cover of each of the functional plant groups described above. The ANOVA model used for these analyses was as follows:

$$Y_{ij} = \mu + \text{block}_i + \text{treatment}_j + \epsilon_{ij}$$

where " μ " is the mean difference between post- and pre-treatment values, block_i is the blocking effect, treatment_j is the site-level harvesting treatment effect (EAM, UAM, or NHM), and ϵ_{ij} is the error term $N(0, \sigma^2)$. All ANOVAs were performed using the PROC GLM statement in SAS for Windows (version 8).

Upper and lower 95 percent confidence intervals around the means were calculated for each site using pooled variance estimates based on plot data. Simple scatter plots of the mean differences with error bars showing lower and upper confidence limits illustrate treatment effects identified by the ANOVAs for each site.

Due to the landscape-level design of this study, analysis of variance was not performed for within-site data. We conservatively assumed that vegetation plots within sites could not be considered independent sample points. Rather, for the within-site data, mean post- minus pre-treatment differences and their associated confidence intervals were computed. For this



analysis, confidence intervals that did not include zero were considered to represent "significant" treatment effects.

RESULTS

Treatment Effects Among Sites (Landscape-scale Analyses)

The MOFEP experimental design allows testing for treatment effects by comparing differences between pre- and post-treatment observations. Tables 2 and 3 provide the results of significant ANOVAs and a list of the site-level pre- and post-treatment mean values used in these analyses, respectively. Significant treatment effects ($\alpha < 0.05$) were detected for mean species richness and percent ground cover per plot, as well as for the relative abundances of several plant groups (tables 2A and B). Noticeable changes in species richness occurred on the control sites (i.e., NHM sites 1, 6, and 8), where richness *decreased* by an average of 1.8 species per plot (95% CI: -3.2 to -0.5, $p=0.02$) from the pre- to post-treatment samples. Conversely, EAM sites (3, 5, and 9) and UAM sites (2, 4, and 7) showed increases in richness by an average of 1.8 species (95% CI: 0.4 to 3.1, $p=0.02$) and 2.3 species (95% CI: 0.9 to 3.6, $p=0.01$) per plot, respectively (table 3, fig. 1A). In all sites, ground cover increased from pre- to post-treatment. NHM sites had the smallest increase in ground cover (2.2% with a 95% CI from 0.8 to 3.7%, $p=0.01$). EAM sites (6.3% with a 95% CI from

4.8 to 7.7%, $p < 0.01$) and UAM sites (6.7% with a 95% CI from 5.5 to 8.4%, $p < 0.01$) increased more in ground cover than did NHM sites (ANOVA contrast (EAM+UAM)/2 vs. NHM, difference estimated to be 3.3%, $p=0.06$) (table 3, fig. 1B).

Significant treatment effects were also observed at the site level for annual and biennial species, woody vines, and legumes. Annuals and biennials, essentially not present on most sites prior to the harvests, increased consistently in mean relative percent cover on all EAM sites (0.5% with a 95% CI from 0.4 to 0.6%, $p < 0.01$). The patterns were less consistent on both UAM and NHM sites, where annual and biennial species increased by an average of 0.2 percent relative cover (95% CI from 0.1 to 0.3%, $p=0.01$), but with confidence intervals for three of the six sites (1, 2, and 4) overlapping zero (fig. 2A). Mean relative percent cover of woody vine species (e.g., *Vitis* spp., *Parthenocissus quinquefolia*, etc.) increased in all sites following treatment, but the increase was most noticeable and consistent for the EAM (3.7% with a 95% CI from 2.9 to 4.5%, $p < 0.01$) and UAM sites (3.3% with a 95% CI from 2.5 to 4.0%, $p < 0.01$). NHM sites (1.6% with a 95% CI from 0.8 to 2.4, $p < 0.01$) had a significantly smaller increase than the harvested sites (ANOVA contrast (EAM+UAM)/2 vs. NHM, difference estimated to be 2.6%, $p=0.02$) (fig. 2B). Mean relative percent cover of legumes (e.g., *Desmodium* spp. and *Lespedeza* spp.) decreased noticeably on all treated sites (UAM: -5.2% with a 95% CI from

Table 2.—Analysis of variance tables for significant variables at the site scale. Testing for treatment effects on structural and compositional parameters: mean post-pre differences in A) mean species richness and mean percent ground cover, and B) mean relative cover of annual/biennial species, woody vines, and legumes.

A)

Source	DF	Species richness			Percent ground cover		
		Sum of squares	F	P	Sum of squares	F	P
Block	2	0.29	0.19	0.83	24.43	14.66	0.01
Treatment	2	29.8	20.01	<0.01	39.56	23.74	<0.01
Error	4	2.98	--	--	3.33	--	--

B)

Source	DF	Annual/biennial abundance			Woody vine abundance			Legume abundance		
		Sum of squares	F	P	Sum of squares	F	P	Sum of squares	F	P
Block	2	0.17	17.39	0.01	16.55	36.99	<0.01	8.66	6.42	0.06
Treatment	2	0.13	13.65	0.02	7.5	16.77	0.01	81.43	60.4	<0.01
Error	4	0.02	--	--	0.89	--	--	2.7	--	--

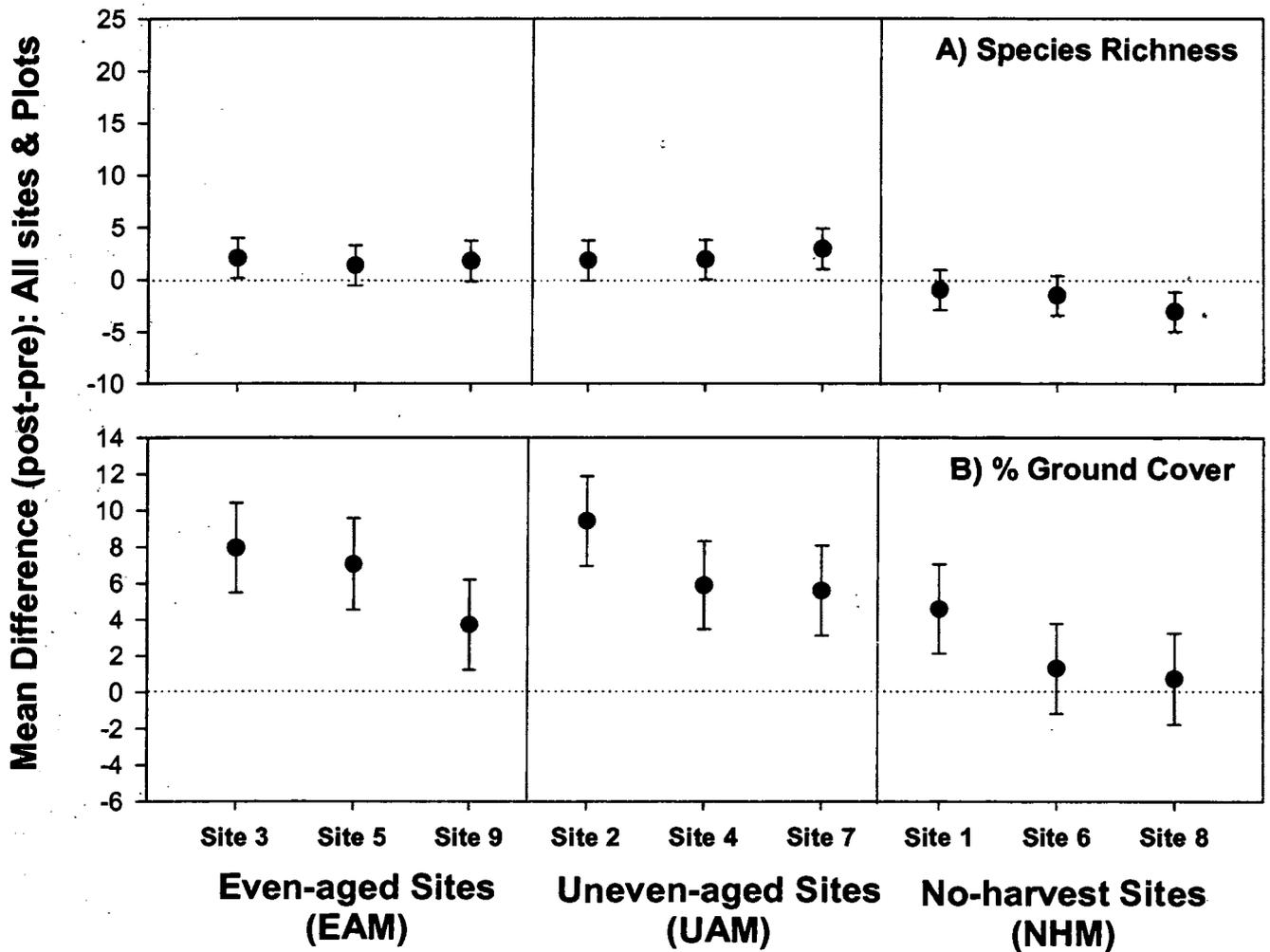


Figure 1.—Mean differences between post- and pre-treatment site-level data for A) mean species richness per plot, and B) mean percent ground cover per plot. Error bars are 95 percent confidence intervals.

Table 3.—Mean values calculated per site and used in ANOVAs to test for treatment effects among sites. “pre” = the mean of pre-treatment data from 1994 and 1995; “post” = the mean of post-treatment data from 1999 and 2000. Units for relative cover are in percent.

block	site	trt	Mean species richness		Mean % ground cover		Relative cover by exotics		Relative cover by annuals / biennials		Relative cover by forbs		Relative cover by graminoids		Relative cover by legumes		Relative cover by shrubs		Relative cover by tree species		Relative cover by woody vines			
			pre	post	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post
1	3	eam	45.3	47.4	21.0	29.0	0.0	0.0	0.2	0.5	10.4	9.8	2.3	4.6	19.8	16.8	9.9	9.9	43.9	40.3	13.3	17.6	0.3	0.4
2	5	eam	56.5	57.9	23.4	30.4	0.1	0.0	0.4	0.9	12.4	11.5	3.8	6.6	25.1	19.0	9.2	9.8	39.1	37.0	9.6	14.8	0.3	0.4
3	9	eam	48.0	49.8	19.4	23.2	0.1	0.1	0.6	1.2	8.7	8.9	4.5	7.6	25.2	21.1	15.8	15.4	42.5	41.3	2.3	3.9	0.3	0.5
1	2	uam	45.6	47.4	26.6	36.0	0.0	0.0	0.4	0.4	10.2	9.8	1.8	4.4	20.3	14.6	11.3	11.3	33.5	32.2	22.4	26.5	0.3	0.8
2	4	uam	52.1	54.1	22.0	27.9	0.0	0.0	0.4	0.5	10.9	11.7	1.9	4.0	25.8	19.8	9.1	10.3	38.7	35.7	12.8	17.4	0.4	0.5
3	7	uam	37.5	40.5	19.7	25.3	0.0	0.1	0.2	0.7	4.8	5.3	2.1	8.8	22.8	19.0	12.0	12.4	43.6	37.9	14.3	15.4	0.2	0.5
1	1	nhm	32.9	32.0	15.6	20.2	0.0	0.0	0.2	0.3	8.3	7.3	1.4	1.3	23.6	25.9	13.4	13.4	42.5	38.5	10.3	12.9	0.1	0.4
2	6	nhm	37.3	35.8	18.3	19.6	0.0	0.0	0.2	0.5	5.8	6.1	2.1	3.6	32.5	32.5	7.4	8.2	46.7	41.7	5.2	7.3	0.1	0.2
3	8	nhm	39.2	36.1	14.8	15.6	0.1	0.1	0.3	0.6	6.3	5.6	2.6	4.9	19.0	21.4	13.6	13.8	50.2	45.0	7.8	7.9	0.3	0.6



Mean Difference (post-pre): All sites & Plots

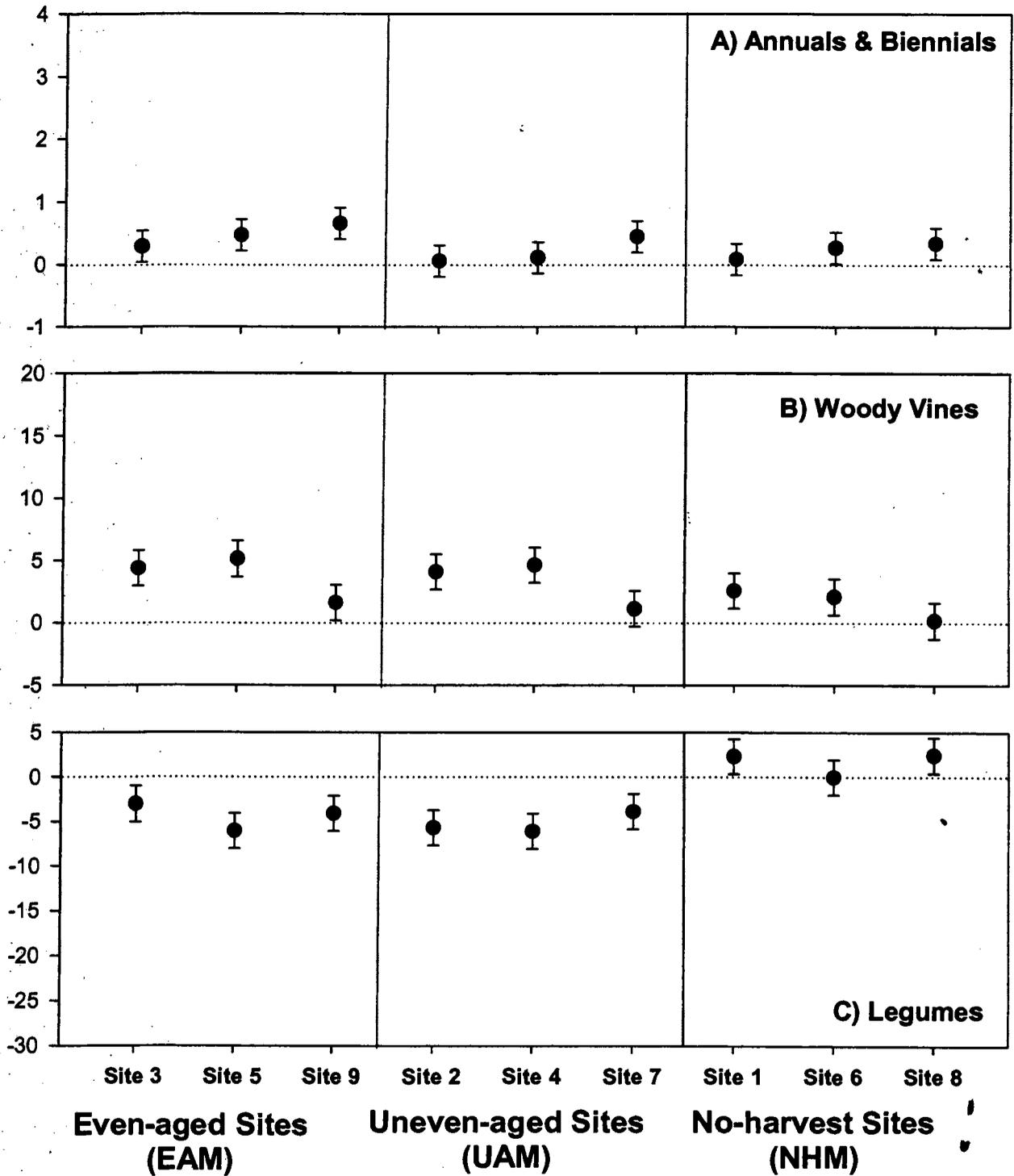


Figure 2.—Mean differences between post- and pre-treatment site-level data for A) mean relative cover by annual/biennial species per plot, B) mean relative cover by woody vines per plot, and C) mean relative cover by legumes per plot. Error bars are 95 percent confidence intervals.

-6.5 to -3.9%, $p < 0.01$; EAM: -4.4% with a 95% CI from -5.7 to -3.1%, $p < 0.01$), while either increasing or remaining unchanged on control sites (1.6% with a 95% CI from 0.2 to 2.9%, $p = 0.03$) (fig. 2C). No significant treatment effects were observed at the site level for other functional groups such as exotics ($p = 0.33$), non-leguminous forbs, herbaceous vines and ferns ($p = 0.27$), grasses and sedges ($p = 0.15$), shrubs ($p = 0.14$), trees ($p = 0.31$), and unknowns ($p = 0.24$) (table 3).

**Treatment Effects Within Sites
("Local Scale" Analyses)**

Given that 69 percent of vegetation plots on EAM sites (147/213) and 43 percent of those on UAM sites (94/218) were not harvested during this first round of treatment (table 1), we

wanted to determine whether the site-level treatment effects described above were also evident *within* treated sites on plots not directly impacted by the harvesting. In other words, we wanted to know whether there was evidence of actual landscape-level changes across the treated sites, or whether the effects were restricted to cut plots only.

In general, there was little evidence of harvesting effects anywhere except on plots directly impacted by tree removal. Comparisons of pre- and post-treatment conditions on uncut plots within treated sites essentially mirrored those observed among control sites for the site-scale analyses presented above. As with no-harvest sites (1, 6, and 8), uncut plots within both EAM and UAM sites decreased noticeably in mean species richness (figs. 3A and 4A) and showed no change in percent ground cover (figs. 3B and

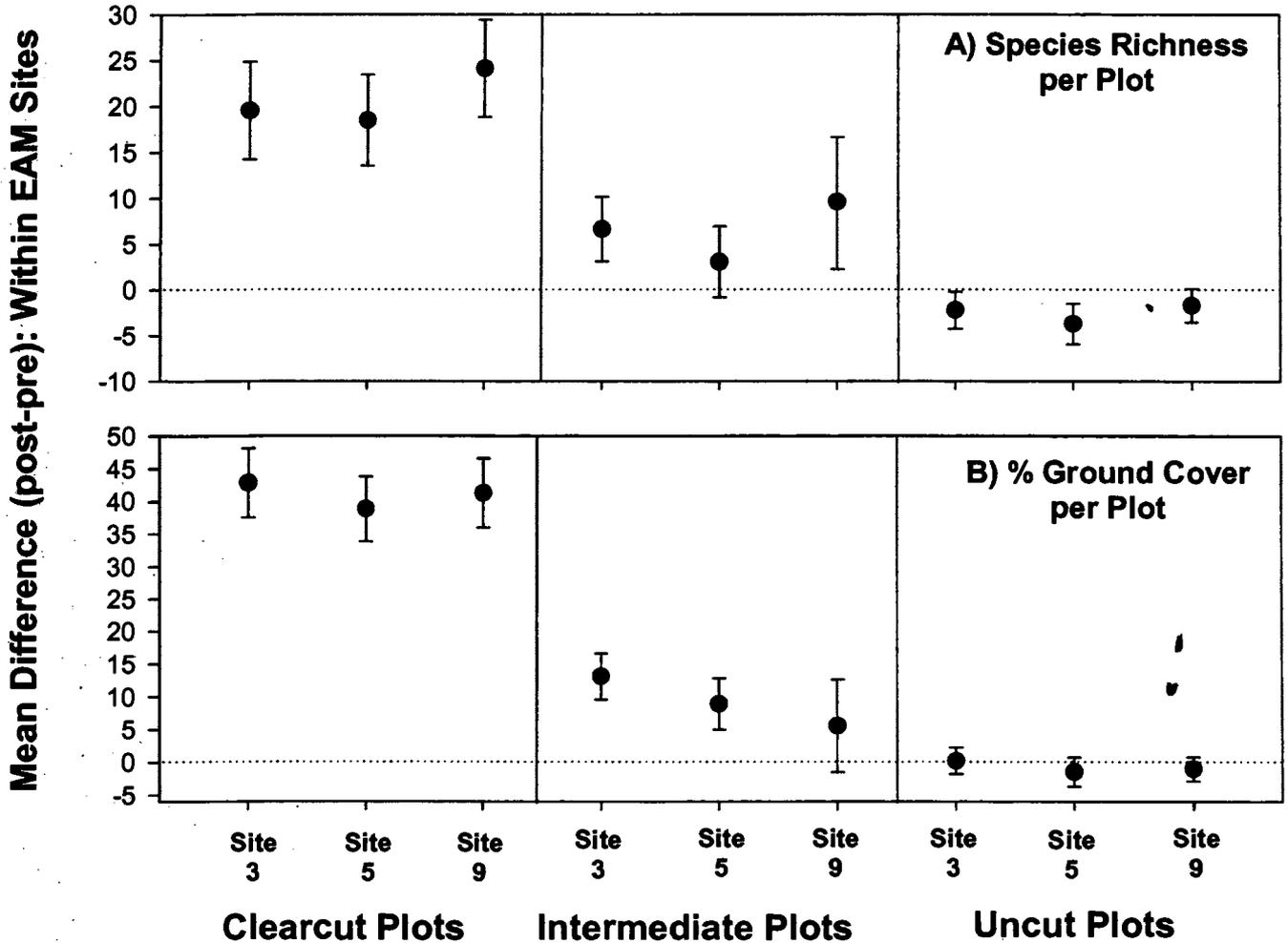


Figure 3.—Mean differences between post- and pre-treatment data within even-aged management sites only for A) mean species richness per plot, and B) mean percent ground cover per plot. Error bars are 95 percent confidence intervals.



4B). Plots subjected to intermediate thinnings (EAM) or single-tree selection (UAM) increased slightly (although usually not significantly) in species richness; plots located in group openings (UAM) or clearcuts (EAM) increased significantly in species richness (figs. 3A and 4A). All harvested plots increased substantially in mean percent total ground cover (figs. 3B and 4B), with native woody vine and shrub species such as *Vitis aestivalis* (summer grape) and *Rubus pensylvanicus* (blackberry) contributing largely to this increase (table 4B).

Within-site responses of functional plant groups following the harvests were somewhat variable, although still similar to those we observed when evaluating site-level means. Annual and biennial species including *Erechtites hieracifolia*

(fireweed), *Erigeron* spp. (daisy fleabanes), and *Gnaphalium* spp. (cudweed) increased their presence on cut plots of all types (clearcuts, group openings, intermediate and selection cuts), although not consistently (figs. 5A and 6A). Woody vines such as *Vitis aestivalis* and *Parthenocissus quinquefolius* (Virginia creeper) increased in abundance across most plots, but most noticeably in clearcuts, group openings, and other cut plots (figs. 5B and 6B). As with the site-level means for both EAM and UAM sites, legumes decreased significantly in abundance on all harvested plots, but remained basically unchanged on most uncut plots (figs. 5C and 6C). This decrease was due primarily to marked declines in the abundance of two very common species, *Desmodium nudiflorum* (common tick trefoil) and *Amphicarpaea bracteata* (hog peanut) (table 4A).

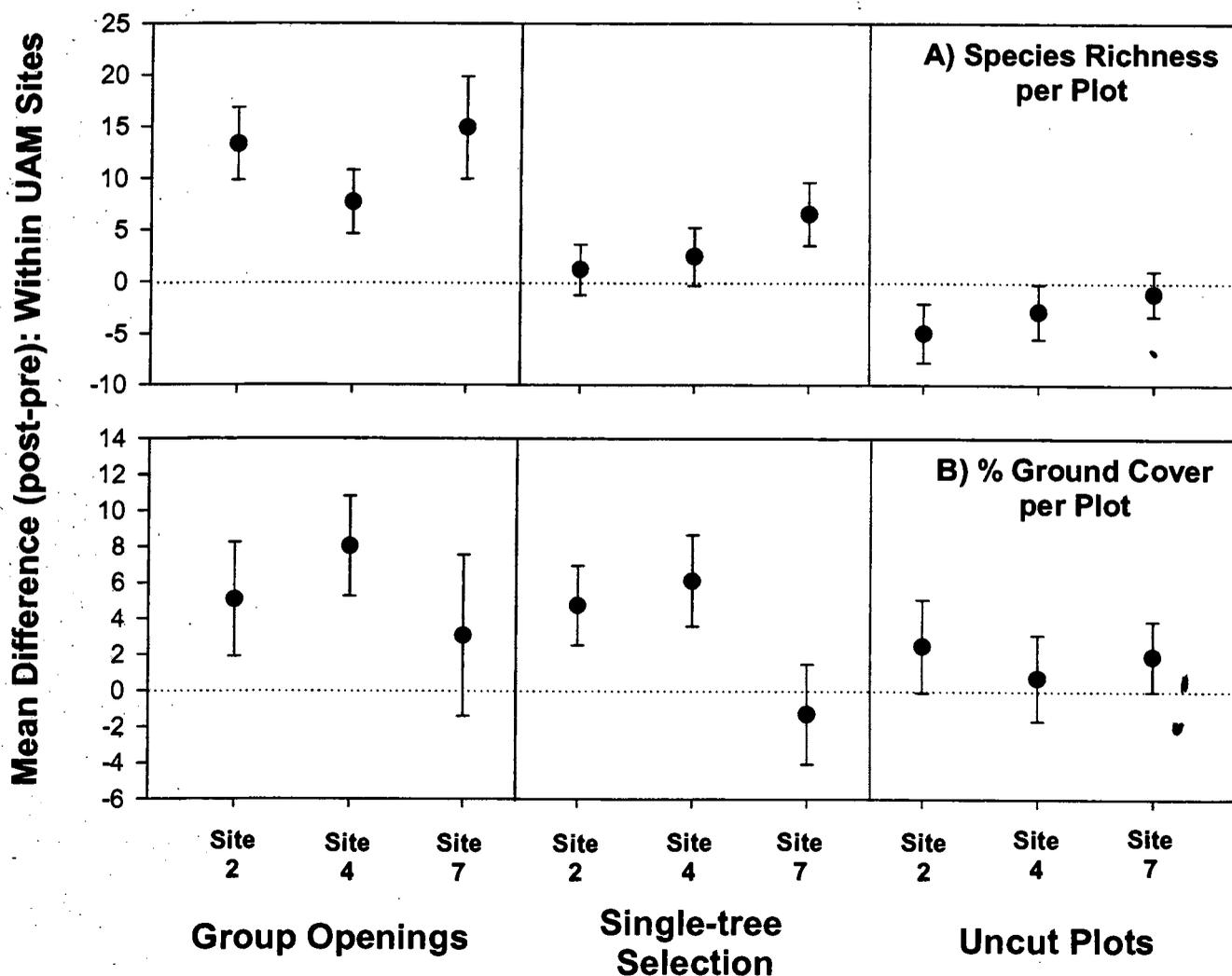


Figure 4.—Mean differences between post- and pre-treatment data within uneven-aged management sites only for A) mean species richness per plot, and B) mean percent ground cover per plot. Error bars are 95 percent confidence intervals.

Table 4A.—Species that showed the greatest decreases in mean relative cover and frequency on plots that had been either clearcut or subjected to intermediate thinnings or single-tree selection

Decreased in: Mean Relative Cover per Plot	Decreased in: Mean Relative Frequency per Plot
Clearcut Plots	
<i>Desmodium nudiflorum</i> (legume)	<i>Galium concinnum</i> (forb)
<i>Amphicarpaea bracteata</i> (legume)	<i>Psoralea psoraloides</i> (legume)
<i>Psoralea psoraloides</i> (legume)	<i>Desmodium nudiflorum</i> (legume)
<i>Cornus florida</i> (understory tree)	<i>Vitis vulpina</i> (woody vine)
<i>Sassafras albidum</i> (understory tree)	<i>Hepatica nobilis</i> (forb)
<i>Cercis canadensis</i> (understory tree)	<i>Cimicifuga racemosa</i> (forb)
<i>Vaccinium stamineum</i> (shrub)	<i>Carex cephalophora</i> (sedge)
<i>Cimicifuga racemosa</i> (forb)	<i>Phryma leptostachya</i> (forb)
<i>Hepatica nobilis</i> (forb)	<i>Viola sororia</i> (forb)
<i>Vaccinium vacillans</i> (shrub)	<i>Botrychium virginianum</i> (fern)
Plots with Intermediate/Selection Cuts	
<i>Amphicarpaea bracteata</i> (legume)	<i>Viola sororia</i> (forb)
<i>Cornus florida</i> (understory tree)	<i>Rubus occidentalis</i> (shrub)
<i>Asimina triloba</i> (understory tree)	<i>Passiflora lutea</i> (vine)
<i>Desmodium nudiflorum</i> (legume)	<i>Agrimonia pubescens</i> (forb)
<i>Sassafras albidum</i> (understory tree)	<i>Carex retroflexa</i> (sedge)
<i>Amelanchier arborea</i> (understory tree)	<i>Cornus florida</i> (understory tree)
<i>Vaccinium vacillans</i> (shrub)	<i>Aristolochia serpentaria</i> (forb)
<i>Cimicifuga racemosa</i> (forb)	<i>Muhlenbergia sobolifera</i> (grass)
<i>Quercus marilandica</i> (tree)	<i>Asimina triloba</i> (understory tree)
<i>Corylus americanus</i> (understory tree)	<i>Smilax pulverulenta</i> (vine)

Table 4B.—Species that showed the greatest increases in mean relative cover and frequency on plots that had been either clearcut or subjected to intermediate thinnings or single-tree selection

Increased in: Mean Relative Cover per Plot	Increased in: Mean Relative Frequency per Plot
Clearcut Plots	
<i>Vitis aestivalis</i> (woody vine)	<i>Vitis aestivalis</i> (woody vine)
<i>Rubus pensylvanicus</i> (shrub)	<i>Panicum boscii</i> (grass)
<i>Quercus alba</i> (tree)	<i>Scleria triglomerata</i> (sedge)
<i>Potentilla simplex</i> (forb)	<i>Rubus pensylvanicus</i> (shrub)
<i>Scleria triglomerata</i> (sedge)	<i>Potentilla simplex</i> (forb)
<i>Pteridium aquilinum</i> (fern)	<i>Parthenocissus quinquefolius</i> (woody vine)
<i>Panicum boscii</i> (grass)	<i>Ulmus alata</i> (understory tree)
<i>Parthenocissus quinquefolius</i> (woody vine)	<i>Heliopsis helianthoides</i> (forb)
<i>Heliopsis helianthoides</i> (forb)	<i>Carex nigromarginata</i> (sedge)
<i>Carex nigromarginata</i> (sedge)	<i>Nyssa sylvatica</i> (tree)
Plots with Intermediate/Selection Cuts	
<i>Vitis aestivalis</i> (woody vine)	<i>Vitis aestivalis</i> (woody vine)
<i>Vaccinium arboreum</i> (shrub)	<i>Sanicula gregaria</i> (forb)
<i>Rubus pensylvanicus</i> (shrub)	<i>Juniperus virginiana</i> (tree)
<i>Nyssa sylvatica</i> (tree)	<i>Ulmus rubra</i> (tree)
<i>Quercus coccinea</i> (tree)	<i>Viola</i> spp. (forb)
<i>Parthenocissus quinquefolius</i> (woody vine)	<i>Carex nigromarginata</i> (sedge)
<i>Ulmus rubra</i> (tree)	<i>Sassafras albidum</i> (understory tree)
<i>Carex nigromarginata</i> (sedge)	<i>Erechtites hieracifolia</i> (forb)
<i>Quercus alba</i> (tree)	<i>Lindera benzoin</i> (understory tree)
<i>Sanicula gregaria</i> (forb)	<i>Cercis canadensis</i> (understory tree)

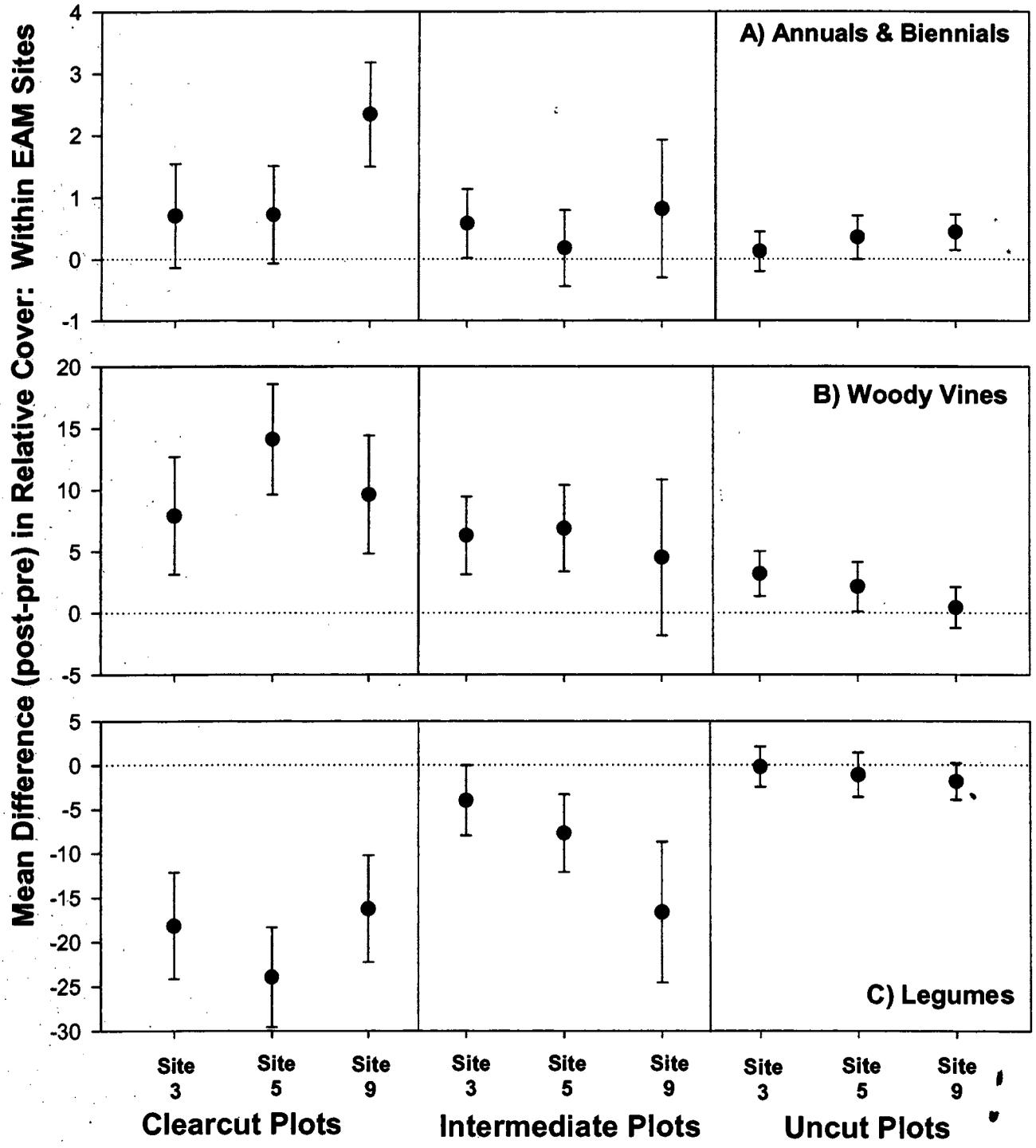


Figure 5.—Mean differences between post- and pre-treatment data within even-aged management sites only for A) mean relative cover by annual/biennial species per plot, B) mean relative cover by woody vines per plot, and C) mean relative cover by legumes per plot. Error bars are 95 percent confidence intervals.

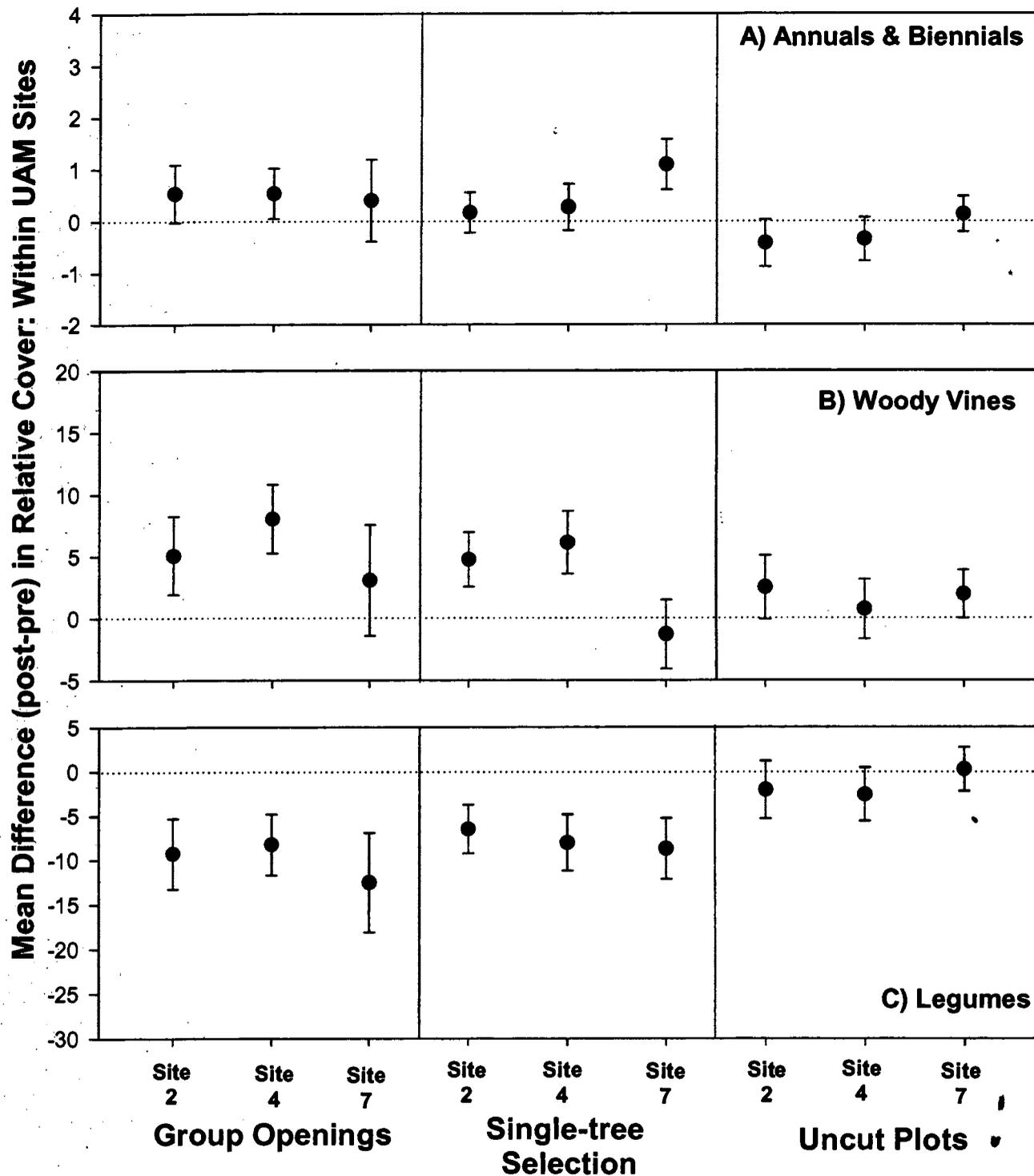


Figure 6.—Mean differences between post- and pre-treatment data within uneven-aged management sites only for A) mean relative cover by annual/biennial species per plot, B) mean relative cover by woody vines per plot, and C) mean relative cover by legumes per plot. Error bars are 95 percent confidence intervals.

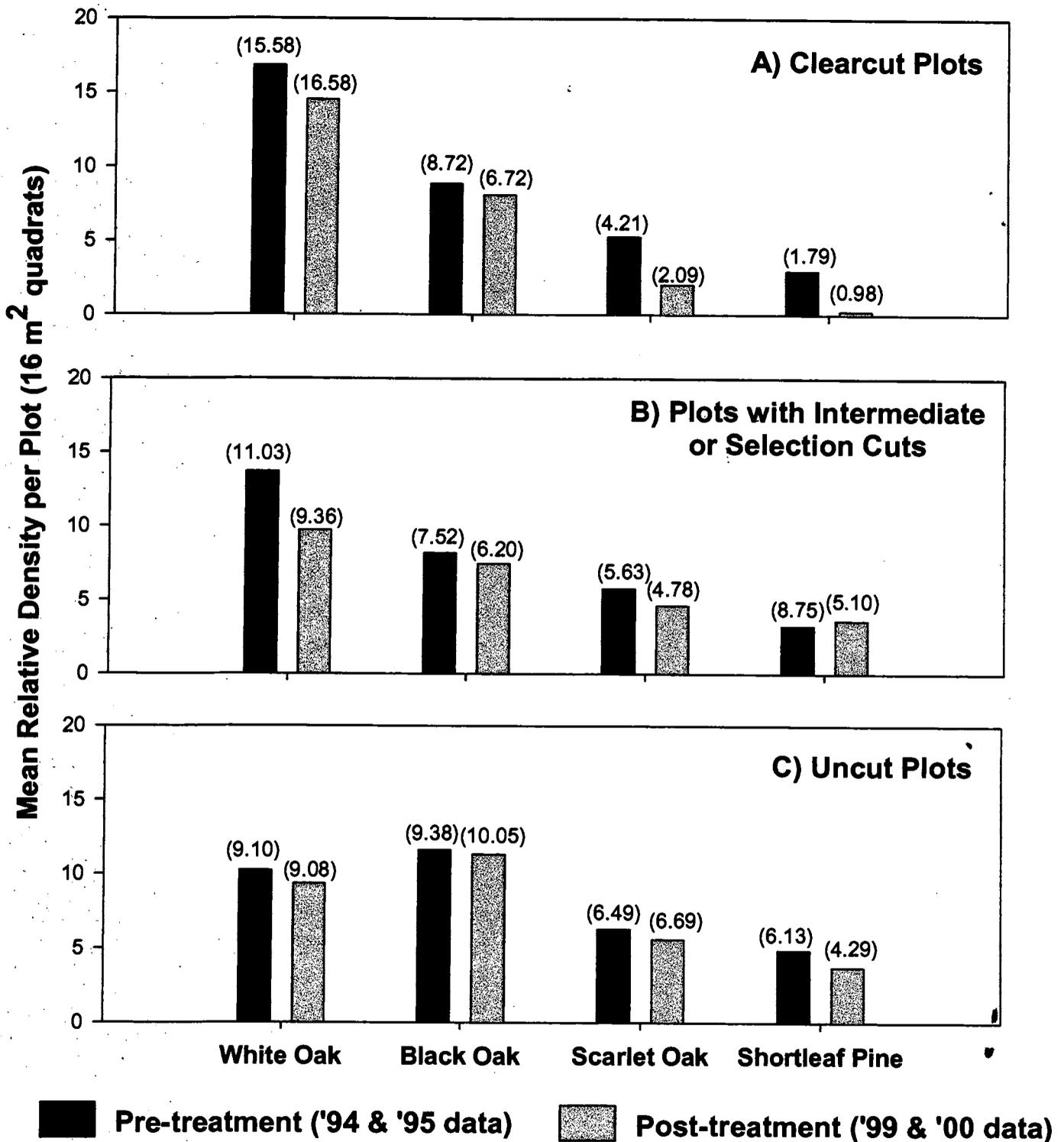


Figure 7.—Comparison of pre- and post-treatment relative densities for white oak (*Quercus alba*), black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), and shortleaf pine (*Pinus echinata*) seedlings (<1 m tall) on plots subjected to A) clearcutting, B) intermediate thinning (EAM sites) or single-tree selection (UAM sites), or C) no cutting. Numbers above bars are standard deviations.

Coverage by graminoids increased across most plots on treated sites, but the increase was generally greater on clearcut and group opening plots, specifically for species such as *Panicum boscii* (panic grass), *Scleria triglomerata* (nut rush), and *Carex nigromarginata* (black-edged sedge). Patterns in average relative cover for all shrubs and trees, and for overall tree density, were less clear and did not reveal clear relationships to the harvesting treatments (table 3). Table 4 lists the ground flora species that changed most drastically from pre- to post-treatment in relative cover and/or frequency on harvested plots.

In addition to evaluating changes in the relative cover and density of all tree species (<1 m tall), we wanted to focus briefly on a few key species of economical and ecological importance within the MOFEP region. To do this, we looked at changes in mean stem density per plot for *Quercus alba* (white oak), *Q. velutina* (black oak), *Q. coccinea* (scarlet oak), and *Pinus echinata* (shortleaf pine). On clearcut plots, shortleaf pine, scarlet oak, and white oak decreased noticeably in mean seedling stem density per plot (fig. 7). On intermediate and/or selectively cut plots, white oak again decreased, but the densities of the other three species did not change appreciably. Little evidence of change in densities was observed for uncut plots.

SUMMARY AND DISCUSSION

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a large-scale, long-term project that experimentally tests for effects of even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) on upland forest components. Pre- (1994, 1995) and post-treatment (1999, 2000) data were collected from 645 permanent vegetation plots as part of the MOFEP ground flora study. Analyses of ground flora data for this report were conducted at two levels: 1) following the experimental model using among-site data in an analysis of variance (ANOVA) framework, and 2) using within-site data to see if ground flora changes in treated sites were confined to harvested plots only.

Patterns in ground flora species richness, total percent ground cover, and species composition observed among treatments at the site level were similar to those observed within treated

sites, among cut and uncut plots. We observed no evidence that changes due to the harvesting have occurred anywhere except on cut plots. In general, patterns among uncut plots on treated sites mirrored those observed among control sites; patterns among intermediate (EAM) and selectively cut (UAM) plots were similar to each other; and plots in clearcuts (EAM) and group openings (UAM) exhibited similar responses for the variables evaluated.

Based on our experience and on existing literature describing early-successional plant responses to canopy removal, we expected that variables such as species richness and ground cover would increase on harvested plots. What we did not expect, however, was the significant decrease in mean plot richness on control sites and on uncut plots within treated sites. One explanation for this decrease may be the exceptionally dry weather in southern Missouri during 1999 and 2000. On cut plots within treated sites, the dramatic increase in light availability may have enabled many plant species to overcome (or at least ignore) the stresses caused by drought. At this point, it is somewhat difficult to confidently describe pre- to post-harvest changes in abundance or frequency for most of the individual plant species encountered on MOFEP sites. Reasons for this difficulty include: 1) normal variations over time in plant populations related to weather, life history traits, and other natural factors not controlled for in this study, 2) the fact that 60 to 70 percent of the species encountered occurred on less than 10 percent of the plots (i.e., very low sample numbers for most species), and 3) year-to-year differences in crew bias and sampling error. Further work is needed to determine if patterns exist (both at landscape and local scales) with regard to which individual species (and groups of species) are decreasing or increasing noticeably in abundance on cut and on uncut plots, and how this might be related to life history traits or some other aspect of plant population biology.

Annual and biennial species, which were essentially not present on MOFEP vegetation plots prior to treatment, increased moderately in mean relative cover after harvests, particularly on clearcut and group opening plots, where they were able to take advantage of the dramatically increased light. Woody vines such as the summer grape (*Vitis aestivalis*) and early-successional shrubs like blackberries (*Rubus*

pensylvanicus) increased drastically in abundance on cut plots from pre- to post-treatment, particularly on clearcut and group opening plots.

Another result that was somewhat surprising was the decline in mean relative cover for legumes, both at the landscape scale among all treated sites, and at a more local scale among all harvested plots within both EAM and UAM sites. A large part of this decline seems to be explained by marked decreases in abundance from pre- to post-treatment for two of the most common ground flora species encountered on MOFEP sites: common tick trefoil (*Desmodium nudiflorum*) and hog peanut (*Amphicarpa bracteata*). Prior to treatment, each of these species typically occurred on 85 to 95 percent of all MOFEP plots, and they were always among the top 10 species in terms of mean relative cover (Grabner *et al.* 1997). These legumes are generalists within a closed-canopy forest environment, but do not appear to be as successful in conditions of increased light. It will be interesting to see if and when these common forest legumes regain their relative dominance on cut plots.

MOFEP is now at the juncture where field observations and experimental analyses must be combined with the concepts of patch dynamics and hierarchy theory to develop a coherent, spatially explicit, across-scale understanding of forest dynamics. Understanding what controls the rate and direction of vegetational change across spatial scales will be critical to developing appropriate management and conservation plans. We have engaged in a long-term, large-scale experiment to evaluate the effects of forest management practices on several ecosystem components. Results from this study suggest that anthropogenically induced disturbances in the form of different forest management practices at a local level (i.e., a stand) can dominate, statistically speaking, the ground-layer vegetation at site scales. But, as our analyses revealed, it is quite possible to show significant treatment effects at the site scale, and yet have these treatment effects spatially confined to the areas actually treated. Post- and pre-treatment differences between 10 and 30 percent for species richness and between 30 and 50 percent for ground cover on 11 percent of all

vegetation plots (i.e., all clearcut plots) within even-aged sites (fig. 3) were large enough to translate into statistically significant differences at the site level. Are the results of this study therefore suggestive of processes that occur at larger, site-level or landscape scales? What would constitute a true site-level effect?

Results from this study highlight the need for a distinction between statistical and biological significance. Whether observed changes in this study are biologically significant may depend on the scale to which we want to reference the change, i.e., are we interested in stand-level or site-level processes. At the stand scale, dramatic differences were observed along a gradient of no harvest, intermediate plots (i.e., thinned areas), and clearcut areas. As MOFEP continues, we will be able to track species invasions, species recovery, and species turnover at the stand level. Site-level questions, on the other hand, will not only focus more on questions that scale up the results gleaned from stand manipulation, but will also need to be expanded to include more process research. For example, will changes in the composition of the understory continue to be proportional to the area treated or is there a point where those changes will become non-linear? In other words, is there a critical level of site-scale fragmentation, where a combination of habitat loss and dispersal limitation affects the heterogeneity of the ground-layer flora at the stand scale?

Because the characteristics of ecological systems at relatively fine scales differ from those at broader scales, these differences must be reflected in the questions and approaches used to study systems (Wiens 1989). Consequently, site-level questions are not merely stand-level questions scaled up. We contend that future efforts should be directed toward developing predictive models that scale stand-level results up to the site level. As with the ground flora study, most projects associated with MOFEP employ some sort of plot or subsampling approach to data collection, and will therefore have similar challenges for interpreting data—before concluding whether or not there is a landscape change. Creative new statistical designs may be needed to address scaling issues and process research within the framework of MOFEP.

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Woody Vegetation Following Even-aged, Uneven-aged, and No-Harvest Treatments on the Missouri Ozark Forest Ecosystem Project Sites

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Abstract.—The Missouri Ozark Forest Ecosystem Project (MOFEP) experimentally tests forest ecosystem response to (a) even-aged management with clearcutting, (b) uneven-aged management with single-tree and group selection, and (c) no-harvesting. The nine MOFEP experimental sites in the southeast Missouri Ozarks are small landscapes ranging from 772 ac (312 ha) to 1,271 ac (514 ha) in extent. In 1996-97, each of the nine sites received one of the three treatments. Clearcutting and thinning affected 26 percent of the total area on the three sites receiving the even-aged management treatment. Selection and group selection harvests affected 57 percent of the total area on the three sites receiving the uneven-aged treatment. The treatments significantly ($P < 0.05$) reduced the mean number of trees, basal area, and canopy cover per acre on the harvested sites, but mean diameter was unchanged. Following treatment, the relative size distribution of trees by diameter class was virtually identical for each of the three treatments. Black oak (*Quercus velutina* Lam.) and scarlet oak (*Q. coccinea* Muenchh.) in combination comprised 60 percent of the harvested basal area; white oak (*Q. alba* L.) and post oak (*Q. stellata* Wangenh.) accounted for an additional 20 to 30 percent. On a percentage basis, harvested trees included more scarlet and black oak basal area and less white oak and shortleaf pine (*Pinus echinata* Mill.) basal area than the sites had prior to harvest. Between 1995 and 1998, the total basal area on no-harvest sites increased an average of 1 ft²/ac (0.2 m²/ha). Trees between 3.3 ft (1 m) tall to 0.5 in. (1.3 cm) d.b.h. increased in number only in stands that were harvested by single-tree and group selection methods. Small trees decreased in all other treatments except those that were not harvested or thinned. Trees between 0.5 in. (1.3 cm) and 1.5 in. (4 cm) d.b.h. decreased in all stands that were harvested; the greatest decrease occurred in clearcut stands. In either size class, differences in pre- and post-harvest abundance were small and species composition did not change consistently as a result of treatments. More than 700 stump sprouts per acre (1,700/ha) occurred in clearcuts; fewer than 120/ac (300/ha) occurred in areas harvested by a combination of single-tree and group selection. Single-tree selection harvests in the uneven-aged treatment and intermediate thinning in the even-aged treatments resulted in 42 and 36 sprouts per acre (104 and 89/ha), respectively. Stands without harvesting averaged fewer than 7 sprouts per acre (17/ha). Overall, the greatest changes in reproduction-sized trees occurred with stump sprouts of which nearly half were oaks. On all sites, white oak had the greatest basal area ingrowth. In addition to providing information on stand and site response to timber harvesting, the results reported in this paper provide information necessary to analyze how other components of the ecosystem (e.g., understory vegetation, animals, microclimate) responded to harvest treatments.

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The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, landscape-scale experiment to test effects of even-aged, uneven-aged, and no-harvest forest management practices on the flora and fauna of upland oak ecosystems (Brookshire and Hauser 1993, Brookshire and Shifley 1997). Because forest harvesting alters forest density, stand size structure, and species composition, identifying differences in pre- and post-harvest forest characteristics is critical for understanding forest change and for interpreting results of other MOFEP studies.

MOFEP was initiated because the impacts of forest management on songbirds and on other non-commodity forest attributes such as diversity of native plant and animal species have been poorly quantified in the Missouri Ozarks. MOFEP provides an opportunity to experimentally measure and statistically test the effects of forest management practices on a suite of ecosystem attributes.

Three management treatments were implemented on the MOFEP sites: (1) even-aged management with harvesting by clearcutting and intermediate thinning, (2) uneven-aged management with harvesting by single-tree selection and group selection, and (3) no-harvest management (see also Sheriff, this proceedings). Even-aged management, as practiced by Missouri Department of Conservation (MDC) managers, uses clearcutting as the principal means of stand regeneration. With this method approximately 10 percent of the acreage in a forest compartment (i.e., a MOFEP site) is clearcut every 10 years for forest regeneration. Thinnings (intermediate cuttings) are conducted periodically within stands to improve quality and increase growing space for residual trees. In the Ozarks, even-aged management is simple to employ, provides excellent regeneration of shade intolerant tree species such as upland oaks (*Quercus* L.) and pine (*Pinus* L.), and provides habitat for wildlife species that prefer early-succession vegetation.

In contrast, uneven-aged management, as practiced by MDC managers, is relatively new to upland oak ecosystems in the Ozarks. Uneven-aged management is commonly practiced in bottomland forests in Missouri and in mixed hardwood forests in the eastern United States where shade tolerant species are prevalent,

competitive, and desirable. Forest management on the Pioneer Forest, a privately owned forest in the Ozarks, suggests that uneven-aged management may be a viable silvicultural alternative in Missouri's upland forests where soils and climate favor oak species and limit competition by undesirable species (Loewenstein 1996). As practiced by MDC managers, uneven-aged management includes single-tree selection and group selection for timber harvest and forest regeneration. Uneven-aged management is more complicated to implement than even-aged management because tree size (and age) distributions within individual stands must be carefully monitored and regulated. However, uneven-aged forests typically have a structurally diverse forest canopy containing both small trees and large-diameter overstory trees over a large contiguous area (Missouri Department of Conservation 1986). Forests managed with uneven-aged methods are thought to be more favorable for forest interior plant and animal species than forests managed with even-aged methods.

Sometimes, managers or land owners choose not to alter or manipulate forest vegetation. For example, managers may desire late-successional or old-growth forests on public lands, and private land owners may choose not to cut trees on their lands. At MOFEP sites, the no-harvest treatment serves two purposes. It demonstrates patterns of forest development that result from natural disturbances and successional processes, and it serves as an experimental control to compare with the two other management practices.

Our paper has four objectives. First, it summarizes the forest harvesting, including the stand-scale effects on tree species density, basal area, and composition. Second, it evaluates site-scale (landscape-scale) effects on tree species density and basal area. Third, it evaluates the effects of harvest treatments on forest regeneration. Finally, it evaluates site-level forest change since inventories began on MOFEP in 1990. Our results and discussion are focused on harvest effects on trees, but the findings are also directly relevant to the other studies in this volume that describe how other components of the forest ecosystem respond to the three forest management treatments.

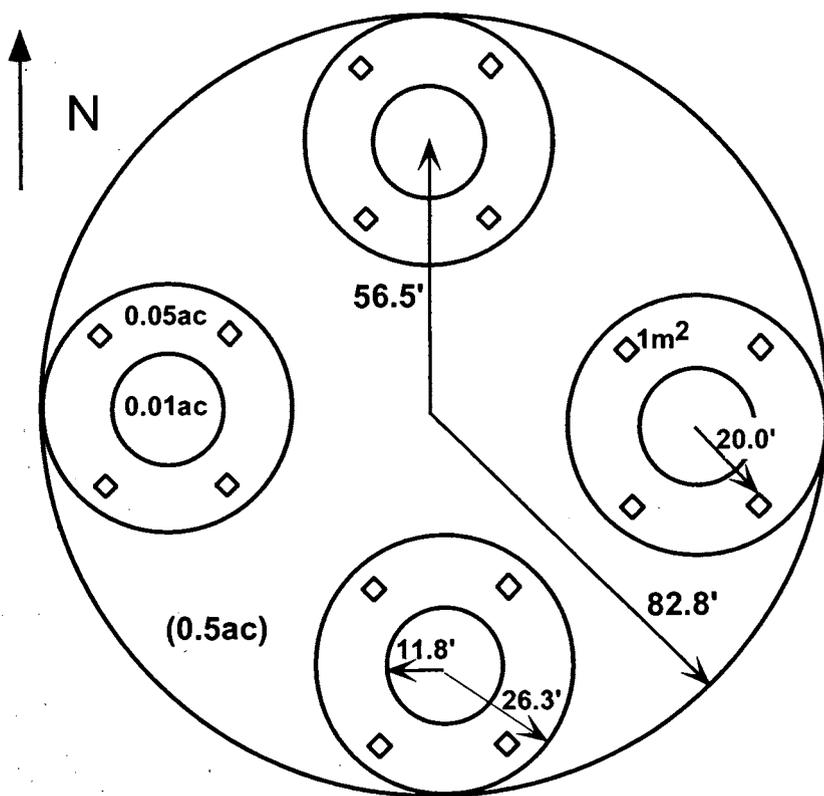


METHODS

Forest Vegetation Sampling and Data Sets

The MOFEP study design is described in detail by Brookshire *et al.* (1997), Sheriff and He (1997), and Sheriff (this proceedings). There are nine study sites (compartments) that range in size from 772 ac (312 ha) to 1,271 ac (514 ha). These were allocated into three "complete" statistical blocks of three sites each. Sites within each block were randomly designated to be managed as even-aged, uneven-aged, or no-harvest, yielding three replicates of each treatment (Sheriff and He 1997). The Missouri Department of Conservation Forest Land Management Guidelines (Missouri Department of Conservation 1986) and the guidelines for managing uneven-aged stands (Law and Lorimer 1989) provided the general recommendations for harvesting in even-aged and uneven-aged MOFEP sites. Also see Sheriff (this proceedings) for additional details on treatments.

Shortly after MOFEP was initiated, each site was divided into areas of common slope and aspect. These were further divided into stands that averaged approximately 12 ac. Stands were used to stratify the placement of permanent vegetation plots (fig. 1). Vegetation plots were randomly located within stands, and each stand received at least one plot. There were 645 vegetation plots established between October 1990 and September 1992. Three additional vegetation plots were added in 1994 to intensify sampling in bottomland areas for a total of 648 permanent inventory plots. Plot center and subplot centers of all vegetation plots were permanently marked with steel rods. Since 1991, these permanent plots have been re-inventoried approximately every 3 years to document the condition of woody vegetation. During each re-inventory within permanent



Size Limits for plots and subplots

- 0.5 acre plot includes trees $\geq 4.5"$ DBH
- 0.05 acre subplot includes trees $\geq 1.5"$ and $< 4.5"$ DBH
- 0.01 acre subplot includes trees ≥ 1 m tall and $< 1.5"$ DBH
- 1m² subplot includes herbaceous vegetation

Down, dead wood transects

56.5' transects (4 per plot) used to measure down dead wood $\geq 2"$ diameter and $\geq 2'$ in length

1 ac = 0.405 ha, 1 ft = 0.305 m

Figure 1.—MOFEP vegetation plot design

plots, live and dead trees ≥ 4.5 in. (11 cm) diameter at breast height (d.b.h.) are sampled in 0.5-ac (0.2 ha) circular plots; trees between 1.5 in. (4 cm) and 4.5 in. (11 cm) d.b.h. are sampled in four 0.05-ac (0.02 ha) circular subplots; and trees at least 3.3 ft (1 m) tall and less than 1.5 in. (4 cm) d.b.h. are sampled in four 0.01-ac (0.004 ha) circular subplots nested within the 0.05-ac subplots. Characteristics recorded for each tree include species, d.b.h. (or size class for trees < 4.5 in. (11 cm) d.b.h.), and status (e.g., live, dead, den, cut, blow-down). Plot and subplot data are combined to obtain plot averages by d.b.h. or size class, and all values are converted to an acre basis for analysis. Additional details about vegetation data collection can be found in Shifley and Brookshire (2000).

We summarized information about the harvested stands (e.g., location, size, area, harvest regime) using spatial data compiled by MDC. We used two data sets to determine the effects of forest harvesting on trees. The first was collected between May 1994 and January 1995 (hereafter referred to as 1995). This inventory was conducted before the first forest harvest entry, which occurred from May 1996 to May 1997. The second data set was collected between October 1997 and June 1998 (hereafter referred to as 1998). We determined forest growth, ingrowth, and mortality during the entire course of MOFEP by comparing data collected in 1991-1992 (hereafter referred to as 1992) to data collected in 1998 in all stands and all MOFEP sites. Growth refers to basal area increases of existing trees ≥ 4.5 in. (11 cm) d.b.h., ingrowth refers to basal area increases for trees that have grown into the ≥ 4.5 in. (11 cm) d.b.h. size class, and mortality refers to all trees ≥ 4.5 in. (11 cm) d.b.h. that have died.

Statistical Analysis

We statistically evaluated pre- and post-treatment differences in the number of tree species per plot, number of trees per acre, quadratic mean diameter, basal area, and percent canopy cover. For quadratic mean diameter and basal area, analyses were conducted by combining data by size classes corresponding to sampling thresholds for vegetation plots and subplots: trees ≥ 3.3 ft (1 m) tall, trees ≥ 1.5 in. (4 cm) d.b.h., and trees ≥ 4.5 in. (11 cm) d.b.h. We also evaluated pre- and post-treatment differences in the number of trees per acre, quadratic mean diameter, and basal areas per acre for the most

abundant tree species: white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muenchh.), shortleaf pine (*Pinus echinata* Mill.), and post oak (*Q. stellata* Wangenh.).

Pre- and post-treatment tree attribute differences were evaluated at the site level using analysis of variance with the following fixed effects model:

$$Y_{ij} = \mu + \text{block}_i + \text{treatment}_j + \epsilon_{ij}$$

Where μ is the mean difference between the pre- and post-treatment attribute, block_i is the block effect, treatment_j is the treatment effect (i.e., harvest treatment), and ϵ_{ij} is the error effect $N(0, \sigma^2)$. Blocks and treatments each received two degrees of freedom, leaving four degrees of freedom for error. For analyses that we conducted with this model, we used an α -level of 0.05. Where overall significance was found, we used a least significant difference test to identify attributes that differed significantly from those of no-harvest sites.

RESULTS AND DISCUSSION

Forest Harvesting

The acreage and volume harvested varied considerably between treatment types (tables 1 and 2). On even-aged treatment sites, approximately 320 ac (130 ha) (11% of the total area) were clearcut and 411 ac (166 ha) (15%) were thinned. Stands that were clearcut averaged 13 ac (5 ha) and stands that were thinned on the even-aged sites averaged 11 ac (4 ha). On uneven-aged sites, 2,124 ac (860 ha) (57%) received single-tree selection harvests, and group openings were created to regenerate the shade intolerant oaks and pine. Group openings 70 ft (21 m) in diameter (i.e., approximately one tree height) were created on south-facing slopes; openings 105 ft (32 m) were created on ridgetops; and openings 140 ft (43 m) in diameter were created on north-facing slopes (Law and Lorimer 1989). In uneven-aged sites, there were between 153 and 267 group openings. These covered a total area of 24 to 46 ac (10 to 19 ha) per site and occupied roughly 5 percent of the area in each cutting unit (table 3). Within group openings, all or nearly all trees were removed. The average cutting unit size averaged 21 ac (9 ha) in the uneven-aged sites. Overall, a greater volume was harvested from uneven-aged sites than from even-aged sites (3.4 million bd ft



Table 1.—Total and percent area harvested and commercial volume harvested in even-aged and uneven-aged sites

Site	Site area ¹ Acres	Area clearcut Acres	Area clearcut Percent	Area thinned ² Acres	Area thinned Percent	Volume harvested ³ Thousand bd ft
Even-aged						
3	889	93	10	211	24	754
5	772	114	15	142	18	927
9	1,141	113	10	58	5	773
Even-aged total	2,802	320	11	411	15	2,454
Uneven-aged						
2	1,271	—	—	876	69	1,146
4	1,183	—	—	735	62	952
7	1,240	—	—	513	41	1,344
Uneven-aged total	3,694	—	—	2,124	57	3,442

¹ Metric conversions are 1 acre = 0.4047 ha.

² Includes intermediate thinning on even-aged management sites and single-tree selection and group selection harvest on uneven-aged management sites.

³ This does not include cull or slash volume; from Brookshire *et al.* 1997.

Table 2.—Number of stands (i.e., cutting units) and stand size for even-aged and uneven-aged sites

Site	No. of stands clearcut	Mean stand size clearcut ¹ (range) Acres	No. of thinned stands ²	Mean stand size thinned ¹ (range) Acres	No. trees ≥4.5" d.b.h. harvested ¹ Trees/acre	Basal area for trees ≥4.5" d.b.h. harvested ¹ ft ² /ac
Even-aged						
3	8	12 (2-32)	22	10 (1-31)	22	16
5	7	16 (7-25)	14	10 (4-27)	29	19
9	9	13 (7-23)	4	15 (12-17)	13	10
Even-aged total	24	13 (2-32)	40	11 (1-31)	21	15
Uneven-aged						
2	—	—	27	32 (3-80)	21	14
4	—	—	55	13 (3-26)	30	20
7	—	—	28	18 (6-51)	12	12
Uneven-aged total	—	—	110	21 (3-80)	21	15

¹ 1 acre = 0.4047 ha, 4.5 in. = 11 cm, 1 tree/ac = 2.47 trees/ha.

² Includes intermediate thinning on even-aged management sites and single-tree selection and group selection harvest on uneven-aged management sites.

Table 3.—Number, total size, and percent area of group openings in uneven-aged cutting units

Site	No. of group openings	Total area of openings ¹	
		Acre	Percent
2	267	46	5
4	221	37	5
7	153	24	5
Uneven-aged total	641	107	5

¹ 1 acre = 0.4047 ha.

vs. 2.5 million bd ft) because more of the total area on the uneven-aged sites was treated with selection and group selection harvests than was thinned or clearcut on the even-aged sites. Moreover, by chance, the total area of the three sites treated with uneven-aged management was about 30 percent greater than the total area of sites treated by even-aged management.

The number of residual trees, the residual basal area, and residual overstory canopy cover within harvested stands or cutting units also differed by treatment (table 4). As expected,

very few residual trees ≥ 1.5 in. (4 cm) d.b.h. remained in clearcut stands except those left to produce seed for forest regeneration or to provide wildlife food and shelter. The residual basal area of clearcut stands was 6 ft²/ac (1.5 m²/ha) compared to 97 ft²/ac (22 m²/ha) prior to harvest; canopy cover was reduced from 86 to 3 percent. Thinned stands in even-aged sites and cutting units harvested by the selection method in uneven-aged sites had roughly a 25 percent reduction in both trees per unit area and basal area; overstory canopy cover was reduced from 86 to 56 percent.

Table 4.—Pre- and post-treatment tree density, basal area, and canopy cover in harvested stands or cutting units

	Trees per acre ¹ (standard deviation)						Basal area (ft. ² /ac) ¹ (standard deviation)				Canopy coverage (standard deviation)	
	≥ 3.3 ft tall		≥ 1.5 in. d.b.h.		≥ 4.5 in. d.b.h.		≥ 1.5 in. d.b.h.		≥ 4.5 in. d.b.h.		(%)	
	1995	1998	1995	1998	1995	1998	1995	1998	1995	1998	1995	1997
Clearcut stands (even-aged treatment)	1,305 (349)	1,277 (230)	437 (138)	17 (9)	136 (13)	8 (2)	97 (4.6)	6 (0.5)	85 (4.9)	6 (0.7)	86 (3.3)	3 (1.0)
Intermediate thinning (even-aged treatment)	1,350 (356)	911 (201)	491 (42)	354 (46)	158 (23)	133 (14)	100 (11.0)	71 (7.5)	86 (13.0)	62 (9.2)	86 (3.6)	55 (8.1)
Selection cutting units (uneven-aged treatment)	1,228 (84)	968 (240)	475 (101)	332 (61)	158 (19)	127 (16)	100 (6.2)	76 (5.8)	87 (2.7)	67 (3.8)	85 (3.8)	57 (12.7)

¹ 3.3 ft = 1 m; 1.5 in. = 4 cm, 4.5 in. = 11 cm, 1 tree/ac = 2.47 trees/ha, and 1 ft²/ac basal area = 0.2296 m²/ha.



In combination, black oak, scarlet oak, white oak, post oak, shortleaf pine, and hickories (*Carya* spp. Nutt.) comprised 95 percent of the live basal area immediately prior to harvest and 96 percent of the harvested basal area. Together, black oak and scarlet oak comprised approximately 60 percent of the harvested basal area; white oak and post oak accounted for an additional 20 to 30 percent of the harvest (fig. 2). Compared to the species composition of the sites prior to harvest, the harvested trees included a greater percentage of scarlet and black oak basal area and a lesser percentage of white oak and shortleaf pine basal area. In the even-aged treatment, the harvested basal areas of scarlet and white oak were nearly equal. However, in the uneven-aged treatment, harvest of scarlet oak was proportionately greater than that of white oak (33 vs. 21% of total). Shortleaf pine was 3 percent of the harvested basal area although it was 9 percent of the total basal area prior to the harvest.

Both harvest treatments removed trees ranging from 5 to more than 29 in. (13 to 74 cm) in diameter. The size distribution of diameters for harvested trees was similar to that of the live trees that were retained (fig. 3). Snags (i.e., standing dead trees) also had a diameter size distribution similar in form to that of live trees.

Diameter distributions for live, cut, and standing dead trees each had a negative exponential (reverse-J) shape. However, compared to the inventory of live trees, the population of snags included a greater proportion of small diameter trees (less than 7 in. [18 cm] d.b.h.) and fewer trees in size classes between 10 and 20 in. d.b.h., regardless of harvest treatment.

Relative to the size distribution of live trees that remained following harvest treatments harvested trees included proportionately more trees greater than 10 in. (25 cm) d.b.h. for even-aged treatments and greater than 15 in. (38 cm) d.b.h. for uneven-aged treatments (fig. 3). Clearcut stands in the even-aged treatment were typically older and included more large trees than the average for untreated stands. Following harvest, the diameter distribution of the live trees was nearly identical for the three treatments (fig. 3).

The q-value is a measure of the shape of a negative exponential (reverse-J) diameter distribution, and it is often used in uneven-aged management to describe desired stand structure. For tree diameter distributions with a negative exponential form, the q-value corresponds to the ratio of the number of trees in a given diameter class to the number of trees in

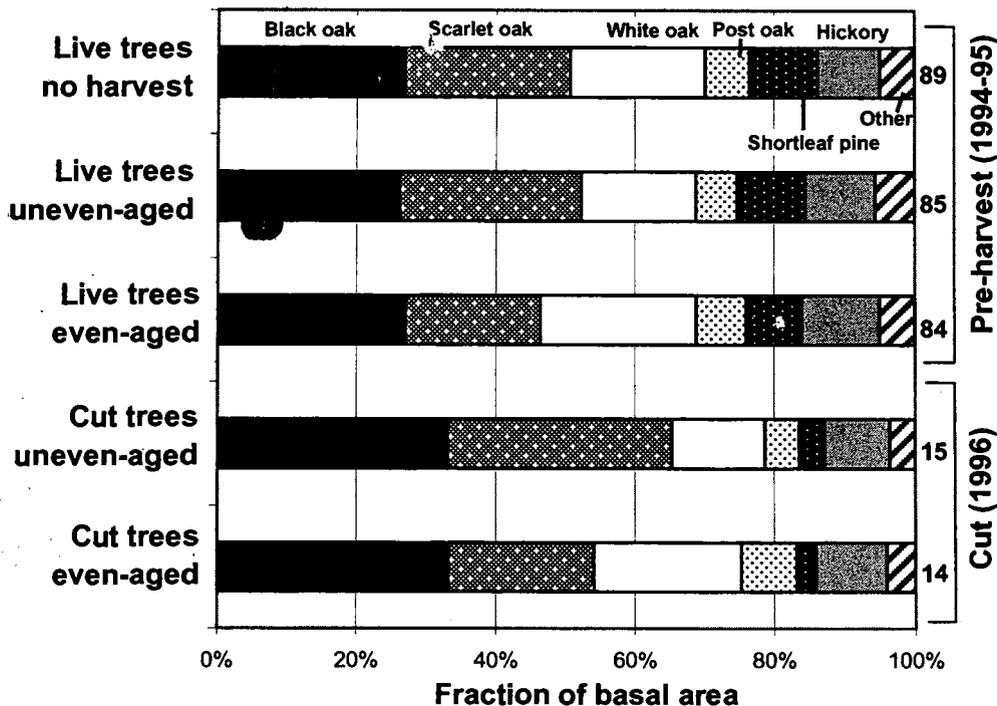


Figure 2.—Proportion of live basal area by species and treatment prior to harvest (1994-95), and proportion of cut basal area by species (1997-98) for the even-aged and uneven-aged treatments. Values are means for three sites in each treatment group. Mean basal area per acre for each category is shown to the right of each bar.

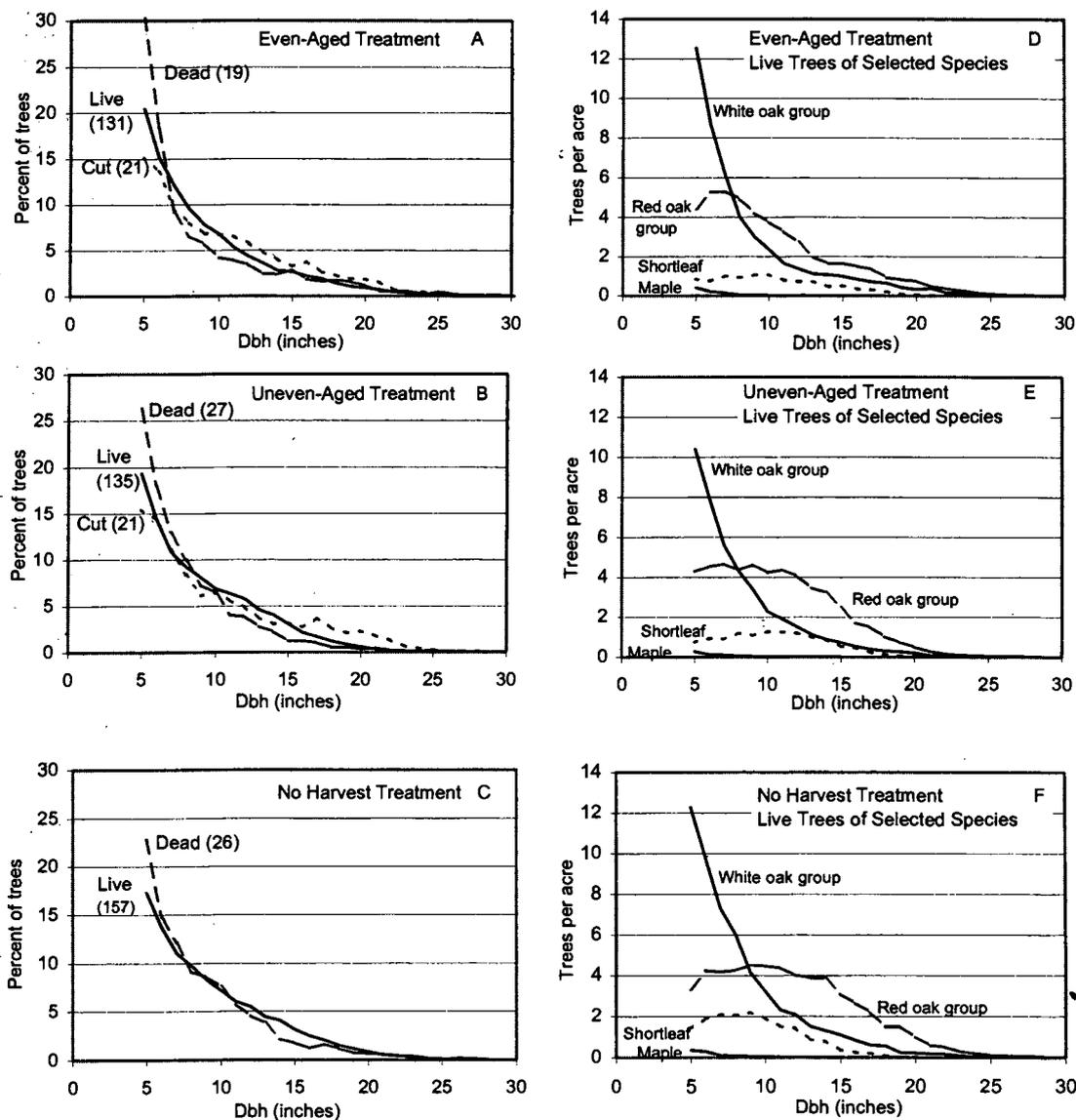


Figure 3.—(A) to (C). Proportion of trees ≥ 4.5 in. (11.4 cm) d.b.h. by diameter class for live, dead, and cut trees, 1998. The mean number of trees per acre for the live, cut, and dead categories is shown adjacent to the live, cut, and dead labels. Values are a composite for all plots in each treatment. All diameter distributions shown follow a negative exponential form. Distribution curves for live trees are virtually identical for each of the three treatments; the q -value for each of the three live tree distributions is 1.2. (D) to (F). Number of live trees by diameter class for the white oak group (white and post oak), the red oak group (black and scarlet oak), the maple group (red and sugar maple), and shortleaf pine, 1998.

the next larger diameter class. When all plots in a treatment were combined, the live tree diameter distributions following harvest were nearly identical for each of the three management treatments. Each had a q -value of 1.2 (computed using 1-in. diameter classes). Individual live tree diameter distributions for maples (*Acer rubrum* L. and *A. saccharum* Marsh.) and for white oaks (white oak and post oak) also had negative exponential diameter distributions (fig.

3). Of the four species groups illustrated, the white oak group (white oak and post oak) dominated the size classes between 5 and 7 in. (13 and 18 cm) d.b.h. The red oak group (black oak and scarlet oak) and shortleaf pine were unimodal in form, and the red oak group had a greater proportion of trees in the larger diameter classes at all sites. We attribute this pattern to greater shade tolerance of white oak and maples, and to the comparatively rapid growth



of the shortleaf pines and trees in the red oak group. The data for smaller diameter classes (fig. 3) show that maple is not increasing.

These results help illustrate that even-aged and uneven-aged forest management systems create very different forest structures (fig. 4). Clearcutting is an intensive tree harvesting method that removes nearly all trees in a treated stand; most large trees that do not have commercial value are cut down in post-harvest "slashing" operations that facilitate regeneration of desirable trees. However, MDC guidelines specify that clearcuts be small in area (a range of 2 to 20 ac [1 to 8 ha] is recommended) to protect water and soil resources and to ensure that different size classes of trees are represented across the forest (Missouri Department of Conservation 1986). Even when the total acres clearcut and thinned are combined, only one-fourth of the total land area was affected by harvest in the even-aged treatment. In contrast, uneven-aged management by the single-tree selection and group selection methods was much more extensive. Harvests occurred over a larger proportion (57%) of uneven-aged sites, explaining why nearly 40 percent more merchantable volume was harvested from uneven-aged sites than from even-aged sites.

The scarlet oak harvest was disproportionately large in the uneven-aged treatment because MDC foresters purposely marked uneven-aged cutting units to retain longer lived tree species such as white oak over the comparatively short-lived tree species such as scarlet oak. In the Ozarks, scarlet oaks are often short lived because they are particularly susceptible to oak decline, largely caused by *Armillaria* root disease (Johnson and Law 1989). Compared to even-age methods, single-tree selection methods used in uneven-aged sites provide greater flexibility to favor long-lived species during timber marking.

Treatment Effects Among Sites

One of MOFEP's strengths is that it was designed to be a long-term, landscape-scale investigation. Although we can address only short-term results at this early stage of the experiment, we can begin assessing some short-term

landscape-scale effects. MOFEP sites (or compartments) serve as contiguous forest "landscapes." For all species combined in our study, there were detectable treatment-level effects for five of nine woody vegetation variables (table 5). Values of variables that changed significantly after harvesting were usually for the larger size classes of trees. For example, there were no significant reductions in the total number of trees per acre although significant decreases were detected for trees ≥ 1.5 in. (4 cm) d.b.h. in the uneven-aged treatment and for trees ≥ 4.5 in. (11 cm) d.b.h. in both even-aged and uneven-aged treatments. One exception was basal area, which decreased significantly in all size classes on harvested sites. As expected, the average canopy cover of harvested sites decreased following harvesting and was significantly lower than the no-harvest sites. We note that the average canopy cover of no-harvest sites also decreased. However, we do not know if this decrease was simply sampling variation or a decrease in canopy cover (e.g., due to tree blowdown, mortality, defoliation), or both. Changes in numbers, diameters, and basal areas for the most abundant species were similar to those of all species combined (table 5). White oak, black oak, and especially scarlet oak stems per acre and/or basal areas of the larger size classes were decreased significantly by harvesting, especially in uneven-aged sites. We found small, but significant changes in post oak basal area for trees ≥ 4.5 in. d.b.h. There were no changes in shortleaf pine abundance, diameter, and basal area.

Even though individual cutting units and stands were impacted by harvesting in both even-aged and uneven-aged sites, we found relatively few site-scale treatment effects. When averaged across an entire site, many vegetation characteristics were not significantly different from those in no-harvest sites. Most changes were detected only for the numbers of trees and basal area per acre. Clearly, both even-aged and uneven-aged harvest treatments impacted the sites, and did so in very different ways (see fig. 4). The first even-aged harvest treatments left mature forests containing large patches (stands) where few mature trees remain. The first uneven-aged harvest treatments left a mature forest having slightly lower density than the pre-harvest forest and containing small patches (group openings) where few trees remain.

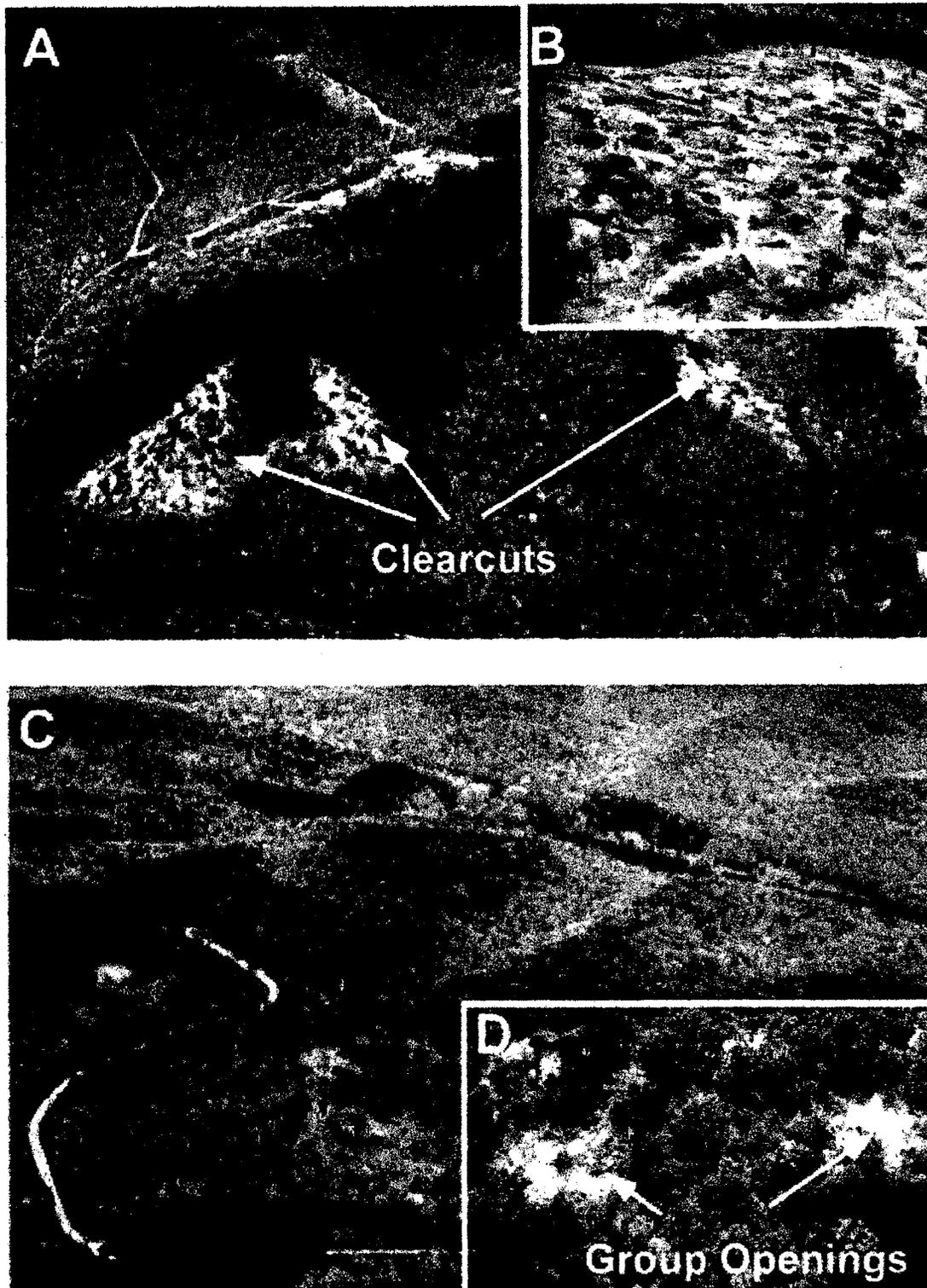


Figure 4.—(A) to (D). Different forest structures are created by even-aged and uneven-aged management. These photographs were taken in April 1997, nearly 1 year after harvesting began. (A). Even-aged MOFEP site 9 illustrating clearcuts. (B). Close-up photograph of a clearcut. Note that few residual trees remain and that a large volume of slash was left on the ground. (C). Uneven-aged MOFEP site 7 illustrating single-tree selection and group openings. (D). Close-up photograph of an area harvested with single-tree selection and group openings. Few trees per acre were removed within single-tree selection cutting units, leaving a nearly closed-canopy forest. Within group openings, all trees were harvested, and some slash remains on the ground.



Table 5.—Pre- and post-treatment means and differences for attributes of all tree species and for white oak, black oak, scarlet oak, shortleaf pine, and post oak. Values differing significantly ($\alpha = 0.05$) from the no-harvest treatment are shown in bold.

Species and attribute ^{a,b}	No-harvest (sites 1, 6, 8)			Even-aged (sites 3, 5, 9)			Uneven-aged (sites 2, 4, 7)			F-value ^c (for difference)	P-value (for difference)
	1995	1998	diff.	1995	1998	diff.	1995	1998	diff.		
All trees											
No. of species per plot	12.7	13.0	0.3	14.5	14.1	-0.4	14.0	14.5	0.5	6.3	0.06
No. of trees > 0 in. d.b.h.	1,180	1,167	-13	1,282	1,183	-99	1,268	1,132	-136	0.3	0.76
No. of trees ≥ 1.5 in. d.b.h.	409	403	-6	451	385	-66	453	362	-91	7.1	0.05
No. of trees ≥ 4.5 in. d.b.h.	155	157	2	149	132	-17	157	135	-22	11.5	0.02
Qmd ≥ 1.5 in. d.b.h.	6.7	6.7	0.0	6.3	6.3	0.0	6.3	6.4	0.1	0.5	0.62
Qmd ≥ 4.5 in. d.b.h.	10.3	10.3	0.0	10.2	10.0	-0.2	10.0	9.9	-0.1	2.3	0.21
Basal area (ft ² /ac) ≥ 1.5 in. d.b.h.	99	100	1	96	82	-14	97	81	-16	22.6	0.01
Basal area (ft ² /ac) ≥ 4.5 in. d.b.h.	89	90	1.0	84	71	-12	85	71	-14	25.0	0.01
Canopy cover (%)	82	69	-13	85	59	-26	84	60	-24	21.9	0.01
White oak											
No. of trees > 0 in. d.b.h.	117	120	3	137	137	0	134	110	-24	10.6	0.03
No. of trees ≥ 1.5 in. d.b.h.	89	93	4	105	101	-4	94	76	-18	5.0	0.08
No. of trees ≥ 4.5 in. d.b.h.	40	43	3	41	38	-3	35	32	-3	7.3	0.05
Qmd ≥ 1.5 in. d.b.h.	6.4	6.4	0.0	6.2	6.0	-0.2	5.7	6.0	0.3	6.1	0.06
Qmd ≥ 4.5 in. d.b.h.	8.9	8.8	-0.1	9.2	9.0	-0.2	8.6	8.5	-0.1	1.4	0.33
Basal area (ft ² /ac) ≥ 1.5 in. d.b.h.	20	21	1.0	22	20	-2	17	15	-2	11.9	0.02
Basal area (ft ² /ac) ≥ 4.5 in. d.b.h.	17	18	1.0	19	17	-2	14	13	-1	14.2	0.02
Black oak											
No. of trees > 0 in. d.b.h.	57	62	5	58	62	4	60	58	2	0.7	0.57
No. of trees ≥ 1.5 in. d.b.h.	32	37	5	38	36	-2	37	38	1	7.0	0.05
No. of trees ≥ 4.5 in. d.b.h.	28	26	-2	29	23	-6	30	24	-6	6.1	0.06
Qmd ≥ 1.5 in. d.b.h.	11.8	10.9	-0.9	10.5	9.7	-0.8	10.6	9.3	-1.3	0.2	0.80
Qmd ≥ 4.5 in. d.b.h.	12.5	12.8	0.3	12.0	11.9	-0.1	11.6	11.4	-0.2	6.0	0.06
Basal area (ft ² /ac) ≥ 1.5 in. d.b.h.	24	24	0	23	19	-4	23	18	-5	14.1	0.02
Basal area (ft ² /ac) ≥ 4.5 in. d.b.h.	24	23	-1	23	18	-5	22	17	-5	10.7	0.02
Scarlet oak											
No. of trees > 0 in. d.b.h.	44	51	7	45	62	17	58	60	2	2.1	0.24
No. of trees ≥ 1.5 in. d.b.h.	32	39	7	35	37	2	43	41	-2	18.3	0.01
No. of trees ≥ 4.5 in. d.b.h.	27	26	-1	25	21	-4	32	25	-7	16.3	0.01
Qmd ≥ 1.5 in. d.b.h.	11.0	10.1	-0.9	9.4	8.2	-1.2	9.8	9.0	-0.8	0.6	0.60
Qmd ≥ 4.5 in. d.b.h.	12.0	12.1	0.1	10.9	10.6	-0.3	11.3	11.2	-0.1	5.4	0.07
Basal area (ft ² /ac) ≥ 1.5 in. d.b.h.	21	22	-1	17	14	-3	23	18	-5	21.7	0.01
Basal area (ft ² /ac) ≥ 4.5 in. d.b.h.	21	21	0	16	13	-3	22	17	-5	21.2	0.01
Shortleaf pine											
No. of trees > 0 in. d.b.h.	26	51	25	18	37	19	19	29	10	1.8	0.28
No. of trees ≥ 1.5 in. d.b.h.	22	47	25	15	35	20	16	26	10	1.4	0.34
No. of trees ≥ 4.5 in. d.b.h.	17	17	0	10	10	0	13	12	-1	4.8	0.09
Qmd ≥ 1.5 in. d.b.h.	8.6	6.3	-2.3	9.1	6.4	-2.7	9.8	7.7	-2.1	0.0	0.99
Qmd ≥ 4.5 in. d.b.h.	9.6	9.7	0.1	11.0	11.1	0.1	10.8	10.9	0.1	0.2	0.80
Basal area (ft ² /ac) ≥ 1.5 in. d.b.h.	9	10	1	7	8	1	8	9	1	2.4	0.21
Basal area (ft ² /ac) ≥ 4.5 in. d.b.h.	9	9	0	7	7	0	8	8	0	1.6	0.31
Post oak											
No. of trees > 0 in. d.b.h.	22	33	11	15	25	10	30	37	7	0.1	0.94
No. of trees ≥ 1.5 in. d.b.h.	15	25	10	13	22	9	16	28	12	0.1	0.91
No. of trees ≥ 4.5 in. d.b.h.	10	10	0	8	7	-1	10	8	-2	4.1	0.11
Qmd ≥ 1.5 in. d.b.h.	8.5	6.9	-1.6	9.4	6.8	-2.6	7.9	5.8	-2.1	0.4	0.72
Qmd ≥ 4.5 in. d.b.h.	10.2	10.2	0.0	11.7	11.3	-0.4	9.7	9.9	0.2	6.2	0.06
Basal area (ft ² /ac) ≥ 1.5 in. d.b.h.	6	7	1	6	6	0	5	5	0	3.8	0.12
Basal area (ft ² /ac) ≥ 4.5 in. d.b.h.	6	6	0	6	5	-1	5	4	-1	21.7	0.01

^a Reported values are per acre except as noted. Metric conversions are 1.5 in. = 4 cm, 4.5 in. = 11 cm, 1 tree/ac = 2.47 trees/ha, and 1 ft²/ac basal area = 0.2296 m²/ha basal area.

^b Qmd = quadratic mean d.b.h. (in inches) for trees in the specified size class.

^c For ANOVA of treatment effects, F has (2,4) degrees of freedom.

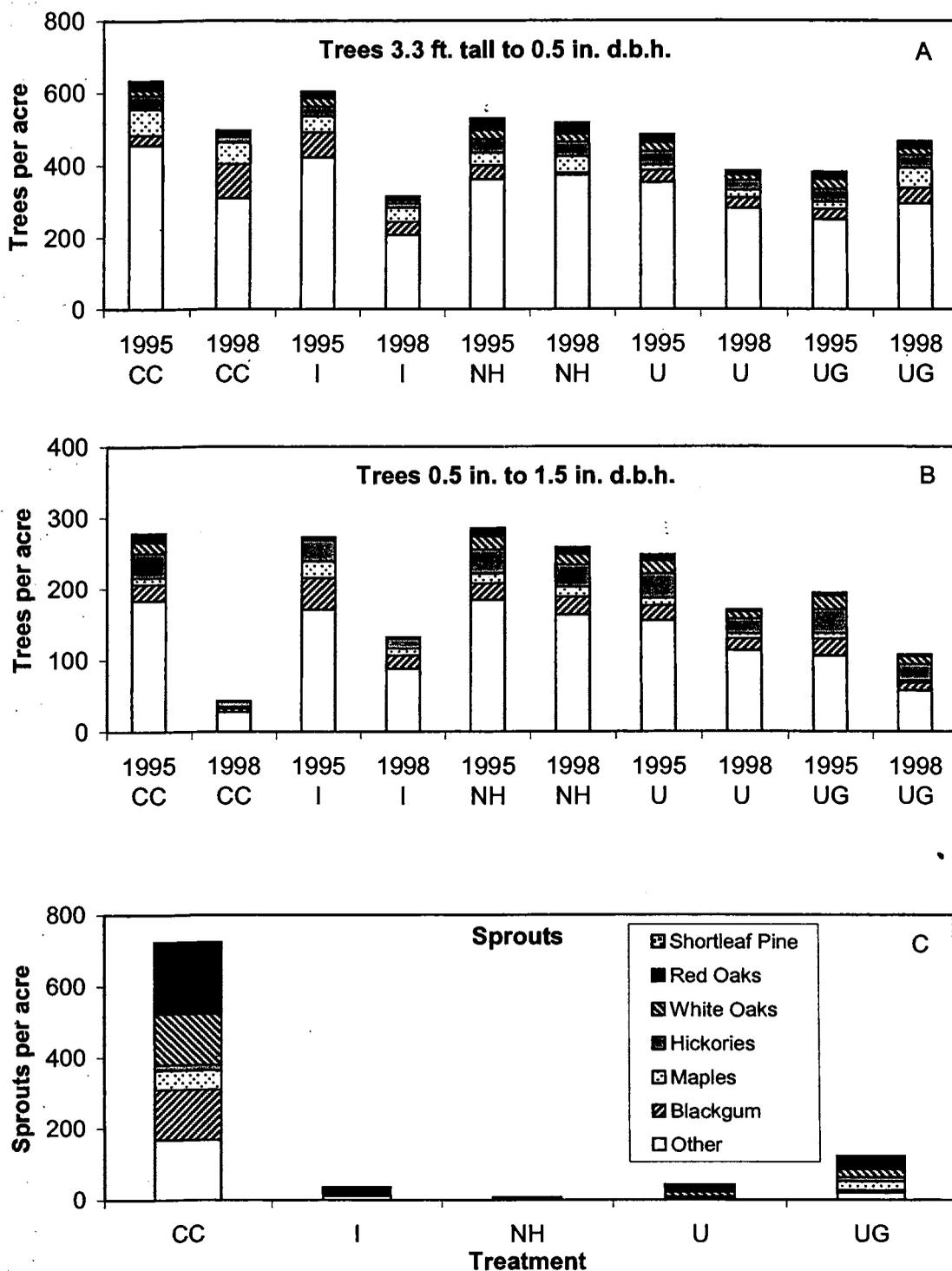


Figure 5.—Number of small trees and sprouts per acre before and after harvest treatments (1995 and 1998). Summaries are for individual plots that were clearcut (CC), received an intermediate harvest as part of the even-aged treatment (I), were left unharvested (NH), received single-tree selection harvest as part of the uneven-aged treatment (U), or received both single-tree and group selection harvesting as part of the uneven-aged treatment (UG). Species shown are: the white oak group (white and post oak); the red oak group (black and scarlet oak); the maple group (red and sugar maple); the hickory group (black, mockernut, pignut, and bitternut hickory); blackgum; shortleaf pine. Values are for (A) trees from 3.3 ft (1 m) tall to 0.5 in. (1.3 cm) d.b.h.; (B) trees \geq 0.5 in. (1.3 cm) to 1.5 in. (4 cm) d.b.h.; and (C) recent sprouts of any diameter. The bars show the proportion attributable to each species group; order of species groups (top to bottom) matches vertical order shown in the legend. One acre = 0.4047ac. 95



However, it is clear that the impact of these treatments on forest structure at site scales (i.e., approximately 1,000-ac compartments) cannot be fully described or understood by evaluating the forest vegetation data with analysis of variance. To better quantify site-scale effects of the different treatments, we need to apply other descriptive measures of the forest structure. These measures should include quantifying the number, area, perimeter, and spatial arrangement of patches of forest having contrasting diameter and/or height distributions (e.g., clearcut stands, group openings, and the matrix of forest between these patches). These statistics would provide a different perspective on the treatment effects.

Forest Reproduction

An important purpose of harvesting by either even-aged or uneven-aged methods is to regenerate a future stand. Therefore, it is important to determine the effects of harvesting on species composition, abundance, and total numbers of trees in the reproduction size class. Trees from 3.3 ft (1 m) tall to 0.5 in. (1.3 cm) d.b.h. increased in number only on plots that were harvested by single-tree and group selection. Small trees decreased on plots in other treatments except those that were not harvested or thinned (fig. 5A). Trees between 0.5 in. (1.3 cm) and 1.5 in. (4 cm) d.b.h. decreased in all treatments; the greatest decrease occurred in clearcut plots (fig. 5B). In either size class, differences in pre- and post-harvest abundance were small, and species composition did not change consistently as a result of treatments. Most trees in these size classes were in the "other" category; of trees in this category, most were dogwoods (*Cornus florida* L.) and sassafras (*Sassafras albidum* [Nutt.] Nees). Neither of these is an overstory species in Ozark forests. More than 700 stump sprouts per acre (1,700/ha) occurred in clearcuts; fewer than 120/ac (300/ha) occurred in areas harvested by a combination of single-tree and group selection (fig. 5C). Single-tree selection harvests in the uneven-aged treatment and intermediate thinning in the even-aged treatments resulted in 42 and 36 sprouts per acre (104 and 89/ha), respectively. Stands without harvesting averaged fewer than 7 sprouts per acre (17/ha). Overall, the greatest changes in reproduction-sized trees occurred with stump sprouts of which nearly half were oaks. Blackgums (*Nyssa*

sylvatica Marsh.) also sprouted prolifically in clearcuts and sprout numbers were similar to those of white oak. The order of sprout abundance followed the expectations for available light at the forest floor: clearcut > group opening > single-tree section or thinning > no harvest (fig. 5C).

Although it is too early to draw definitive conclusions with the data collected only 2 years after harvesting, cutting apparently has had very little effect on the species composition or abundance of the reproduction layer. During the next few years, we anticipate that oaks will become more abundant in the reproduction layer within harvested areas, especially in clearcuts and group openings, primarily because of oak stump sprouting.

Oak stump sprouting is an important source of regeneration in upland hardwood forests throughout the Central Hardwood region (Dey and Jensen, this proceedings; Johnson 1992; Sander *et al.* 1984; Weigel and Johnson 1998). In clearcuts, stump sprouts may provide most of the oaks that will later grow into dominant or codominant canopy positions (Johnson 1975, Weigel and Johnson 1998). The contribution of stump sprouts to oak regeneration depends upon many factors. Some important factors are parent tree species, age, and diameter (Sander *et al.* 1984, Weigel and Johnson 1998). Large (> 8 in. [20 cm] d.b.h.) black oaks and scarlet oaks are more likely to stump sprout than large white oaks (Sander *et al.* 1984). Younger oaks sprout more readily than older ones and smaller diameter oaks sprout more readily than larger ones (Weigel and Johnson 1998).

We do not know the exact number of reproduction-sized oak trees needed to ensure adequate regeneration, but oak regeneration is seldom a problem in even-aged stands in this part of the Missouri Ozarks. However, it is not clear to what extent oak regeneration will be successful in uneven-aged stands because oak seedlings require about one-third full sunlight for maximum photosynthesis (Law and Lorimer 1989) and uneven-aged stands may not provide enough sunlight for oak seedlings to compete with other tree species. For Missouri Ozark forests, Larsen *et al.* (1999) recommended a residual basal area of about 50 ft²/ac (12 m²/ha) to ensure adequate oak regeneration in stands harvested only by single-tree selection methods. On MOFEP sites, the residual basal area in

selection harvest cutting units was 67 ft²/ac (15 m²/ha), considerably higher than recommended by Larsen *et al.* (1999) for single-tree selection if used alone. However, uneven-aged harvesting at MOFEP followed the guidelines of Law and Lorimer (1989), who recommended using group openings nested within single-tree selection cutting units to encourage oak regeneration. Accordingly, MOFEP single-tree selection cutting units within uneven-aged sites contained from 153 to 267 group openings (or about 5% of the area of cutting units) to enhance oak regeneration. Moreover, the residual basal area within single-tree selection cutting units (excluding the group openings) is within the recommendations made by Law and Lorimer (1989). Our analysis was conducted too soon after harvesting to determine how successful the combination of single-tree selection and group openings will be over the long term in providing adequate oak regeneration on MOFEP sites. Monitoring the regeneration dynamics of all MOFEP treatments will continue in order to measure effects on forest regeneration.

Forest Dynamics

Forest species composition is always changing. Some trees continue to grow while others die and are eventually replaced. Human-caused disturbances such as timber harvesting often create the most striking short-term changes in species composition, but natural disturbances and succession also alter species composition over time. To evaluate some of these changes for the most abundant tree species on MOFEP sites, we compared the growth, ingrowth, and mortality of individual tree species and species groups for trees ≥ 4.5 in. (11 cm) d.b.h. in each treatment and site.

From 1992 to 1998, white oak had the greatest net basal area growth on no-harvest sites and a net basal area increase on three of six sites receiving harvest treatments despite substantial white oak removal (fig. 6). We attribute this greater net growth rate to white oak's initial high abundance, moderate growth rate, high ingrowth rate, and low natural mortality (fig. 6). Because white oak is moderately shade tolerant (Rogers 1990), the steady increase of white oak net growth in no-harvest sites and moderate losses of white oak in harvested sites were expected. Its moderate shade tolerance allows some white oak regeneration to persist in the

forest's partial shade. Once regeneration is established, white oak seedlings can be recruited into larger size classes in natural canopy gaps or in openings created by harvesting. Recruitment of white oaks into the ≥ 4.5 in. (11 cm) diameter class explains the large amount of white oak ingrowth shown in figure 6. Moreover, white oaks are less susceptible to disease or decline than the common red oak species, and they often live longer than red oaks (Hicks 1998, Rogers 1990), explaining the low white oak mortality on all MOFEP sites. Shortly after MOFEP was initiated, Pallardy (1995) predicted that white oak would become more important in the overstory. His prediction was based upon analysis of the first MOFEP inventory data set that showed that white oak was much more abundant in the understory compared to species in the red oak group and shortleaf pine (Pallardy 1995). Data collected on MOFEP thus far support Pallardy's prediction.

Black oak had low to moderate net basal area growth increases on no-harvest sites 1 and 6 but a net loss on no-harvest site 8 (fig. 6). Scarlet oak had modest net basal area growth on all no-harvest sites. Both black oak and scarlet oak had net basal area losses on all sites that received harvest treatments (fig. 6) because of low ingrowth rates, high mortality rates, and substantial harvesting. We expected greater black oak ingrowth than we observed because of its moderate shade tolerance and moderate growth rate (Sander 1990). Even though black oak is considered moderately shade tolerant, black oak seedlings and saplings must not be as shade tolerant as those of white oak or else we would have observed greater black oak ingrowth. We did not anticipate much scarlet oak ingrowth because it is shade intolerant (Johnson 1990); substantial regeneration and recruitment of scarlet oak would typically require a major canopy-removing disturbance.

High mortality of both black oak and scarlet oak was not surprising. Both species are susceptible to oak decline and to *Armillaria mellea* (Bruhn *et al.* 2000). As indicated previously, oak decline is often attributed to *Armillaria* root disease in the Missouri Ozarks (Bruhn *et al.* 2000, Johnson and Law 1989). The abundance of *Armillaria mellea*, the most virulent of the *Armillaria* species documented in the study area, is positively correlated with black oak and scarlet oak abundance on MOFEP sites and is correlated with very gravelly and drought-prone

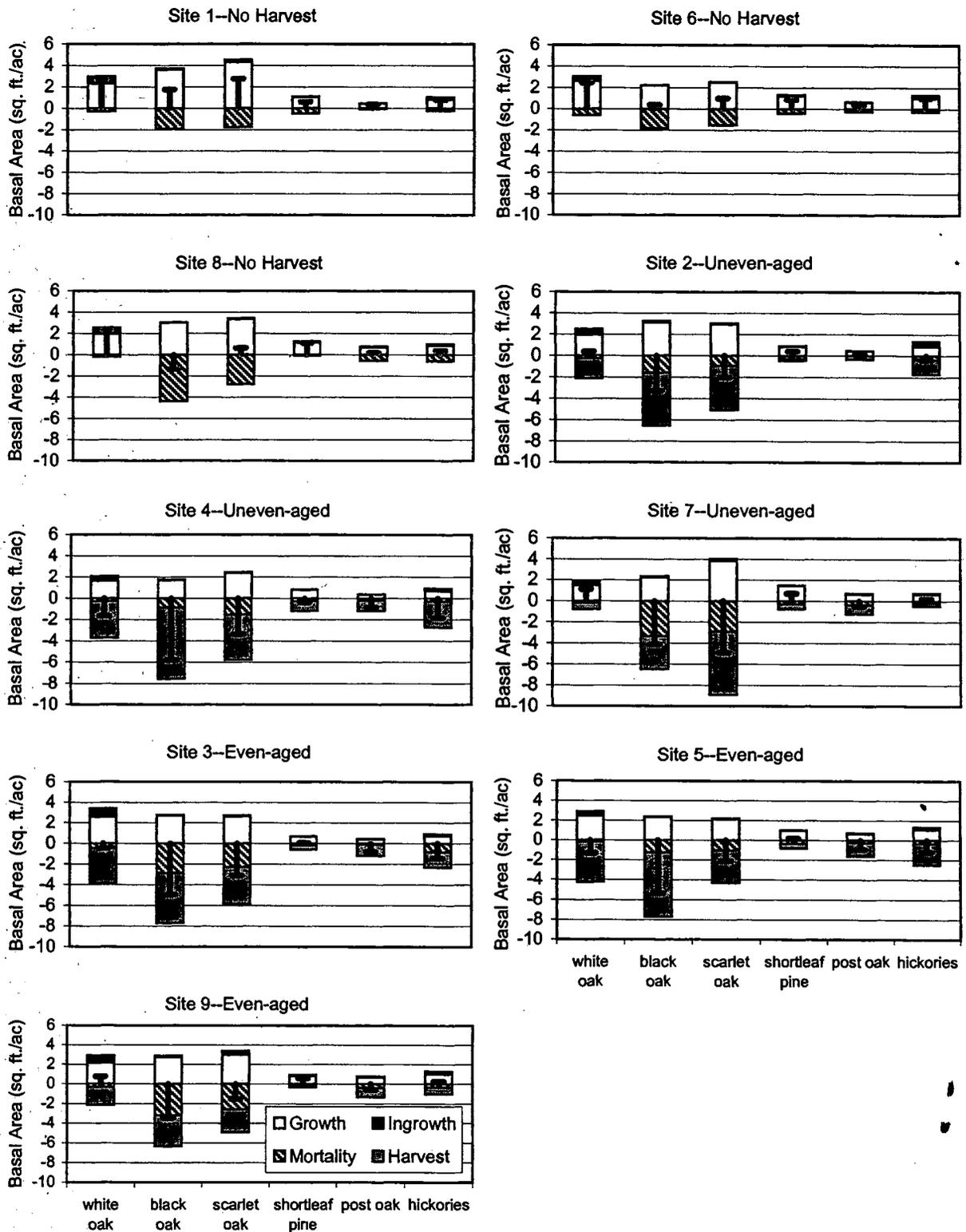


Figure 6.—Growth of initial trees, ingrowth, mortality, and harvest of trees ≥ 4.5 in. (11 cm) d.b.h. for the most abundant trees species. Values show mean basal area change per acre for trees on each site. The line within the bar of each species shows the net change in basal area when mortality and harvest are subtracted from growth and ingrowth. The hickory group includes black, mockernut, and pignut hickory. One ft^2/ac of basal area = $0.2296 \text{ m}^2/\text{ha}$.

SUMMARY

and acidic soils associated with summit, shoulder, and shoulder ridge landform positions and with gravelly hillslope sediments from the Roubidoux and upper Gasconade bedrock formations (Bruhn *et al.* 2000). Soils having these characteristics are much more extensive on MOFEP sites 7 and 8 (Meinert *et al.* 1997), thus explaining the greater black oak and scarlet oak mortality observed on these two sites.

Shortleaf pine had negligible ingrowth and little mortality during the sampling period and maintained a modest, positive net growth on nearly every site (fig. 6). This modest positive net growth of shortleaf pine was also found on harvested sites because relatively few shortleaf pine trees were removed. The hickory group, which includes pignut hickory (*C. glabra* Mill.), mockernut hickory (*C. tomentosa* Nutt.), and black hickory (*C. texana* Buckl.), had modest but positive net growth on no-harvest sites and negligible or modest net basal area decreases on harvested sites (fig. 6).

These findings have implications for MOFEP overstory vegetation composition in the future. On no-harvest sites, we expect white oak to become much more abundant over time because the absence of harvest disturbances will favor the growth of longer lived, more shade-tolerant species such as white oak. Similarly, we also expect white oak to become more abundant on uneven-aged sites because single-tree selection harvesting favors species that are more shade tolerant and because more scarlet oak was harvested on uneven-aged sites. However, we do expect some eventual recruitment of black oak and scarlet oak in uneven-aged group openings. Overstory composition will likely change the least on even-aged sites: clearcutting leaves behind very few residual trees so there is little opportunity to alter species composition except through thinning. Moreover, most of the forest regeneration on even-aged sites appears to be from both white oak group and red oak group sprouts. It is difficult to predict composition changes for the other species because their abundances are so low. However, it appears that shortleaf pine basal area will increase on all treatments because of modest but positive net growth.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, landscape-scale experiment to test effects of even-aged, uneven-aged, and no-harvest forest management practices on the flora and fauna of upland oak ecosystems. Three management treatments have been implemented on the MOFEP sites: (1) even-aged management with harvest by clearcutting and intermediate thinning, (2) uneven-aged management with harvest by single-tree selection and group selection, and (3) no harvest.

On even-aged treatment sites, approximately 320 ac (130 ha) (11%) were clearcut and 411 ac (166 ha) (15%) were thinned. Stands that were clearcut averaged 13 ac (5 ha) in size, and stands that were thinned on the even-aged sites averaged 11 ac (4 ha). In uneven-aged treatment sites, 2,124 ac (860 ha) (57%) were harvested. On uneven-aged sites, stands were grouped into cutting units that averaged 21 ac (9 ha) in size. Clearcutting removed more trees per cutting unit than thinning or single-tree selection, although a greater total merchantable volume was cut on uneven-aged sites.

Black oak and scarlet oak in combination made up approximately 60 percent of the harvested basal area; white oak and post oak accounted for an additional 20 to 30 percent of the harvest. In the even-aged treatment, the harvested basal areas of scarlet and white oak were nearly equal. In the uneven-aged treatment, however, harvest of scarlet oak was proportionately greater than that of white oak.

On both even-aged and uneven-aged sites for all species combined, there were decreases in trees per acre and in basal area per acre. Changes that differed significantly from those of the no-harvest control were usually detected for the larger size classes of trees. One exception was basal area, which decreased significantly in all size classes on harvested sites. The average canopy cover of all sites decreased, and decreased significantly more on harvested sites. Changes in numbers, diameters, and basal areas for the most abundant species were similar to those for all species combined.



Abundance in reproduction-sized trees did not change consistently as a result of treatments. We found that the greatest changes in reproduction occurred with stump sprouts. Clearcuts had the greatest number of sprouts, followed by areas harvested by a combination of single-tree and group selection. Some sprouting occurred in thinned and selectively harvested stands. Few sprouts were found in non-harvested stands.

From 1992 to 1998, white oak had the greatest net basal area growth on no-harvest sites. Black oak had low to modest net basal area growth increases on no-harvest sites 1 and 6 but a net loss on no-harvest site 8. Scarlet oak had modest net basal area growth on no-harvest sites. Both black oak and scarlet oak had net basal area losses on all sites that received harvest treatments because of a low ingrowth rate, a high mortality rate, and substantial harvesting. Shortleaf pine had negligible ingrowth during the sampling period, but maintained a modest, positive net growth, even on sites that received harvest treatments because relatively few shortleaf pines were removed. Among the other most abundant tree species, there was little net growth during the sampling period on all sites regardless of harvest treatment.

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Stump Sprouting Potential of Oaks in Missouri Ozark Forests Managed by Even- and Uneven-aged Silviculture

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Abstract.—We evaluated the stump sprouting potential of white oak, black oak, and scarlet oak in relation to tree age, stem diameter, and overstory density in Ozark forests managed by even-aged and uneven-aged silvicultural systems. In eastern North America, few studies have evaluated the influence of a forest canopy on the potential of hardwood stumps to sprout and contribute to regeneration. The Missouri Ozark Forest Ecosystem Project (MOFEP) gave us an opportunity to study oak stump sprouting in relation to tree characteristics and residual overstory density resulting from various regeneration methods.

One growing season after the clearcut, single-tree, and group selection harvests implemented on MOFEP sites in 1996, we measured sprout growth on 701 stumps of white oak (*Quercus alba* L.), scarlet oak (*Q. coccinea* Muenchh.), and black oak (*Q. velutina* Lam.). Stumps were selected from plots (primarily on Ecological Landtypes 17 and 18) within uneven- and even-aged compartments. Stumps averaged 9.3 in. (23.6 cm) in diameter (range 1.7 to 33.3 in. [4.3 to 84.5 cm]) and 61 years in age (range 38 to 169 years). By the end of the first growing season after harvest, 78 percent of the oak stumps had produced a live sprout. Stump sprout frequency was high for small diameter and young trees, regardless of species. However, sprouting probability declined more rapidly with increasing stump diameter or age for white oak than it did for scarlet oak and black oak. Scarlet oak and black oak produced more sprouts (mean = 12) per stump than white oak (mean = 8). Overstory density (e.g., clearcut vs. single-tree gaps) had no detectable effect on oak stump sprouting probability or on the number of sprouts per stump. However, increasing overstory density reduced the height of the tallest stem in each stump sprout clump. The tallest stem within a sprout clump averaged 2.8 ft (0.85 m) in the single-tree selection treatment compared to 4.0 ft (1.2 m) in the clearcut treatment. Sprouting potential, height of the dominant sprout, and sprout clump density decreased with increasing stump diameter and tree age for all species regardless of overstory density.

In Missouri Ozark forest ecosystems, the composition and structure of the overstory and

advance reproduction present before regeneration disturbances largely determines the composition of the future forest (Dey *et al.* 1996). Large advance reproduction and stump sprouts are the most competitive sources of oak reproduction. Their development is greatest where light intensities exceed 50 percent of full sunlight (Gottschalk 1994) because most oaks are intermediate in shade tolerance (e.g., white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), and northern red oak (*Q. rubra* L.)) or are shade intolerant (e.g., post oak (*Q. stellata* Wangenh.))

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and scarlet oak (*Q. coccinea* Muenchh.). Therefore, regeneration methods such as clearcutting and shelterwood harvesting have been recommended to managers of oak forests, and methods such as single-tree selection have not been considered appropriate for sustainable management of oak ecosystems (Marquis and Johnson 1989, Sander and Clark 1971, Sander and Graney 1993). Ironically, some interest groups are advocating uneven-aged silvicultural systems (e.g., single-tree selection) to preserve forest aesthetics and for other reasons. Consequently, Federal and State forest managers are now applying regeneration methods to create uneven-aged forests in the Ozarks, despite the uncertainty that these methods can sustain desired forest composition and conditions. Forest managers and scientists do not fully understand the dynamics of oak regeneration and recruitment that result from uneven-aged harvest methods, especially when they are applied to mature, fully stocked forests in the Ozarks.

Sustainable recruitment of oak into the overstory in stands managed by uneven-aged silvicultural systems depends on sufficient numbers of large oak reproduction in the understory (Larsen *et al.* 1999). This reproduction can arise from advance reproduction as seedling sprouts or from stump sprouts created by harvesting. Foresters must manage stand density and structure carefully because understory light levels, which are directly related to the forest canopy, affect development of oak reproduction.

Long-term survival of oak advance reproduction (i.e., seedling sprouts) is low beneath closed-canopied forests, especially on productive sites where subcanopies of shade tolerant species reduce understory light levels to as low as 1 percent of full sunlight, far below the light compensation point of oaks (Dey and Parker 1996, Hanson *et al.* 1987, Loftis 1990). Forest managers and scientists have long recognized the important relationship between the occurrence of abundant large oak advance reproduction as seedling sprouts and overstory density (Carvell and Tryon 1961). More recently, Larsen *et al.* (1997) found in Ozark forests that the chance of having abundant large oak advance reproduction was improved when overstory density was maintained at relatively low stocking (i.e., 58 percent stocking according to Gingrich 1967). In contrast, there is less known about the persistence and competitiveness of

oak stump sprouts that develop in single-tree gaps and in small group openings. Most studies of oak stump sprouting have dealt with how sprouts develop in clearcuts, or large openings (Cobb *et al.* 1985, Johnson 1977, Lynch and Bassett 1987, Ross *et al.* 1986, Weigel and Johnson 1998, Wendel 1975).

The purpose of this study was to determine the effect of overstory density, forest canopy crown cover, and individual tree characteristics on the sprouting potential and growth performance of sprouts arising from oak stems cut by chainsaw in a timber harvest operation. We present an assessment of sprouting capacity and growth performance for white oak, black oak, and scarlet oak in Missouri Ozark forests harvested by the clearcut, group selection, or single-tree selection regeneration method. Longer term monitoring will provide valuable insight into the persistence of stump sprouts growing under a partial forest canopy and their recruitment potential in small canopy gaps.

METHODS

We monitored stump sprouting of oak trees in stands harvested by the clearcut, group selection, or single-tree selection regeneration method as part of the Missouri Ozark Forest Ecosystem Project (MOFEP). MOFEP is described in Brookshire and Shifley (1997), Shifley and Brookshire (2000), and other papers in this volume. Timber harvesting was completed in the fall of 1996 and was immediately followed by slashing (i.e., cutting) of unmerchantable stems in the winter of 1996-1997. A total of 70 vegetation plots (0.5-ac [0.2 ha]) were used to sample oak stumps in stands harvested by clearcutting (21 plots from sites 3, 5, and 9) and in stands harvested by uneven-aged methods (i.e., group selection and single-tree selection) (49 plots from sites 2, 4, and 7) on Ecological Landtypes 17 and 18 (Brookshire *et al.* 1997). All plots that were clearcut were sampled, and approximately 50 percent of the more accessible uneven-aged management plots were sampled. On each vegetation plot, oak stumps were randomly selected and spatially referenced to a plot or subplot center. At each plot or subplot center, no more than 5 stumps were chosen for each species. A total of 701 stumps were selected to represent the range of stump diameters present on MOFEP harvest units (table 1).

Table 1.—*Distribution of oak stumps by species and harvest treatment sampled on Missouri Ozark Forest Ecosystem Project sites*

Species	Clearcut	Group selection	Single-tree selection	Total
White oak	155	97	124	376
Scarlet oak	67	26	55	148
Black oak	71	46	60	177
Total	293	169	239	701

During the winter of 1996-1997, before sprouting occurred, a 0.5- to 2-in. (1 to 5 cm)-thick disc was cut from the top of each of the 701 oak stumps to determine tree age. Stumps were tagged, the diameter of each stump was measured, and stumps were referenced to plot or subplot center by azimuth and distance. Stumps averaged 9.3 in. (23.6 cm) in diameter (range 1.7 to 33.3 in. [4.3 to 84.6 cm]) and 61 years in age (range 38 to 169 years). In the spring of 1998, one growing season after harvest, stumps were revisited to count the number of sprouts and measure the height of the tallest sprout.

In the summer of 1995 (before timber harvesting) and again in the summer of 1997 (after logging and slashing operations), ocular estimates of forest canopy crown cover were made on each 0.5-ac (0.2-ha) vegetation plot according to procedures outlined in Grabner (2000). Crown cover was measured above each ground

flora quadrat and above each plot and subplot center, resulting in a total of 21 observations per vegetation plot. These were averaged to give an estimate of crown cover for each 0.5-ac (0.2-ha) plot in which stump sprouts were monitored. In 1998, basal area and trees per acre for trees \geq 4.5 in. (11.4 cm) d.b.h. were determined for each 0.5-ac (0.2-ha) circular permanent vegetation plot according to procedures outlined by Jensen (2000). Pre- and post-harvest stand conditions are summarized in table 2.

The probability of an oak stump producing at least one live sprout at the end of the first growing season was modeled using logistic regression (SAS Institute Inc. 1995). Independent variables considered included stump diameter, tree age, species, and measures of stand density and forest crown cover. For a subset of stumps that sprouted, regression analysis (SAS Institute Inc. 1991) was used to evaluate relationships between the response

Table 2.—*Average pre-harvest and post-harvest stand density and crown cover^a by harvest treatments for the Missouri Ozark Forest Ecosystem Project plots used in this study*

Harvest treatment	Basal area ^b Feet ² /acre	Trees per acre ^b	Crown cover Percent
Pre-harvest			
Even-aged	84 \pm 6	149 \pm 17	85 \pm 2
Uneven-aged	85 \pm 1	157 \pm 18	84 \pm 4
Post-harvest			
Even-aged	7 \pm 6	9 \pm 9	3 \pm 4
Uneven-aged	62 \pm 16	122 \pm 39	58 \pm 17

^a The pre-harvest inventory was conducted in 1995. Post-harvest crown cover was measured in 1997, and stand density was determined in 1998.

^b 1 ft²/ac = 0.2296 m²/ha; 1 tree/ac = 2.47 trees/ha.

variables (number of sprouts and height of the tallest sprout) and an array of independent tree and stand variables similar to those used in the logistic regression analysis.

SD = stump diameter (inches),
 AGE = tree age at stump height (years),
 OAK1 = 0 for white oak and black oak,
 and 1 for scarlet oak, and
 OAK2 = 0 for white oak and scarlet oak,
 and 1 for black oak.

RESULTS

Survival

By the end of the first growing season after harvest, 78 percent of the oak stumps had produced at least one live sprout. One of the best models for predicting stump sprouting probability was:

$$P = [1 + \exp \{- (5.9991 - 0.2413SD - 0.0475AGE + 1.527OAK1 + 1.4122OAK2)\}]^{-1} \quad (1)$$

where: P = probability of producing at least one live sprout at the end of the first growing season,

Other models (table 3) were significant (p-values < 0.001) and provided good fits to the data according to the Hosmer and Lemeshow (2000) test. Including a dummy variable (OAK1 and OAK2) for species resulted in the lowest Akaike's information criterion (AIC_c) (271 for the model in Equation (1)), which was adjusted for small sample sizes according to Burnham and Anderson (1998). In the first set of nested models (i.e., the upper group of models) in table 3, adding species to the model substantially improved model performance as indicated by ΔAIC_c. Models that have an AIC_c that is 7 to 10 units lower than any other model within a family of nested models are considered superior

Table 3.—Logistic regression models and diagnostic statistics for the probability that an oak stump will produce at least one live sprout at the end of the first growing season after being harvested by either clearcut, group selection, or single-tree selection harvesting

MODELS ^a (includes group opening data)	AIC _c	ΔAIC _c	Fit ^b
SD ^c	471	200	0.28
AGE ^c	292	21	0.94
SD ^c +AGE ^c	284	13	0.64
SD+AGE ^c +(SD x AGE)	286	15	0.59
SD ^c +OAK1 ^c +OAK2 ^c	441	170	0.48
AGE ^c +OAK1+OAK2	290	19	0.55
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c	271	0	0.41
SD+AGE+(SD x AGE)+OAK1 ^c +OAK2 ^c	273	2	0.76
MODELS (excludes group opening data)			
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c	271	0	0.69
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c +CC	273	2	0.75
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c +BA	273	2	0.71
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c +TPA	273	2	0.79
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c +BA+TPA	275	4	0.22
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c +BA+TPA+CC	276	5	0.16
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c +BA+TPA+(BA x TPA)	277	6	0.07
SD ^c +AGE ^c +OAK1 ^c +OAK2 ^c +BA+TPA+CC+(BA x TPA)	278	7	0.25

^a Where models are of the form: $P = [1 + \exp\{- (\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n)\}]^{-1}$ and SD = stump diameter (inches); AGE = tree age at stump height (years); OAK1 = 0 for white and black oak, and 1 for scarlet oak; OAK2 = 0 for white oak and scarlet oak, and 1 for black oak; TPA = trees per acre; BA = basal area (feet²/acre); and CC = crown cover of forest canopy (%).

^b Probability value for Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000).

^c Indicates significance of parameter (P ≤ 0.05) based on Wald χ² statistic.



(Burnham and Anderson 1998). Both black oak and scarlet oak had higher sprouting probabilities in year 1 than white oak for a given stump diameter and tree age (fig. 1). For all oak species, sprouting probabilities decreased with increasing stump diameter and age. As stump diameter and age increased, sprouting probabilities dropped more rapidly for white oak than for black oak or scarlet oak.

We evaluated the significance of stand density and crown cover on sprouting probability with the models presented in table 3. Inclusion of stand density or crown cover did not significantly improve model goodness of fit, and parameters for stand density and crown cover were each judged insignificant based on the Wald χ^2 statistic, despite overall model significance. Again the model with the lowest AIC_c was Equation (1). It does not appear that a partial forest canopy affects stump sprouting and first-year sprout survival.

Height

Increasing overstory density significantly reduced height of the tallest sprout regardless of oak species (fig. 2). Stump sprouts in clearcuts, which had an average residual basal area of 7 ft²/ac (1.6 m²/ha), were about 1 foot taller (30 cm) on average than sprouts under a single-tree selection canopy, which had an average residual basal area of 62 ft²/ac (14.2 m²/ha). In clearcuts, white oak sprouts averaged 3.6 ft (1.1 m), scarlet oak 4.5 ft (1.4 m), and black oak 4.3 ft (1.3 m). Stand density measures (i.e., basal area and trees per acre and crown cover) were highly correlated with each other (Pearson correlation coefficients were consistently about 0.91 with p-values of <0.001). Models that contained combinations of basal area, trees per acre, and crown cover had serious multicollinearity problems as indicated by analysis of variance inflation factors, eigenvalues, condition index, and proportion of variance diagnostics (Neter *et al.* 1985, SAS Institute Inc. 1991). In addition, parameter estimates for these variables were individually non-significant where the overall model was highly significant. Consequently, we present three height models, each containing

only one measure of stand density or overstory crown cover, that express the relationship between sprout height, and tree and stand characteristics (table 4).

Black oak and scarlet oak sprouts were significantly taller (about 0.7 and 1.0 ft taller [0.2 and 0.3 m], respectively, on average) than those of white oak for given tree diameter, age, and stand condition (table 4). Both tree diameter and age were negatively related to height of the tallest sprout for all oak species (fig. 2).

Sprout Numbers

Including measures of stand density and crown cover did not improve our ability to explain variation in sprout clump density (based on adjusted R²), nor were parameter estimates of these variables significant. Sprout clump density was similar in clearcuts and single-tree selection harvest units. However, tree age and diameter were negatively related to the number of sprouts per stump after the first year regardless of oak species (fig. 3). Numbers of sprouts per stump were significantly different among the red and white oak groups (scarlet oak = black oak > white oak), and the following model was selected as the best fit (F = 8.14, p-value = <0.0001, R²_{adj} = 0.10):

$$S = 17.09666 + 3.8806OAK1 + 3.93426OAK2 - 0.03101SD - 0.15368AGE \quad (2)$$

where: S = number of sprouts per stump at the end of the first growing season,
SD = stump diameter (inches),
AGE = tree age at stump height (years),
OAK1 = 0 for white and black oak, and 1 for scarlet oak, and
OAK2 = 0 for white oak and scarlet oak, and 1 for black oak.

Black oak and scarlet oak stumps each produced about 4 more sprouts per stump than white oaks across the range of stump diameters and tree ages observed in this study. On average, black oak and scarlet oak stumps each produced 12 sprouts per stump compared to 8 sprouts for white oak.

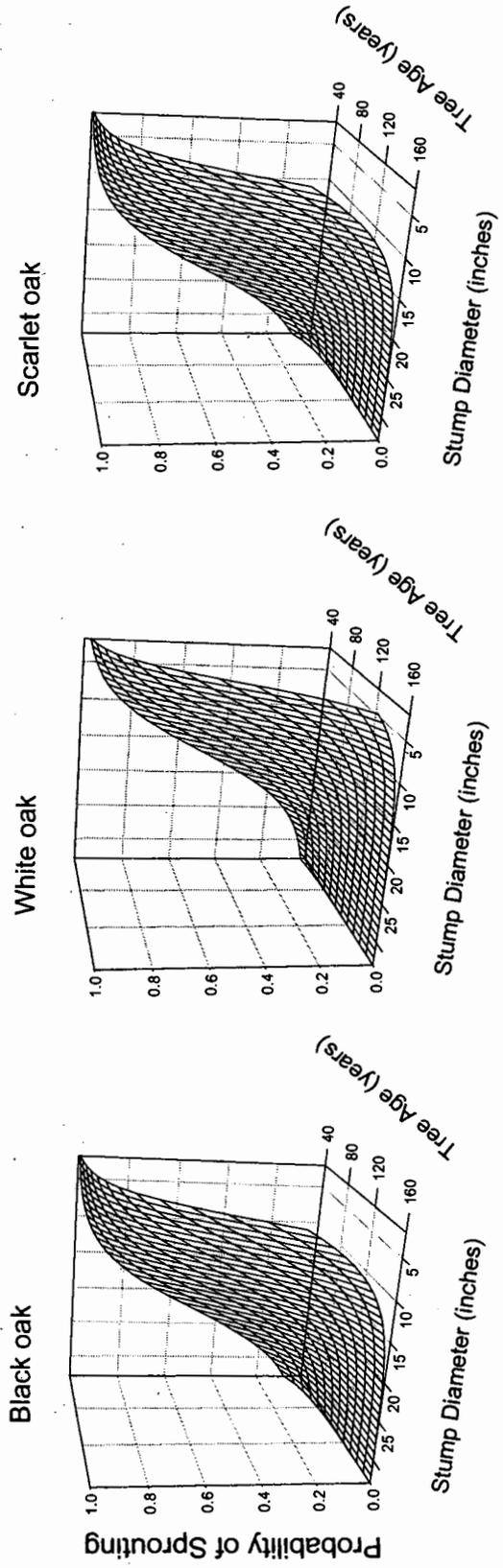
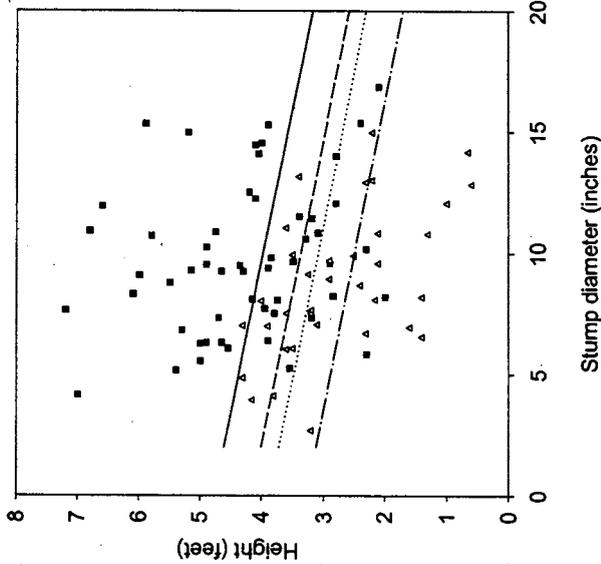


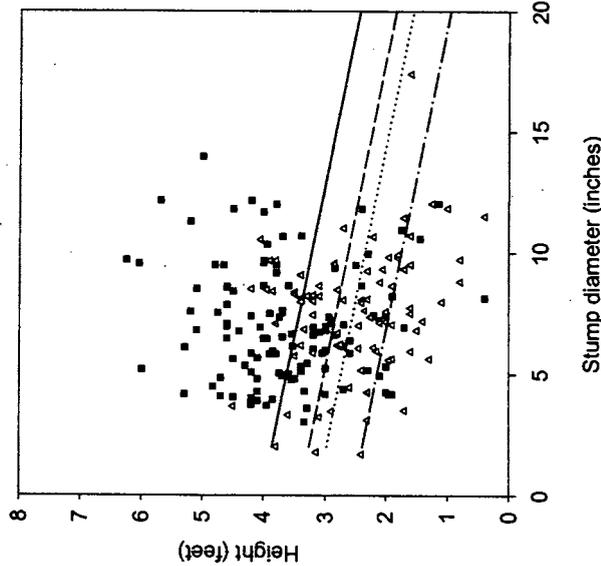
Figure 1.—Probability of producing at least one live sprout at the end of the first growing season in relation to stump diameter and tree age for black oak, white oak, and scarlet oak. Plotted lines are based on Equation (1). 1 inch = 2.54 cm.



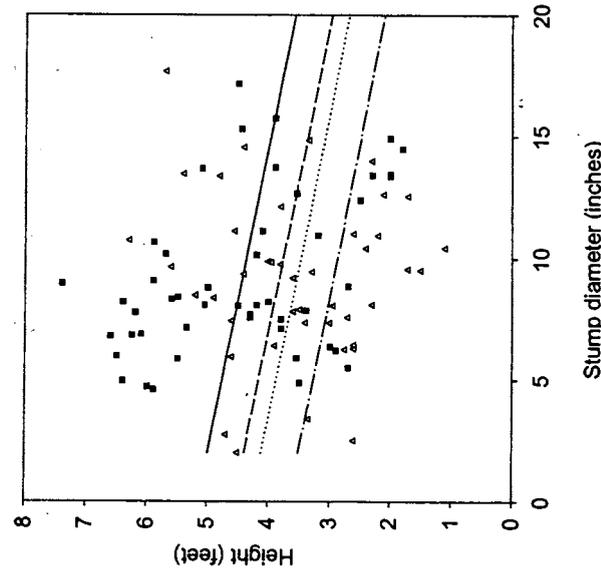
Black oak



White oak



Scarlet oak



- Basal Area = 7 ft²/ac; Age = 60 years
- Basal Area = 62 ft²/ac; Age = 60 years
- Observed Sprouts in Clearcuts
- ▲ Observed Sprouts in Selection Cuts
- - - Basal Area = 7 ft²/ac; Age = 100 years
- · - Basal Area = 62 ft²/ac; Age = 100 years

Figure 2.—First-year height of the dominant stump sprout for black oak, white oak, and scarlet oak in relation to stump diameter, tree age, and overstory density. Plotted lines are based on the equations presented in table 4. 1 inch = 2.54 cm; 1 foot = 0.3048 m; 1 ft²/ac = 0.2296 m²/ha.

Table 4.—Regression models of first-year height of tallest sprout in relation to tree species, diameter and age, and stand density

Model	Regression model ^a	Overall model F-value (p-value)
1	$HT = 5.12483 + 1.08725OAK1 + 0.73658OAK2 - 0.0741SD - 0.01751AGE - 0.00771TPA$	20.16 (<0.001)
2	$HT = 5.03427 + 1.13404OAK1 + 0.74591OAK2 - 0.07888SD - 0.015AGE - 0.01605BA$	19.65 (<0.001) [*]
3	$HT = 5.13286 + 1.08193OAK1 + 0.73915OAK2 - 0.07647SD - 0.01704AGE - 0.01795CC$	21.53 (<0.001)

^a Where:

HT = height (feet) of the tallest sprout at the end of the first growing season,
 SD = stump diameter (inches),
 AGE = tree age at stump height (years),
 OAK1 = 0 for white and black oak, and 1 for scarlet oak,
 OAK2 = 0 for white oak and scarlet oak, and 1 for black oak,
 TPA = trees per acre,
 BA = basal area (feet²/acre), and
 CC = crown cover of forest canopy (%).

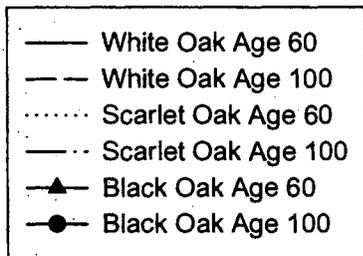
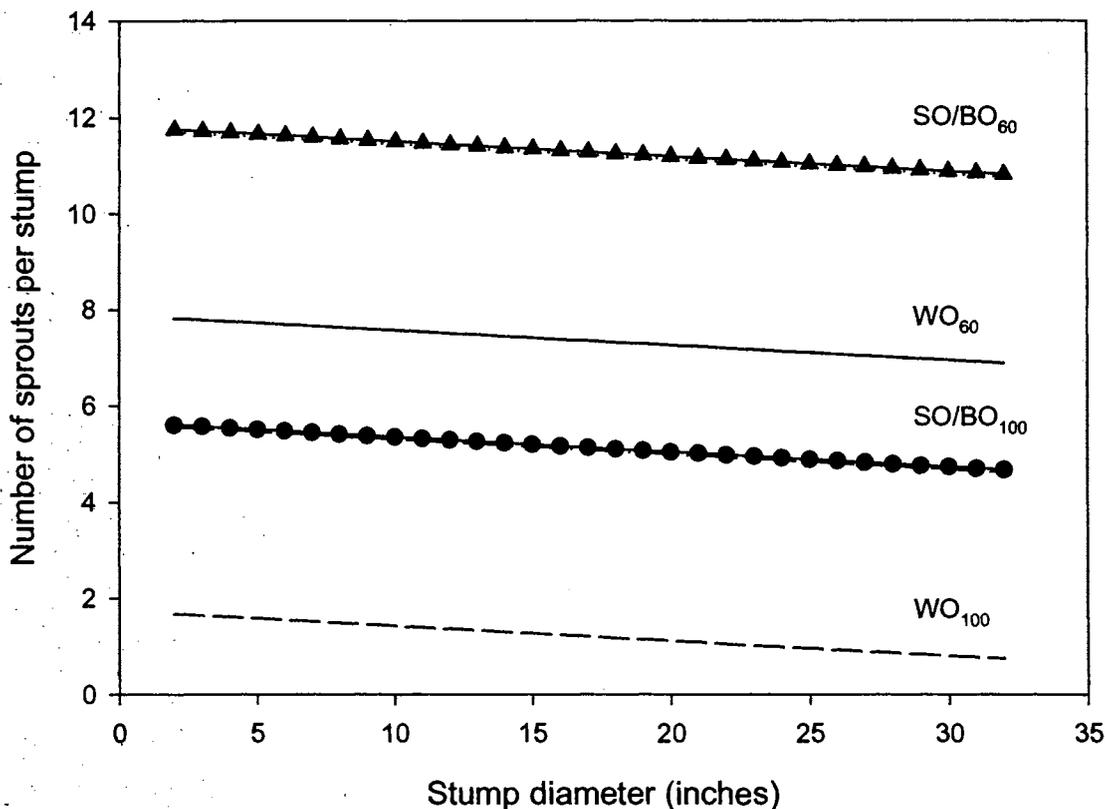


Figure 3.—Predicted sprout clump density 1 year after harvesting by stump diameter and for selected ages of scarlet oak, black oak, and white oak. Plots are based on Equation (2). 1 inch = 2.54 cm.



DISCUSSION

For all oak species in our study, sprouting probability decreased with increasing diameter and age. Similarly, declines in sprouting frequency with increasing diameter and age have been reported for black oak, scarlet oak, white oak, and northern red oak (Johnson 1975, 1977; Lynch and Bassett 1987; Weigel and Johnson 1998), and pin oak (*Quercus palustris* Muenchh.), cherrybark oak (*Q. falcata* var. *pagodifolia* Ell.), and willow oak (*Q. phellos* L.) (Kabrick and Anderson 2000). These studies sampled oak stumps over a wide range of diameters and ages. In some research studies, oak sprouting frequencies were high and there were low correlations between tree age and (1) sprouting frequency, (2) height and diameter of the dominant sprout, and (3) number of sprouts per stump (Gardiner and Helmig 1997, Kabrick and Anderson 2000, Lynch and Bassett 1987, Wendel 1975). These results usually occurred when the sample oaks were relatively young and uniformly small in diameter (e.g., 28-year-old water oak (*Quercus nigra* L.)).

The sprouting probabilities of black oak and scarlet oak were similar, and both species were more likely to sprout than white oaks of similar size and age. Similarly, Johnson (1977) observed that scarlet oak and black oak had greater sprouting probabilities than white oak after 1 year in Missouri Ozark clearcuts. We found that black oak and scarlet oak exhibited greater sprouting probabilities at larger diameters and greater ages than white oak (fig. 1). Similar species differences in sprouting probability were also observed by Weigel and Johnson (1998) in southern Indiana clearcuts. They also found that sprouting probability decreased more rapidly in white oak than it did in black oak, scarlet oak, and northern red oak as stem diameter and age increased.

Overstory density, as measured by basal area, stems per acre, or forest canopy crown cover, did not significantly affect the probability of producing at least one live sprout the first year after harvesting for white oak, black oak, or scarlet oak. Stumps in clearcuts were as likely to sprout as trees of similar sizes and ages in single-tree selection or group selection openings. However, increasing overstory density and canopy cover significantly reduced the height of the tallest sprout by the end of the first growing

season in all oak species. In contrast, a partial forest overstory did not affect the initial sprout density.

Gardiner and Helmig (1997) studied the development of water oak stump sprouts in a 28-year-old plantation that had been thinned from below to 40 percent or 60 percent basal area. They found that overstory density was not related to the probability of sprouting because all stumps produced sprouts in this young oak stand. In a mature bottomland oak forest in southeast Missouri, Kabrick and Anderson (2000) reported that stumps of pin oak, cherrybark oak, and willow oak in single-tree gaps sprouted as readily as stumps of upland oaks in clearcuts (Johnson 1977, Weigel and Johnson 1998). Their sprouting frequencies were also comparable to open-grown stump sprouts in this study.

In our study, scarlet oak produced the tallest dominant sprouts at the end of the first year, followed closely by black oak. Sprouts of these species were significantly taller than those of white oak (fig. 2). Sprout heights in clearcuts were slightly higher than those reported by Johnson (1977) for upland oaks in the Missouri Ozarks and by Weigel and Johnson (1998) for oaks in southern Indiana. Stump sprouts under a single-tree selection canopy were slightly taller than 1-year sprouts of pin oak, willow oak, and cherrybark oak growing in single-tree gaps in a bottomland forest in southeast Missouri (Kabrick and Anderson 2000).

Black oak and scarlet oak stump sprout clump densities were similar (mean = 12 sprouts per stump), and both species produced more sprouts per stump than white oak (mean = 8 sprouts per stump) (fig. 3). In southeast Missouri, pin oak, cherrybark oak, and willow oak averaged 9, 16, and 20 sprouts per stump, respectively, for stumps in single-tree gaps (Kabrick and Anderson 2000). Johnson (1977) reported sprout clump densities for upland white oak and black oak (mean = 8 sprouts per stump) and scarlet oak (mean = 12 sprouts per stump) in Missouri Ozark clearcuts that were similar to those in our study.

Even though stand density and canopy cover did not affect initial stump sprouting probability or sprout density, they may affect stump sprout long-term survival and recruitment into the

overstory. Oak advance reproduction is more likely to accumulate and grow large when understory light intensities are 50 percent or more of full sunlight (Gottschalk 1994). Single-tree selection harvest in mature, closed-canopied hardwood forests may not appreciably increase light levels at the forest floor (Fischer 1979, Marquis 1988). Thus, low light levels may limit oak advance reproduction, including stump and seedling sprouts, under a moderate to heavy overstory. Overstory density is important for developing large oak advance reproduction in Missouri Ozark (Larsen *et al.* 1997) and Lower Peninsula of Michigan (Johnson 1992) oak ecosystems, where the probability of having large oak reproduction was greatest at stocking levels between 30 and 60 percent (according to Gingrich 1967). Larsen *et al.* (1999) recommended maintaining overstory density at 63 ft²/ac (14.5 m²/ha) on average over a 20-year cutting cycle to favor oak recruitment in forests managed to produce an uneven-aged structure in the Missouri Ozarks. However, the effect of an overstory on stump sprout potential in oaks is not well known and few studies address this situation. Most recently, Gardiner and Helmig (1997) and Kabrick and Anderson (2000) studied stump sprouting under a bottomland overstory. These studies were too short-term to provide any indication of the ability of stump sprouts to survive and develop under a forest overstory. The overstory in our single-tree selection stands (mean basal area = 62 ft²/ac [14.2 m²/ha]) did reduce the height of the tallest stump sprout. The long-term survival and recruitment success of these sprouts remains unknown.

SUMMARY

Oak stump sprouts are important in obtaining adequate oak regeneration. In young stands, stump sprouting may account for most of the reproduction. In older stands, stump sprouts can supplement advance reproduction populations to ensure the adequacy of oak in the new forest. Managers need to be able to predict the contribution of stump sprouts to the overall population of oak reproduction to judge whether (1) reproduction is adequate, (2) artificial regeneration by planting or direct seeding is needed to supplement natural reproduction, (3) competition control is needed to maintain oak in a free-to-grow state, or (4) harvesting should be delayed to give time for the development of large advance reproduction.

The contribution of oak stump sprouts to oak regeneration potential is predictable, and estimates based on tree, stand and site characteristics can be made before harvesting. In this study, we demonstrated that stem diameter and age are primary factors that determine the probability of sprouting, density of sprouts, and height growth of the dominant sprout for individual trees. We also noted that sprouting potential and sprout growth vary by oak species.

Overstory density is important in determining long-term survival of oak stump sprouts and success of oak recruitment into the overstory. Further monitoring of stump sprouts in this study will provide valuable information on their contribution to oak regeneration in stands managed by uneven-aged management, and it will provide a quantitative basis for assessing the fate of oak stump sprouts developing under a partial forest overstory. Managers can use these results to help determine when uneven-aged management is appropriate and to manipulate stand stocking to promote oak reproduction and recruitment.

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Tree Cavity Estimation and Verification in the Missouri Ozarks

Randy G. Jensen¹, John M. Kabrick², and Eric K. Zenner³

Abstract.—Missouri forest management guidelines require that cavity trees and snags be provided for wildlife. Missouri Ozark Forest Ecosystem Project (MOFEP) timber inventories provided opportunities to determine if cavity tree and snag densities in a mature second-growth oak-hickory-pine forest meet forest management guidelines, to evaluate the effects of the first-entry harvesting on cavity tree densities in even-aged, uneven-aged, and no-harvest management systems, and to determine if cavity abundance differed among tree species, tree diameter, hole diameter, and location on the tree. We examined 54,452 live trees and snags during two pre-harvest data collection periods and during a third post-harvest data collection period. Pre-harvest cavity tree and snag densities were near or above optimum recommendations specified in the management guidelines. After timber harvests, cavity tree densities were above optimum recommendations in even-aged and no-harvest sites and slightly below optimum recommendations on uneven-aged sites. Snags were well above optimum recommendations on no-harvest and uneven-aged sites and only slightly below optimum on even-aged sites after timber harvests. Blackgum (20%) had the highest occurrence of tree cavities and shortleaf pine (1%) had the lowest, compared to oaks (2-10%) and hickories (7-11%). Basal cavities were the most abundant cavities overall (44%), particularly in trees <18 in. (46 cm) and >26 in. (66 cm) diameter at breast height (d.b.h.). For all tree species, larger diameter classes had a higher proportion of trees with cavities.

A second study was conducted to verify the accuracy of cavity estimation procedures and to investigate the reliability of general survey cavity estimates. We conducted an intensive cavity search and inventory in twenty-four, 0.5-ac (0.2 ha) vegetation plots before and after clearcut harvesting. In each plot, approximately 75 trees \geq 4.5 in. (11 cm) d.b.h. were intensively examined for tree cavities and potential tree cavities during the winter of 1995-1996. During the winter of 1996-1997, following clearcutting, we relocated trees thought to have cavities or potential cavities and dissected them with a chain saw for cavity verification and measurement. Overall, our intensive search yielded twice as many cavity trees as found during the timber inventory. However, only 55 percent of openings initially judged to lead to a tree cavity actually did. Conversely, 18 percent of openings thought to be potential cavities were found to be cavities. Many of the tree cavities would not be suitable for many wildlife species that use cavities. Only 13 percent of the estimated cavities and 23 percent of the actual cavities fit the criteria of having a hole at least 1 in. (2.5 cm) diameter, 10 ft (3 m) or more above ground, and with a 2x2x4 in. (5x5x10 cm) cavity. More information on the cavity characteristics, including hole size, tree height, tree diameter, and internal dimensions, required by different wildlife species is needed to aid managers in selecting (retaining) the cavity trees most beneficial for wildlife species.

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Snags and tree cavities provide important habitats for at least 89 species of wildlife in Missouri (MDC 1985). Snags provide habitat, food, and singing and feeding perches for wildlife (MDC 1986b). Cavities in live trees and snags provide escape cover, thermal protection, rearing areas for young, and food storage locations for many mammals, birds, reptiles, and amphibians (MDC 1985, 1986b). In Missouri forest habitats, at least 10 species are primary cavity excavators, meaning they construct cavities in trees; at least 22 species are secondary cavity users that use existing cavities (Hardin and Evans 1977, MDC 1985). Twenty-two percent of Missouri's bird species are cavity nesters, of which 60 percent declined in populations from 1966 to 1994 (Wilson 1996). Because so many species rely on snags and tree cavities to meet their basic life requirements, management activities that affect snag and cavity tree abundance can have a direct impact on their populations.

The Missouri Ozark Forest Ecosystem Project (MOFEP) was initiated in 1989 to document the effects of even-aged, uneven-aged, and no-harvest forest management practices on the ecology of the oak-hickory-pine forest of the southeast Missouri Ozarks (Brookshire and Hauser 1993, Brookshire *et al.* 1997, Kurzejeski *et al.* 1993). MOFEP was designed to be a long-term study at a landscape scale looking at many ecological attributes that traditionally have not received much attention. One such study is determining the abundance and size of cavity trees and snags and the effect of forest management on their distributions.

Different silvicultural management systems may have different effects on snag and cavity abundance at the site scale. For example, because even-aged intermediate thinnings and uneven-aged management focus on the harvest of single trees or groups of trees, managers examine each tree more closely than with clearcutting in even-aged management. Thus, managers have a greater chance of detecting, and more flexibility in controlling, the number and distribution of snags and cavity trees with uneven-aged management compared to clearcutting in even-aged management. With even-aged management, where clearcutting is used for tree regeneration, a smaller proportion of the site (approximately 10%) is harvested during each re-entry and very few trees are left behind, including snag and cavity trees. This

means that there are more opportunities to decide whether to leave or harvest trees containing cavities suitable for wildlife during intermediate thinnings or selection cuts, even though cavity trees may be considered inferior for timber production. The MOFEP cavity and snag study is documenting changes in cavity tree and snag densities and characteristics with even-aged, uneven-aged, and no-harvest management.

The objectives of this paper were to 1) document the density of tree cavities and snags on MOFEP sites both before and after first-entry harvesting in even-aged, uneven-aged, and no-harvest sites and compare these to the Forest Land Management Guidelines for Missouri; 2) report trends in the pre-treatment cavity data with regard to cavity tree species, tree diameter, hole diameter, and hole height on the tree; 3) verify the reliability of tree cavity estimates by dissecting cavity trees; and 4) discuss implications of cavity use by wildlife. In this paper, "holes" refer to openings in tree boles or branches, "cavities" refer to the hollow within tree boles or branches with an opening to the tree exterior, and "dens" refer to cavities that are being used by wildlife species.

METHODS

The MOFEP study design is described in detail by Brookshire *et al.* (1997), Sheriff and He (1997), and Sheriff (this proceedings). Nine study sites (compartments), ranging in size from 772 ac (313 ha) to 1,275 ac (516 ha), were allocated into three "complete" statistical blocks of three sites each. A management system (i.e., even-aged, uneven-aged, or no-harvest) was randomly assigned to sites within a block, yielding three replicates of each treatment (Sheriff and He 1997). The management system was applied at the site level, and management was implemented at the stand level. Each site was divided into many stands in which forest vegetation composition and age, and environmental characteristics were similar. The Missouri Department of Conservation Forest Land Management Guidelines (Missouri Department of Conservation 1986) and the guidelines for managing uneven-aged stands (Law and Lorimer 1989) provided general recommendations for harvesting in even-aged and uneven-aged MOFEP sites. See Sheriff (this proceedings) for additional details on treatments.



We conducted two different studies to address our objectives. In the first study, we used the *general overstory cavity inventories* to document the density of tree cavities and snags in two inventories before, and one inventory after, first entry harvesting in even-aged, uneven-aged, and no-harvest sites and compared the observed densities to the Forest Land Management Guidelines for Missouri (objective 1). We also used these data to identify trends in the pre-treatment cavity data with regard to cavity tree species, tree diameter, and hole height on the tree (objective 2). In the second study, we used data from an *intensive cavity survey and verification* to verify the reliability of tree cavity estimates (objective 3). The data sources used for these studies are described below.

General Overstory Cavity Inventories

Cavity data were collected on 50,845 live trees and 3,607 snags as part of the MOFEP woody

vegetation study on the original 645, 0.5-ac (0.2 ha) vegetation plots in 1990-1992 and three new plots in 1994 (total of 648 vegetation plots). All trees used in these analyses were individually tagged with a number. These trees and ingrowths were re-inventoried in 1994 and 1995 prior to MOFEP timber harvest in 1996 and were inventoried again in 1997-1998. Overstory cavity data were collected on all trees ≥ 4.5 in. (11 cm) diameter breast height (d.b.h.) and on snags that were at least 8 ft (2.4 m) tall and ≥ 6 in. (15 cm) d.b.h. Tree species, d.b.h., crown class, and the presence of holes thought to lead to cavities were recorded. Data collected on holes included hole diameter class, hole height class, and cavity formation type (natural or wildlife excavated) (table 1). Holes that went into or underneath tree roots were considered cavities but were rare. Live trees with cavities on dead branches were considered live cavity trees. Cavity trees were defined as having one or more holes that were ocularly estimated to be a minimum 1 in. (2.5 cm) in diameter or to have a

Table 1.—Codes and descriptions used to quantify wildlife cavities in trees ≥ 4.5 in. d.b.h. on the MOFEP cavity and overstory forest vegetation study

Formation code	Cavity type	Description	
1	Natural	Hollow; formed by decay after a branch breaks off a tree.	
2	Excavated	Hollow; formed primarily by woodpeckers and aided by decay. Usually circular with smooth edges.	

Size code (Pre-treatment)	Cavity diameter	Size code (Post-treatment)	Cavity diameter (Post-treatment)
1	≤ 5 in.	0.5	≤ 0.75 in.
2	$5 < x \leq 12$ in.	1.0	$0.75 < x \leq 1.25$ in.
3	> 12 in.	1.5	$1.25 < x \leq 1.75$ in.
		2.0	$1.75 < x \leq 2.25$ in.
		2.5	$2.25 < x \leq 2.75$ in.
		3.0	$2.75 < x \leq 3.50$ in.
		4.0	$3.50 < x \leq 4.50$ in.
		5.0	$4.50 < x \leq 5.50$ in.
		etc.	

Location code (Pre-treatment)	Height above groundline	Location code (Post-treatment)	Height above groundline
1	< 5 ft	0.1	Ground or root
2	$5 \leq x < 15$ ft	0.2	≤ 4 in.
3	$15 \leq x < 25$ ft	1	$4 \text{ in.} \leq x < 5$ ft
4	$25 \leq x < 35$ ft	2	$5 \text{ ft} \leq x < 15$ ft
5	≥ 35 ft	3	$15 \text{ ft} \leq x < 25$ ft
		4	$25 \text{ ft} \leq x < 35$ ft
		5	≥ 35 ft

minimum dimension of 0.75 x 1.25 in. (1.9 x 3.2 cm) for oval holes. The hole diameter recorded was the widest diameter in the narrowest axis of the hole. In most cases trees were examined on at least two sides. Holes within reach were examined to determine if a cavity was present. A more detailed discussion of the woody vegetation data collection procedure is provided by Jensen (2000).

Because of the large number of trees, cavity data were collected during both dormant and growing seasons. We found a slightly greater number (< 2%) of cavities during the dormant season for holes high on trees, probably because it was easier to identify cavities in tree canopies without leaves. However, we feel that the difference between dormant season and growing season cavity inventories was small and unbiased with respect to harvest treatment, tree species, and tree size, so we proceeded with our analyses with the data pooled across season.

Intensive Cavity Survey and Verification

During the winter of 1995-1996, a more intensive search for cavities was conducted in 24 vegetation plots containing 1,439 overstory trees, scheduled to be clearcut during the summer and fall of 1996. For this intensive survey, we used binoculars to help estimate if a hole led to a cavity. A clinometer was used to determine the hole height. In this portion of the study there was no minimum hole diameter requirement, but data were not collected on potential cavities in the 0.5 in. (1 cm) size class formed by woodpeckers due to the very large number of them. Potential cavities in this size class formed by other means were recorded. The hole diameter was estimated in half-inch (1 cm) size classes for holes < 3 in. (7.5 cm) and in 1 in. (2.5 cm) size classes for larger holes (table 1). Holes were classified as being in a live or dead section of a live tree and the height to width ratio of the hole was recorded. Trees were thumped with an axe to determine if they sounded hollow or decayed. For this intensive cavity survey, cavities were defined as having a minimum depth into the tree of 3 in. (7.5 cm) or a depth of at least half the diameter of the stem if in small branches. Other data collected on cavity trees and other overstory trees included tree species, d.b.h., crown class, and a tree condition code. The overstory tree tag number was painted on cavity trees to aid in relocation.

Data were also collected on holes determined to be potential cavities (except on the excavated half inch [1.3 cm] size class). For the intensive cavity survey, potential cavities were defined as holes in early stages of cavity formation that did not meet our minimum cavity dimension requirements.

During the tree harvest in 1996, researchers recorded log lengths of each tagged tree removed. The tree tag number was painted on felled tree tops, cull logs, and non-merchantable tree sections to ensure that the entire length of each of the original trees could be accounted for during cavity verification. During the winter of 1996-1997 and before slashing was done, the plots were revisited and the cavity data verified. Cavity trees left as culls or of unmerchantable size were felled with a chainsaw. The initial data were used as an aid to finding the original holes. The original cavity estimates were verified by measuring relocated holes and potential holes on felled trees. A drafting compass was used to measure hole diameters. A chainsaw was used to dissect the stems above and below holes. The internal cavity dimensions (maximum width, minimum width, and depth) were recorded. The hole was designated as an actual cavity if it met or exceeded the minimum size requirements, or it was designated as a potential cavity if internal dimensions were smaller.

RESULTS

General Overstory Cavity Inventories

Cavity and Snag Guidelines vs. MOFEP Findings

For this discussion, pole timber included the trees < 10 in. (25 cm) d.b.h., small sawtimber included those from 10 to 19 in. (25 to 48 cm) d.b.h., and large sawtimber trees were greater than 19 in. (48 cm) d.b.h. (fig. 1). Based on the general overstory cavity inventory on the 648 vegetation plots prior to treatment, MOFEP sites had cavity tree densities well above the minimum recommended in the Forest Land Management Guidelines (MDC 1986a) for poles (2.3 vs. 1/ac or 4.0 vs. 2.5/ha), small sawtimber (3.7 vs. 2/ac or 9.1 vs. 5/ha), and large sawtimber (1.3 vs. 0.5/ac or 3.0 vs. 1/ha). Cavity tree density was just below the optimum recommendations for poles (2/ac or 5/ha) and small sawtimber (4/ac or 10/ha), and above for large sawtimber (1/ac or 3/ha).

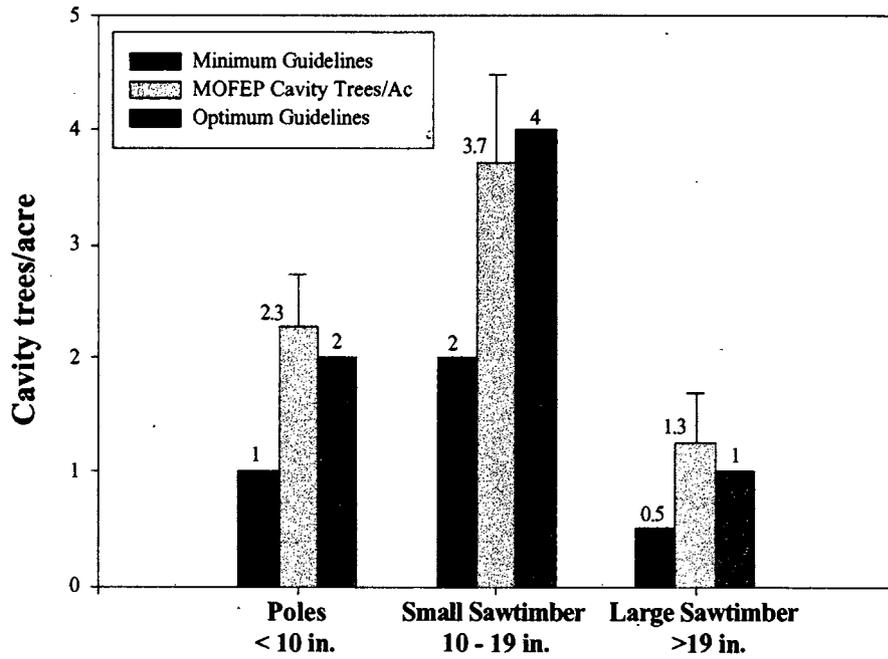


Figure 1.—Pre-harvest cavity tree (≥ 4.5 in. (11 cm) d.b.h.) densities for pole timber, small sawtimber, and large sawtimber on all MOFEP sites compared to the land management guidelines for Missouri's heavily forested areas. Error bars are 95 percent confidence intervals for site means. Numbers on bars indicate site means or minimum and optimum recommendations.

Following harvest treatments in 1996, there was a reduction in cavity tree density in even-aged (-0.6/ac or -1.5/ha) and uneven-aged (-0.6/ac or -1.5/ha) sites, and an increase in no-harvest (+1.2/ac or +3.0/ha) sites compared to pre-harvest cavity tree density. These estimates are for the entire site, which included both harvested and unharvested stands. For all size

classes, cavity tree density was slightly above the optimum recommendation of seven cavity trees/ac (17/ha) on no-harvest (7.2/ac or 17.8/ha) sites and on even-aged (8.5/ac or 21.0/ha) sites and slightly below the optimum recommendation for uneven-aged (6.1/ac or 15.1/ha) sites (fig. 2).

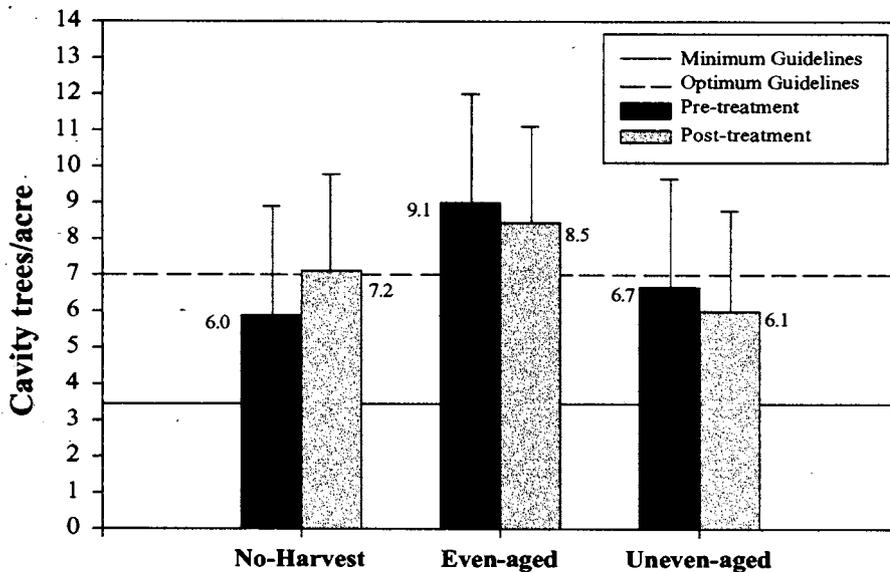


Figure 2.—Pre-harvest and post-harvest cavity tree densities (≥ 4.5 in. (11 cm) d.b.h.) by forest management on MOFEP sites compared to the land management guidelines (combined size classes) for Missouri's heavily forested areas. Error bars are 95 percent confidence intervals for site means. Numbers on bars indicate treatment means.

On the no-harvest sites, 82 percent of the pre-treatment cavity trees remained alive in the winter of 1998-1999, 11 percent became snags, and 7 percent fell to the ground. On the harvested sites, 21 percent of the pre-treatment cavity trees on uneven-aged sites and 16 percent on the even-aged sites were cut. Kabrick *et al.* (this proceedings) give a more detailed description of the overstory tree conditions on MOFEP sites before and after the 1996 harvest.

Snag densities on MOFEP sites in 1994 and 1995 were above the optimum levels for pole timber (4.0 vs. 2/ac or 9.9 vs. 5/ha) and large sawtimber (0.3 vs. 0/ac or 0.7 vs. 0/ha), and they were below optimum for small sawtimber (2.9 vs. 4/ac or 7.2 vs. 10/ha) but above the minimum recommendations (2/ac or 5/ha) (fig. 3). For all snag size classes combined, snag densities in even-aged sites were below the optimum snag recommendation (5.2 vs. 6/ac or 13 vs. 15/ha) but above optimum in no-harvest (8.8 vs. 6/ac or 22 vs. 15/ha) and uneven-aged (7.5 vs. 6/ac or 19 vs. 15/ha) sites. Following the tree harvest, 1998 snag densities rose

slightly in no-harvest (9.2/ac or 23/ha) sites and more in uneven-aged (9.9/ac or 24/ha) sites but stayed about the same in even-aged (5.1/ac or 13/ha) sites (fig. 4).

Cavities by Tree Size, Height on Trees, and Tree Species

Whereas the number of trees in 2 in. (5 cm) diameter classes had a negative exponential diameter curve, the proportion of live trees with a cavity had a positive exponential curve (q-value of 1.5) with increasing diameter classes. Most trees (33%) were in the 6 in. (15 cm) d.b.h. class, but only 1.7 percent of these had noticeable cavities (fig. 5). Three percent of the trees were in the 18 in. (46 cm) d.b.h. size class and 17 percent of these trees had cavities. Only 0.1 percent of trees were larger than 27 in. (69 cm) d.b.h., but 68 percent of these trees contained cavities. The trend of increasing occurrence of cavities with increasing tree diameter was also observed within species and species groups (fig. 6) and has been noted by others (Allen and Corn 1990, Healy *et al.* 1989).

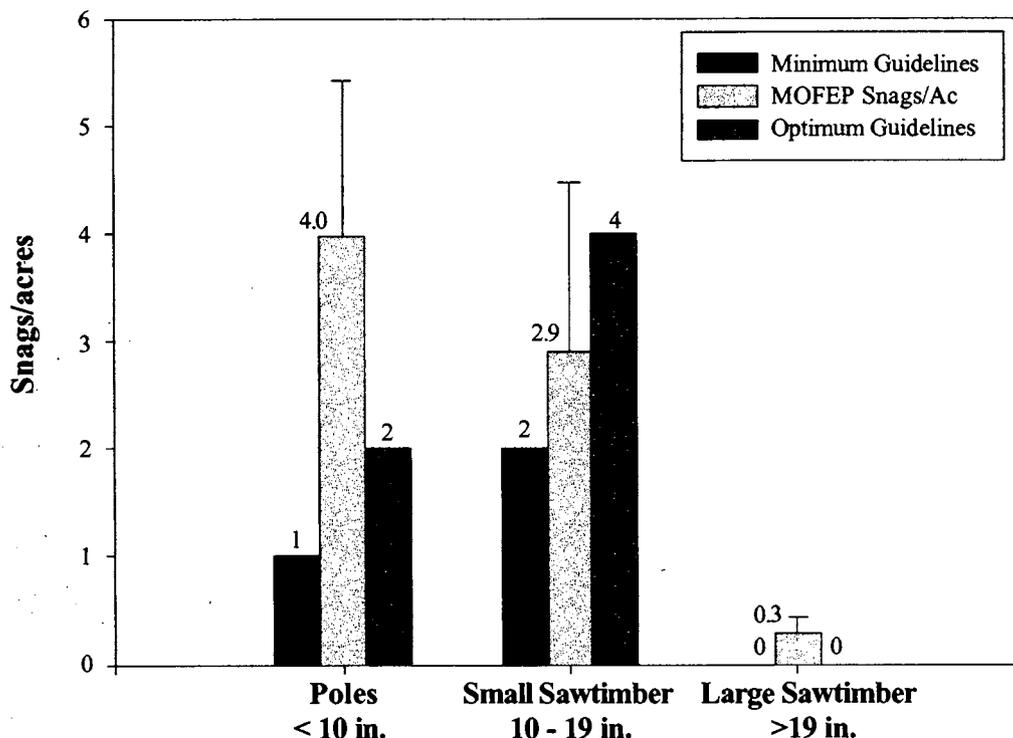


Figure 3.—The density of snags (≥ 6 in. (15 cm) d.b.h.) on pre-treatment MOFEP vegetation plots in 1994-1995, and a comparison to the recommended snag guidelines for Missouri's heavily forested regions. Error bars are 95 percent confidence intervals for site means. Numbers on bars indicate site means or minimum and optimum recommendations.

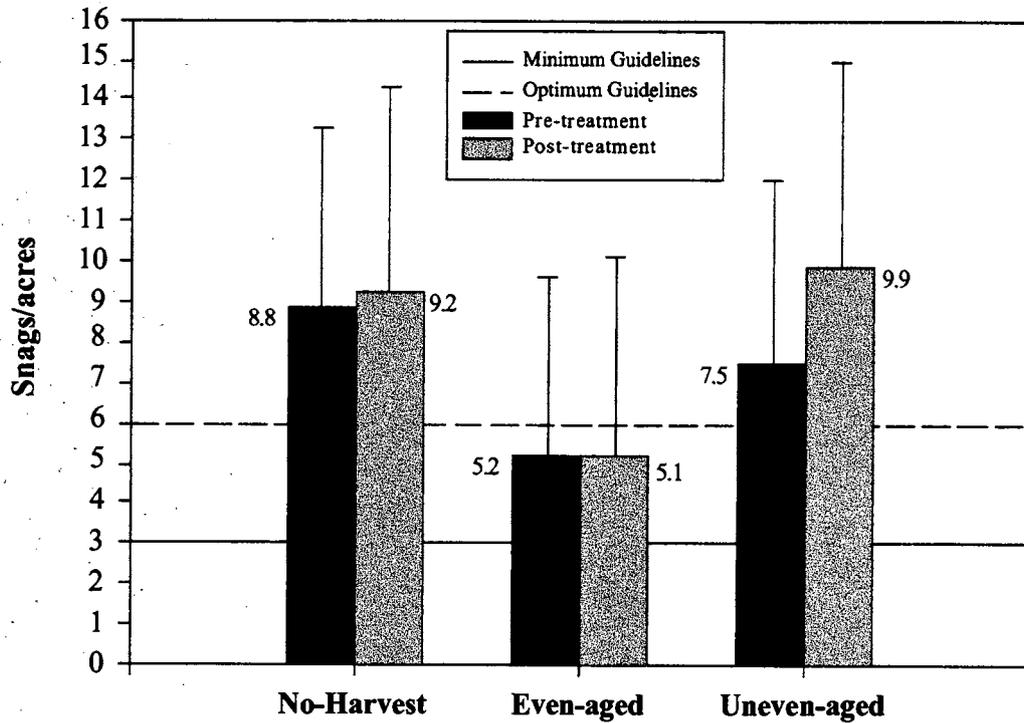


Figure 4.—Pre-harvest and post-harvest snag densities (≥ 6 in. (15 cm) d.b.h.) by forest management on MOFEP sites compared to the land management guidelines (combined size classes) for Missouri's heavily forested areas. Error bars are 95 percent confidence intervals for site means. Numbers on bars indicate site means.

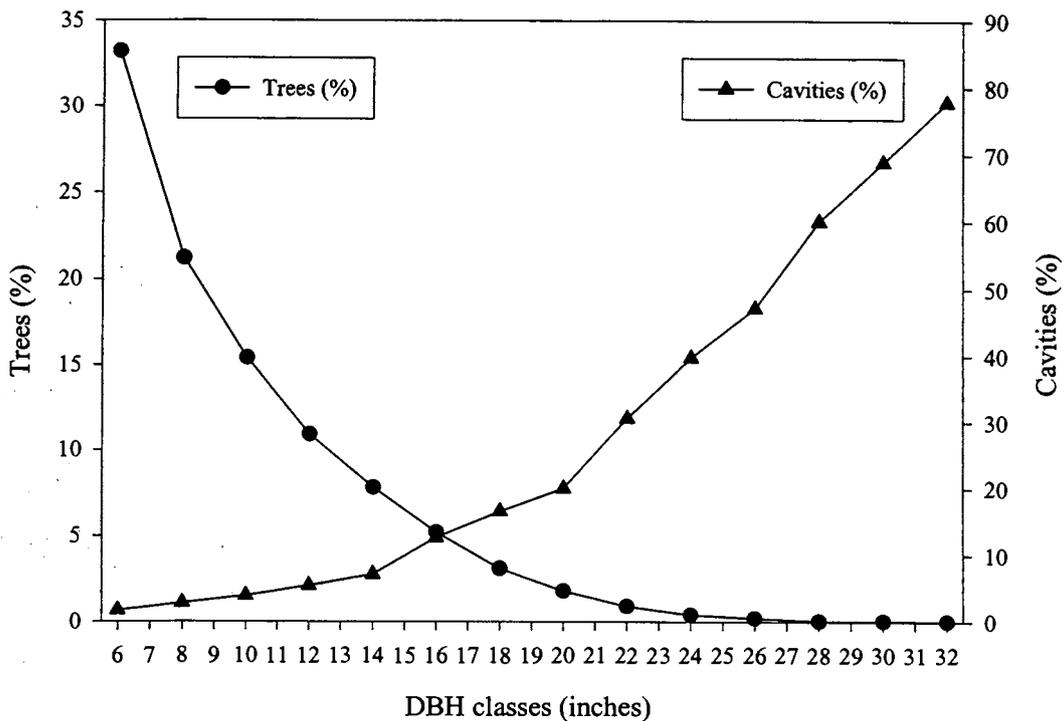


Figure 5.—Pre-treatment diameter distribution of overstory trees (≥ 4.5 in. (11 cm) d.b.h.) on MOFEP sites and the corresponding percent of cavity trees by size class.

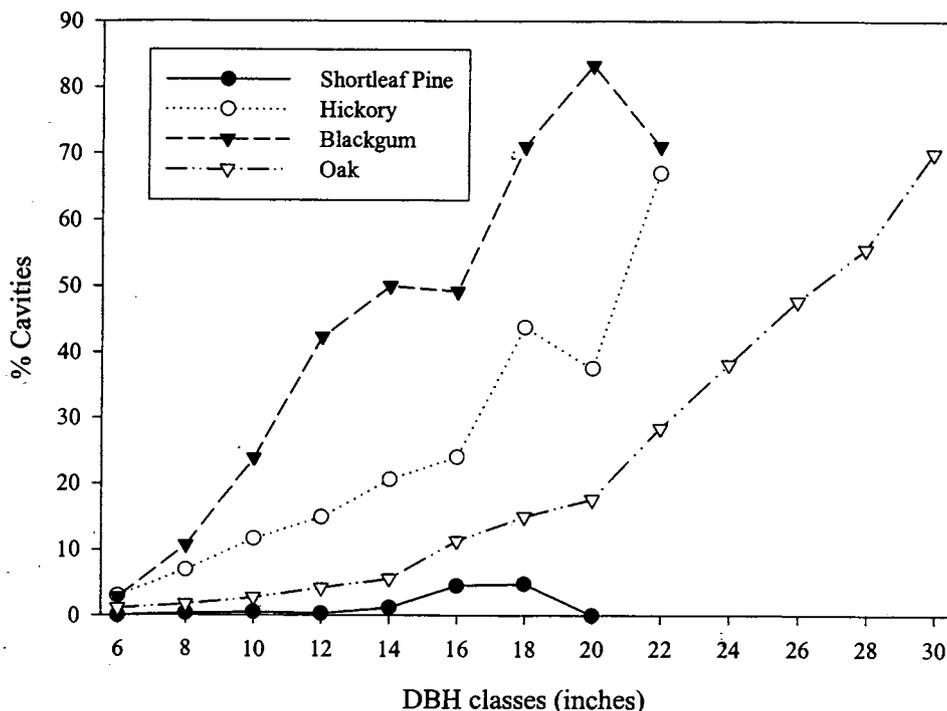


Figure 6.—The pre-treatment percentage of cavity trees by 2 in. (5 cm) size classes for select species and species groups (≥ 5 in. (13 cm) d.b.h.) on MOFEP sites. The last data point for each species or species group includes larger trees when their sample size would have been less than 10 otherwise.

Basal cavities (< 5 ft or 1.5 m above ground) made up 44 percent of all cavities located and were present in 58 percent of the cavity trees. For trees ≤ 12 in. (30 cm) d.b.h., there were more basal cavities present than all other cavity

heights (> 5 ft) combined. For diameter classes other than 18, 22, and 24 in. (or 46, 56, and 61 cm) d.b.h., where most cavities were in the 20 ft (6 m) height class, basal cavities were again the predominant height location. Cavities at least

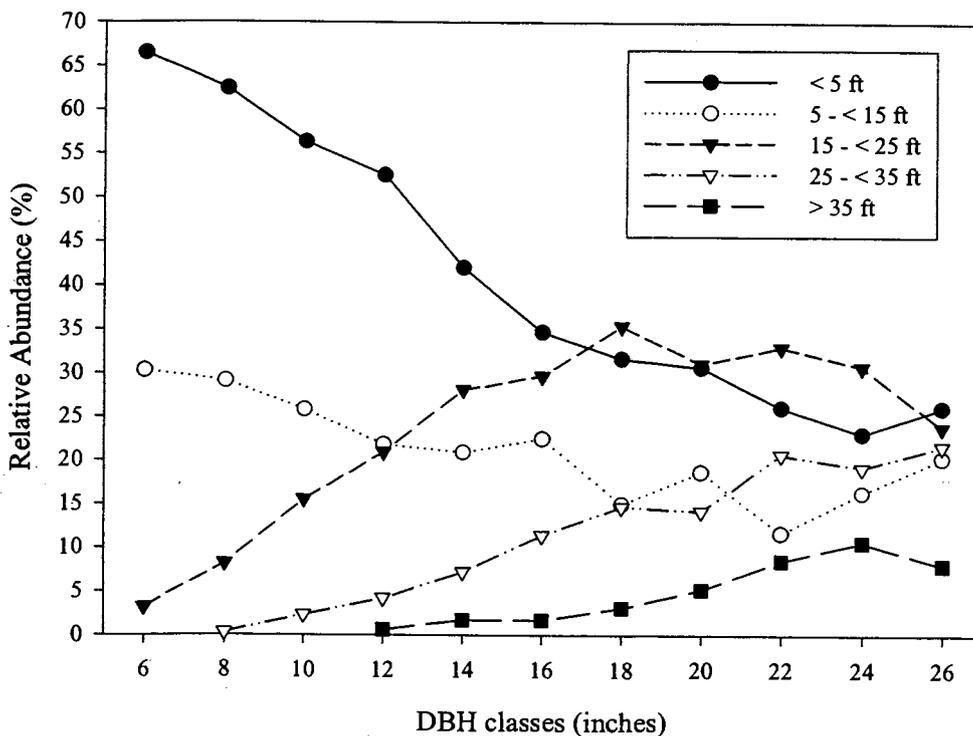


Figure 7.—The relative abundance of cavity hole height locations on trees (≥ 5 in. (13 cm) d.b.h.) prior to MOFEP timber harvests by 2 in. (5 cm) size classes.



35 ft (10.7 m) above ground were found only in trees 12 in. (30 cm) d.b.h. and larger (fig. 7).

Cavities were detected in 5 percent of all overstory trees, but there were differences among tree species. For example, cavities were found in 20 percent of blackgums (*Nyssa sylvatica* Marsh.) but in 1 percent of shortleaf pines (*Pinus echinata* Mill.) (fig. 8). Cavity occurrence was low for the three most abundant tree species: white oak (*Quercus alba* L.) (2%), black oak (*Q. velutina* Lam) (5%), and scarlet oak (*Q. coccinea* Muenchh) (4%). These three oak species made up 63 percent of the live overstory trees on MOFEP sites in 1995, but blackgum was only 2 percent of the population. Post oak (*Q. stellata* Wangenh) (10%) had the highest abundance of cavities of the oaks.

Intensive Cavity Survey and Verification

On plots scheduled to be clearcut, 1,439 standing trees were intensively examined prior to harvest and 484 cavities and 358 potential cavities in 410 trees were found. Twenty-two live cavity trees/ac (54/ha) had holes in the 1-in. (2.5 cm) diameter class or larger. Compared

to our general cavity survey in which we found only 10 cavity trees/ac (25/ha), the intensive search located more than twice the number of cavity trees. However, we still needed to verify if cavity and potential cavity estimates made with the intensive cavity search on standing trees were indeed cavities. Following the 1996 timber harvest, we relocated 222 holes thought to be cavities and 184 potential cavities on 215 trees that were dissected after the timber harvest and before slashing operations. Here we found that only 55 percent (122) of the holes that were thought to be cavities actually were cavities, but that 18 percent (33) of the potential cavities turned out to also be cavities. We therefore overestimated the number of actual cavities when surveying standing trees; the actual number of cavities was only 70 percent of our estimate. This estimate verification only applies to the subset of cavities and potential cavities relocated from the original intensive search. It does not include new cavities that may have existed but were not detected in the intensive cavity search on standing trees because the timber sale contract prohibited an intense inspection of *all* trees at the time of harvest.

For species in which we relocated at least 10 trees with cavities, we were most accurate in

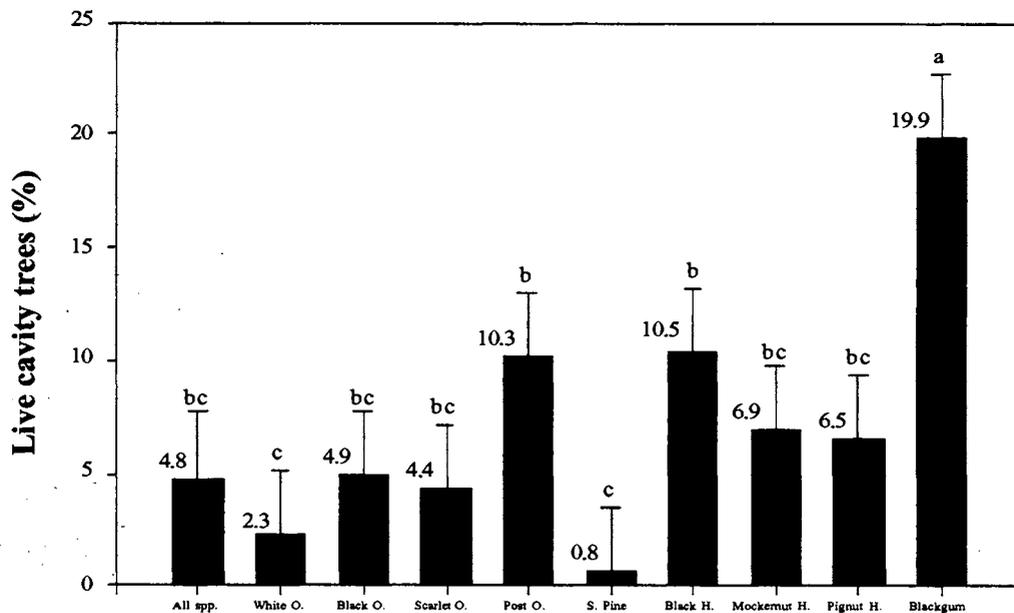


Figure 8.—The relative abundance of cavity trees for all trees (≥ 4.5 in. (11 cm) d.b.h.) and the most abundant tree species on MOFEP sites prior to harvest. Error bars are 95 percent confidence intervals for site means. Different letters indicate significant differences in abundance of live cavity trees (%) among species based on a Tukey test. Same or shared letters indicate no significant difference at $\alpha = 0.05$ level.

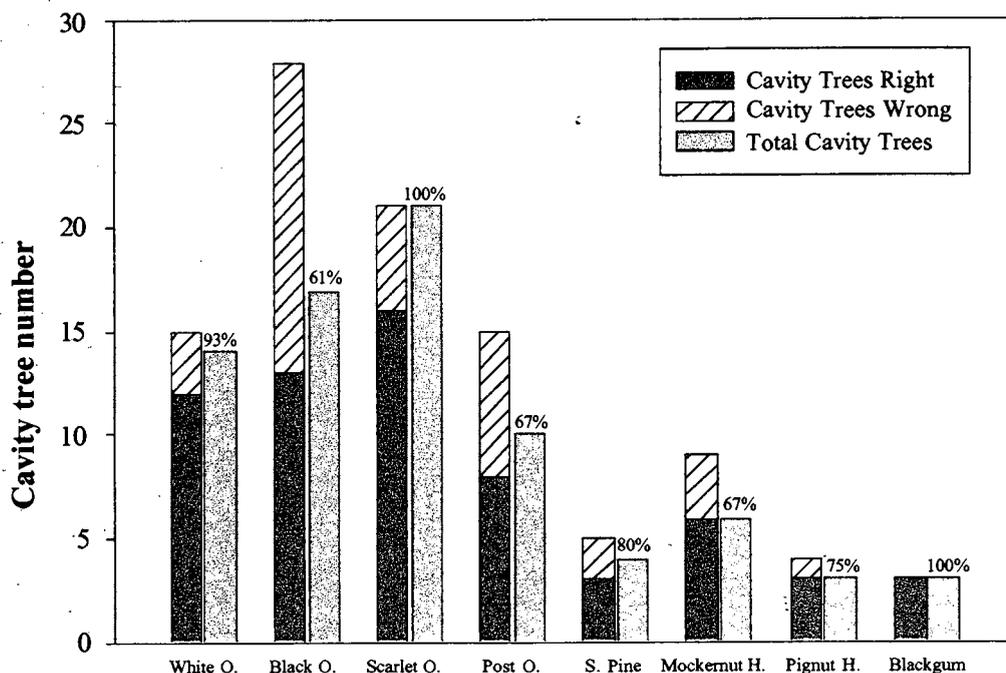


Figure 9.—The number of cavity trees by species estimated by an intensive cavity search, including the number of confirmed cavity trees of the original estimate (dark gray), cavities that were not confirmed (hatched), and the total number of cavity trees including potential cavities that turned out to be cavities (light gray). The number above the light gray bar indicates this proportion of the original cavity estimate.

calling a tree a cavity tree in white oak (80%) and scarlet oak (76%) and least successful in black oak (46%), post oak (53%), and black hickory (*Carya texana* Buckl.) (58%) (fig. 9). However, some holes thought to be potential cavities were actually found to lead to a cavity as well. By accounting for these potential cavity holes that were found to be cavities, the proportion of cavity trees was again equal to our original estimate for scarlet oak and near the estimate for white oak (93%). However, the verified number of black oak cavity trees was only 61 percent of the original estimate.

Even though we could accurately estimate cavity tree density for some species, we could not always accurately estimate the number of holes leading to cavities within individual cavity trees. For example, we accurately estimated cavity tree density for scarlet oak, although the number of holes successfully estimated to lead to a cavity for scarlet oak cavity trees was only 51 percent of the original estimate. We were less

successful (29% correct) at estimating black hickory holes leading to cavities. White oak holes were estimated correctly as leading to a cavity on 82 percent of the sample.

The presence of cavities was more successfully identified with decreasing height on the tree (fig. 10). For cavities > 30 ft (9 m) above ground, only 57 percent were correctly identified compared to 91 percent for cavities ≤ 10 ft (3 m) above ground. The presence of large diameter holes increased cavity estimation accuracy, reaching 100 percent with holes ≥ 4 in. (10 cm) in diameter (fig. 11). This contrasts with only 16 percent of the half-inch diameter holes that were correctly called cavities. The total number of cavities of this size class was 40 percent of the original estimate after including potential cavities that turned out to be cavities. Estimated cavities were correctly identified in 63 percent of the sample in live portions of trees but in only 35 percent of the sample in dead limbs.

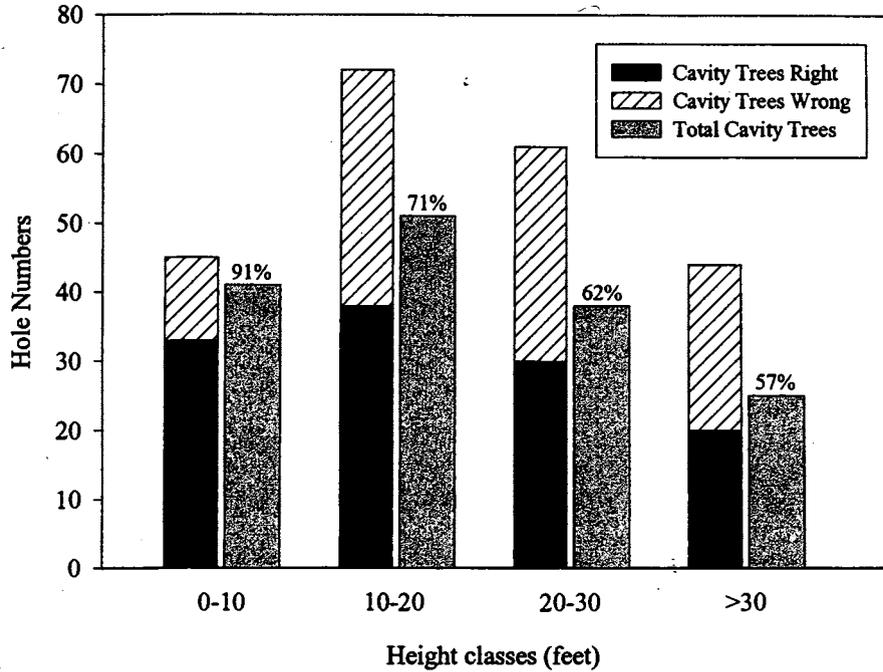


Figure 10.—The proportion of holes correctly estimated to lead to a cavity with an intensive cavity search by hole height class, including the number of confirmed cavities of the original estimate (dark gray), cavities that were not confirmed (hatched), and the total number of cavity trees including potential cavities that turned out to be cavities (light gray). The number above the light gray bar indicates this proportion of the original cavity estimate.

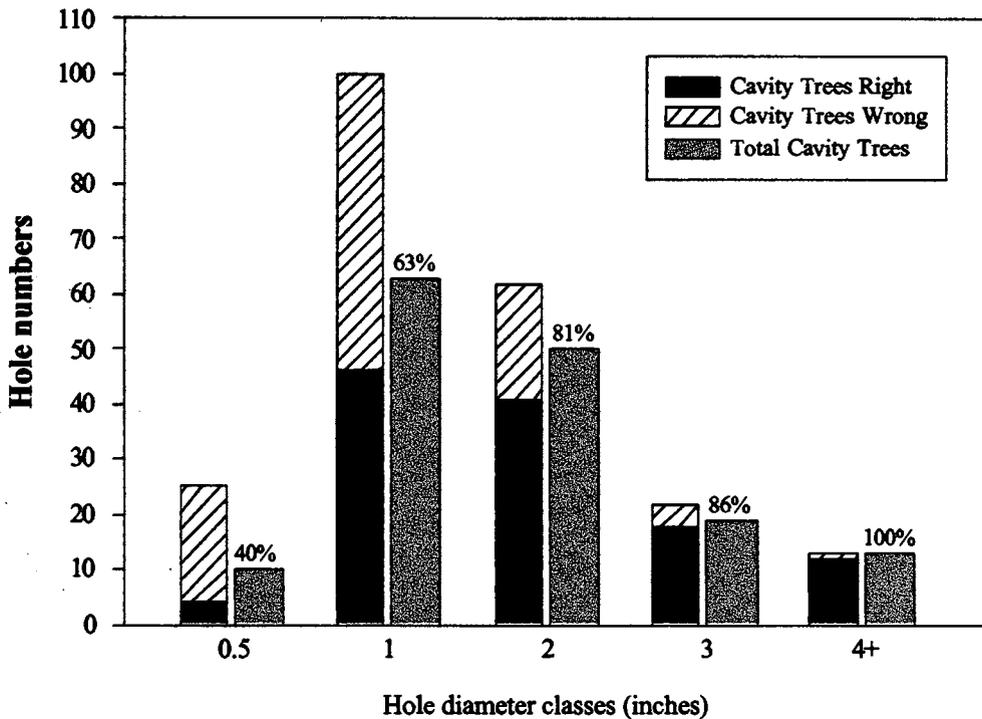


Figure 11.—The proportion of holes that were successfully estimated to lead to a cavity with an intensive cavity search by hole diameter class, including the number of confirmed cavity trees of the original estimate (dark gray), cavities that were not confirmed (hatched), and the total number of cavity trees including potential cavities that turned out to be cavities (light gray). The number above the light gray bar indicates this proportion of the original cavity estimate.

DISCUSSION

General Overstory Cavity Inventories

Cavity and Snag Guidelines vs. MOFEP Findings

The Missouri Department of Conservation has established guidelines for cavity and snag densities for heavily forested regions of Missouri (MDC 1985, 1986a). Prior to harvest treatments, the cavity tree density was close to the optimum guidelines for no-harvest and uneven-aged sites and above optimum guidelines in even-aged sites. Moreover, even though harvesting reduced cavity tree densities, the post-harvest cavity densities on both even-aged and uneven-aged sites remained above or near optimum at the site scale.

Because we found that large diameter trees had substantially more cavities than small diameter trees and large diameter trees are also a criterion for determining which stands will be harvested, the greatest opportunities for managing for cavity species lie in the conscious management of larger trees. There is potential for cavity densities to decrease at a faster or slower rate with uneven-aged treatments. Because more trees on larger areas are evaluated for harvesting during each re-entry, managers have more opportunities to either improve timber quality by removing poor-quality trees, which may have or will develop cavities, or to identify and protect cavity trees from being cut. However, these two objectives are not necessarily mutually exclusive. For example, Healy *et al.* (1989) found 2.9 times as many cavities in unthinned oak stands compared to thinned stands in Massachusetts, but also found that 89 percent of the rough culls and 63 percent of the rotten cull trees did not have cavities. These trees could be removed through timber stand improvement with minimal impact on cavity tree densities. Moreover, preferred timber—those trees left in the forest as growing stock—can also have cavities. Healy *et al.* (1989) found that 28 percent of the cavity trees in central Massachusetts were classified as preferred timber trees, often having holes high in the tree or on limbs. In the MOFEP intensive cavity survey, 37 percent of the cavity trees thumped with an axe had solid 8-ft (2.4 m) butt logs that were or could become merchantable saw logs. Fifteen percent sounded hollow only below 4.5 ft (1.4 m), and 48 percent sounded hollow above and below 4.5 ft.

When we combine the snag size classes, uneven-aged sites actually had a much higher increase in snag densities after harvesting (7.7 to 10/ac or 19 to 26/ha, fig. 4) than even-aged or no-harvest sites. This increase is most likely due to the number of trees that were double girdled with a chainsaw. Tree girdling as part of slashing operations was taken advantage of mostly on site 2, where snag density increased most dramatically from 5.5 to 12 snags/ac (14 to 30/ha). Since the 1998 inventory, we have observed, however, that many of these girdled trees have fallen down. We will be able to document this during the next inventory scheduled to begin in 2001. Snag numbers and basal areas on MOFEP sites prior to treatment are reported in Shifley *et al.* (1997); snag numbers ≥ 4.5 in. (11 cm) d.b.h. post-treatment are reported in Kabrick *et al.* (this proceedings).

Cavities by Tree Size, Height on Trees, and Tree Species

In our mature second-growth forest with little past forest management, the proportion of cavity trees increased exponentially with tree diameter. Conversely, the number of live trees decreased exponentially with increasing diameter classes. Consequently, leaving some large (i.e., ≥ 18 in. (46 cm) d.b.h.) trees on site in single-tree selection and even-aged intermediate harvests, where cavity tree densities are lower than desired, would be a simple way to obtain higher levels of cavity tree densities.

Most of the cavities located on trees were basal cavities (< 5 ft (1.5 m) height). Although basal dens may be used for escape cover and caching food by some wildlife species, for many wildlife species these cavities may be unsuitable for rearing young or winter survival. Although there is much to learn in the oak-hickory-pine forest, the gray squirrel (*Sciurus carolinensis*) is the only secondary cavity user known to nest in cavities below 10 ft (3 m) height on trees in forest interiors (MDC 1985). On the other hand, the northern saw-whet owl (*Aegolius acadicus*), another secondary cavity user, is not known to nest below 20 ft (6 m) and can nest as high as 40 ft (12 m); the barred owl (*Strix varia*) is not known to nest below 30 ft (9 m) (MDC 1985). However, few cavities were detected high above ground in this study. Protecting trees with cavities high above ground during timber harvest would thus increase the most limiting class of cavities for secondary cavity nesters without compromising timber quality.



The highest proportion of live trees containing cavities occurred in blackgum (20%). However, our examination of blackgums showed that many individuals of this species were nearly hollow throughout, and the cavities often extended into secondary branches. Moreover, cavities with entry holes high on blackgum boles often did not have bottoms until near ground line. This decay pattern may be partly due to blackgum's diffuse-porous wood structure that does not compartmentalize decay as effectively as ring-porous wood structures like those found in oaks and hickories (Shigo 1984, Shigo and Marx 1977). It is unknown to date if these kinds of cavities have much value for wildlife. The next highest proportion of cavities occurred in black hickory (11%) and post oak (10%), both of which are abundant on MOFEP and provide hard mast for wildlife food. Many of their cavities are much smaller than those in blackgum and may provide better nesting habitat. Shortleaf pine had very few cavities (1%) and is not likely to provide very many cavities in Ozark forests.

Intensive Cavity Survey and Verification

We identified 50 percent fewer holes with the general cavity survey compared to the more intensive cavity survey. The search effort during the general survey was similar to the methods that forest managers use while conducting a forest stand inventory or when selectively marking trees for harvest. In the general survey, 5 percent of live overstory trees were called cavity trees. When verifying cavity trees, we found 80 percent of the white oak and 46 percent of the black oak were correctly called cavity trees. Allen and Corn (1990) reported 20 percent of the live trees had cavities in the Missouri Ozark oak-hickory forest, but they restricted their sampling to dominant and codominant canopy classes, excluding intermediate and suppressed crown classes and shortleaf pines. They found 3.5 times as many medium (2 to 4 in. or 5.1 to 10.2 cm in diameter) cavities and 5 times as many large (> 4 in. or > 10.2 cm diameter) cavities in black oak compared to white oak. In 1939, Dalke (1948) found dens large enough for squirrels in 10 percent white oak, 8 percent black oak, and 7 percent scarlet oak, in trees at least 12 in. (30 cm) d.b.h., on Deer Run State Forest near present-day MOFEP sites.

Wildlife Management Implications

Most of the cavities (44%) were located near the ground and are suspected to be a result of the past fire history of the Ozarks (Guyette and Larsen 2000). These cavities can serve as escape cover for wildlife, but there are no secondary cavity users known to nest below 5 ft (1.5 m) in forest interior habitats (MDC 1985). Only 12 percent of the cavity trees had a hole at least 25 ft (7.6 m) high in the general survey. Dalke (1948) found that 38 percent of squirrel dens were at the ground line and were characterized as escape or hiding dens. The rest were in the bole or limbs of trees and considered home dens.

Many of the cavities verified in the intensive survey may provide very little benefit to wildlife species. Our minimum size for a cavity (3 in. or 8 cm deep into a tree) was perhaps too small in this study to get a good baseline estimate of *usable cavity* densities and distributions. This may have caused us to overestimate the number of usable cavities for many wildlife species. Estimating the number of usable cavities requires better information about cavity sizes and tree locations needed by specific wildlife species. For example, gray tree frogs (*Hyla chrysoscelis* and *H. versicolor*) and the broad-headed skink (*Eumeces laticeps*) are known to use cavities, but specific information about the dimensions or height requirements are lacking. Other small species may use cavities, but they may not yet be identified in the literature.

The white-footed mouse (*Peromyscus leucopus*) and deer mouse (*Peromyscus maniculatus*) made up about 90 percent of the small mammals captured before and after MOFEP timber harvests (Fantz and Renken 1997 and this proceedings). Although these two species are not listed in the Missouri Department of Conservation snag and cavity guidelines as cavity users, Dooley and Dueser (1990) found that all of the deer mice and many of the white-footed mice used arboreal nests. White-footed mice used tree cavities more frequently in the absence of deer mice. Deer mice used cavities located higher above ground in the presence of white-footed mice. Dooley and Dueser describe the arboreal nests as most frequently being in bole cavities with hole diameters < 0.75 in. (2 cm).

If we had more detailed information about den requirements of deer mice, we would better understand the cavity tree species that potentially provide suitable dens for this species. For example, if a hypothetical deer mouse required a den with a 1 in. (2.5 cm) diameter hole, at least 10 ft (3 m) high on the tree, with interior cavity dimensions of at least 2 x 2 in. (5 x 5 cm) and 4 in. (10 cm) deep, only 13 percent of the 222 dissected cavities would meet the requirements. Seventy-five percent of the holes meeting these criteria were in white oak and scarlet oak, but a higher proportion of white oak trees (41%) contained cavities with these requirements than did scarlet oak (20%). Only 2 of the 52 estimated cavities in black oak fit this criteria.

CONCLUSIONS

This paper reports baseline findings on a large cavity tree and snag data set collected while conducting tree inventory. Overall, we found that both even-aged and uneven-aged management decreases the cavity tree density on MOFEP sites immediately after harvesting. Snags decreased on even-aged sites, but increased on uneven-aged sites because many trees were double girdled rather than slashed. Snags and cavity tree densities have thus far remained near or above the optimum density recommended by Missouri Department of Conservation Guidelines (MDC 1985, 1986a and b). However, it remains unclear if snag and cavity tree densities will remain near or above optimum levels with future harvests.

There were important relationships between tree diameter and tree species and resulting cavity tree densities. Large diameter trees were more likely to contain cavities than small diameter trees, and blackgums were more likely to have cavities than oaks, hickories, or short-leaf pines. Most cavities were found < 5 ft (1.5 m) above ground. Our cavity verification study showed that we more accurately identified cavities in white oaks and scarlet oaks and less accurately in black oak, post oak, and black hickory. This may largely be due to differences in decay patterns among tree species. Hole sizes and locations also affect the accuracy of cavity estimates. As expected, estimation accuracies were greater when holes leading to cavities were larger or located nearer to the ground. There is much to learn about the internal characteristics of cavity trees to assist forest managers in saving the best cavity trees for wildlife when

selectively harvesting trees. Cavity data collected further into the cutting rotation of MOFEP should assist managers in keeping an adequate supply of cavity trees for wildlife. Future studies should also be directed at investigating the tree cavity characteristics required by different wildlife species during the most limiting season to ensure healthy wildlife populations.

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Harvest-associated Disturbance in Upland Ozark Forests of the Missouri Ozark Forest Ecosystem Project

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Abstract.—The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, multidisciplinary, landscape-based research program studying effects of even-aged (EAM), uneven-aged (UAM), and no-harvest (NHM) management on forest communities. The first MOFEP timber harvests occurred from May through November 1996. Harvest-related disturbance occurred on 69 of 180 permanent 0.2-ha study plots in which interactions between *Armillaria* populations, forest structure, and forest management are being studied. On each of these 69 plots, we mapped and measured 1) all injured non-harvested trees ≥ 5.0 cm d.b.h. (diameter at breast height) and their injuries, 2) all stumps and girdled trees, and 3) all vehicle paths. Roots ≥ 1.0 cm diameter and their injuries were characterized in 0.2-m deep \times 0.25-m² excavations beneath skidder tracks that passed through the 69 study plots. Excavations exposed an average of 1.0 m of root, and multiple- and single-haul skid trails averaged 1.3 vs. 0.7 injuries per meter of discovered root, respectively. Skidder tracks disturbed an estimated 3 percent of the forest floor, resulting in > 900 root injuries per hectare harvested. Partial cutting occurred on 56 of our 69 disturbed plots (14 EAM and 42 UAM). In 22 partially cut plots (15 UAM and 7 EAM), all trees ≥ 5.0 cm d.b.h. (both injured and non-injured) were mapped and characterized. Approximately 11 percent of non-harvested saplings and 3 percent of larger stems were broken, shattered, uprooted, or pushed over; an additional 4 percent of saplings and 10 percent of larger stems incurred xylem-exposing injuries; and another approximately 3 percent of non-harvested trees incurred phloem wounds. Average wound size was smaller for saplings than for larger stems, but percentage stem circumference injured was similar (27 vs. 23 percent, respectively). Frequency of buttress root injury increased with tree d.b.h. An average 62 percent of all injured plot trees occurred ≤ 2.0 m from vehicle paths, whereas 54 percent of trees this close to vehicle activity were injured. For the 22 completely mapped plots, we used stepwise logistic regression to explore each tree's probability of injury based on tree characteristics, harvest-related factors, and site factors. Probability of stem injury was positively associated with north- to east-facing slopes, the length of truck haul road passing through the study plot, and the number of stumps ≥ 45 cm diameter created within the study plot. Probability of stem injury was negatively associated with stem quality, distance from vehicle paths, day of year harvested, two specific logging crews, and UAM.

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Silvicultural thinning and single-tree selection operations are planned disturbance events that produce a suite of outcomes influencing long-term forest structure dynamics in a number of ways (e.g., Dey 1994). We categorize the results of harvest operations as intended, collateral, or accidental. The intended result is a prescribed adjustment of stand structure and composition to provide a planned flow of values over time—for example, some combination of commercial wood products, wildlife habitat improvement, and aesthetic values. Collateral products are the inherent results of the harvest that may or may not serve an intended purpose (e.g., stump populations and skidding disturbance). For example, managers may anticipate that stump-sprouting will provide desirable regeneration (see Dey and Jensen, this proceedings), yet stumps and their root systems represent potential food bases for increasing root-infecting fungus inoculum potential over time (e.g., *Armillaria* root disease, see Termorshuizen 2000, Wargo and Harrington 1991). Similarly, managers may anticipate that forest floor disturbance caused by skidding activity will create valuable seedbeds, yet this form of disturbance also injures roots, thus increasing, to some extent, tree vulnerability to infection (e.g., Popoola and Fox 1996, Weaver 1974). Accidental products of harvest are neither essential to the harvest nor completely avoidable. The most important accidental products are physical injuries to residual live stems and root systems. While large stem injuries directly reduce wood product values over time through discoloration and decay, wound compartmentalization anywhere on a tree reduces the volume of energy storage tissue in the tree (Shigo 1984, 1985; Shigo and Tippett 1981), and root and buttress injuries have been shown to facilitate infection and decline (Benzie *et al.* 1963, Kessler 1992, Popoola and Fox 1996, Weaver 1974).

Levels of individual harvest disturbance components vary both spatially and temporally across the landscape. Factors determining patterns of local disturbance intensity include topography, initial stand structure and composition, the silvicultural system applied, the harvest design and methods employed, the skill level and sense of purpose of harvest crews, the season of harvest, and the weather encountered. Overall, the challenge is twofold. First, we need to understand the incremental relationships between levels of individual harvest disturbance components and consequent levels of tree

damage capable of inciting forest decline (Manion and Lachance 1992). This knowledge is needed to guide efforts to set acceptable limits on the components of harvest disturbance.

Because forest decline disease syndromes with similar symptoms can result from various interactions among numerous factors (Manion and Lachance 1992), it is important to know the extent to which declines in a specific region reflect recurrent causal themes (e.g., *Armillaria* root disease) with implications for forest management. Foresters have attributed a major role in upland Ozark oak decline to *Armillaria* root disease (Johnson and Law 1989). We have identified *Armillaria gallica* Marxmüller & Romagn., *A. mellea* (Vahl:Fr.) P. Kumm., and *A. tabescens* (Scop.) Emel in these forests and have evaluated their ecological distributions (Bruhn *et al.* 2000). Harvest-related disturbances and *Armillaria* root disease fit the concepts of "inciting" and "contributory" factors in the decline spiral model (Manion and Lachance 1992).

RESEARCH GOALS AND OBJECTIVES

Our overall goal is to understand the ecological distributions and activities of *Armillaria* species in the Ozark Highlands, with specific respect to each other, to silvicultural and natural disturbances, and to forest structure dynamics.

Clearly, evaluation of harvest disturbances first requires their documentation. Our primary objective in this phase of our studies was to explicitly map and measure all harvest-related disturbance caused by 1996 MOFEP timber harvest activities on the study plots included in *Armillaria* root disease studies. Spatially explicit disturbance data will permit us to revisit injured trees to evaluate wound response, defect development, growth, decline, and survival. To further study the context within which these disturbances took place, and as a basis for future evaluation of their ramifications with respect to forest structure, we have mapped and measured all trees ≥ 5.0 cm d.b.h. on randomly selected plots within which disturbance was documented. Future evaluations of value losses due to injury-initiated forest product defects, *Armillaria* root disease, and other forest decline factors will build on our baseline documentation of harvest disturbance factors, summarized here.



METHODS

Plot Selection

The Missouri Ozark Forest Ecosystem Project (MOFEP) comprises nine upland forest sites (266 ha to 527 ha in size) in southeastern Missouri (Shifley and Brookshire 2000, Sheriff, this proceedings). These sites are arranged in three blocks of three sites each, with three silvicultural systems (i.e., even-aged management (EAM), uneven-aged management (UAM), or no-harvest management (NHM) applied to one site each in each block for a time period equivalent to an EAM rotation (100 - 150 years). Upland forest predominates; overstory vegetation is mostly mature second-growth *Quercus*, *Carya*, and *Pinus echinata* Mill. (Shifley *et al.* 2000). Sites 1 through 6 and 9 occur in the Current-Black River Oak-Hickory Forest Breaks Landtype Association (LTA), characterized by extensive bedrock dissection. Sites 7 and 8 occur in the Current-Eleven Point River Hills LTA, with gentler relief. The bedrock stratigraphy, landforms, and soils in these LTAs have been described (Kabrick *et al.* 2000).

In 1993 - 1994, we randomly selected 180 of the total 648 MOFEP 0.2-ha vegetation study plots, stratified by ecological landtype (ELT) over all nine sites, for studies of *Armillaria* species ecology, forest disturbance, and vegetation dynamics (Bruhn *et al.* 2000). The first set of MOFEP harvests (May - November 1996, see Kabrick *et al.*, this proceedings) disturbed 69 of our 180 plots. Harvest activity on these 69 plots took the form of EAM clearcuts on 13 plots and partial cutting on 56 plots (14 EAM intermediate thinning and 42 UAM single- or single- and group-tree selection). We report here on 1) root damage detected by excavations beneath skid trail tracks adjacent to all 69 plots (table 1), and 2) non-harvested stem injury in the 56 partially cut plots (table 2).

Data Collection

Shortly after harvest was completed in a stand, all injured and intentionally girdled stems ≥ 5 cm d.b.h., all stumps ≥ 5 cm diameter, and all vehicle paths in each of the 69 disturbed *Armillaria* study plots were mapped and measured for future spatial analysis. Roads and skid trails were characterized as haul roads or as multiple- or single-haul skid trails. For 22 of the 56 partially cut plots (15 UAM and 7 EAM

plots), we have completed total stem maps (i.e., including non-injured trees ≥ 5 cm d.b.h.).

As soon as possible after harvest, we examined belowground woody lateral roots (≥ 1 cm diameter) for injury. For this purpose, we randomly located four small-scale forced-water excavations (0.5 m x 0.5 m x 0.2 m deep) immediately adjoining our plots in the two tracks within each vehicle path that entered each study plot (table 1). Forest floor disturbance was recorded at the site of each excavation as the maximum depth of forest floor displacement and/or compression by the vehicle track. Within each excavation, the diameter, length, depth, and dimensions of any injuries were recorded for each woody root segment encountered. A total of 145 excavations were made in multiple-haul skid trails and 110 were made in single-haul skid trails.

The following data were collected for all mapped stems: species, d.b.h., canopy position, condition (i.e., living, moribund, died post-harvest, or died pre-harvest) and pre-injury suitability (+/-) as a crop tree. The shortest distance to a vehicle path (and whether that path was a road or a multiple- or single-haul skid trail) was recorded for all trees ≤ 2.0 m from a vehicle path. All injuries on residual stems were categorized as: 1) only phloem penetrated, 2) xylem exposed, or 3) stem broken. The position and dimensions of each injury were recorded as height above ground level to wound base, maximum wound length along the stem axis, maximum wound width perpendicular to the stem axis, and maximum depth of xylem penetration. It would have been impractical to graphically determine individual wound surface area. Instead, we expressed wound area as the traditional index calculated by multiplying maximum wound length by maximum circumferential wound width. Ohman (1970) reported that although actual wound area ranged from one-half to two-thirds of the index value, both calculations were good indicators of probability of value loss. Stump-top diameter and identity (at least genus) were recorded for all mapped stumps.

Our study plots are characterized for analysis by MOFEP block, landtype association, and slope position, aspect, and steepness. Harvest disturbance at each plot has been characterized by silvicultural system, 1996 harvest activity class, day of year harvested, length of each class of vehicle trail, diameter distribution of the stump population, and harvest crew identity.

Table 1.—Distribution of the 255 skid trail excavations^a used to evaluate root injury associated with 1996 harvest disturbance

Site ^b	Block	Silvicultural system ^c	1996 activity ^d	ELT ^e	No. of excavations	
					Mult-haul skid trails	Single-haul skid trails
2	1	UAM	STS	11	12	4
				17	8	4
				18	8	0
			S/GTS	11	4	4
				17	0	0
				18	4	4
3	1	EAM	CC	11	0	0
				17	0	0
				18	4	0
			INT	11	0	4
				17	4	0
				18	9	6
4	2	UAM	STS	11	12	0
				17	4	8
				18	12	8
			S/GTS	11	4	0
				17	4	4
				18	0	0
5	2	EAM	CC	11	0	4
				17	4	4
				18	12	0
			INT	11	4	8
				17	0	0
				18	4	0
7	3	UAM	STS	11	4	4
				17	12	0
				18	4	0
			S/GTS	11	0	8
				17	4	0
				18	0	0
9	3	EAM	CC	11	0	4
				17	0	0
				18	4	4
			INT	11	0	0
				17	0	0
				18	0	0
Total					145	110

^a Each excavation is 0.25 m² square x 0.2 m deep = 0.05 m³.

^b See Sheriff (this proceedings, table 1, figures 1 and 3).

^c Silvicultural systems: UAM, uneven-aged management; EAM, even-aged management.

^d 1996 harvest activity: STS, single-tree selection; S/GTS, single- and group-tree selection; CC, clearcut; INT, intermediate thinning.

^e Ecological landtype (ELT) (broad sense): 11, ridgetops; 17, south- to west-facing slopes; 18, north- to east-facing slopes.

Table 2.—Characteristics of the 56 permanent 0.2-ha vegetation/*Armillaria* study plots that experienced thinning or selection harvest disturbance in 1996

Site-plot	Mapping ^a complete	Block	Trtmt ^b	1996 activity ^c	ELT ^d	Slope position ^e	Length ^f (m)			Harvest crew	Day of year	No. of stumps ^g	
							Road	Skid1	Skid2			≥ 25 cm	≥ 45 cm
2-16	No	1	U	STS	18	3	0	47	38	1	261	6	6
2-18	No	1	U	STS	11	5	0	41	27	1	262	5	2
2-19	No	1	U	STS	11	5	0	0	57	1	255	3	1
2-25	No	1	U	STS	18	3	0	0	0	2	276	5	0
2-28	No	1	U	S/GTS	18	3	0	0	78	2	235	14	6
2-30	No	1	U	S/GTS	11	5	0	46	18	15	184	13	5
2-31	No	1	U	STS	17	3	0	55	41	15	189	8	3
2-32	Yes	1	U	S/GTS	11	5	0	0	57	15	164	21	6
2-33	No	1	U	STS	18	4	0	37	7	2	213	4	3
2-34	No	1	U	STS	11	5	48	22	20	2	221	6	1
2-67	No	1	U	STS	11	5	46	0	14	2	225	4	1
2-68	No	1	U	STS	11	5	0	25	0	2	228	0	0
2-69	Yes	1	U	STS	17	3	0	49	31	2	248	4	2
2-70	No	1	U	STS	17	4	0	0	24	2	251	0	0
2-72	No	1	U	S/GTS	18	4	0	38	56	2	226	3	2
3-29	Yes	1	E	IH	11	5	47	0	70	1	224	10	2
3-30	Yes	1	E	IH	18	4	0	65	0	1	226	12	5
3-52	Yes	1	E	IH	17	4	0	37	50	4	179	12	4
3-56	No	1	E	IH	18	3	0	0	121	3	290	10	8
3-61	Yes	1	E	IH	18	3	0	0	94	1	241	7	6
3-63	No	1	E	IH	18	4	0	0	81	1	241	7	5
3-70	Yes	1	E	IH	11	5	46	47	14	2	178	8	7
4-15	Yes	2	U	S/GTS	11	5	0	50	26	7	193	11	2
4-16	No	2	U	STS	17	3	0	0	22	7	196	11	4
4-24	No	2	U	STS	11	5	42	65	74	5	197	10	4
4-26	No	2	U	S/GTS	11	5	16	0	0	6	192	20	16
4-28	Yes	2	U	S/GTS	17	3	0	0	66	6	192	17	6
4-30	Yes	2	U	STS	18	3	0	58	17	5	165	10	7
4-31	No	2	U	STS	11	5	50	0	0	6	213	10	3
4-33	Yes	2	U	STS	18	3	0	0	35	5	213	8	3
4-35	No	2	U	STS	18	3	0	0	0	8	274	4	0
4-36	No	2	U	STS	17	3	0	0	45	7	171	16	6
4-37	No	2	U	STS	17	3	0	24	0	7	178	9	3
4-38	Yes	2	U	STS	18	3	0	0	120	7	267	16	6
4-42	Yes	2	U	S/GTS	11	5	0	35	0	7	165	26	8
4-49	No	2	U	STS	18	3	0	32	33	8	242	13	0
4-60	No	2	U	STS	11	5	44	12	0	5	190	21	2
4-70	No	2	U	STS	18	3	0	50	0	5	175	19	3
4-71	Yes	2	U	S/GTS	17	3	0	32	29	5	175	10	5
5-1	Yes	2	E	IH	11	5	47	22	43	8	189	12	6
5-2	Yes	2	E	IH	18	3	0	47	37	8	189	7	4
5-12	No	2	E	IH	11	5	46	0	26	6	182	11	4
5-30	No	2	E	IH	11	5	36	18	28	8	177	14	7
5-33	No	2	E	IH	11	5	0	9	38	5	245	8	5
5-48	No	2	E	IH	11	5	0	0	71	7	207	12	1
7-35	Yes	3	U	STS	17	3	0	56	55	11	171	10	1
7-41	Yes	3	U	STS	11	5	0	51	52	11	127	14	8

(Table 2 continued on next page)

(Table 2 continued)

Site-plot	Mapping ^a complete	Block	Trtmt ^b	1996 activity ^c	ELT ^d	Slope position ^e	Length ^f (m)			Harvest crew	Day of year	No. of stumps ^g	
							Road	Skid1	Skid2			≥ 25 cm	≥ 45 cm
7-43	No	3	U	STS	17	4	0	63	57	11	148	13	7
7-47	Yes	3	U	STS	11	5	33	0	58	10	140	8	3
7-52	No	3	U	S/GTS	11	5	34	0	8	10	140	14	8
7-55	Yes	3	U	STS	18	3	0	89	0	9	177	8	6
7-58	Yes	3	U	S/GTS	11	5	0	41	54	9	177	14	6
7-63	No	3	U	STS	11	5	0	0	0	9	226	5	4
7-65	Yes	3	U	STS	17	4	0	13	42	9	234	6	3
7-66	No	3	U	S/GTS	17	3	0	39	39	9	234	8	7
9-17	No	3	E	IH	18	3	0	58	0	12	135	18	10

^a Mapping completed: Yes – All non-injured and injured stems ≥ 5.0 cm d.b.h. within the plot were mapped; No – Within the plot, all injured stems ≥ 5.0 cm d.b.h. as well as all non-injured stems ≥ 5.0 cm d.b.h. and ≤ 2.0 m from vehicle trails were mapped.

^b Experimental treatment: E – even-aged management; U – uneven-aged management.

^c 1996 harvest activity: STS – single-tree selection; S/GTS – single- and group-tree selection; IH – Intermediate harvest.

^d Ecological Landtype (broad sense): 11 – ridge-top; 17 – south- to west-facing slope; 18 – north- to east-facing slope.

^e Slope position: 3 – lower slope; 4 – break from mid-slope to ridge; 5 – ridges.

^f Length (within plot): Road – truck haul road; Skid1 – multiple-haul skidder trails; Skid2 – single-haul skidder trails.

^g Number of stumps: The number of stumps on the plot that had a stump-top diameter of ≥ 25 cm or ≥ 45 cm.

Statistical Analyses

To explore hypothesized relationships between site and disturbance factors and the extent of root injury observed in multiple- vs. single-haul vehicle track excavations, root damage in each excavation was characterized both as 1) the number of injuries per (0.25 m²) excavation, and 2) the number of injuries per meter of root length. Excavations that contained no roots ≥ 1.0 cm diameter did not contribute to our calculations of number of injuries per meter of root length, whereas all 255 excavations contributed to our calculations of number of injuries per excavation. Number of injuries per meter of root length represents the root population beneath skidder tracks in our study plots, whereas number of injuries per excavation can be applied to our estimated proportion of forest floor area under skidder tracks to estimate the extent of root injury throughout harvested stands. These two dependent variables were used to compare root injury occurring beneath multiple- vs. single-haul skid trail tracks. Correlations between these two dependent variables and slope percent, depth of forest floor displacement, and day of year harvested were also examined separately for single- and multiple-haul skid trails.

We selected 37 variables (28 binary classification and 9 continuously distributed) documenting characteristics of location, individual trees,

and disturbance (table 3) for use in stepwise logistic regression analysis (SLR; see Sokal and Rohlf 1995) of factors that might explain the different patterns of tree injury encountered on the 22 plots for which we have mapped all stems. The dependent variable was the probability that an observed tree became injured during the harvest operation. All 37 independent variables were selected on the basis of *a priori* hypotheses of relationship to the dependent variable. The stepwise model-selection method (PROC LOGISTIC, $\alpha = 0.05$; SAS/STAT System Release 8.00, SAS Inst., Inc., Cary, NC) was used to eliminate variables that did not help explain the pattern of trees injured.

To evaluate the SLR model, PROC LOGISTIC used the SLR model to assign each tree a probability, p , of injury during harvest. PROC LOGISTIC also calculated the number of different pairs of stems in which injury was observed and not observed for the two members of the pair, as the product (Observed) \times (Total - Observed). A measure of each model's predictive strength was then evaluated as its percent concordant, percent discordant, and percent tied (SAS/STAT System Release 8.00, SAS Inst., Inc., Cary, NC). Percent concordance is the percent of all possible pairs of stems for which the larger probability of injury (p) was associated with the injured stem, percent discordance is the percent of pairs of stems for which the larger probability of injury (p) was associated



Table 3.—Variables included in stepwise logistic regression analyses of harvest disturbance

Type of variable Variable group	No. of variables
Binary (classification) variables	
Ecological Landtype (broad sense) ^a	3
Landtype Association	2
Logging crew identity ^b	13
Silvicultural system ^c	2
Slope position ^d	3
Statistical block ^e	3
Stem quality ^f	2
Continuously distributed variables	
Day of year harvested	1
Distance to nearest vehicle path (m)	1
Numbers of stumps ^g	2
Slope (percent) at plot center	1
Stem d.b.h. (cm)	1
Vehicle activity ^h (m)	3

^a Ridgetop, south- to west-facing slope, or north- to east-facing slope.

^b Each of the 13 logging crews assigned to harvest one or more of our study plots was represented as a binary (classification) variable.

^c Even- or uneven-aged management.

^d Ridge, transition from ridge to upper slope, or lower slope position.

^e Block 1: sites 1–3; block 2: sites 4–6; block 3: sites 7–9.

^f Stem either of potential crop quality or not.

^g Number of stumps within each plot of stump-top diameter ≥ 25 cm or ≥ 45 cm.

^h Total length of trail within each plot, by activity class: truck haul road, or multiple- or single-haul skidder trail.

with the non-injured stem, and percent tied is the percent of pairs of stems for which both were equally likely to be injured (i.e., p equal).

Our SLR model can be field tested in two ways. First, and most straightforward, as we complete the mapping of non-injured trees for additional partially harvested *Armillaria* study plots, we can apply our model to those data sets (which will also represent the 1996 harvest). Alternatively, we can test our model during the next MOFEP harvest, but this approach may be biased if the next harvest proceeds differently.

RESULTS

Vehicle Path Root Injury

Roots ≥ 1.0 cm diameter were found in 92 percent of the 145 multiple-haul and 87 percent of the 110 single-haul skid trail excavations. Root length, diameter, and depth were similar for multiple- vs. single-haul trail excavations, and occurrences of these two trail types were similarly distributed among harvest dates and with respect to slope steepness (table 4). Nevertheless, approximately twice as many injuries were found beneath multiple- vs. single-haul trails on both a per excavation and a per meter root length basis (table 4). Both number of injuries per excavation and number of injuries per meter of root length were skewed distinctly to the right, with 0 injuries found in 41 percent of multiple- and 70 percent of single-haul excavations, and ≥ 9 injuries per excavation and ≥ 10 injuries per meter of root length found in only 1 excavation in each trail class.

Mean lengths of the three types of vehicle path in each of the 56 partially harvested plots were highly variable (table 5). No apparent differences were detected in vehicle path length between EAM and UAM plots for any of the trail types using Student's t -test ($P > 0.05$). However, the overall mean length of single-haul trails averaged 44 percent greater than that of multiple-haul trails (35.2 m vs. 24.5 m, respectively; $t = 2.06$, $P = 0.05$). Presuming approximately 1.0 m vehicle track width in a 3 m wide vehicle path, then plots averaged approximately 24 m² and 35 m² under vehicle tracks in multiple- and single-haul trails, respectively. These figures extrapolate to approximately 122 m² per hectare and 176 m² per hectare, respectively, or 1.22 percent and 1.76 percent of the forest floor disturbed by multiple- and single-haul skidder tracks. Extrapolating from 1.13 and 0.55 injuries per 0.25 m² excavation under multiple- vs. single-haul skid trail tracks, respectively, we estimate approximately 551 and 387 root injuries per harvested hectare beneath multiple- and single-haul skidder tracks, respectively.

Forest floor disturbance by multiple- and single-haul skidder tracks ranged in depth from 0.4 to 19.0 cm and from 0.6 to 12.0 cm, respectively (see table 4). Disturbance in multiple-haul (but not single-haul) skid trails was positively correlated with slope steepness and day of year harvested (table 6). Neither number of injuries per excavation nor number of injuries per meter

Table 4.—Mean values for root characteristics, forest floor disturbance, percentage slope, and day of year harvested, for excavations beneath single- and multiple-haul skid trail tracks

Variable	Single-haul skid trail			Multiple-haul skid trail		
	Mean	N	SD	Mean	N	SD
Root diameter ^a (cm)	1.76	266	0.97	1.84	393	0.94
Root depth ^a (cm)	10.84	266	4.82	9.99	393	5.20
Root length ^a (m)	97.64	110	84.73	109.52	145	82.47
Injuries per m root ^a	0.74	96	1.58	1.34	134	2.06
Injuries per excavation ^b	0.55	110	1.25	1.13	145	1.46
Disturbance ^c (cm)	4.38	96	2.19	5.06	145	3.13
Slope percent	20.3	96	12.13	21.1	145	10.44
Day of yr harvested	191.7	96	37.9	206.5	145	36.9

^a Root diameter, root depth, root length, and number of injuries per meter root length are based on the population of root segments encountered in all excavations.

^b Number of injuries per excavation is based on all excavations.

^c Disturbance is the maximum depth of forest floor displacement and/or compression by the vehicle track at each excavation site.

Table 5.—Lengths of vehicle paths (m) within 0.2-ha plots by treatment^a

Vehicle/Activity class	UAM		EAM		All Plots	
	Mean	SD	Mean	SD	Mean	SD
Truck haul road	7.4	16.2	15.9	22.3	9.5	18.1
Multiple-haul skid trails	25.4	25.0	21.6	24.3	24.5	24.7
Single-haul skid trails	31.0	27.7	48.1	35.6	35.2	30.5

^a Based on 42 uneven-aged management plots and 14 even-aged management plots.

of root length was apparently correlated with slope steepness or day of year harvested for either trail type (table 6). Nevertheless, number of injuries per meter of root length in single-haul trails (but not multiple-haul trails) was positively correlated with forest floor disturbance (table 6).

Proportions of Trees Damaged

For summarization, non-harvested stems were classified as saplings (5.0 – 11.0 d.b.h.), poles (11.1 – 29.9 d.b.h.), and sawtimber (≥ 30 d.b.h.), and stem damage was categorized as broken, xylem exposed, or phloem exposed. Proportions of trees in all three size classes experiencing

each category of damage were similar for commercial tree species (table 7) vs. all tree species (data not shown). There appears to be very little difference in the patterns of damage occurring in plots partially cut by UAM vs. EAM systems (table 7). Overall, while similar proportions of trees in each size class were damaged, there was a greater tendency for sapling stems to be broken (table 7).

Size and Location of Xylem-exposing Injuries

The size of the largest xylem-exposing wound on damaged trees was highly variable (table 8), with means of 539, 1,040, and 1,877 cm², respectively, for saplings, pole-size, and sawtimber-size trees. Corresponding mean percentages



Table 6.—Correlation coefficients (and corresponding *P* values) for root injury beneath multiple- vs. single-haul skid trails with forest floor disturbance, percent slope, and day of year harvested

	Forest floor disturbance	Percent slope	Day of year harvested
Multiple-haul trails			
Injuries per excavation	0.081 (0.35)	0.070 (0.42)	-0.103 (0.24)
Injuries per meter root Disturbance	0.068 (0.44)	0.086 (0.32)	0.003 (0.97)
		0.248 (0.003)	0.262 (0.002)
Single-haul trails			
Injuries per excavation	0.171 (0.10)	-0.173 (0.092)	-0.056 (0.59)
Injuries per meter root Disturbance	0.267 (0.009)	-0.023 (0.82)	-0.034 (0.74)
		-0.081 (0.41)	0.101 (0.30)

Table 7.—Categorization of stems (percent) of commercial species by "most severe injury" class, d.b.h. class, and silvicultural system

System ^a	D.b.h. class											
	5.0 – 11.0 cm				11.1 – 29.9 cm				≥ 30.0 cm			
	Broken ^b	Xylem ^c	Phloem ^d	Uninjured	Broken	Xylem	Phloem	Uninjured	Broken	Xylem	Phloem	Uninjured
UAM	9.6	5.1	1.9	83.4	3.1	10.7	2.4	83.8	2.4	10.2	3.3	84.1
EAM	12.8	2.6	6.1	78.6	3.3	10.3	4.0	82.5	4.7	8.2	3.5	83.5
Combined	10.5	4.4	3.2	82.0	3.2	10.5	3.0	83.3	3.0	9.7	3.3	84.0

^a UAM, uneven-aged management, based on 15 completely mapped plots; EAM, even-aged management, based on 7 completely mapped plots.

^b This category includes stems uprooted, pushed over, shattered, permanently bowed, and/or broken off at a point precluding future merchantability.

^c Xylem exposed.

^d Phloem damaged, without immediately exposing xylem.

of stem circumference damaged by these wounds were more consistent among stem size classes, ranging from 23 percent for pole- and sawtimber-size trees to 27 percent for saplings (table 8). Largest xylem-exposing wounds occurred consistently in the butt log portions of damaged trees, averaging 33 cm, 36 cm, and 25 cm above ground level for saplings, pole- and sawtimber-size trees, respectively.

The largest xylem-exposing wounds on all injured saplings occurred above the root buttress on the bole (table 9). As tree size class increased, the percentage of trees with the largest xylem-exposing wounds involving buttress roots increased (table 9). The proportion of trees with the largest xylem-exposing wounds involving a buttress root was greater for both pole- and sawtimber-size trees in plots under EAM vs. UAM (table 9).

Relationship of Vehicle Activity to Non-harvested Stem Damage

In the 22 completely mapped plots, 67 percent of all injured stems were located ≤ 2.0 m from a vehicle track, with no apparent difference between UAM and EAM plots or among stem size classes (table 10). All 56 of our disturbed plots averaged a total of 69.2 m of vehicle path, including 9.5 m of haul road and 59.7 m of skid trails (table 5). With skid trails averaging 3 m wide, we estimate that 67 percent of all injured stems occurred on approximately 23 percent of the non-road plot area. In all 56 plots, over 50 percent of saplings ≤ 2.0 m from a haul road or skid trail were injured (table 11). The mean percentage of pole stems injured ranged from 35 percent along single-haul skid trails to 51 percent along multiple-haul skid trails. Fifty percent and 19 percent of non-harvested sawtimber stems ≤ 2.0 m from multiple- or single-haul skid trails, respectively, were injured (table

Table 8.—Dimensions of largest xylem-exposing injury on trees of commercial species, by d.b.h. class and silvicultural system

Wound feature ^a	D.b.h. class								
	5.0 – 11.0 cm			11.1 – 29.9 cm			≥ 30.0 cm		
	N	Mean	SD	N	Mean	SD	N	Mean	SD
Even-aged Management (14 plots)									
Area (cm ²)	18	671	1,226	68	1,025	1,097	7	683	706
% Stem Circumf.	18	26	10	66	22	10	5	12	7
Height (cm)	18	34	31	75	30	46	13	44	138
Uneven-aged Management (42 plots)									
Area (cm ²)	66	504	588	177	1,046	1,178	49	2,047	3,813
% Stem Circumf.	66	27	11	173	23	11	44	24	35
Height (cm)	66	32	36	188	38	97	63	21	55
Combined									
Area (cm ²)	84	539	764	245	1,040	1,154	56	1,877	3,598
% Stem Circumf.	84	27	10	239	23	11	49	23	33
Height (cm)	84	33	35	263	36	86	76	25	75

^a Wound area index (cm²) calculated as the product of maximum wound length and width, percent of stem circumference affected at the point of maximum wound width, and height (cm) to wound base.

Table 9.—Location (percent) of largest xylem-exposing injuries on injured stems of commercial species, by d.b.h. class and silvicultural system

System ^a	D.b.h. class								
	5.0 – 11.0 cm			11.1 – 29.9 cm			≥ 30.0 cm		
	Bole ^b	Root ^c	Both	Bole	Root	Both	Bole	Root	Both
EAM	100.0	0.0	0.0	75.7	13.0	11.4	35.0	60.0	5.0
UAM	100.0	0.0	0.0	89.2	6.2	4.6	63.8	28.7	7.5
Combined	100.0	0.0	0.0	85.5	8.0	6.6	59.2	33.7	7.1

^a EAM, even-aged management, based on 14 plots; UAM, uneven-aged management, based on 42 plots.

^b Injuries that do not extend into contact with the forest floor.

^c Injuries that expose lateral root xylem.

11). A comparable percentage for sawtimber trees ≤ 2.0 m from haul roads could not be determined because all sawtimber trees ≤ 2.0 m from haul roads in our plots had been harvested.

Harvest and Site Characteristics Related to Tree Injury

Our SLR model showed that a tree's likelihood of being injured was greater in 1) plots with northern to eastern slope aspects ($P < 0.001$), and 2) plots where more large stumps were created ($P < 0.001$) (table 12). A tree's likelihood of becoming injured was lower in 1) UAM plots



Table 10.—*Distribution of injured stems with respect to distance from vehicle tracks, potential crop tree designation, and silvicultural system^a*

D.b.h. class (cm)	All Injured trees			Injured crop trees		
	≤ 2.0 m	> 2.0 m	% Injured ≤ 2.0 m	≤ 2.0 m	> 2.0 m	% Injured ≤ 2.0 m
Uneven-aged Management (15 plots)						
5.0 – 24.9	420	266	61.2	295	151	66.1
25.0 – 44.9	98	35	73.7	92	33	73.6
45.0 – 64.9	3	4	42.9	3	4	42.9
Even-aged Management (7 plots)						
5.0 – 24.9	165	129	56.1	110	63	63.6
25.0 – 44.9	25	7	78.1	25	5	83.3
45.0 – 64.9	4	1	80.0	3	1	75.0

^a Data from haul roads and multiple- and single-haul skid trails were combined for all plots representing each silvicultural system.

Table 11.—*Frequency of stem injury in close proximity to three classes of vehicle activity, with respect to potential crop tree designation^a*

D.b.h. class (cm)	All trees within 2.0 m			Crop ^b trees within 2.0 m		
	Injured	Uninjured	% Injured	Injured	Uninjured	% Injured
Truck haul roads						
5.0 – 24.9	80	64	55.6	62	56	52.5
25.0 – 44.9	22	30	42.3	20	30	40.0
45.0 – 64.9	0	0	— ^c	0	0	— ^c
Multiple-haul skidder trails						
5.0 – 24.9	161	100	61.7	113	87	56.5
25.0 – 44.9	39	37	51.3	36	34	51.4
45.0 – 64.9	3	5	37.5	3	3	50.0
Single-haul skidder trails						
5.0 – 24.9	338	243	58.2	221	200	52.5
25.0 – 44.9	61	112	35.3	58	108	34.9
45.0 – 64.9	4	13	23.5	3	13	18.8

^a Data from 42 UAM and 14 EAM plots were combined for each vehicle activity class.

^b Stems of commercial species were classified as crop trees if their condition prior to harvest activity would have permitted them to be considered potential crop trees.

^c Not applicable, no trees.

($P < 0.001$), 2) plots harvested later in the summer and autumn ($P < 0.001$), and 3) plots harvested by crew number 5 and crew number 8 ($P < 0.001$) (table 12). Potential crop trees were less likely to be injured than cull trees or non-commercial species ($P < 0.001$) (table 12). Also, a tree's likelihood of becoming injured decreased with increasing distance from the nearest vehicle track ($P < 0.001$) and increased with increasing within-plot haul road length ($P < 0.001$) (table 12). Concordance and discordance values for this SLR model were 82.6 percent and 16.3 percent, respectively (table 12).

DISCUSSION

As a component of the long-term MOFEP program, our study documents the suite of harvest disturbances in a spatially explicit manner, as a contribution toward understanding the ecological relationships between disturbance factors, individual tree and forest health, and consequent forest structure in upland Ozark forests. The 1996 MOFEP harvests occurred in stands that had not been harvested for at least 40 years. Sheriff (this proceedings) has described

the silvicultural prescription process. For both the EAM- and (especially) the UAM-designated sites, an important objective of this first set of harvests was to shift stand structure toward the desired silvicultural model. Therefore, the 1996 MOFEP EAM thinning and (especially) the UAM single-tree selection harvests were not yet typical of either EAM or UAM.

Nor does the analysis of a single set of harvests reflect the more frequent stand entries inherent with UAM. More frequent stand entry should involve: 1) shorter time intervals between disturbances; 2) greater cumulative length of both single- and multiple-haul skid trails during the equivalent of an EAM rotation period; 3) a tendency to recognize and re-use the most convenient multiple-haul trails, resulting in a third class of skid trail, repeated multiple-haul; 4) correspondingly greater cumulative levels of root and stem damage during the equivalent of an EAM rotation; and 5) no clear regeneration harvest at a location until it is designated for group-tree selection. More frequent stand entry also presents *Armillaria* species with more stable temporal and spatial distributions of infection courts and woody food base resources.

Table 12.—Results of stepwise logistic regression analysis to identify factors associated with probability of stem injury during harvest

Model	Explanatory variables ^a			Predictive evaluation ^b			
	Intercept	Variable name	Parameter estimate	Pr > Wald Chi-square	Percent concord.	Percent discord.	No. pairs
Complete plots, All trees	4.0620				82.6	16.3	1,338,805
		Stem quality	-0.8328	< 0.001			
		Distance	-1.9584	< 0.001			
		ELT 18	+1.0381	< 0.001			
		Day of year	-0.0111	< 0.001			
		Crew no. 8	-1.9545	< 0.001			
		Crew no. 5	-0.6858	< 0.001			
		Uneven-aged management	-0.5388	< 0.001			
		Truck haul road length	+0.0151	< 0.001			
	No. stumps ≥ 45 cm dia	+0.1230	< 0.001				

¹ Variable names: Stem quality, +/- potential crop-quality stem pre-harvest; Distance, stem distance from nearest vehicle trail; ELT 18, northern to eastern slope aspect; Day of year, calendar day of year harvested; Crew no., identity of logging crew that harvested the plot. The significance test used by PROC LOGISTIC is based on the Wald statistic (Sokal and Rohlf 1995; SAS/STAT System Release 8.00, SAS Inst., Inc., Cary, NC).

² No. Pairs represents the product (Observed) * (Total - Observed), the number of possible pairwise combinations of stems for which the specified scenario (injury) was observed and not observed for the two members of the pair. For each stem in each model, SLR assigned a probability, p, that injury would be observed. "Percent Concordant" is the percentage of pairs for which the larger probability of injury (p) was associated with the stem on which injury was observed. "Percent Discordant" is the percentage of pairs for which the larger probability of injury (p) was associated with the stem on which injury was not observed (SAS/STAT System Release 8.00, SAS Inst., Inc., Cary, NC).



EAM involves more dramatic harvest disturbances, but longer intervals between disturbances. While stems injured during thinning may deteriorate further because they remain in the stand longer, regeneration by clearcut eliminates almost all injured stems. And while a clearcut creates the greatest volume and most thorough distribution of potential woody food base resources for *Armillaria*, it is not yet clear how the longer interval between thinning and clearcutting affects the inoculum potential of the three *Armillaria* species in the area and their relative abilities to capture the woody resources made available by a clearcut.

The relationship between physical injury and tree decline is associated with the processes by which trees respond physiologically to injury. Trees do not restore the function of injured tissues or tissues that die in the wound response. Instead, trees expend energy to "compartmentalize" these tissues (Shigo 1984).

Compartmentalization is a variably effective process for containment of microbial colonization, involving both the sacrifice of ray and xylem tissues pre-dating injury and an attempt to overgrow the injury as quickly as possible (Shigo 1984). Because ray parenchyma tissues within compartments die in the process, an injured tree's energy storage capacity is correspondingly reduced, impairing its abilities to respond to subsequent stress or infection (Shigo 1985). The extension of stain and decay slows greatly once a wound is overgrown, as closure seals the injured tissue from further desiccation and aeration (Basham 1978). Thus, smaller wounds generally result in smaller compartments, faster wound closure, and less discoloration and decay.

Trees attempt to compartmentalize root injuries and infections in the same manner as stem injuries (Shigo and Tippett 1981). The success of the compartmentalization process in a tree root depends on the physiological condition of the tree and the nature of any pathogenic challenge. A tree's physiological response to stress or injury diverts energy that might also be needed to compartmentalize root injuries or infections, and in doing so, temporarily increases root concentrations of carbon and nitrogen forms preferred by *Armillaria* species (Wargo 1996).

Skidder tracks covered an estimated 3 percent of the forest floor, resulting in > 900 root injuries per hectare harvested. There were no differences between EAM and UAM plots in the mean length of single- or multiple-haul skid trails. If this pattern remains true for future partial cuts, then a much greater proportion of the forest floor will be skidded over with UAM than with EAM during an EAM rotation-equivalent period of time. We are not aware of any other studies characterizing skid trail damage to subterranean woody roots. Consequently, we have no case studies with which to compare the levels of root damage we observed, and are not presently able to predict the magnitude of their effect(s) on forest health. Comparative evaluation of root disease level relative to distance from skid trails will eventually clarify this issue. Weaver (1974) showed that *A. tabescens* infected and colonized wounded peach roots more readily than non-wounded roots. Popoola and Fox (1996) found that root-pruned black currant plants were more readily infected by both *A. gallica* and *A. mellea* compared with non-injured plants, and that *A. mellea* infection resulted in higher levels of twig and root mortality on both pruned and non-injured plants than *A. gallica*.

The positive correlation between forest floor disturbance in multiple-haul skid trails and slope steepness was anticipated (table 6). However, the positive correlation between forest floor disturbance in multiple-haul skid trails and harvest day of year (table 6) is misleading, because very few of our plots were harvested early in the spring when soil moisture is especially conducive to soil displacement and compaction. Only 5 of our 56 study plots happened to be harvested as early as May, and the last 10 were harvested in September and October (table 2). Earlier harvesting in sites 7 and 9 than in sites 2 through 5 resulted in some very severe rutting (locally ≥ 60 cm deep), which, however, did not occur close to our plots. Forest managers in sites 7 and 9 rationalized correctly that ruts would close with time. Because so few of our plots were harvested early, our correlation analysis apparently detected increasing disturbance associated with the late season rise in soil moisture. The lack of correlation for both root injury indices with slope steepness and day of year harvested (table 6) is also probably misleading. The small correlation coefficients

observed are probably associated with the very rocky soils characteristic of the upland Ozarks and with complete displacement of some injured root segments from more disturbed tracks on steeper slopes. "Number of injuries per meter of root length" was positively correlated with forest floor disturbance, but only in single-haul skid trails. We attribute this to more frequent displacement of damaged root material from more heavily used trails. On rocky soils, combined displacement and compaction may not be adequate indicators of either disturbance or root damage. Overall, we consider our extrapolated estimates of root damage at the site level to be conservative.

We expect approximately 15 percent sapling stem mortality in partially cut plots under both EAM and UAM, because of the effects of suppressed forest canopy position on their ability to recover from injury (Nyland 1994). The greater proportion of saplings injured than larger trees is undoubtedly due to their greater density, the fact that they are small enough to safely run over, and the focus of loggers' attention on avoiding damage to larger stems. Sapling destruction is of special concern in UAM because: 1) the greater frequency of stand entries with UAM provides more frequent opportunities to damage residual stems; and 2) UAM depends on a constant supply of appropriately distributed advance regeneration from which to select future crop trees (Daniel *et al.* 1979, Nyland 1994). The extent to which old skid routes are used in future UAM harvests will largely determine how much total sapling destruction occurs.

The largest xylem-exposing wound on each injured tree averaged 539 cm² for saplings and 1,877 cm² for sawtimber stems, respectively, and covered approximately 25 percent of stem circumference for both size classes (table 8). Because the barrier zone produced by the vascular cambium during compartmentalization extends substantially beyond the wound margins (Shigo 1984, 1985), the percent stem circumference actually affected by an injury is much greater than wound dimensions suggest. Several relatively long-term studies have addressed the prognosis for wounds on various tree species in different climatic zones. For example, Benzie *et al.* (1963) found that yellow birch injuries increased in size during the year after wounding, whereas sugar maple injuries did not. Smith *et al.* (1994) found that injuries > 322 cm² on Appalachian hardwoods often

require over 15 years to close. Basham (1978) observed that sugar maple injuries inflicted during the spring closed faster than autumn injuries of the same size, leading to greater defect development from autumn vs. spring injuries. Basham (1978) also found that wounds that penetrated the xylem resulted in substantially greater defect than wounds that exposed but did not penetrate the xylem. Lamson and Smith (1988) found no d.b.h. growth loss associated with injuries > 645 cm² during the 5 years following thinning in Appalachian hardwoods.

The greater frequency of buttress root damage on larger trees (table 9) is doubtless due to the increase in buttress size and exposure as trees grow. The frequency of buttress injury is also expected to increase with the total length, degree of curvature and number of turns in skid trails, and with increasing length of skidded logs. In addition, loggers may presume that buttress root injuries are less important than stem injuries because trees with buttress root injuries can often be harvested before the associated defect extends into the valuable butt log. In fact, Benzie *et al.* (1963) found that decay in yellow birch and sugar maple was much more commonly associated with 4-year-old buttress root injuries than with stem injuries, although decay generally had not yet progressed into the butt log. Kessler (1992) found an association between buttress root injuries and branch dieback in black oak.

Non-harvested stem damage was heavily concentrated ≤ 2.0 m from vehicle paths (tables 10 and 11). Two-thirds of all injured stems occurred in the approximate 23 percent of plot area (excluding permanent haul roads) that was ≤ 2.0 m from a vehicle path. Skid trails were not predesignated for this harvest, and merchantable tree-length logs were skidded to decks alongside haul roads. Fifty and eighteen percent, respectively, of the non-harvested sawtimber trees ≤ 2.0 m from a multiple- or single-haul skid trail were injured. We need to emphasize that stem damage incurred during harvest constrains the professional forester's subsequent freedom to implement silvicultural guidelines, subjugating considerations of stand structure to the removal of damaged stems (e.g., Ohman 1970). In this light, a study of residual stem damage resulting from whole-tree harvest thinning of northern hardwoods found that predesignation of skid trails greatly reduced the level of damage to residual stems (Ostrofsky *et*



al. 1986). The potential benefits to be derived from logger education and careful harvest layout are clear (Bruhn 1986, Dey 1994, McNeel and Copstead 1994, Nyland 1994, Ostrofsky *et al.* 1986). While it is not possible to completely avoid residual stem damage, it is important to realize that we will live with the effects of harvest disturbance for a long time.

While relationships detected by stepwise logistic regression (SLR) are not necessarily causal, SLR is a valuable tool for exploring potential relationships in a data set. Our SLR analysis of the probability of tree injury during the first MOFEP harvest included only factors of MOFEP experimental design (i.e., silviculture system and statistical block) or of direct hypothetical interest (table 3). As such, the results are instructive in designing future planned comparisons. A few of the detected associations merit emphasis. Two of the 13 logging crews involved with our 56 plots were associated with less damage than the other crews. Crew 5 harvested seven plots, and crew 8 harvested five plots (table 2). It would be difficult to determine whether these two crews were assigned easier plots to harvest, harvested the plots they were assigned more carefully, or both. All skidding was accomplished with rubber-tired tractors hauling merchantable tree-length logs. Meyer *et al.* (1966) found that rubber-tired tractors skidding tree-length logs caused excessive damage compared with log-length skidding. The generally lower probability of injury under UAM in this first MOFEP harvest may be partly due to the skidding of fewer and smaller stems out of or through plots under this system than under EAM. Probability of stem injury was also associated with the number of large stumps created within plots. Stump size is directly related to merchantable tree length. The greater probability of injury in stands with northern to north-eastern slope aspects is likely due to higher soil moisture levels and higher site index values in these more productive stands (J. M. Kabrick, personal communication). The declining probability of stem injury as the growing season progressed is explained by the progressive tightening of bark with the advancing growing season. Overall, the 82.6 percent concordance of our SLR model suggests that important variables determining probability of stem injury were included (tables 3 and 12).

Loss of commercial tree value due to direct stem injury depends heavily on the tree species, its initial condition, and the desired product mix

(e.g., veneer, lumber, or charcoal). We have deliberately refrained at this time from predicting the economic consequences of 1) different types and sizes of stem injury, 2) different frequencies of stem injuries, and 3) levels of structural root damage associated with skidder tracks. We have also refrained from predicting the economic costs of reducing disturbance levels. Nevertheless, the documentation approach we have taken provides the baseline data necessary for followup studies of dynamics of wood products quality (e.g., mortality, rates of wound closure and defect development) as well as dynamics of forest health and structure. Results of this and related studies will facilitate evaluation and enhancement of forest operation guidelines to maintain or improve overall forest health.

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Landscape-level Effects of Forest Management on Bird Species in the Ozarks of Southeastern Missouri

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Abstract.—This study was designed as an experiment to test how bird populations in an extensively forested landscape respond to small (group and single-tree selection) and large (clearcut) openings. Our objectives are to test the landscape-level effects of even-aged and uneven-aged forest management relative to no-harvest management on population density and reproductive success for forest-interior and early-successional bird species. Pre-treatment data were gathered during the period 1991 through 1995, treatments were applied in 1996 and early 1997, and post-treatment data have been collected from 1997 through the present. Immediately following treatment, populations of forest-interior species declined on all study sites. Post-treatment, forest-interior species responded both positively and negatively to the even-aged and uneven-aged treatments. For early-successional species, changes in density were positive in response to both even-aged and uneven-aged treatment types. Neither nest predation rates nor nest parasitism rates increased following treatment. From a landscape-level perspective, our findings indicate that the short-term effects of even-aged management are mixed, positive and negative, for forest-interior species and that the response by early-successional species is greater for even-aged than for uneven-aged management.

Planning for the MOFEP bird study began in 1989 and we have collected data since 1991. At the time this study was being planned, much of the work that had been done on migratory forest songbirds had been conducted in landscapes comprising mixtures of forest and other habitats, but in areas where forest was fragmented and a lesser component of the landscape. We were concerned that processes that

affected avian populations in these landscapes also might be at work in landscapes dominated by forest, so we collaborated with scientists in related disciplines in the design and implementation of the MOFEP experiment. While we have been working on MOFEP, other researchers have turned their attention to forest-dominated landscapes and the effects of forest management on migratory forest birds. The other studies that have been done, such as Thompson *et al.* (1992), Annand and Thompson (1997), and Robinson and Robinson (1999), have been observational or correlational in nature. An important distinction to note is that MOFEP is a manipulative experiment. Thompson *et al.* (2000) recommended that, while observational studies can provide insights into the processes that affect bird populations, manipulative experiments such as MOFEP should be conducted to test and confirm key hypotheses that are generated by the observational/correlational studies. Taken together, the results of all these studies should provide forest managers with important insights into the effects of their management decisions on the forest bird community.

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The MOFEP bird study was designed to experimentally test how avian populations in an extensively forested landscape respond to even-aged and uneven-aged forest management, by examining how large (clearcut) and small (group and single-tree selection) openings affect avian abundance and demographic patterns at the landscape level, and whether or not timber harvest constitutes a negative disturbance of the habitat. Studies in central Missouri had shown that those species of migratory songbirds that required the interior of mature forest responded negatively to forest fragmentation in a number of ways. They avoided forest fragments even though the fragments often were hundreds of times larger than the typical breeding territory (Hayden *et al.* 1985). They occurred at reduced densities on the smallest of those fragments where they did occur (Wenny *et al.* 1993). They had reduced pairing success on smaller fragments (Gibbs and Faaborg 1990, Van Horn *et al.* 1995) and showed reduced nesting success of those nests that occurred as fragments got smaller in size (Donovan *et al.* 1995). Both nest predation and cowbird parasitism were shown to be mechanisms causing these patterns (O'Conner and Faaborg 1993, Donovan *et al.* 1995).

Timber harvest changes the composition of the avifauna of a forest by reducing, for a period of time, habitat quality for species that require mature trees. On the other hand, it improves habitat quality for species that use clearings or early-successional habitats, again for a period of time. Even-aged management creates large openings (clearcuts) that are unsuitable for forest-interior birds (King *et al.* 1996). In contrast, uneven-aged management produces a heterogeneous habitat of mature trees interspersed with small openings that may or may not be suitable for forest-interior birds and may or may not be sufficiently open to attract early-successional species (Dickson *et al.* 1995, Lent and Capen 1995, Thompson *et al.* 1995).

Once a clearing has been created, the interface between the forest and the clearing is an edge. Recent studies have shown that edge habitats are correlated with a number of negative effects for migrant songbirds, including increased brood parasitism and increased nest predation (Paton 1994, Faaborg *et al.* 1995). The occurrence of negative edge effects, however, is not uniform among landscapes or regions. In general, landscapes that are composed of forest and non-forest habitats, especially agriculture,

often show high rates of nest parasitism and predation (Robinson 1992, Robinson and Wilcove 1994, Faaborg *et al.* 1995). Edges created by timber harvest within a forested landscape, however, generally show lower rates of nest parasitism and predation (Lent and Capen 1995, King *et al.* 1996). Strong relationships between the amount of forest cover within landscapes and nest parasitism and nest predation rates have been found by Donovan *et al.* (1997, 2000), Hartley and Hunter (1998), Hochachka *et al.* (1999), and Robinson *et al.* (1995).

Thompson *et al.* (1992) studied the effects of even-aged management on the abundance of several forest-interior and early-successional forest bird species, and Annand and Thompson (1997) compared the effects of even-aged forest management and uneven-aged forest management on the abundance of a similar set of forest bird species. These studies were conducted in the heavily forested Ozarks of south Missouri. Both studies found that individual species responded differently to the different treatments: some forest-interior species responded negatively to even-aged cuts, but some responded positively; some early-successional species were found in both smaller and larger openings, but some were found only in larger openings. Robinson and Robinson (1999) studied the effects of uneven-aged management on birds in southern Illinois. They found apparently depressed levels of two forest-interior species within treated areas. Among early-successional birds, only the species that responded to smaller openings were found.

Much of the work cited above has occurred since the MOFEP experiment began in 1989. Our goal was and continues to be to measure the landscape-level effects of even-aged and uneven-aged management on select forest songbirds via a manipulative experiment. Given the recent studies that show how landscape context plays a significant role in determining what, if any, edge effects occur, and the observational studies on forest management that have been conducted, we are in an even better position with the MOFEP bird study to assess the effects of these two forest management practices on populations of forest songbirds.

In this paper we present a synopsis of 5 years of pre-treatment data and post-treatment data from 3 years following the first set of treatments on the MOFEP sites. We discuss the successes

and difficulties we have encountered during the course of our study. In an ongoing process, we are analyzing the bird study data and will report the results of these analyses in other outlets, as well. Our first paper was written prior to this symposium and was submitted as Gram *et al.*, (in prep.).

OBJECTIVES

The overall, long-term objectives of the MOFEP bird study are:

1. To determine differences in breeding densities of some common forest songbirds in forest managed by the even-aged, uneven-aged, and no-harvest methods,
2. To determine rates of nest parasitism, nest predation, and reproductive success for these songbirds in forests managed by the even-aged, the uneven-aged, and no-harvest methods.

METHODS

The MOFEP sites have been described in detail elsewhere (Brookshire *et al.* 1997). Bird data were gathered during the periods 1991-1995 and 1997-the present. Treatments were applied during 1996 and early 1997.

Initially, we selected five forest-dwelling species for intensive study: Ovenbird (see table 1 for scientific names), worm-eating warbler, Kentucky warbler, wood thrush, and Acadian flycatcher. Data also were gathered on other neotropical migrant forest birds, including species such as indigo bunting and blue-winged warbler that are associated with forest edge or second growth. These were selected because:

- 1) they are territorial and vocal, thus allowing estimates of their densities via spot-mapping;
- 2) their nests are generally accessible for monitoring of reproductive success;
- 3) we had comparable data on abundance and demography of these species from fragmented habitats in prior or concurrent studies.

In fact, we gathered data on all forest birds, including species such as scarlet tanager, yellow-throated warbler, and eastern wood pewee. The list is extensive (table 1). However, for most of these species, we gathered only

Table 1.—Bird species for which density data were collected

Focal Forest-Interior Species

Acadian flycatcher (*Empidonax virescens*)
 Wood thrush (*Hylocichla mustelina*)
 Worm-eating warbler (*Helmitheros vermivorus*)
 Ovenbird (*Seiurus aurocapillus*)
 Kentucky warbler (*Oporornis formosus*)

Focal Early-successional Species

Blue-winged warbler (*Dendroica pinus*)
 Prairie warbler (*Dendroica discolor*)
 Yellow-breasted chat (*Icteria virens*)
 Hooded warbler (*Wilsonia citrina*)
 Indigo bunting (*Passerina cyanea*)

Other Forest-Interior Species for which Density Data Were Collected

Pileated woodpecker (*Dryocopus pileatus*)
 Yellow-billed cuckoo (*Coccyzus americanus*)
 Great crested flycatcher (*Myiarchus crinitus*)
 Eastern wood pewee (*Contopus virens*)
 Eastern phoebe (*Sayornis phoebe*)
 Carolina chickadee (*Parus carolinensis*)
 Eastern tufted titmouse (*Parus bicolor*)
 White-breasted nuthatch (*Sitta carolinensis*)
 Carolina wren (*Thryothorus ludvicianus*)
 Blue-gray gnatcatcher (*Poliophtila caerulea*)
 Yellow-throated vireo (*Vireo flavifrons*)
 Red-eyed vireo (*Vireo olivaceus*)
 Black-and-white warbler (*Mniotilta varia*)
 Northern parula (*Parula americana*)
 Cerulean warbler (*Dendroica cerulea*)
 Yellow-throated warbler (*Dendroica dominica*)
 Pine warbler (*Dendroica pinus*)
 Louisiana waterthrush (*Seiurus motacilla*)
 Scarlet tanager (*Piranga olivacea*)
 Summer tanager (*Piranga rubra*)

Other Early-successional Species for which Density Data Were Collected

Mourning dove (*Zenaida macroura*)
 Eastern bluebird (*Sialia sialis*)
 White-eyed vireo (*Vireo griseus*)
 Common yellowthroat (*Geothlypis trichas*)
 Northern cardinal (*Cardinalis cardinalis*)
 Rufous-sided towhee (*Pipilo erythrophthalmus*)
 Field sparrow (*Spizella pusilla*)



spot-mapping density data because their nests are located in the forest canopy where we cannot monitor them to determine reproductive success.

To facilitate study, each of the nine study areas was laid out in a grid system for orientation and subdivision. Grid lines run E-W and N-S and were approximately 300 m apart. Trees along grid lines were permanently marked with orange paint. Junctions were flagged and identified as to location on the grid. To equalize effort among the nine study sites, the exterior portions of the larger sites (study areas 1 - 4, 6, 7, and 9) were excluded from study, resulting in sampling areas per site that ranged from 278 to 355 ha.

Bird densities were determined through spot-mapping (Robbins 1970). Each study area was divided into seven spot-mapping plots, each of which was approximately 45 ha in size. Each plot was visited 8 to 10 times at 2- to 3-working-day intervals from mid-May through the end of June. Mappers used enlarged topographic maps of the spot-map plots to orient themselves and marked all detections of birds on their maps, along with the path used in making the map. Workers were instructed to use a different route across the plot from the one used in the prior visit. One map was produced each day a spot map plot was visited; most maps took 3 to 4 hours to complete. To determine densities, composite maps were compiled for each species. To locate territories, we looked for clusters of observations (≥ 3). In addition to the density data for each plot each year, territory locations have been entered into a GIS system.

To determine reproductive success, nests were located and monitored while spot-mapping and by deliberate searching from mid-May through July. Nest locations were recorded on enlarged topographic maps and marked on-site by flagging. Nests were monitored every 3-5 days until nest fate was determined. Evidence of predation and parasitism was noted as part of data collection procedures. This produced reproductive data and a permanent record of nest locations. Daily survival rates were calculated using the methods of Mayfield (1961, 1975) as modified and categorized by the protocol for the Breeding Biology Research Database (BBIRD) program (Martin *et al.* 1997).

Birds also were captured in mist nets and banded to examine movements and return

rates. During the pre-treatment phase of the study, 13 mist net lines, each containing 12 nets (36-mm mesh) set 50 m apart, were placed systematically throughout each study area on the east-west grid lines. Following treatment on the even-aged sites, two of the net lines were modified as follows: instead of following grid lines, nets were placed at 50-m intervals along the border of a clearcut, with one end attached to a tree at the edge and the net strung towards the interior of the cut. Net lines (and net locations) were marked on the topographic maps to ensure consistent placement of nets on an annual basis. Each net line was run for two consecutive mornings from dawn to noon. All birds captured in the nets were identified, aged, sexed, banded with U.S. Fish and Wildlife Service bands, and released.

Each summer, 24-27 field assistants helped us conduct the bird study. The students were enrolled in an Undergraduate Research Internship through the University of Missouri-Columbia, which provided a stipend, research credit, and a chance to do independent projects.

RESULTS

Avian Density

In this paper, we have focused our attention on five forest-interior species (ovenbird, worm-eating warbler, Acadian flycatcher, wood thrush, and Kentucky warbler) and four species of early-successional birds (indigo bunting, hooded warbler, yellow-breasted chat, and prairie warbler). We were interested in answering two questions: 1) Do treatments affect the densities of forest-interior birds? 2) To what extent do early-successional birds respond to the treatments?

Table 2 lists the focal species and displays the number of study sites on which they were detected each year throughout the study. Four of the five focal forest-interior species have been observed on all nine sites every year. The exception, Kentucky warbler, has been detected on a majority of the sites each year, but exists in low densities and was observed on all nine sites only in one year, 1992. Three of the four focal early-successional species were detected on some or all of the study sites prior to the treatments, but all four have been observed much more consistently since then.

Table 2.—The number of study sites on which the focal species were detected each year

Species	1991	1992	1993	1994	1995	1997	1998	1999
Acadian flycatcher	9	9	9	9	9	9	9	9
Wood thrush	9	9	9	9	9	9	9	9
Ovenbird	9	9	9	9	9	9	9	9
Worm-eating warbler	9	9	9	9	9	9	9	9
Kentucky warbler	7	9	6	5	8	6	7	7
Yellow-breasted chat	1	3	2	6	5	6	7	7
Prairie warbler	0	2	2	0	2	2	4	4
Hooded warbler	0	0	0	0	0	4	5	6
Indigo bunting	2	8	8	9	9	9	9	9

Figures 1-5 show the observed densities of the forest-interior species during the pre-treatment phase of the study, 1991-1995, and during the first 3 years of observed densities following treatment, 1997-1999. The populations of all five forest-interior species dropped from the pre-treatment period to the post-treatment period, including those on the untreated (control) sites. It is possible that the timber harvest activity constituted a disturbance in a large area, and that it had effects beyond the boundaries of the treated sites, even to the point of affecting populations on the nearby control sites. Gram *et al.* (2001) reported that many species showed evidence of changes in density in the post-treatment period, with both declines and increases in densities across all species groups and treatments following the timber harvest in 1996. Even so, we are able to see possible treatment effects on several species.

The response to the treatments varied among the forest-interior species. Ovenbirds declined more on both the even-aged and uneven-aged treatments than on the control sites (fig. 1). Wood thrushes initially declined on both treatments and the controls, but have increased on the even-aged sites during the post-treatment period (fig. 4). Kentucky warblers have never been found in high densities on any of the MOFEP sites, but seem to have responded to the treatments and increased on both treatment sites after timber harvest (fig. 5). Worm-eating warblers declined initially on both treatment types and the control sites, but since have rebounded on all three (fig. 2). Acadian flycatchers declined on both types of treatment and the controls (fig. 3).

A number of early-successional birds responded positively and dramatically to the newly available habitat created by the treatments on the 10-12 percent of the study sites that were disturbed (see figs. 6-9). However, because we are examining bird populations at the landscape (study site) scale, conversion of densities to number of territories per 100 ha for entire study sites diluted the numbers, making total increases relatively small. Indigo buntings responded dramatically to both treatments, increasing their densities many fold in the post-treatment period on both even-aged and uneven-aged sites (fig. 6). Yellow-breasted chats responded to both treatments, especially the even-aged treatment, by increasing density on both treatment types (fig. 8). Prairie warblers seemed to respond only to the even-aged treatment (fig. 9). Hooded warblers were practically non-existent on the study areas prior to treatment and have moved into the cuts produced by both treatments (fig. 7). No species showed greater density increases on the uneven-aged treatment sites versus the even-aged sites, but several species showed greater increases on the even-aged sites versus the uneven-aged sites.

Avian Reproduction

To this point in the study, we have found and monitored over 1,600 nests. However, when these data are divided by species, year, and treatment, the number of nests per category can be too small to be useful for examination. For this paper, therefore, we grouped the data from all of the nests that we have monitored into three guilds: 1) tree-nesting forest-interior birds, 2) ground-nesting forest-interior birds, and 3) shrub-nesting early-successional birds.

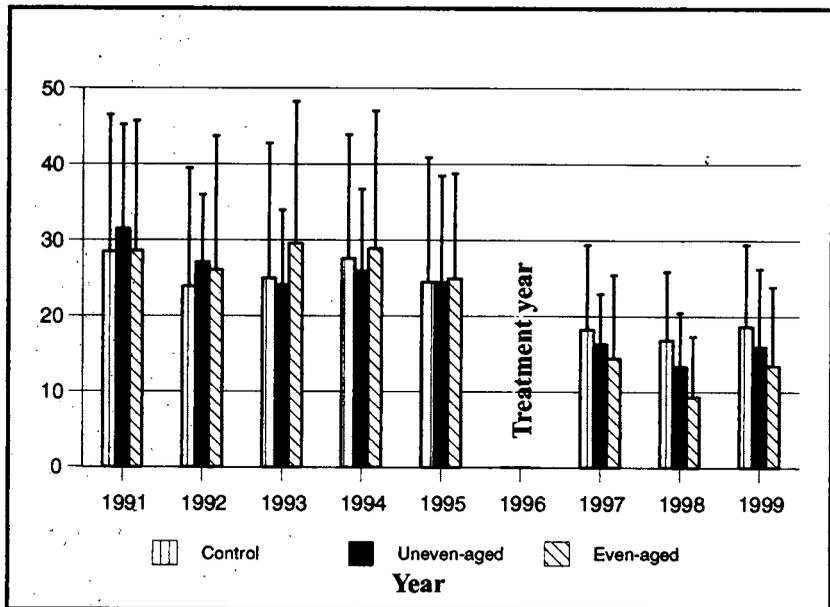


Figure 1.—Mean densities (number of territories per 100 ha) and standard errors for overnird, 1991-1995 and 1997-1999.

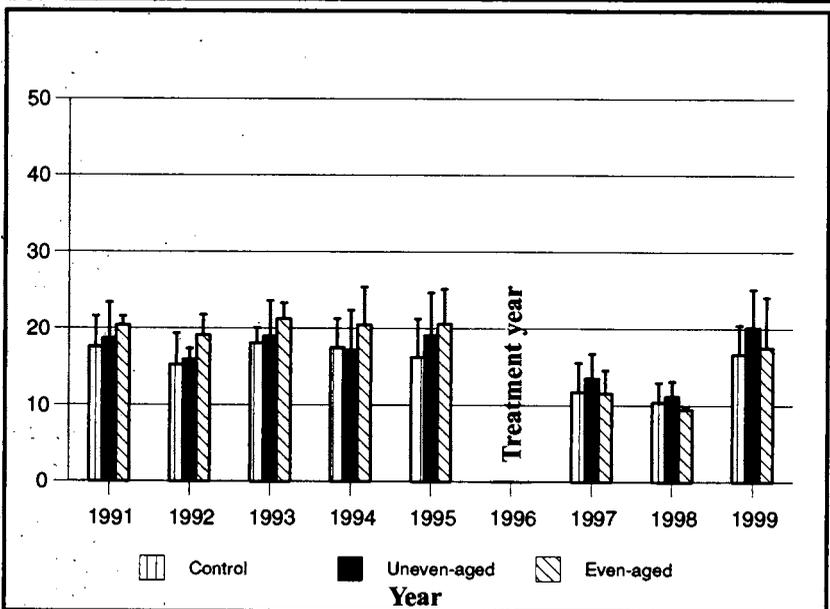


Figure 2.—Mean densities (number of territories per 100 ha) and standard errors for worm-eating warbler, 1991-1995 and 1997-1999.

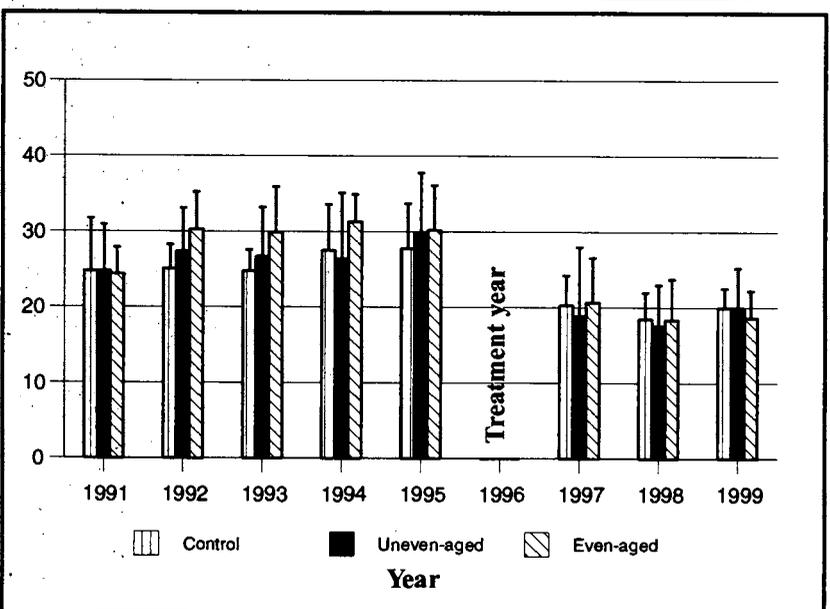


Figure 3.—Mean densities (number of territories per 100 ha) and standard errors for Acadian flycatcher, 1991-1995 and 1997-1999.

Figure 4.—Mean densities (number of territories per 100 ha) and standard errors for wood thrush, 1991-1995 and 1997-1999.

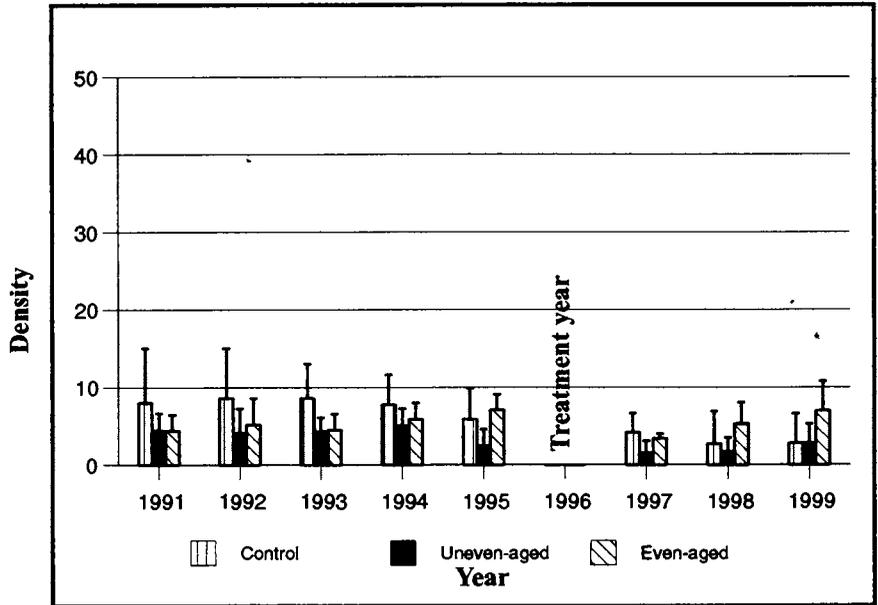


Figure 5.—Mean densities (number of territories per 100 ha) and standard errors for Kentucky warbler, 1991-1995 and 1997-1999.

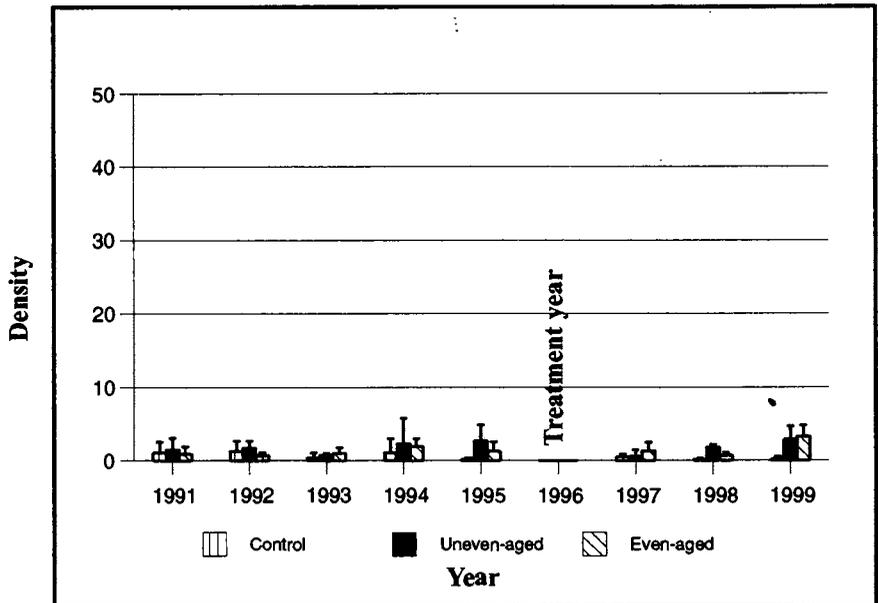
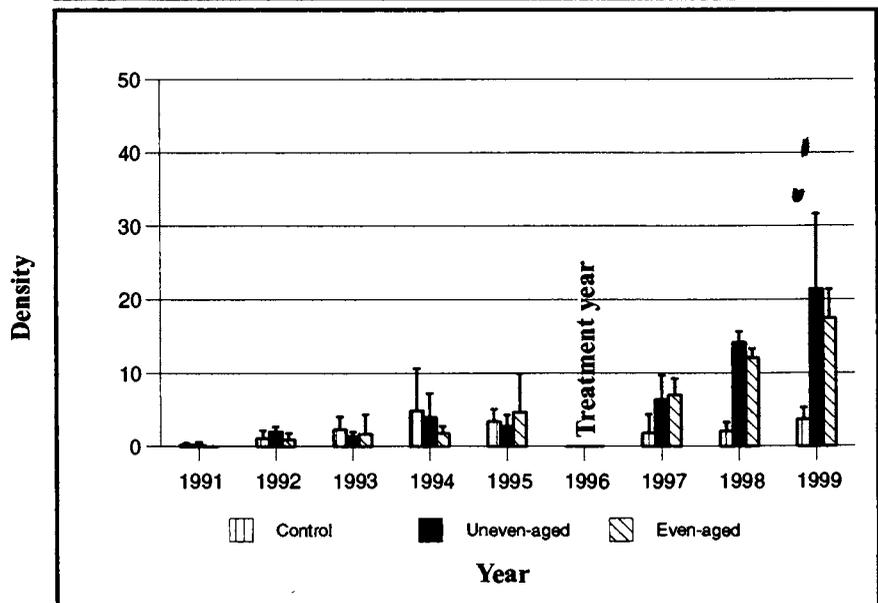


Figure 6.—Mean densities (number of territories per 100 ha) and standard errors for indigo bunting, 1991-1995 and 1997-1999.



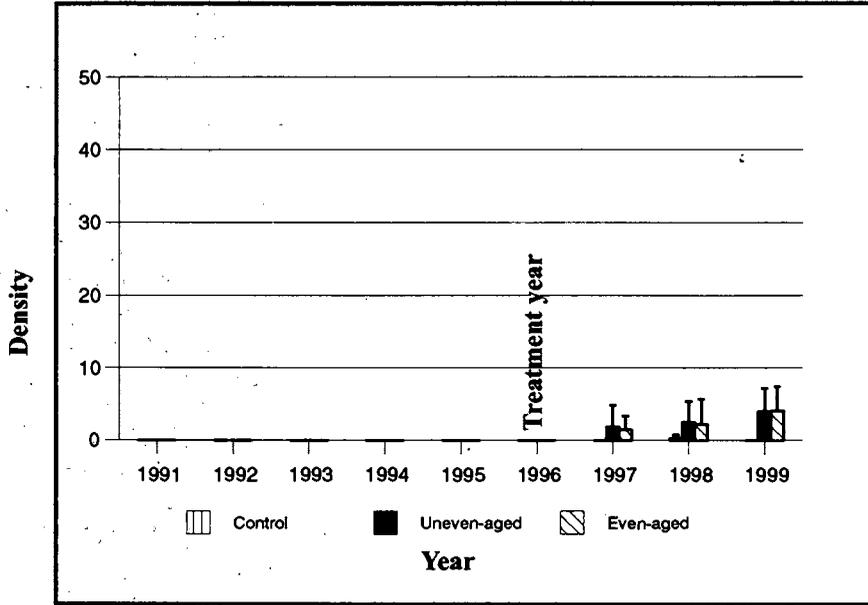


Figure 7.—Mean densities (number of territories per 100 ha) and standard errors for hooded warbler, 1991-1995 and 1997-1999.

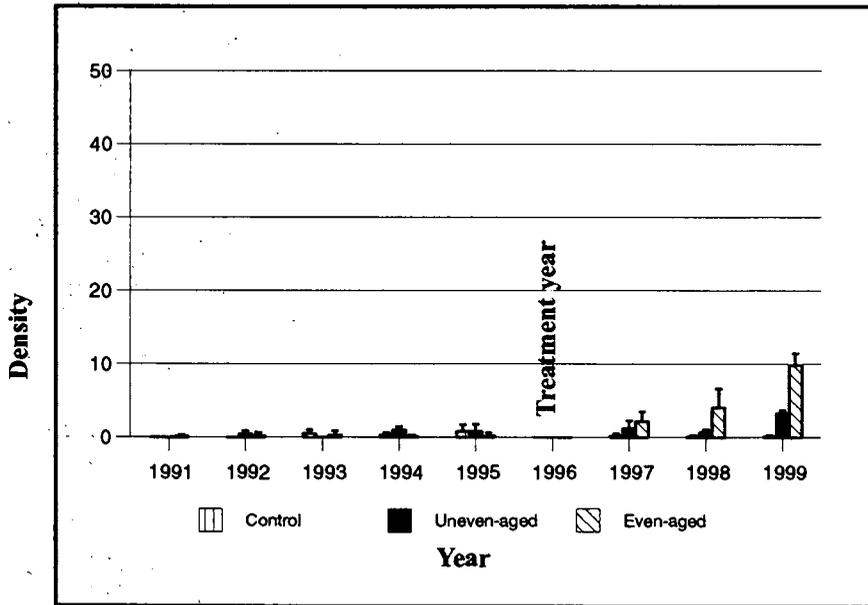


Figure 8.—Mean densities (number of territories per 100 ha) and standard errors for yellow-breasted chat, 1991-1995 and 1997-1999.

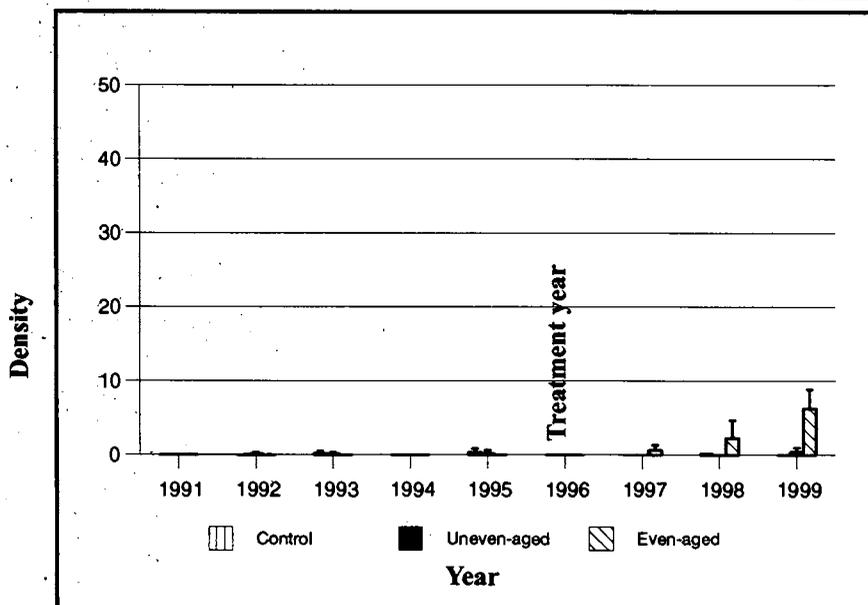


Figure 9.—Mean densities (number of territories per 100 ha) and standard errors for prairie warbler, 1991-1995 and 1997-1999.

We calculated daily survival rates and rates of brood parasitism for these groups, subdividing the data for the study sites by treatment type during the pre-treatment and post-treatment periods (see tables 3-5).

During the pre-treatment period, we monitored between 84 and 142 nests of tree-nesting forest-interior species annually (table 3). Daily survival rates ranged from 0.95 to 0.98 per year and the rate of brood parasitism ranged from 0 to 16.7 percent. During the post-treatment period we found between 107 and 172 nests annually. Post-treatment daily survival rates ranged from 0.95 to 0.98; they were similar among treatments and were comparable to those observed prior to treatment. Rates of brood parasitism in the several treatment categories ranged from 0 to 10.1 percent and were within the pre-treatment range of observations. The predominant species in our sample were Acadian flycatcher, wood thrush, and red-eyed vireo, but we also have data from yellow-billed cuckoo, summer and scarlet tanagers, eastern wood pewee, and eastern phoebe.

Nests of ground-nesting forest-interior birds were somewhat harder to find than those of tree-nesters, and not as many species placed their nests on or near the forest floor. As a result, we monitored fewer ground nests, between 38 and 63 annually, during the pre-treatment period, and 39 to 102 nests annually post-treatment (table 4). Daily survival rates pre-treatment ranged from 0.89 to 0.97 and brood parasitism rates ranged from 0 to 14.3

percent. Post-treatment daily survival rates ranged from 0.94 to 0.98; as above, they were similar among treatments and were comparable to those observed prior to treatment. Rates of brood parasitism post-treatment ranged from 0 to 7.1 percent and most were within the range observed prior to treatment. The predominant species in our sample were ovenbird, worm-eating warbler, and black-and-white warbler, but we also have data from Kentucky warbler, Louisiana water thrush, and Carolina wren.

Nests of shrub-nesting early-successional species were uncommon prior to treatment, but the number that we found and monitored was rising during the pre-treatment period and rose dramatically post-treatment (table 5). Most of the nests found in the pre-treatment period were indigo bunting. The rising number of nests found in 1993-1995 did not represent an increase in density of buntings (see figure 6), but instead represented increased attention to the species in anticipation of the upcoming treatment. Pre-treatment daily survival rates ranged from 0.86 to 1.00, but sample sizes were low. Brood parasitism rates ranged from 0 to 7.7 percent. Post-treatment, daily survival rates ranged from 0.92 to 1.00 and brood parasitism rates ranged from 0 to 25.0 percent. The predominant species in our sample were indigo bunting and northern cardinal, but we also have data from mourning dove, hooded warbler, yellow-breasted chat, common yellowthroat, blue-winged warbler, prairie warbler, and white-eyed vireo.

Table 3.—Daily survival rates (DSR) and parasitism rates for tree-nesting forest-interior songbirds, 1991-1995 and 1997-1999

	Control			Uneven-aged			Even-aged		
	No. Nests	# Par. (%)	DSR	No. Nests	# Par. (%)	DSR	No. Nests	# Par. (%)	DSR
1991	39	1 (2.6)	0.96	18	3 (16.7)	0.97	27	0 (0)	0.95
1992	37	1 (2.7)	0.95	30	0 (0)	0.95	25	0 (0)	0.97
1993	64	4 (6.3)	0.96	35	1 (2.9)	0.95	36	1 (2.8)	0.98
1994	35	1 (2.9)	0.96	28	0 (0)	0.95	32	0 (0)	0.96
1995	64	5 (7.8)	0.96	29	1 (3.4)	0.95	49	2 (4.1)	0.97
1997	69	7 (10.1)	0.95	47	2 (4.3)	0.95	56	2 (3.6)	0.96
1998	44	1 (2.3)	0.95	27	1 (3.7)	0.95	36	1 (2.8)	0.97
1999	33	0 (0)	0.98	35	0 (0)	0.96	44	1 (2.3)	0.95



Table 4.—Daily survival rates (DSR) and parasitism rates for ground-nesting forest-interior songbirds, 1991-1995 and 1997-1999

	Control			Uneven-aged			Even-aged		
	No. Nests	# Par. (%)	DSR	No. Nests	# Par. (%)	DSR	No. Nests	# Par. (%)	DSR
1991	15	0 (0)	0.92	17	0 (0)	0.97	19	0 (0)	0.95
1992	18	0 (0)	0.96	19	1 (5.3)	0.95	16	1 (6.3)	0.96
1993	18	0 (0)	0.94	14	1 (7.1)	0.94	6	0 (0)	0.89
1994	15	1 (6.7)	0.97	19	0 (0)	0.97	21	1 (4.8)	0.95
1995	21	3 (14.3)	0.95	21	1 (4.8)	0.96	21	0 (0)	0.97
1997	34	1 (2.9)	0.94	29	1 (3.4)	0.95	39	2 (5.1)	0.96
1998	21	0 (0)	0.98	14	1 (7.1)	0.95	21	0 (0)	0.94
1999	7	0 (0)	0.94	10	0 (0)	0.95	22	0 (0)	0.98

Table 5.—Daily survival rates (DSR) and parasitism rates for shrub-nesting early-successional songbirds, 1991-1995 and 1997-1999

	Control			Uneven-aged			Even-aged		
	No. Nests	# Par. (%)	DSR	No. Nests	# Par. (%)	DSR	No. Nests	# Par. (%)	DSR
1991	0	--	--	1	0 (0)	1.00	1	0 (0)	1.00
1992	0	--	--	0	--	--	1	0 (0)	1.00
1993	3	0 (0)	0.96	7	0 (0)	0.98	1	0 (0)	0.90
1994	10	0 (0)	0.97	5	0 (0)	0.98	5	0 (0)	0.95
1995	6	0 (0)	0.86	4	1 (25.0)	0.93	17	0 (0)	0.98
1997	7	0 (0)	0.92	11	1 (9.1)	0.93	10	0 (0)	0.96
1998	3	0 (0)	1.00	24	2 (8.3)	0.94	15	0 (0)	0.97
1999	7	0 (0)	0.95	58	5 (8.6)	0.97	44	3 (6.8)	0.97

To biologically interpret daily survival rate, one can convert the figure into "nesting success" as follows: the probability that a nest will survive the entire nesting cycle is calculated by raising the figure to the exponent of the number of days in the nesting cycle for a particular species.

However, because the data presented herein are composites for guilds that are composed of species with different lengths of nesting cycles, nest success cannot be calculated for the guilds. We have calculated nesting success elsewhere (Gram *et al.*, in prep.) and calculated that nest success rates averaged 29 percent for the five species for which there were 50 or more nests in the data (Acadian flycatcher, ovenbird, worm-eating warbler, wood thrush, and indigo bunting). There did not appear to be any distinguishable changes in nest success from pre- to post-treatment.

Mist Netting

As with the other data, we subdivided the mist netting data by treatment type for the pre-treatment and post-treatment periods (see table 6). The number of birds caught per net line (a net line consists of 12 nets that have been run for two consecutive mornings) ranged from 5.18 (± 1.52) to 13.74 (± 3.36) birds during the pre-treatment period. The rate of recapture of previously banded birds ranged from 2.5 to 9.2 percent. Post-treatment, the number of birds caught per net line remained low (in fact, dropped) on the control sites to 3.84 (± 1.77) to 6.51 (± 0.67) birds per line, while the capture rate climbed somewhat to 11.88 (± 3.96) to 15.79 (± 3.92) birds on the uneven-aged sites. In 1997 the slash from the timber harvest prevented us from placing any nets in the

Table 6.—Mist netting results, 1991-1995 and 1997-1999

	Control			Uneven-aged			Even-aged			No. recaptured
	No. Birds Net- ted	No. Caught Per Net Line (SE)		No. Birds Net- ted	No. Caught Per Net Line (SE)		No. Birds Net- ted	No. Caught Per Net Line (SE)		
1991	250	7.58 (0.23)		358	10.85 (5.99)		334	10.12 (0.73)		—
1992	329	9.14 (1.69)		327	9.09 (1.01)		313	8.70 (2.57)		24 (2.5%)
1993	280	7.78 (1.14)		337	9.36 (3.88)		269	7.47 (2.17)		70 (7.9%)
1994	428	10.97 (0.92)		536	13.74 (3.36)		461	11.82 (4.50)		104 (7.3%)
1995	255	6.54 (2.62)		251	6.44 (2.38)		202	5.18 (1.52)		65 (9.2%)
1997	215	6.51 (0.67)		392	11.88 (3.96)		328	9.94 (2.54)		18 (1.9%)
1998	162	4.91 (0.90)		478	14.48 (2.42)		560	16.97 (5.89)		23 (1.9%)
1999	92	3.84 (1.77)		379	15.79 (3.92)		624	26.00 (12.83)		36 (3.3%)

clearcuts on the even-aged sites and our capture rate was similar to pre-treatment numbers at 9.94 (\pm 2.54) birds per line. After nets were placed around the borders of clearcuts in 1998, however, the capture rate shot up to 16.97 (\pm 5.89) birds and climbed further to 26.00 (\pm 12.83) birds in 1999. Post-treatment, the rate of recapture of banded birds on all sites was low and remained low, ranging from 1.9 to 3.3 percent.

DISCUSSION

We have generated a very large set of data describing the composition, abundance, and reproductive success of the forest bird community of the Ozarks of southeastern Missouri, and have data in hand with which to begin developing an understanding of the response of these species to two types of forest management applied to the MOFEP sites. We have density data for forest songbirds at the level of an entire study site for the nine MOFEP sites. This level of data is unique in the country. We have accompanying data from monitoring the nests of these birds. These data will allow us to consider both abundance and reproductive success when we seek to determine the effects of forest management on the bird community.

We have, however, encountered unanticipated difficulties that must be addressed as the MOFEP experiment and the bird study continue. The most serious of these difficulties arose in the even-aged sites, where the downed material (mostly felled tree tops) and the explosion of growth (the most problematic of which

was grape vine) prevented our workers from penetrating the interior of the largest of the clearcuts. This was not a big problem initially, because observers could scan all the way across the cuts. By the third year post-treatment, however, the newly sprouted trees grew beyond head height, severely limiting our capability to spot-map the entire opening. The tangle of downed material and vines, and the profusion of small stems, also prevented our personnel from searching for nests beyond the edges of the openings. When we recognized that we had a problem, we created narrow paths through several of the clearcuts as a possible solution. From these paths we were better able to survey the cuts and doubled or nearly doubled the number of observed territories for early-successional species within the openings. We therefore recommend that, after subsequent rounds of treatment, paths be cleared immediately following treatment in large, even-aged cuts, and that these paths be marked and maintained in the post-treatment years. As the stands that were treated in 1996 grow, we will continue to monitor the situation so that we also will be able to recommend the time period through which such paths must be maintained. We have taken steps to eliminate or reduce the likelihood that these "bird paths" will negatively affect the results of our study or the other MOFEP studies by 1) avoiding the sampling plots for the other studies, 2) creating narrow paths, 3) making the paths meander through the cuts, and 4) siting the paths so they do not open at the edges of the cuts.



Another difficulty that we encountered concerned mist netting in the forest. Although we have captured and banded thousands of birds during the course of the study, it is only because of the very large number of nets employed across the landscape that we have captured very many birds at all. When examined critically, the capture rates for our mist netting effort in mature forest have been disappointingly low and raise questions as to the return in data for the effort required to collect it. Since the treatments were applied, capture rates have picked up in both even-aged and uneven-aged treatment types, especially in the even-aged openings. We speculate that this has occurred for two reasons: 1) the influx of early-successional birds, and 2) the dense vegetation in the openings also attracts family groups of forest-interior species once the young have fledged. We recommend that future mist netting be targeted to address specific issues and needs of the bird study, rather than conducted generally across the landscape.

Because MOFEP is a long-term experiment that will go on for 100 years or longer, it would be premature in the extreme to draw final conclusions based upon only 3 years of data following the very first treatment. There are, however, trends in the composition and the demographics of the avifauna that can be discerned and reported, even at this early point in the experiment. First of all, it appears that the treatments have not caused the dire consequences that might have been predicted 10 years ago. The forest-interior species that were of concern when the study was initiated remain dominant and important parts of the species composition of the study sites. Reproductive success, as measured by daily survival estimates for nests, did not decline. Brood parasitism did not increase. In addition, early-successional species have responded to the habitat created by the treatments, resulting in an increase in the diversity of the avifauna on the study sites.

As the MOFEP experiment continues, it will be important to continue monitoring birds for a number of reasons. Determining the responses of the different species to the different treatments will be critical to understanding the functioning of the Ozark forest and the implications of active management. The first treatments affected only a small percentage of the overall area. The openings that were created will

close in with regenerated forest, and the composition of the avifauna within those openings will be dynamic and changing. It can be assumed that the early-successional species will plateau and then decline as the new forest begins its long maturation process; at some point, the forest-interior species will begin to reoccupy the space (Johnston and Odum 1956). Knowledge about when and how these changes take place will help us predict what will happen in subsequent treatments.

As treatments are applied at intervals through time, a mosaic of different-aged forest will be created on the study sites. It will take a number of cutting cycles before the age composition of the forest and the interspersed of treated stands will approximate the long-term condition that will be attained after a full rotation of 100 years. The composition and demographics of the avifauna probably will remain in flux until that time, so regular, if not constant, monitoring of the bird population will be required to remain on top of the situation. We hope that the data we have gathered and the techniques we have tried and implemented will be valuable to the researchers who will follow us, and will allow them to make informed decisions about data collection and interpretation in the future. Ultimately, of course, the goal of this study is to provide to forest managers the information they need to manage the birds and all the other components of the Ozark forest ecosystem.

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Short-term Responses of the Small Mammal Communities to Forest Management Within Missouri Ozark Forest Ecosystem Project Sites

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Abstract.—We conducted a capture-recapture study on the north-east-facing slopes of the MOFEP sites in south central Missouri to determine the initial effects of even- and uneven-aged forest management on species composition, species richness, and relative abundance of the small mammal communities. We compared changes between pre-treatment (1994-1995) and post-treatment (1998-2000) measures. Species richness ranged from two to six species per site across years; eight different species were caught across all nine sites and years. Overall small mammal relative abundance estimates ranged from 0.23 to 7.75 individuals captured per 100 trap nights per site across years. Qualitative and quantitative evaluations indicate that forest management had no short-term effect on species composition or species richness, but did have an effect upon total small mammal relative abundance 2, 3, and 4 years after harvest. Even-aged management, and uneven-aged management to a lesser extent, appeared to have dampened a natural decline in small mammal relative abundance that was observed on control sites. Relative abundance estimates on treated sites were slightly higher than those on control sites.

Interest in North American forests has evolved from one of exploitation, to managed timber harvests, to conservation of the forest ecosystem. With this increased interest in managing forests for wildlife as well as trees, and in managing for all animals, not just game, threatened, or endangered species, natural resource management agencies have found they need information about the effects of their silvicultural practices on wildlife communities. Small mammals are an important component of forest ecosystems. They are prey for a number of predators, disperse plant seeds and mycorrhizal fungi spores, consume significant amounts of insects, including pest species, aerate and mix the soil through tunneling activity, create refuge tunnels used by other wildlife, and add to the organic content of forest soils (Elkinton *et al.* 1996, Madison 1997, Maser *et al.* 1978, Spurr and Barnes 1980).

Forest management changes the structure and composition of the forest, especially conventional clearcutting, which can drastically alter forest wildlife habitat. Several researchers have evaluated the initial effects of forest management, mainly clearcutting, on small mammal communities inhabiting North American coniferous and deciduous forests and have reported different results (Buckner and Shure 1985; Clough 1987; Gashwiler 1959, 1970; Hooven and Black 1976; Kirkland 1974, 1977, 1978; Kirkland *et al.* 1985; Krull 1970; Lovejoy 1975; Martell 1983; Martell and Radvanyi 1977; Monthey and Soutiere 1985; Probst and Rakstad 1987; Ramirez and Hornocker 1981; Steventon *et al.* 1998; Sullivan 1979; Sullivan and Sullivan 1982; Sullivan *et al.* 1999; Tevis 1956; Verme and Ozoga 1981; Von Trebra *et al.* 1998; Yahner 1992). These differences emphasize the importance of potential sources of variation, including forest type, population levels of individual species in surrounding forests, study design, site variation, and specific management practices, in the pattern of responses of small mammals to forest management (Clough 1987, Kirkland 1990).

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A review of 21 published studies evaluating the initial responses (sites were clearcut 6 or fewer years before sampling) of small mammals to conventional clearcutting of temperate North American forests revealed a general pattern of positive responses in small mammal populations in both coniferous and deciduous forests (Kirkland 1990). There was an initial increase in overall relative abundance on recent clearcuts reported in 15 of 20 studies. The effect of cutting on species richness and species composition was more variable. Eight studies reported an initial increase in species richness after clearcutting, four studies reported a decrease, and five studies reported no change. Species composition provided a more detailed look at small mammal community responses than species richness. Researchers reported species caught in uncut forests but not in clearcuts (mean=2.0, range=1-4 species), species caught in clearcuts but not in uncut forests (mean=2.4, range=1-5 species), no appearance or disappearance of species after clearcutting, and the appearance of non-forest dwelling mammals (for example, *Zapus* spp. and *Microtus* spp.) on clearcut areas.

Many studies specifically addressed changes in *Peromyscus* spp. populations following logging. Most concluded that there are more deer mice (*Peromyscus maniculatus*) on logged areas compared with adjacent forested habitat (Ahlgren 1966; Gashwiler 1959, 1970; Hooven and Black 1976; Martell and Radvanyi 1977; Tevis 1956; Verme and Ozoga 1981; Yahner 1992). Only one known study examined the effects of even-aged forest management on white-footed mice (*Peromyscus leucopus*) in Midwest oak-hickory forests (Root *et al.* 1990). In that study, population trends were similar between clearcut and control areas, although clearcuts generally had greater numbers of white-footed mice.

The Missouri Ozark Forest Ecosystem Project (MOFEP), initiated in 1989, is a long-term scientific experiment designed to examine the effects of forest management practices (even- and uneven-aged management) on multiple ecosystem components of southern Missouri's oak-hickory (*Quercus* spp. - *Carya* spp.) forest (Brookshire *et al.* 1997, Sheriff and He 1997, Sheriff this proceedings). Nine approximately 400-ha study sites have been established in Reynolds, Carter, and Shannon Counties. Each site is a compartment, which is the Missouri Department of Conservation's basic forestry

management unit (Missouri Department of Conservation 1986). Each compartment is a collection of smaller units (stands). These nine sites are grouped into three blocks that each contain a no-harvest (control), uneven-aged management, and even-aged management site.

Studies of the effects of forest management on wildlife communities typically examine responses at the forest stand level. The MOFEP experiment provides a unique opportunity to examine responses at the compartment and landscape levels. The long-term experiment also provides the opportunity to examine conditions of small mammal communities before treatment, rather than solely after treatment. This paper reports on the initial (2, 3, and 4 years after first-entry timber harvest) effects of even- and uneven-aged forest management on the species composition, species richness, and relative abundance of small mammal communities occupying northeast-facing slopes of the MOFEP sites.

METHODS

Study Design and Field Sampling

To characterize the MOFEP small mammal communities, we conducted a capture, mark, and recapture study. Trapping occurred during April and May of 1994-1995 (pre-treatment) and 1998-2000 (post-treatment) (table 1). No trapping occurred during timber harvest (1996) and slashing (which continued until June 1997). Trapping was not conducted during Missouri's annual spring firearms turkey season in late April.

We randomly selected two locations on northeast-facing slopes on each of the nine MOFEP sites. At each location, a 12 x 12 station trapping grid was constructed with 25 m between stations (7.56-ha grid, two grids per site). We sampled only on northeast-facing slopes because we believed these locations would contain more small mammals due to a moister environment when compared to southwest-facing slopes. We selected 7.56 ha as a grid size to fit upon available northeast-facing slopes and to attempt to maximize the number of available traps within a grid. Only two grids were sampled per site for several reasons. First, the number of northeast-facing slopes large enough to contain a 7.56-ha grid was limited on several sites. Secondly, we estimated that one person

Table 1.—Trapping periods for small mammals on northeast-facing slopes of MOFEP sites, 1994-2000. No trapping occurred during timber harvest (1996) and slashing (which continued through June 1997).

Year	Block 1	Block 2	Block 3
1994	06-12 April	04-10 May	18-24 May
1995	12-18 April	10-16 May	24-30 May
1996	no trapping		
1997	no trapping		
1998	07-13 April	05-11 May	20-26 May
1999	06-12 April	03-09 May	18-24 May
2000	03-09 April	08-14 May	22-28 May

could check, rebait, and reset all traps within two 7.56-ha grids within an average workday. Grids within each block were simultaneously sampled during a 6-night trapping period (six grids sampled during the same 6-night trapping period). One Sherman small mammal box trap (7.7 x 8.9 x 22.9 cm) baited with a mixture of peanut butter and rolled oats was placed at each station. Traps were checked for captured animals and rebaited once daily. Captured animals were identified to species, individually marked by toe-clipping (except eastern chipmunks (*Tamias striatus*) and eastern woodrats (*Neotoma floridana*) were individually marked with nontoxic, waterproof markers), and released at the point of capture. Traps were disinfected with a dilute (10%) chlorine bleach solution between trapping periods as a precautionary measure against possible exposure to hantavirus. Yunker and Randa (1999) reported that this type of trap disinfection has no adverse effect on trappability of small mammals. Additional details about the study design are presented in Fantz and Renken (1997).

Deer mice and white-footed mice both occur in southern Missouri, and field identification of live animals is difficult due to overlap in external morphological characteristics (Schwartz and Schwartz 1981). We conducted standard body length measurements (total length, tail length, hind foot length, and ear length) and used measurements reported in Schwartz and Schwartz (1981) to distinguish between the two species (table 2).

Sites received varying degrees of treatment in 1996-1997 (Sheriff this proceedings), and trapping grids on these sites were impacted differently by these treatments. On the three uneven-aged sites, 83 percent, 99 percent, and 100 percent of the grids were within treated areas. On the three even-aged sites, 0.01 percent, 17 percent, and 32 percent of the grids fell within a clearcut, and 0 percent, 3 percent, and 23 percent were impacted by intermediate cutting. No less than 359 m separated the two trapping grids on a site.

Table 2.—Characteristics used to distinguish between *Peromyscus* spp. captured on northeast-facing slopes of the MOFEP sites

Characteristic	Species	
	<i>Peromyscus maniculatus</i>	<i>Peromyscus leucopus</i>
Tail	Sharply bicolored; Tuft at tip	Not sharply bicolored; More sparsely furred and scaly, without tuft at tip
Tail length	< 63 mm	63 mm or greater
Hind foot length	< 20 mm	20 mm or greater
Ear length	< 15 mm	15 mm or greater



Data Analysis

Differences in species composition, species richness, and relative abundance of small mammal communities among treatments and years were qualitatively and quantitatively evaluated. Including pre-treatment data in the analysis allowed us to incorporate pre-existing conditions into our understanding of animal responses to treatment. A pre-treatment analysis of the MOFEP small mammal communities was presented in Fantz and Renken (1997).

The short-term effects of forest management on species composition were qualitatively examined. We compared species occurrences in pre-treatment and post-treatment periods to determine if individual species were affected by treatment. Specifically, we looked for species that were captured during pre-treatment but were absent after treatments, or species that were not captured during pre-treatment but were caught following treatments.

Species richness within small mammal communities was defined as the number of species caught on a site within a year. To test for the effects of treatments on species richness, we compared the mean species richness change on control sites to the mean species richness change on treatment sites using a randomized complete block analysis of variance (ANOVA) model (SAS 1989). Mean species richness change was defined as the difference between the pre-treatment (1994/1995) mean species richness and post-treatment mean species richness for each site for 1998, 1999, and 2000 separately. We then used these difference values for each site in the ANOVA to evaluate treatment effects. The main effects in the ANOVA model were block and treatment, with the block*treatment interaction used as the error term. An alpha level of 0.1 was used because of the small sample size ($n=9$) in the experiment (Sheriff and He 1997).

Small mammal relative abundance was defined as the number of individuals (excluding recaptures) captured per grid per 100 trap nights. One trap night is defined as one trap open for one night. Relative abundance estimates for each grid were calculated by dividing the total number of individuals captured on that grid by the total number of trap nights per grid (864 trap nights). Relative abundance estimates were averaged by site for each year. To test for the effect of treatment on relative abundance, we

compared the mean relative abundance change on control sites to the mean relative abundance change on treatment sites using a randomized complete block ANOVA model (SAS 1989). The main effects in the ANOVA model were block and treatment, with the block*treatment interaction used as the error term. An alpha level of 0.1 was used because of the small sample size ($n=9$) in the experiment (Sheriff and He 1997).

RESULTS

Eight species of small mammals were captured on northeast-facing slopes of the MOFEP sites during 1994-1995 and 1998-2000. One species was an insectivore (Elliot's short-tailed shrew, *Blarina hylophaga*), two were sciurid rodents, (eastern chipmunk; southern flying squirrel, *Glaucomys volans*), and the remaining five species were cricetid mice and rats (woodland vole, *Microtus pinetorum*; eastern woodrat; golden mouse, *Ochrotomys nuttalli*; white-footed mouse; deer mouse). Scientific and common names follow Schwartz and Schwartz (1981), except for Elliot's short-tailed shrew, which follows George *et al.* (1981, 1982).

The species trapped most often were the white-footed mouse and deer mouse. Both species were captured on most sites across years. White-footed mice represented between 37 and 54 percent of individuals (all species combined) captured on all nine sites across years, and deer mice were between 24 and 52 percent of individuals (all species combined) captured on all nine sites across years. Field identification of *Peromyscus* spp. is difficult, especially for juveniles, and these two species may be lumped in future analyses. Eastern chipmunks were the third most frequently captured species (between 1 and 13 percent of individuals captured on all nine sites across years). The remaining five species were sporadic captures across sites and years.

Even-aged and uneven-aged forest management had no short-term effect on the species composition of the small mammal community on northeast-facing slopes. Species composition by treatment type for pre-treatment years combined compared to post-treatment years combined did not change (table 3). Most species (Elliot's short-tailed shrew, golden mouse, white-footed mouse, deer mouse, eastern chipmunk) were trapped on all treatment types during both pre-treatment and post-treatment

Table 3.—Small mammal species composition of northeast-facing slopes of MOFEP sites. A plus means the species was captured at least once on at least one site within that treatment type and sampling period, and a minus means it was not captured during sampling. Pre-treatment represents 1994-1995 combined, and post-treatment represents 1998-2000 combined. CON = control sites, UAM = uneven-aged management sites, EAM = even-aged management sites.

Species	Time period / Treatment					
	Pre-treatment			Post-treatment		
	CON	UAM	EAM	CON	UAM	EAM
<i>Blarina hylophaga</i>	+	+	+	+	+	+
<i>Tamias striatus</i>	+	+	+	+	+	+
<i>Glaucomys volans</i>	-	-	+	-	+	+
<i>Microtus pinetorum</i>	+	-	-	-	-	+
<i>Neotoma floridana</i>	+	+	+	-	+	+
<i>Ochrotomys nuttalli</i>	+	+	+	+	+	+
<i>Peromyscus leucopus</i>	+	+	+	+	+	+
<i>Peromyscus maniculatus</i>	+	+	+	+	+	+

sampling. The exceptions were the eastern woodrat, woodland vole, and southern flying squirrel. Eastern woodrats were not captured on control sites during post-treatment, although they were still captured within harvested sites during post-treatment. Only two woodland voles and six southern flying squirrels were trapped across all years, so it's impossible to draw any conclusions about these two species.

Species richness estimates per site ranged from two to six species (table 4). The number of species on each site typically did not vary by

more than one species between pre-treatment and post-treatment years. Species richness means by treatment type ranged from 3.0 to 4.7 (table 5). There were no treatment effects on species richness 2, 3, or 4 years after timber harvest (1998, $F_{2,4}=0.75$, $MSE=1.75$, $P=0.53$; 1999, $F_{2,4}=1.13$, $MSE=3.58$, $P=0.41$; 2000, $F_{2,4}=1.70$, $MSE=3.86$, $P=0.29$).

Overall small mammal mean relative abundance estimates per site ranged from 0.23 individuals per 100 trap nights to 7.75 individuals per 100 trap nights (table 6). Mean relative abundance

Table 4.—Species richness estimates by site and year for small mammals inhabiting northeast-facing slopes of MOFEP sites

Site	Pre-treatment		Post-treatment		
	1994	1995	1998	1999	2000
Control					
1	5	4	3	2	4
6	4	3	4	4	4
8	4	6	2	3	2
Uneven-aged management					
2	5	4	3	4	4
4	4	5	3	3	3
7	2	3	3	3	3
Even-aged management					
3	3	5	3	5	6
5	3	3	5	6	5
9	3	4	3	2	3

Table 5.—Mean species richness estimates (standard error) by treatment type and trapping period for small mammals inhabiting the northeast-facing slopes of MOFEP sites. Pre-treatment represents the 1994/1995 mean.

Treatment	Pre-treatment 1994/1995	Post-treatment		
		1998	1999	2000
Control	4.3 (0.4)	3.0 (0.6)	3.0 (0.6)	3.3 (0.7)
Uneven-aged	3.8 (0.7)	3.0 (0.0)	3.3 (0.3)	3.3 (0.3)
Even-aged	3.5 (0.3)	3.7 (0.7)	4.3 (1.2)	4.7 (0.9)

estimates by treatment type ranged from 0.73 to 3.95 (fig. 1). We observed treatment effects on mean relative abundance 2, 3, and 4 years after timber harvest (1998, $F_{2,4}=4.21$, $MSE=2.17$, $P=0.10$; 1999, $F_{2,4}=6.20$, $MSE=15.96$, $P=0.06$; 2000, $F_{2,4}=9.07$, $MSE=5.71$, $P=0.03$).

DISCUSSION

Treatment had no effect on species composition and species richness of the small mammal communities inhabiting the northeast-facing slopes of the MOFEP sites. White-footed mice, deer mice, and eastern chipmunks were annually caught on most sites. The remaining five species were sporadic, localized captures. Six additional small mammal species (least shrew, *Cryptotis parva*; southeastern shrew, *Sorex*

longirostris; eastern mole, *Scalopus aquaticus*; hispid cotton rat, *Sigmodon hispidus*; prairie vole, *Microtus ochrogaster*; southern bog lemming, *Synaptomys cooperi*) have been caught in pitfall and funnel traps used for capturing amphibians and reptiles on MOFEP sites, but we believe that these species most likely will not be captured on the small mammal grids. The two shrews are often caught in pitfall traps but rarely caught in box traps, and the fossorial eastern mole is seldom captured in conventional small mammal traps. Hispid cotton rats, prairie voles, and southern bog lemmings prefer grassy areas (Schwartz and Schwartz 1981), and very few (four, seven, and five individuals, respectively) were captured. The most likely place and time to have captured these three species would have been on 1- to 2-year-old clearcuts when the ground flora was relatively more sparse.

Table 6.—Mean relative abundance estimates (standard error) (individuals captured / 100 trap nights) by site and year for small mammals inhabiting northeast-facing slopes of the MOFEP sites

Site	Pre-treatment		Post-treatment		
	1994	1995	1998	1999	2000
Control					
1	6.54 (0.06)	2.43 (0.81)	0.64 (0.06)	0.87 (0.41)	1.22 (0.52)
6	2.37 (0.29)	3.82 (1.04)	2.66 (0.46)	0.98 (0.29)	1.91 (0.17)
8	1.91 (0.17)	3.76 (1.33)	0.23 (0.23)	0.35 (0.12)	0.35 (0.00)
Uneven-aged management					
2	2.89 (0.81)	2.49 (1.56)	1.33 (0.29)	2.37 (0.41)	1.91 (0.87)
4	1.45 (0.06)	1.68 (0.64)	1.50 (0.35)	1.50 (0.12)	1.27 (0.23)
7	1.22 (0.29)	5.56 (1.62)	0.75 (0.41)	2.03 (0.06)	0.75 (0.17)
Even-aged management					
3	3.01 (0.35)	3.99 (1.22)	2.14 (0.87)	7.75 (4.17)	4.51 (2.08)
5	0.93 (0.35)	1.56 (0.64)	1.79 (0.52)	3.53 (3.07)	2.08 (0.46)
9	1.04 (0.00)	1.97 (1.04)	0.52 (0.17)	0.58 (0.23)	0.93 (0.23)

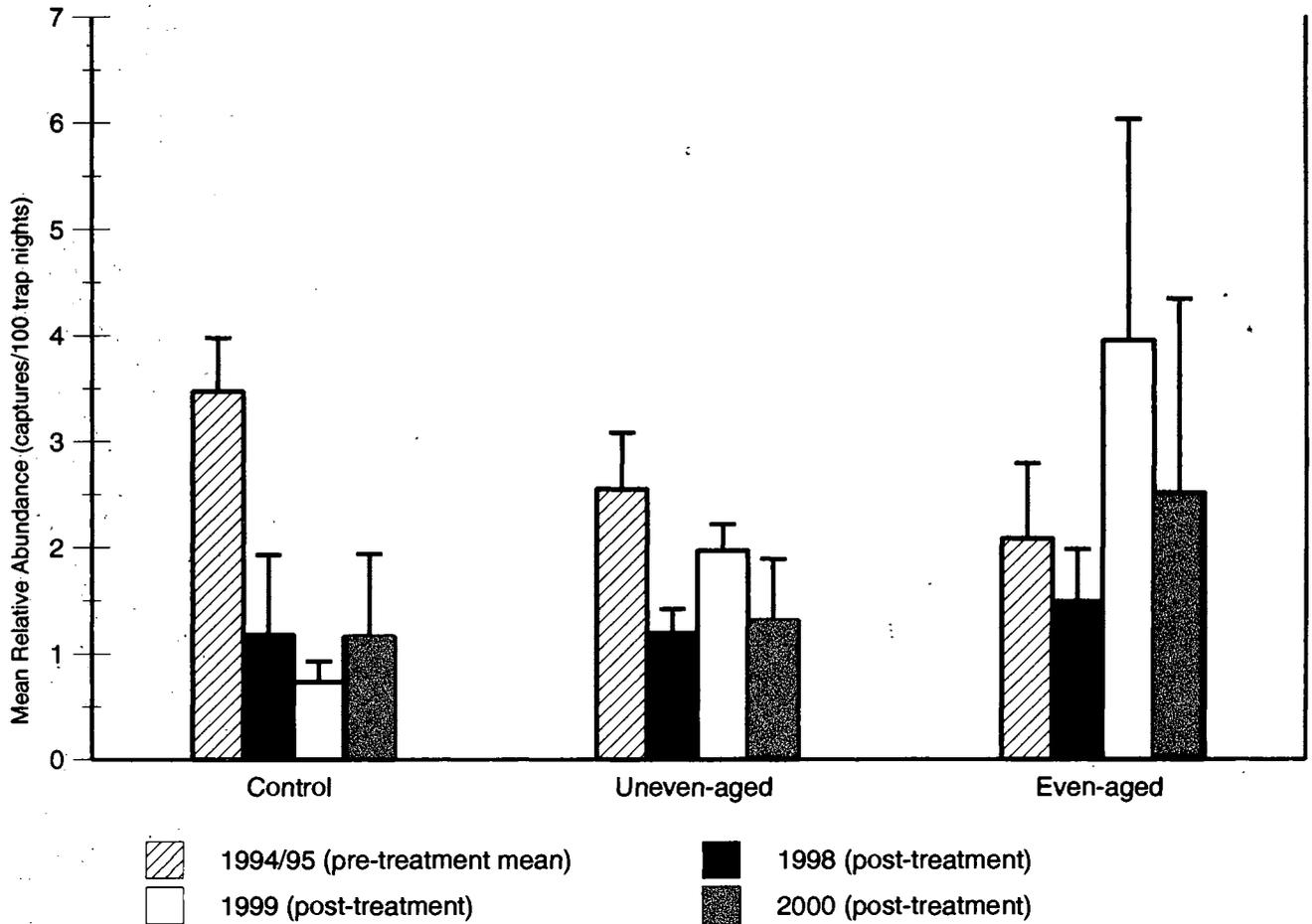


Figure 1.—Mean relative abundance estimates (individuals captured / 100 trap nights) by treatment type and trapping period for small mammals inhabiting northeast-facing slopes of the MOFEP sites. Standard errors are shown by the lines at the top of the bars.

Treatment did have an effect on the overall relative abundance of small mammals 2, 3, and 4 years after timber harvest. It appears that there was a natural decline in mean overall small mammal relative abundance, which was evident on the control sites. Even-aged management, and uneven-aged management to a lesser extent, appeared to have dampened this natural decline. Relative abundance estimates on treated sites were slightly higher than those on control sites. We think forest management may have dampened this decline by increasing available food sources and providing better cover for protection against most predators.

Temperate forest small mammals are characterized by seasonal and multi-annual population fluctuations in response to a variety of density-dependent and density-independent factors. Yahner (1992) reported significantly lower

numbers of individuals during a drought year that presumably reduced the availability of terrestrial arthropods as a food resource. Arthropods, hard mast, soft mast, seeds, and green vegetation are the primary foods of the small mammal species inhabiting MOFEP sites (Hamilton 1941, Schwartz and Schwartz 1981, Whitaker 1966). Clearcut areas can produce large quantities of fruits, seeds, and insects (Ahlgren 1966, Hoooven 1973, Lovejoy 1975, Tevis 1956). Perry *et al.* (1999) reported that in the Ouachita Mountains of Arkansas and Oklahoma, soft mast production did not significantly differ among five timber harvest treatments the first year after timber harvest, but was significantly greater in harvested stands (both even- and uneven-aged management stands) when compared to unharvested stands 3 years after cutting. Five years after cutting, they reported significantly greater soft mast



production in shelterwood cuts and clearcuts (80-100 times greater than unharvested stands) when compared to single-tree selection, group selection, or unharvested stands.

The results presented in this paper are a preliminary look at the responses of the small mammal communities to even- and uneven-aged forest management on the MOFEP sites. Our plans are to sample in 2001 and then suspend sampling for a few years. We plan to further analyze data to examine the effects of forest management on small mammal communities and investigate species-specific and trophic group responses. Collaboration with other MOFEP researchers, especially those working on the invertebrate, hard mast, soft mast, and botany studies, may provide insight into the variation we observed.

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Immediate, Landscape-scale Impacts of Even-aged and Uneven-aged Forest Management on Herpetofaunal Communities of the Missouri Ozark Forest Ecosystem Project

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Abstract.—We examined the immediate, landscape-scale impacts of even-aged and uneven-aged forest management on the species composition, species richness, and relative abundance of herpetofaunal communities and selected focal groups of species during the second and third years following initial tree harvest on Missouri Ozark Forest Ecosystem Project (MOFEP) sites in southern Missouri. We compared these measures of the pre-treatment (1992-1995) community to measures of the 1998 and 1999 post-treatment communities. We did not observe changes in species composition, species richness, and overall amphibian and reptile relative abundance in 1998 or 1999 because of the first-entry harvest within sites. Landscape-scale impacts also were not observed in the relative abundances of woodland salamanders (*Plethodon* spp.) and a group of small snakes (prairie ring-necked snake (*Diadophis punctatus arnyi*), northern redbellied snake (*Storeria occipitomaculata occipitomaculata*), and western smooth earthsnake (*Virginia valeriae elegans*)). We did observe a landscape-scale effect on pond-breeding salamanders (*Ambystoma* spp.) and skinks (*Eumeces* spp.). Even-aged and uneven-aged forest management appeared to dampen a natural oscillation in *Ambystoma* relative abundance estimates on southwest-facing slopes and resulted in an increase in *Eumeces* relative abundance on northeast-facing slopes in 1998. Potential mechanisms for these observed impacts and future analysis plans are discussed.

Most studies of the impacts of timber harvest upon amphibians and reptiles have focused upon the effects within forest stands. Amphibian and reptile populations, however, move among stands, can be impacted by the environmental conditions within adjacent stands, and are dependent upon population dynamics that occur across many stands. The Missouri Department of Conservation manages forests with the compartment as the basic unit of management (Missouri Department of Conservation 1986): A compartment, which is typically about 415 ha in size, consists of smaller units of stands. Forest management practices, such as

even-aged and uneven-aged management, are applied to compartments as a whole with stands of trees manipulated to achieve desired forest conditions (Missouri Department of Conservation 1986). Hence, an investigation of the effects of forest management at a landscape scale of the compartment is reasonable and desirable because forestry practices are applied to compartments, and because amphibian and reptile populations are likely affected by forces working at a scale greater than forest stands.

Past studies of the effects of timber harvest on amphibians and reptiles demonstrated that salamanders declined sharply in recently harvested stands (Ash 1988; Blymer and McGinnes 1977; DeGraaf and Yamasaki 1992; Dupuis *et al.* 1995; Enge and Marion 1986; Harper and Guynn 1999; Harpole and Haas 1999; Herbeck and Larsen 1999; Petranka *et al.* 1993, 1994; Pough *et al.* 1987; Sattler and Reichenback 1998), whereas some reptiles increased in abundance on recently cut stands (Goldingay *et al.* 1996, Raphael 1988). The

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estimated number of years required for salamander abundances to recover varied from about 20 years (Ash 1997) to more than 50 years (Petranka *et al.* 1993, 1994), depending on region, species, and definition of recovered population abundance (Ash 1997, Ash and Pollack 1999, Petranka 1999). Clearly, forest management has a local impact on herpetofaunal communities. On a larger geographic scale, forest fragmentation, as measured by percent forest cover, distance to forest edge, island size, and tree basal area, was associated with reduced species distribution and diversity for some amphibians in temperate (Gibbs 1998, Hager 1998) and tropical (Marsh and Pearman 1997, Pearman 1997) regions.

The goal of our study was to experimentally examine the landscape-scale effects of forest management on amphibian and reptile communities. For this report we tested the short-term (the second and third years after harvest) impacts of even-aged and uneven-aged forest management on amphibian and reptile community species composition, species richness, and relative abundance on nine compartments (which will be called sites for the remainder of this paper) in the Missouri Ozarks. With 6 years of data (4 years of pre-treatment and 2 years of post-treatment data), we evaluated the effects of management on measures of the amphibian and reptile community and the relative abundance of four taxonomic focal groups during the second and third years after timber harvest.

METHODS

Sampling Design and Field Sampling Methods

The overall design and location of MOFEP are described in Sheriff and He (1997) and Sheriff (this proceedings). Details about the timber harvest, or treatment, which occurred in 1996 and the sites are included elsewhere (Brookshire *et al.* 1997, Meinert *et al.* 1997). To examine the landscape-scale effect of even-aged and uneven-aged forest management on the species composition, species richness, and relative abundance of amphibian and reptile communities, we trapped amphibians and reptiles at 12 modified Jones (1981) design arrays randomly placed on southwest-facing slopes (Ecological Landtype 17) and northeast-facing slopes (Ecological Landtype 18) on each

site. Of the 12 arrays, 6 were placed on southwest-facing landscapes and 6 were placed on northeast-facing landscapes (Renken 1997). Twelve arrays were used per site because we believed that two technicians could check all traps at 12 arrays within an average work day. Southwest-facing and northeast-facing slopes were sampled because they comprise 68-83 percent of the area within the sites. For further details about the arrays and reasons for selecting this technique for sampling amphibians and reptiles at MOFEP sites, see Renken (1997).

Arrays were open for trapping during 20 March - 2 July and 19 August - 28 October 1992 (165 days); 4 March - 2 July and 30 August - 30 October 1993 (174 days); 25 February - 1 July and 29 August - 2 November 1994 (183 days); 27 February - 30 June and 29 August - 2 November 1995 (184 days); 25 February - 26 June and 28 August - 30 October 1998 (188 days); and 24 February - 30 June and 25 August - 29 October 1999 (187 days). All arrays on a site were checked for captured animals approximately every 3 to 5 days. The nine sites were grouped into three blocks of three sites each (randomized block design) to account for the influence of location on observed results (Sheriff and He 1997). All arrays within a block were checked on the same day.

Captured animals were identified to species, toe clipped or ventral scale clipped with a unique mark, and released approximately 5-7 m from the traps. Turtles were marked by filing notches in marginal scutes. During 1993, 1994, 1995, 1998, 1999, and the later part of 1992, Eastern American toads (*Bufo americanus americanus*) and central newts (*Notophthalmus viridescens louisianensis*) were given a batch mark unique for the sampling year. All other species were given unique individual marks. During this research, approximately 19,600 individuals were captured during the pre-treatment period (1992-1995) and approximately 10,000 individuals were captured during the post-treatment period.

Data Analysis

Differences in species composition of amphibian and reptile communities among treatments between pre-treatment (1992 through 1995) and post-treatment (1998 and 1999) periods were quantitatively and qualitatively described. Indices of similarity (Jaccard 1901) in species

composition between pre-treatment and post-treatment periods for each slope type (southwest-facing or northeast-facing) were computed for each site. An index of 1.00 meant the species composition between pre-treatment and post-treatment periods was identical. A randomized complete block analysis of variance (ANOVA; SAS 1989) using the interaction term of treatment and block as the error term was used to test the effect of treatment upon the Jaccard's indices calculated for the species composition of the sites. Similarity indices were log transformed for the analysis so that model residuals were normally distributed (Snedecor and Cochran 1980). We used an alpha of 0.1 for this test because of the low power (N=9) of the experiment (Sheriff and He 1997). In a qualitative evaluation of immediate effects of forest management on species composition, we examined species occurrences in pre-treatment and post-treatment periods to determine if species were affected by treatment. In particular, we looked for species that were not captured following treatment and for species captured only following treatment.

We defined the species richness of a site to be the number of species caught at a site within a year and slope type. To determine if treatment had an effect on species richness, we tested the numerical difference between the mean species richness observed in the pre-treatment period and the species richness observed in 1998 or 1999 for each site in a randomized complete block ANOVA. We used the treatment by block interaction term as the error term to test for differences among treatments and an alpha of 0.10 because of the low power (N=9) of the experiment.

Relative abundance estimates of animals at each array were derived by summing the number of individuals captured at each array (recaptures were not included) for each year and dividing by the total number of trap days (number of days the array was open for sampling) for that year. One trap day was defined as one array operating for one day. We defined trap days as such because all 10 traps (1 pitfall and 9 funnel traps) at an array were not independent of one another. We then standardized estimates as number of captures per 100 trap days. Mean annual relative abundance estimates for each slope type (six arrays within each slope type) within each site then were calculated. We then calculated the difference between mean pre-treatment and 1998 or 1999

overall amphibian and reptile relative abundance estimates for each site and slope type, and tested for the effect of treatment on these differences in a randomized complete block ANOVA using the treatment by block interaction term as the error term for testing the main effects among treatments. We used an alpha level of 0.1 because of the small sample size (N=9) of the experiment (Sheriff and He 1997).

We were also interested in the effect of treatment upon the relative abundance of four taxonomic focal groups of species (*Ambystoma* spp., *Plethodon* spp., *Eumeces* spp., and a group of selected small snakes: *Diadophis punctatus arnyi*, *Storeria occipitomaculata occipitomaculata*, and *Virginia valeriae elegans*). We chose to focus on groups of species rather than individual species for several reasons. Our research goals emphasized effects of forest management on communities, but groups of species within a community may respond in opposite ways to forest management. Presumably, species within a focal group shared similar ecological habits and taxonomic characteristics that make them more or less vulnerable to forest management. Captures of individuals within focal groups also were more numerous and exhibited less within-site variability than did many individual species. Using focal groups made our analyses more robust and we were more likely to observe an effect if one existed. We calculated and analyzed the relative abundance estimates of these four focal groups in the same manner as we calculated and analyzed estimates of overall amphibian and reptile relative abundance.

RESULTS

The species composition and species richness of the amphibian and reptile community on either southwest-facing or northeast-facing slopes were not affected by even-aged or uneven-aged forest management during the second and third years following the 1996 timber harvest. We did not observe a difference in Jaccard's similarity indices (table 1) among treatments (southwest-facing slopes, $F_{2,4}=0.14$, $MSE=0.0001$, $P=0.87$; northeast-facing slopes, $F_{2,4}=1.83$, $MSE=0.007$, $P=0.27$) when comparing pre-treatment to post-treatment communities. In our qualitative analysis, we suspect the occurrence of only one species, the northern rough greensnake (*Opheodrys aestivus aestivus*), (table 2) may be related to the effects of treatment. Northern



Table 1.—Means (and standard errors) of Jaccard's similarity indices for each treatment by slope type for MOFEP sites during 1992-1995 and 1998-1999. The indices are a measure of the similarity in species composition of pre-treatment and post-treatment amphibian and reptile communities. An index of 1.0 means the communities were identical.

Treatment	Jaccard's similarity indices	
	Southwest-facing slopes	Northeast-facing slopes
Control	0.73 (0.02)	0.71 (0.04)
Even-aged	0.74 (0.02)	0.74 (0.01)
Uneven-aged	0.75 (0.04)	0.78 (0.0)

rough greensnakes had not been captured in even-aged sites following harvest even though they had been captured during the pre-treatment period. They also were not captured on northeast-facing slopes in uneven-aged sites in the post-treatment period. Their absence may be due to the short post-treatment period reported in this paper or it may be related to treatment. Further sampling will help us answer that question. Species richness of amphibian and reptile communities (table 3) on either slope type also was not affected by even-aged or uneven-aged forest management (southwest-facing slopes, $F_{2,4}=1.08$, $MSE=3.47$, $P=0.42$; northeast-facing slopes, $F_{2,4}=2.45$, $MSE=11.44$, $P=0.20$).

Even-aged and uneven-aged forest management did not immediately affect the overall relative abundance of amphibians and reptiles on the sites. Overall relative abundance of amphibians and reptiles was not affected by treatment on either slope type and in either post-treatment year (southwest-facing slopes, 1998, $F_{2,4}=2.36$, $MSE=92.7$, $P=0.21$; 1999, $F_{2,4}=1.40$, $MSE=42.8$, $P=0.36$; northeast-facing slopes, 1998, $F_{2,4}=0.38$, $MSE=62.4$, $P=0.71$; 1999, $F_{2,4}=0.11$, $MSE=7.47$, $P=0.90$; fig. 1). We also did not observe landscape-scale treatment effects upon *Plethodon* spp. or small snake relative abundance on either slope type (*Plethodon* spp., southwest-facing slopes, 1998, $F_{2,4}=1.45$, $MSE=23.4$, $P=0.34$; 1999, $F_{2,4}=0.49$, $MSE=5.95$, $P=0.64$; northeast-facing slopes, 1998, $F_{2,4}=1.01$, $MSE=75.1$, $P=0.44$; 1999, $F_{2,4}=0.82$, $MSE=6.4$, $P=0.50$, fig. 2; small snakes, southwest-facing slopes, 1998, $F_{2,4}=1.46$, $MSE=0.88$, $P=0.34$; 1999, $F_{2,4}=0.27$, $MSE=0.08$, $P=0.78$; northeast-facing slopes, 1998, $F_{2,4}=0.78$, $MSE=0.74$, $P=0.52$; 1999, $F_{2,4}=0.50$, $MSE=0.41$, $P=0.64$, fig. 3).

We did observe an effect of treatment on *Ambystoma* spp. relative abundance on southwest-facing slopes in 1998 and 1999 (fig. 4a) and on *Eumeces* spp. relative abundance on northeast-facing slopes in 1998 (fig. 5b). Both even-aged and uneven-aged management appeared to dampen a natural *Ambystoma* spp. oscillation in relative abundance estimates that occurred on control sites in the post-treatment period (southwest-facing slopes, 1998, $F_{2,4}=4.64$, $MSE=0.57$, $P=0.09$; 1999, $F_{2,4}=5.20$, $MSE=1.52$, $P=0.08$). *Eumeces* spp. relative abundance appeared to be greater on northeast-facing slopes on even-aged and uneven-aged management sites than on control sites in the second year after harvest ($F_{2,4}=4.05$, $MSE=1.33$, $P=0.11$). This effect, however, was not observed in 1999 ($F_{2,4}=1.23$, $MSE=0.68$, $P=0.38$). There was no effect of treatment on *Ambystoma* spp. relative abundance on northeast-facing slopes (1998, $F_{2,4}=0.12$, $MSE=0.06$, $P=0.89$; 1999, $F_{2,4}=2.19$, $MSE=3.54$, $P=0.23$; fig. 4b) or on *Eumeces* spp. relative abundance on southwest-facing slopes (1998, $F_{2,4}=2.34$, $MSE=0.67$, $P=0.21$; 1999, $F_{2,4}=0.70$, $MSE=1.66$, $P=0.55$; fig. 5a).

DISCUSSION

The lack of an immediate, landscape-scale treatment effect upon the species composition, species richness, and overall amphibian and reptile relative abundance of the MOFEP sites was not unexpected. Because a relatively small proportion of the forest (approximately 10 percent of a site) was harvested and disturbed during this first timber harvest, we did not expect to observe landscape-scale impacts to such general measures, such as species composition and overall relative abundance, of the

Table 2.—The species composition of MOFEP amphibian and reptile communities within control, even-aged, and uneven-aged management sites on southwest-facing and northeast-facing slopes during the pre-treatment (1992-1995) and immediate post-treatment (1998-1999) years. An X denotes the capture of at least one individual of that species during the pre-treatment period. An O denotes the capture of a species during the post-treatment period.

Species	Species presence within treatment types and by slope types											
	Southwest-facing slopes						Northeast-facing slopes					
	Control		Even-aged		Uneven-aged		Control		Even-aged		Uneven-aged	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Spotted salamander <i>Ambystoma maculatum</i> (Shaw)	X	O	X	O	X	O	X	O	X	O	X	O
Marbled salamander <i>Ambystoma opacum</i> (Gravenhorst)	X	O	X	O	X	O	X	O	X	O	X	O
Eastern tiger salamander <i>Ambystoma tigrinum tigrinum</i> (Green)							X					
Central newt <i>Notophthalmus viridescens</i> <i>louisianensis</i> Wolterstorff	X	O	X	O	X	O	X	O	X	O	X	O
Dark-sided salamander <i>Eurycea longicauda</i> <i>melanopleura</i> (Cope)	X	O	X	O	X	O	X	O	X	O	X	O
Cave salamander <i>Eurycea lucifuga</i> Rafinesque	X	O	X	O	X	O	X	O	X	O	X	O
Four-toed salamander <i>Hemidactylium scutatum</i> (Schlegel)	X	O	X	O	X	O	X	O	X		X	O
Western slimy salamander <i>Plethodon albagula</i> Grobman	X	O	X	O	X	O	X	O	X	O	X	O
Southern red-backed salamander <i>Plethodon serratus</i> Grobman	X	O	X	O	X	O	X	O	X	O	X	O
Eastern American toad <i>Bufo americanus americanus</i> Holbrook	X	O	X	O	X	O	X	O	X	O	X	O
Fowler's toad <i>Bufo fowleri</i> Hinckley	X	O	X	O	X	O	X	O	X	O	X	O
Blanchard's cricket frog <i>Acris crepitans blanchardi</i> Harper	X						X					
Gray treefrogs <i>Hyla chrysoscelis</i> - <i>Hyla</i> <i>versicolor</i> complex	X	O	X	O	X	O	X		X	O	X	O
Northern spring peeper <i>Pseudacris crucifer</i> <i>crucifer</i> (Wied - Neuwied)	X	O	X	O	X	O	X	O	X	O	X	O
Eastern narrow-mouthed toad <i>Gastrophryne carolinensis</i> (Holbrook)	X	O	X		X		X	O				O
American bullfrog <i>Rana catesbeiana</i> Shaw							X					
Northern green frog <i>Rana clamitans melanota</i> Rafinesque	X	O	X	O	X	O	X	O	X	O	X	O
Pickerel frog <i>Rana palustris</i> LeConte	X	O	X	O	X	O	X	O	X	O	X	O
Southern leopard frog <i>Rana sphenoccephala</i> Cope	X	O	X	O	X	O	X	O	X	O	X	O
Three-toed box turtle <i>Terrapene carolina triunguis</i> (Agassiz)	X	O	X	O	X	O	X	O	X	O	X	O
Northern fence lizard <i>Sceloporus undulatus</i> <i>hyacinthinus</i> (Green)	X	O	X	O	X	O	X	O	X	O	X	O



(Table 2 continued)

Species	Species presence within treatment types and by slope types											
	Southwest-facing slopes						Northeast-facing slopes					
	Control		Even-aged		Uneven-aged		Control		Even-aged		Uneven-aged	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Southern coal skink <i>Eumeces anthracinus</i> <i>pluvialis</i> Cope	X	O	X	O	X	O	X	O	X	O	X	O
Common five-lined skink <i>Eumeces fasciatus</i> (Linnaeus)	X	O	X	O	X	O	X	O	X	O	X	O
Broad-headed skink <i>Eumeces laticeps</i> (Schneider)	X	O	X	O	X	O	X	O	X	O	X	O
Little brown skink <i>Scincella lateralis</i> (Say)	X	O	X	O	X	O	X	O	X	O	X	O
Eastern six-lined racerunner <i>Cnemidophorus sexlineatus</i> <i>sexlineatus</i> (Linnaeus)							X					
Western wormsnake <i>Carphophis vermis</i> (Kennicott)	X	O	X	O	X	O	X	O	X	O	X	O
Eastern yellow-bellied racer <i>Coluber constrictor</i> <i>flaviventris</i> Say	X	O	X	O	X	O	X	O	X	O	X	O
Prairie ring-necked snake <i>Diadophis punctatus amyi</i> Kennicott	X	O	X	O	X	O	X	O	X	O	X	O
Black ratsnake <i>Elaphe obsoleta obsoleta</i> (Say)	X	O	X	O	X	O	X		X	O	X	O
Eastern hog-nosed snake <i>Heterodon platirhinos</i> Latreille	X	O	X	O	X	O	X	O	X	O	X	O
Speckled kingsnake <i>Lampropeltis getula holbrooki</i> Stejneger			X		X		X				X	
Red milksnake <i>Lampropeltis triangulum</i> <i>syspila</i> (Cope)	X	O	X	O	X	O	X		X		X	O
Common watersnake <i>Nerodia sipedon sipedon</i> (Linnaeus)	X		X		X						X	O
Northern rough greensnake <i>Opheodrys aestivus aestivus</i> (Linnaeus)	X	O	X		X	O			X		X	
Midland brownsnake <i>Storeria dekayi wrightorum</i> Trapido	X	O	X	O	X	O	X	O	X	O	X	O
Northern red-bellied snake <i>Storeria occipitomaculata</i> <i>occipitomaculata</i> (Storer)	X	O	X	O	X	O	X	O	X	O	X	O
Orange-striped ribbonsnake <i>Thamnophis proximus</i> <i>proximus</i> (Say)	X	O		O	X	O	X	O	X	O	X	O
Eastern gartersnake <i>Thamnophis sirtalis sirtalis</i> (Linnaeus)	X	O	X	O	X	O	X	O	X	O	X	O
Rough earthsnake <i>Virginia striatula</i> (Linnaeus)	X		X		X	O	X		X		X	
Western smooth earthsnake <i>Virginia valeriae elegans</i> Kennicott	X	O	X	O	X	O	X	O	X	O	X	O
Osage copperhead <i>Agkistrodon contortrix</i> <i>phaeogaster</i> Gloyd	X	O	X	O	X	O	X	O	X	O	X	O
Timber rattlesnake <i>Crotalus horridus</i> Linnaeus	X		X	O				O	X	O	X	
Western pygmy rattlesnake <i>Sistrurus miliarius streckeri</i> Gloyd						O						

Table 3.—Means and standard errors for species richness estimates by treatment type and slope type on MOFEP sites during pre-treatment (1992-1995) and post-treatment (1998, 1999) periods. Species richness is the number of species captured within a slope type within a site.

Species richness estimates						
Treatment	Southwest-facing slopes			Northeast-facing slopes		
	Pre-treatment	1998	1999	Pre-treatment	1998	1999
Control	24.1 (0.8)	23.7 (1.3)	22.3 (0.9)	24.0 (1.4)	23.3 (0.9)	19.3 (0.7)
Even-aged	22.8 (0.3)	24.7 (2.0)	23.0 (2.0)	23.0 (0.4)	24.7 (1.7)	23.0 (0.6)
Uneven-aged	22.8 (0.9)	24.3 (0.3)	22.0 (1.7)	22.1 (1.7)	22.7 (1.2)	22.7 (0.3)

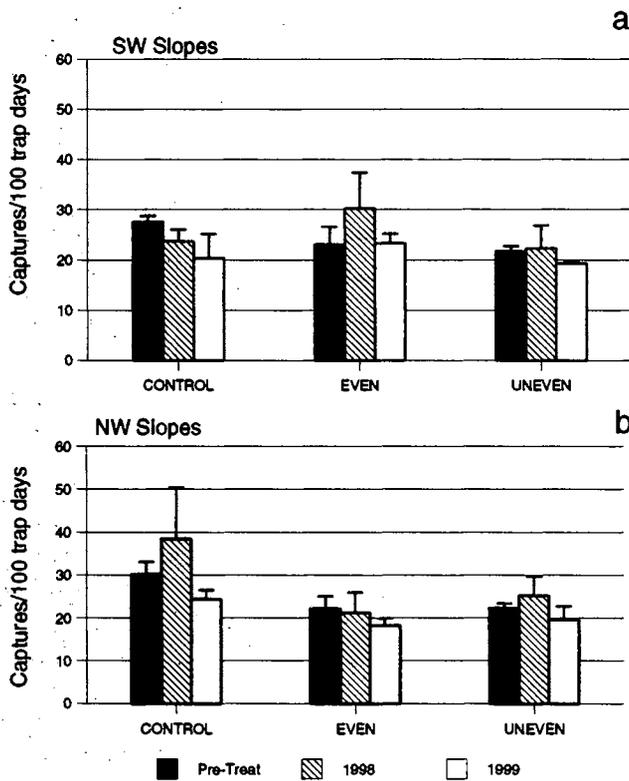


Figure 1.—Means and standard errors for overall amphibian and reptile relative abundance on southwest-facing (a) and northwest-facing (b) slopes during pre-treatment, 1998, and 1999.

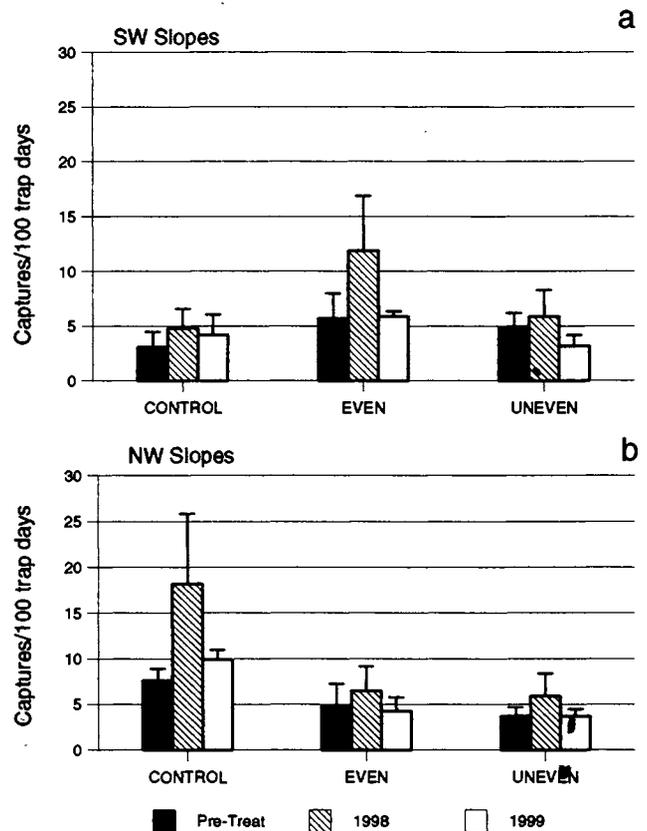


Figure 2.—Means and standard errors for *Plethodon* spp. relative abundance on southwest-facing (a) and northwest-facing (b) slopes during pre-treatment, 1998, and 1999.

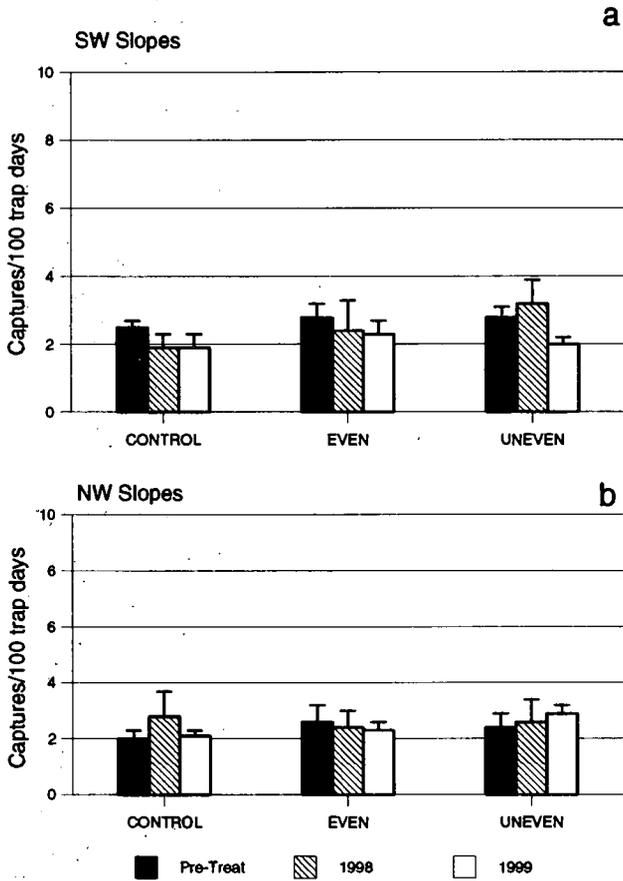


Figure 3.—Means and standard errors for small snake relative abundance on southwest-facing (a) and northeast-facing (b) slopes during pre-treatment, 1998, and 1999.

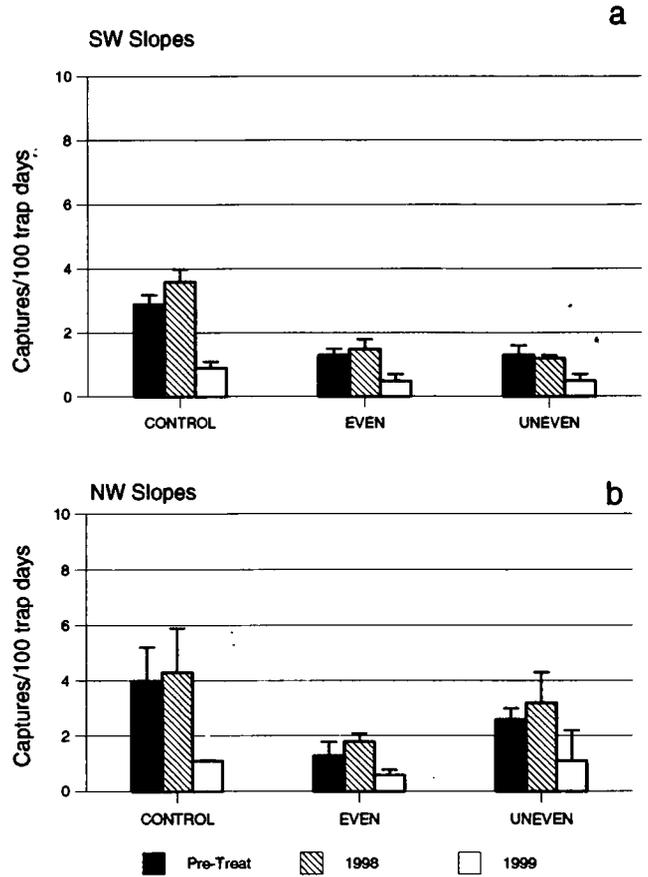


Figure 4.—Means and standard errors for *Ambystoma* spp. relative abundance on southwest-facing (a) and northeast-facing (b) slopes during pre-treatment, 1998, and 1999.

herpetofaunal community. We suspect that if impacts are detected to such general measures, they will be observed when a greater proportion of the forest area has been cut. Landscape-scale impacts, however, may still not be detected in those future surveys because even-aged and uneven-aged sites are likely to provide a mix of old trees (100+ year old trees) in undisturbed habitat, intermediate-aged trees (30 to 50 years old) in recovering habitat, and a small proportion of young trees (20 years old or less) in recently disturbed habitat. This mix may still support the diversity of species and result in overall amphibian and reptile capture rates similar to those observed in herpetofaunal communities prior to the initial 1996 timber harvest and in control sites.

The effect of landscape-scale forest management was probably better evaluated when impacts upon focal groups of species were examined. A general measure such as overall amphibian and reptile relative abundance may change if the impact was dramatic and more widespread on the landscape, but might not change with smaller, more subtle changes following the first tree harvest. Subtle changes are more likely to affect specific species groups, which respond in different ways to habitat alterations. It appeared even-aged and uneven-aged forest management on southwest-facing slopes dampened a natural oscillation in *Ambystoma* spp. relative abundance estimates observed on southwest-facing slopes of the control sites. In 1998, *Ambystoma* spp. relative

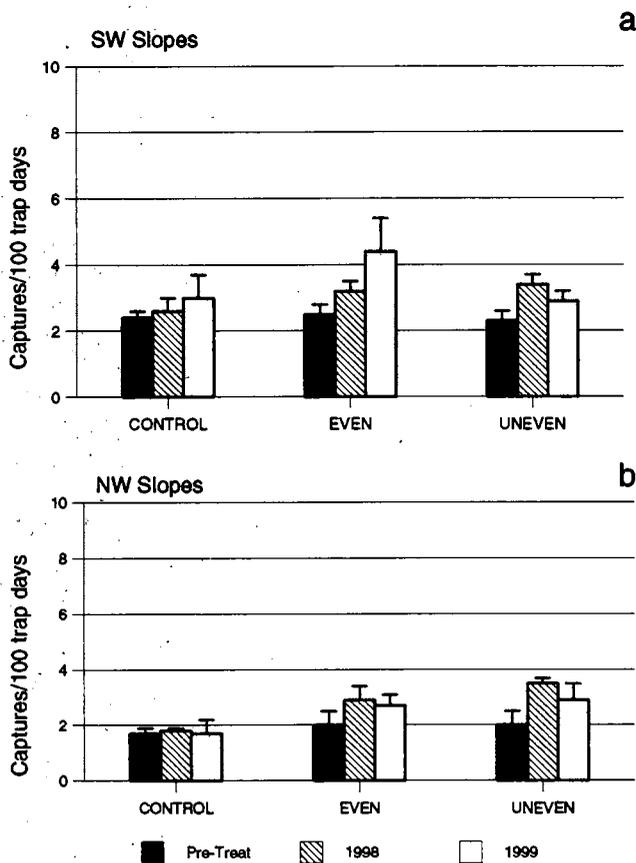


Figure 5.—Means and standard errors for *Eumeces* spp. relative abundance on southwest-facing (a) and northeast-facing (b) slopes during pre-treatment, 1998, and 1999.

abundance on control sites increased while this group's relative abundance remained the same on even-aged and uneven-aged sites. In 1999, all treatment types showed a decline in salamander relative abundance, yet on control sites the decline was dramatic compared to the decline observed on even-aged and uneven-aged sites, which displayed relative abundances already smaller than relative abundances on control sites. We suspect the dampened oscillations of *Ambystoma* spp. on southwest-facing slopes of even-aged and uneven-aged management sites were the result of salamanders electing not to move in, near, or through the drier, more hostile conditions of recently cut forest on southwest-facing slopes, even when it

appeared conditions were conducive (in 1998) for much salamander movement as evidenced by the increased relative abundance observed on the control sites. Although salamanders are typically thought to move no more than a few hundred meters from breeding ponds (Kleeberger and Werner 1983, Madison 1997, Williams 1973), we have learned from the pre-treatment period capture data that these salamanders are more widespread in distribution in the upland forest and were moving farther (up to 1,500 m) from the few breeding ponds (Renken 1997) than what has been reported (also see Gordon 1968). There is evidence to suggest pond-breeding salamanders either move out of or avoid entering recently harvested forest areas (deMaynadier and Hunter 1998, 1999; Raymond and Hardy 1991). Other researchers have noted that salamanders retreat underground when soil surface conditions are dry and harsh for these moisture-dependent animals (Semlitsch 1983). We suspect salamanders that occupy southwest-facing slopes of even-aged and uneven-aged management sites restricted their movements upon and through those slopes after harvest to avoid desiccation.

An increase in *Eumeces* spp. relative abundance following timber harvest was a more expected result of forest management. Although reptile responses to forest management have been studied less than amphibian responses, other workers have noted that lizards are more abundant in recently harvested moist forests (Goldingay *et al.* 1996). We suspect the warmer (Zheng *et al.* 2000), drier soil surface conditions and change in vegetation structure caused by the opening of the forest canopy and increased sunlight to the forest floor following harvest were conducive to these lizards and possibly the prey they feed upon. The significant increase in relative abundance on northeast-facing slopes within even-aged and uneven-aged sites, but not on southwest-facing slopes, is likely due to the smaller variation around relative abundance estimates for all treatment types on the northeast-facing slopes and to the more dramatic changes in soil temperature (Zheng *et al.* 2000) and likely in soil moisture that resulted from the harvest on northeast-facing slopes.

**SUMMARY**

In summary, we did not observe any landscape-scale impacts of treatment upon the species composition and richness, and overall amphibian and reptile relative abundance within the sites. We also did not observe any treatment impacts on *Plethodon* spp. and small snake relative abundance. Treatment impacts were observed on pond-breeding salamanders (*Ambystoma* spp.) and skinks (*Eumeces* spp.), but depended upon slope type and length of time following harvest.

We plan to continue sampling amphibian and reptile communities through 2001 and then sporadically sample, perhaps 3 years out of 5, through the rest of the MOFEP experiment. Less sporadic sampling may also be conducted several years immediately before and after succeeding tree harvest entries, which at this time are scheduled to occur every 15 years.

We emphasize that the results presented in this paper are an initial look at the impacts of even-aged and uneven-aged forest management on amphibian and reptile communities. We plan to further analyze data to examine amphibian and reptile response in the spring and fall seasons separately and focus on specific species that are sufficiently abundant in the data to allow analysis. We also plan to soon report updated findings to managers and the scientific community. An important task for us and every investigator succeeding us will be to continually analyze and examine data, and report results so the information is communicated to managers, administrators, and the general public. We think we have only begun to learn how the herpetofaunal community is responding to forest management in this immediate, post-treatment period.

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Impact of Timber Harvest on Species Accumulation Curves for Oak Herbivore Communities of the Missouri Ozarks

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Abstract.—We report the effects of two timber harvest methods, even-aged and uneven-aged harvest, versus no harvest on species accumulation curves for leaf-chewing herbivores of *Quercus alba* and *Q. velutina* in the Missouri Ozarks. The study was part of a larger project, the Missouri Ozark Forest Ecosystem Project (MOFEP). Herbivores were sampled four times during the year (early May, June, July, and late August) for each of 4 years after cutting. Species accumulation curves were generated by plotting the total number of species recorded per leaf area sampled in all stands (N=6 stands/site) within a site in May 1997, the first census of the first year following cutting, and then adding the number of new species encountered in each subsequent census through the end of 2000. Treatment effects first became apparent in 1998. Uneven-aged management tended to reduce the rate of species accumulation across years for *Q. alba* compared to no harvest (control) and even-aged management, although marginally so. In contrast, even-aged management significantly increased the rate of species accumulation on *Q. velutina* compared to no harvest, with uneven-aged curves lower than no harvest. The May and June censuses contributed most to the treatment effect for *Q. alba* and *Q. velutina*, respectively. We interpret these results to mean that the treatments either increased or decreased population size relative to controls, thus resulting in an increased or decreased probability, respectively, of sampling a species. Species accumulation curves were lower for younger forests, suggesting that continued cutting, regardless of harvesting method, will reduce species richness of this herbivore fauna.

A major concern for natural area managers is the impact that management will have on the biodiversity of managed areas. One component of biodiversity is the total number of species (i.e., species richness) found in any one location. Changing the nature of the habitat through active management (e.g., harvesting timber), or in some cases absence of manipulation (e.g., protection as old growth), can lead to changes in the ability of species to use that

habitat. Whether an individual species increases or decreases in abundance as a result of some management option will depend on the ecology and life history of the particular species involved. When the effects on communities of organisms are considered, changes in total species richness will be the sum of the reactions of all individual species making up the community, with some species perhaps showing positive population responses to management, and

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others showing negative responses. Because species have intrinsic value unto themselves (Wilson 1988) and changes in species richness can be linked to changes in various ecosystem functions (Hart *et al.* 2001), an important goal of managers is to define management regimes that limit loss of native species.

Species accumulation curves provide one way to assess the effects of management on species richness. Such curves represent the cumulative number of species encountered as sample size is increased in either time or space. When management has a negative effect on species richness, the species accumulation curve should be shallower or level off at a lower number of samples compared to that for unmanaged habitats. When management has a positive effect on species richness, more new species will be accumulated with fewer number of samples compared to control locations. Species accumulation curves have been used to compare the effectiveness of different sampling techniques to estimate arthropod diversity (Longino and Colwell 1997), to compare canopy versus understory insect diversity (DeVries *et al.* 1997, Le Corff and Marquis 1999), and to determine the effects of natural disturbance on plant community diversity (Vandermeer *et al.* 2000).

During the years 1993-2000, we assessed the impact of two alternative forest harvesting regimes on the community structure and abundance of leaf-chewing insects feeding on white (*Quercus alba*) and black oak (*Quercus velutina*) in the southeastern portion of the Missouri Ozarks. This study is part of a larger multi-collaborator experiment, the Missouri Ozark Forest Ecosystem Project (MOFEP) (Sheriff, this proceedings), designed to determine the impacts of alternative forest harvesting regimes on the overall biodiversity and long-term productivity of these oak-hickory forests. The first harvest entry was completed; it was the first of a continuing series of periodic harvests to be implemented on a 15-year cycle in the even-aged and uneven-aged harvest units. We sampled the herbivore communities of the same stands, and the same trees within those stands, 3 years before cutting and 4 years after cutting. In each year, we sampled four times to account for predictable changes in community composition as the season progressed. Because the specific stands we sampled were not harvested, our sampling results reveal the landscape-level effects of harvesting on species accumulation.

We present here species accumulation curves for stands within regions undergoing two harvesting regimes (even-aged versus uneven-aged management) and a no-harvest (control) treatment. First, we determined the degree to which the species accumulation curves differed among the three treatments, with increasing numbers of samples over time (censuses and years), and we did so separately for the two host plants, *Q. alba* and *Q. velutina*. Second, we asked whether different times of year (different censuses) contributed differentially to treatment effects and to the overall 4-year pattern. The herbivore faunas of these oak species change dramatically in composition across the season, particularly between May and the rest of the the year. It is of interest to know, therefore, whether different portions of the fauna contribute equally to any observed treatment effects. Impacts on species richness *per se* and species turnover will be described in another publication (Marquis *et al.*, in rev.).

We predicted that both treatments would decrease species richness, resulting in lower species accumulation curves compared to unharvested forest regions. Three results from our initial pre-treatment sampling led us to predict a decrease. First, we found that total abundance of insect herbivores was greatest on trees located on north- and east-facing slopes as compared to trees on south- and west-facing slopes, for both *Q. alba* and *Q. velutina* (Marquis and Le Corff 1997). Thinning of the forest (uneven-aged management) would open the canopy, and increased proximity to clearcuts (even-aged management) would expose sampled trees and their insects to more open abiotic conditions. Both would be similar to the abiotic conditions of south- and west-facing slopes. Fewer individual insects would result in fewer species sampled. Second, prior to cutting, we found fewer species in the canopy of oaks than in the understory on saplings and low-hanging branches of mature trees (Le Corff and Marquis 1999). The canopy environment should be more similar to a thinned forest or clearcut edge than closed understory. Third, we found some evidence that younger forests have fewer insects (Marquis and Le Corff 1997). If opening up the forest simulates earlier successional stages, then fewer insects would be expected, and in turn, fewer species would be sampled. Finally, we expected the greatest decline in the uneven-aged management forest tracts, because a larger portion of their area was affected by cutting, and many stands that we sampled in

uneven-aged sites were thinned whereas none of our sampled even-aged stands were within a clearcut.

METHODS

Overall MOFEP Design

The MOFEP design (Brookshire *et al.* 1997, Sheriff, this proceedings) includes nine sites of approximately 400 ha each. At the onset of the study (1993), each of these sites was assigned to one of three cutting treatments: control, even-aged, or uneven-aged (N=3 sites/treatment). Pre-treatment sampling was conducted from 1993 to 1995, and cutting occurred in 1996, during which no data were collected. Post-treatment sampling began in 1997 and has continued through 2000. Sites were blocked by geographic proximity and other general characteristics (Sheriff and He 1997). The results presented here are for the post-treatment years only. We are testing whether these treatments affect species accumulation curves at the landscape scale, that is, across entire sites, since none of the stands in the control and even-aged sites, and only a portion of the uneven-aged sites, were altered directly by the cutting.

General Census Methods

Data presented here are for ground-level censusing (0.5 to 2.5 m) on a mixture of saplings and low-hanging branches of sub-canopy to canopy *Q. alba* and *Q. velutina* trees. The same trees and the same stands were censused each year and across years. Five trees each of *Q. alba* and *Q. velutina* were chosen haphazardly from those available within a stand, given a minimum leaf number criterion of 600 leaves per *Q. alba* individual and 200 leaves per *Q. velutina* individual, and a total of 3,000 and 1,000 leaves per stand for *Q. alba* and *Q. velutina*, respectively. When only trees with fewer numbers of leaves were available, more trees were marked. Trees that died within the time span of this study were replaced with nearby neighbors of the same species to maintain a comparable sample size. Sampled trees were spread over approximately 0.2 to 0.8 ha per stand.

To measure insect species richness, leaves on saplings or marked branches of trees were searched both top and bottom, as were associated branches and the main stem of the tree. The number of leaves on marked branches of each tree or sapling was counted in June of each year to estimate the amount of leaf area searched each census. Leaf-chewing insects encountered were classified to species or morphospecies, using a combination of photographs and detailed species descriptions. Each field worker was given training in identification prior to sampling and had a list of descriptions for all species sampled. At no time were leaves collected. All insects were left intact on the plant unless individuals could not be positively identified to species; these unknowns were taken back to the laboratory for rearing and photographing. Each unknown was given a unique sample number and description, and this information was entered into a database. An insect of unknown species was photographed and then observed throughout development until it could be verified as a previously-recognized species or classified as a species new to our inventory.

Post-treatment Censuses (1997-2000)

Leaf, Tree, and Stand Sample Size

During the four post-treatment years, we sampled an average (± 1 SE) of 855 ± 54 and $2,296 \pm 109$ leaves per stand on *Q. velutina* (N=43 stands) and *Q. alba* (N=54 stands), respectively. Using the average leaf size for *Q. velutina* (96.7 cm^2) and *Q. alba* (58.7 cm^2) (N=200 undamaged leaves for each species, each from a different tree), we sampled an average of *ca* 8.3 m^2 and 13.5 m^2 of foliage/stand on *Q. velutina* and *Q. alba*, respectively. Within each stand, the leaves were distributed among 5-12 trees per oak species. For *Q. alba*, we sampled six stands in each of the nine sites. For *Q. velutina*, it was not always possible to locate appropriate sized trees in every stand, so the number of stands/site ranges from 3 to 6 (N=43 total stands). The location of stands within each site was chosen randomly, except that in even-aged sites, we restricted the list of potential sites to the area scheduled to be cut in the second round of cutting in 2011; in so doing, we ensured that our stands were not located within clearcuts.



Number of Samples and Site Sampling Schedule

Due to changes in herbivore abundance and composition through the year (Marquis and Whelan 1994), trees were censused four times per year: early May, late June, late July, and late August-early September. Each census required 2 weeks to complete. In 1997 and 1998, the order of sampling of sites was the same as in pre-treatment sampling: sites 6, 5, and 4 of block 2; sites 3, 2, and 1 of block 2; and sites 7, 8, and 9 of block 3 (see Sheriff, this proceedings). Because we were concerned that the order of sampling might affect census results, especially in the May census when species are rapidly completing their life cycle before leaf hardening, we randomized the order in which we sampled blocks in the May censuses of 1999 (3, 2, 1) and 2000 (1, 2, 3), keeping the order of sites within blocks the same as in previous years.

Data Analysis

Species accumulation curves were generated by plotting the total number of species recorded in all stands within a site in the first census (May) of 1997 and then adding the number of new

species encountered for each successive census through the last census (August) of the year 2000. Although we sampled multiple trees within stands and multiple stands within sites, we chose to calculate species accumulation at the site level because site was the level at which treatments were actually applied. For each census, data were pooled across all stands within each site and cumulative species richness values were weighted by the leaf area sampled. Because the amount of leaf area/site varied slightly among years, data points for 1998-2000 were weighted by the running average of leaf area sampled (e.g., cumulative richness values for 1998 censuses were divided by the mean area sampled in 1997 and 1998). Separate curves were generated for *Q. alba* and *Q. velutina*. To examine the effect of the cutting treatments, block, year, and census on the pattern of species accumulation, we used repeated-measures analysis of variance (Littell *et al.* 1991). Treatment and block were the between-subject fixed effects, and year and census and their interactions with treatment and block were the within-subjects effects. Profile analyses (Littell *et al.* 1991, von Ende 1993) were conducted to determine when effects were significant (i.e., between which pairs of successive censuses and years). We estimated

Table 1.—Repeated measures ANOVA testing for treatment and block effects on the cumulative number of species per square meter of leaf area. *F*-approximations are based on Wilk's-Lambda test statistic. *Ndf* and *Ddf* are numbers of degrees of freedom in the numerator and denominator, respectively, for calculating the *F*-statistic for within subject effects.

Source	Between subjects							
	<i>Quercus alba</i>				<i>Quercus velutina</i>			
	df	MS	F	P	df	MS	F	P
Treatment (T)	2	0.62	3.48	0.1331	2	2.86	13.67	0.0163
Block (B)	2	1.49	8.43	0.0368	2	13.28	62.92	0.0009
Error	4	0.17			4	0.21		
Source	Within subjects							
	<i>Quercus alba</i>			<i>Quercus velutina</i>				
	Ndf/Ddf	F	P	Ndf/Ddf	F	P		
Year (Y)	3/2	140.31	0.0071	3/2	101.00	0.0098		
Census (C)	3/2	87.52	0.0113	3/2	98.56	0.0101		
Y X C ¹	9/36	49.16	0.0001	9/36	26.92	0.0007		
Y X T	6/4	1.48	0.3676	6/4	1.02	0.5157		
Y X B	6/4	4.00	0.1005	6/4	3.00	0.1532		
C X T	6/4	0.62	0.7157	6/4	1.50	0.3627		
C X B	6/4	1.98	0.2644	6/4	2.48	0.1994		
Y X C X T ¹	18/36	0.70	0.2529	18/36	1.67	0.2610		
Y X C X B ¹	18/36	1.55	0.7853	18/36	2.98	0.1053		

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

the contribution of individual censuses to the overall 4-year pattern by graphically comparing the mean effect of each census on species accumulation. Sufficient degrees of freedom were not available to test some interactions in these profile analyses (see table 1). The α -level was considered to be $P \leq 0.05$ unless otherwise indicated.

RESULTS

Species Accumulation Across Years

For both *Q. alba* and *Q. velutina* (fig. 1), the number of species sampled per leaf area in 1997, the first year following timber harvest, was approximately equal across treatments. For

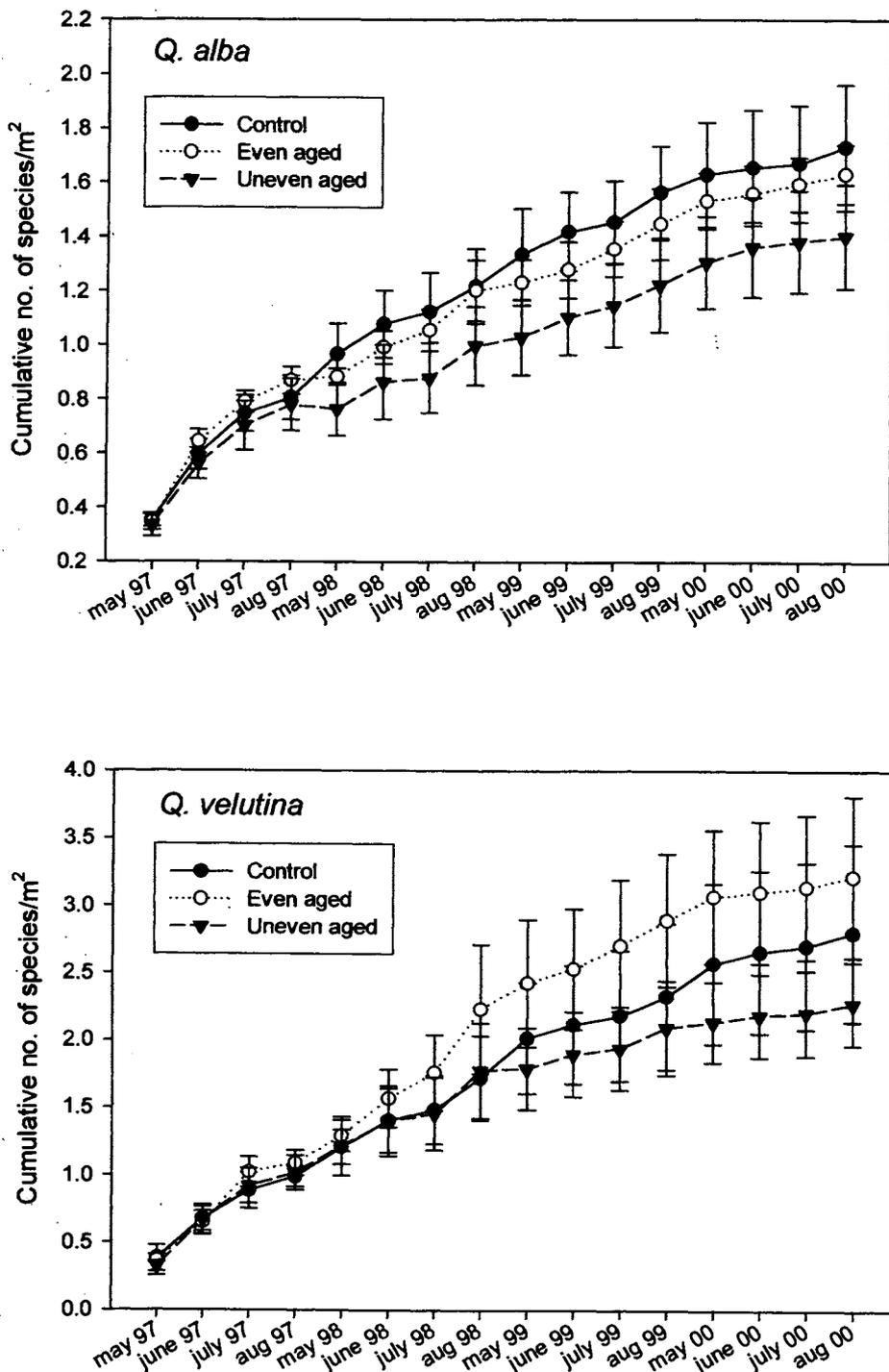


Figure 1.—Effect of harvest treatments on species accumulation curves across all four censuses for the years 1997-2000 on *Quercus alba* and *Q. velutina*. Values are the mean number of new species (\pm SE) accumulated per square meter of leaf area since the previous census.



Q. alba, mean numbers of new species sampled per square meter of leaf area searched at the end of the August 1997 census were 0.79 ± 0.08 , 0.86 ± 0.05 , and 0.7 ± 0.10 for control, even-aged, and uneven-aged treatments, respectively, while for *Q. velutina* these values were 0.98 ± 0.08 , 1.08 ± 0.09 , and 0.90 ± 0.02 , respectively. Thereafter, treatments diverged for both species. Both the significant census ($P < 0.011$) and year ($P < 0.0098$) effects for both species (table 1) and the shape of the curves (fig. 1) indicate that a significant number of new species continued to be added to the list in both *Q. alba* and *Q. velutina* throughout the 4-year period. By the end of 2000, we had recorded a total of 174 and 195 species of leaf-chewing insects on *Q. velutina* and *Q. alba*, respectively. A large majority of these species were rare: 12 percent were represented by a single individual and 16 percent were represented by only two to five individuals. Only one species was exotic, the Asiatic oak weevil, *Crytepistomus castaneus* Roelofs.

Control and even-aged treatments had higher species accumulation over time for *Q. alba*, but not significantly so for the entire study period (fig. 1) (table 1, $P = 0.133$). For *Q. velutina*, treatment ($P = 0.016$) was significant. For this species, control sites had intermediate numbers of new species compared to even-aged treatment (highest) and uneven-aged treatment (lowest) (fig. 1, table 2). Profile analysis showed that contrasts between years were not significant ($P > 0.13$).

Table 2.—Adjusted least squared means (\pm standard error) of cumulative number of species per square meter of leaf area for *Q. alba* and *Q. velutina* in August 2000. Means with different letters are significantly different.

Block	<i>Quercus alba</i>	<i>Quercus velutina</i>
1	$1.62 \pm 0.096ab$	$2.54 \pm 0.22a$
2	$1.86 \pm 0.096a$	$3.74 \pm 0.22b$
3	$1.29 \pm 0.096b$	$2.02 \pm 0.22a$
Treatment	<i>Quercus alba</i>	<i>Quercus velutina</i>
Control	$1.73 \pm 0.096a$	$2.80 \pm 0.22ab$
Even-aged	$1.63 \pm 0.096a$	$3.22 \pm 0.22a$
Uneven-aged	$1.40 \pm 0.096a$	$2.26 \pm 0.22b$

Species accumulation curves varied significantly by block for both *Q. alba* ($P = 0.037$) and *Q. velutina* ($P = 0.0009$) (table 1, fig. 2). For each species, block 2 had the highest curve, with blocks 1 and 3 similar in average number of accumulated species at the end of the 4 years (fig. 2, table 2). Profile analyses by year showed that the majority of the block effect for both species occurred after 1997, as only the contrast between 1997 and 1998 was significant for each species ($P = 0.032$ and 0.031 , for *Q. alba* and *Q. velutina*, respectively).

These block differences appear to be due in part to the differences in management histories of the sites, with individual blocks containing sites of similar ages. The total number of species accumulated per site at the end of 2000 was significantly negatively correlated with the year in which the sites came under the protection of the Missouri Department of Conservation (i.e., site acquisition year). This correlation was significant for 3 of 4 years for *Quercus alba* ($r = -0.77$ to -0.82 , $P = 0.006-0.01$) and for all 4 years for *Q. velutina* ($r = -0.74$ to -0.79 , $P = 0.01-0.02$) (fig. 3). Repeated-measures ANOVA showed that the effect of site acquisition year on total number of accumulated species at the end of each year was marginally significant for both *Q. alba* ($P = 0.103$) and *Q. velutina* ($P = 0.086$).

Species Accumulation by Census Across Years

For both *Q. alba* ($P = 0.011$) and *Q. velutina* ($P = 0.010$), censuses varied significantly in the rate at which species accumulated over time (table 1). Profile analysis showed that the significant treatment effect in *Q. velutina* was due mainly to the difference in treatments between the June and July censuses (fig. 3, $P = 0.036$, all other contrasts $P > 0.41$). In contrast, the strongest treatment effect in *Q. alba* occurred in the May census (fig. 4). Block differences in *Q. alba* were significant between the June and July censuses ($P = 0.01$), and marginally so between the July and August censuses ($P = 0.06$). For *Q. velutina*, block differences were significant between May and June ($P = 0.009$), between June and July ($P = 0.04$), and marginally so between July and August ($P = 0.06$).

The steeper slopes for the May censuses, followed by the August census, for both *Q. alba* (fig. 4) and *Q. velutina* (fig. 5) indicate that these

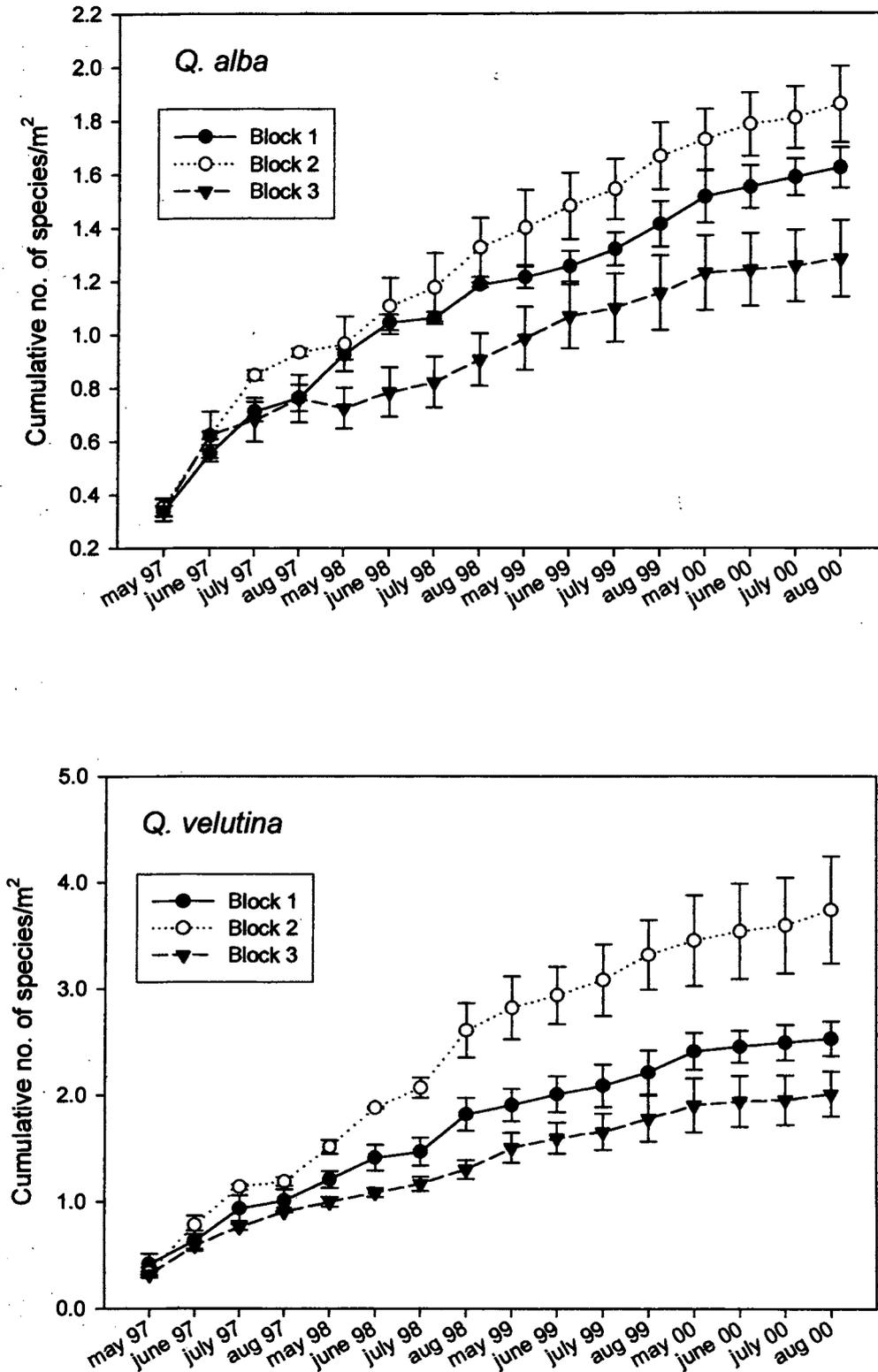


Figure 2.—Effect of block on species accumulation curves across all four censuses for the years 1997-2000 on *Quercus alba* and *Q. velutina*. Values are the mean number of new species (\pm SE) accumulated per square meter of leaf area since the previous census.

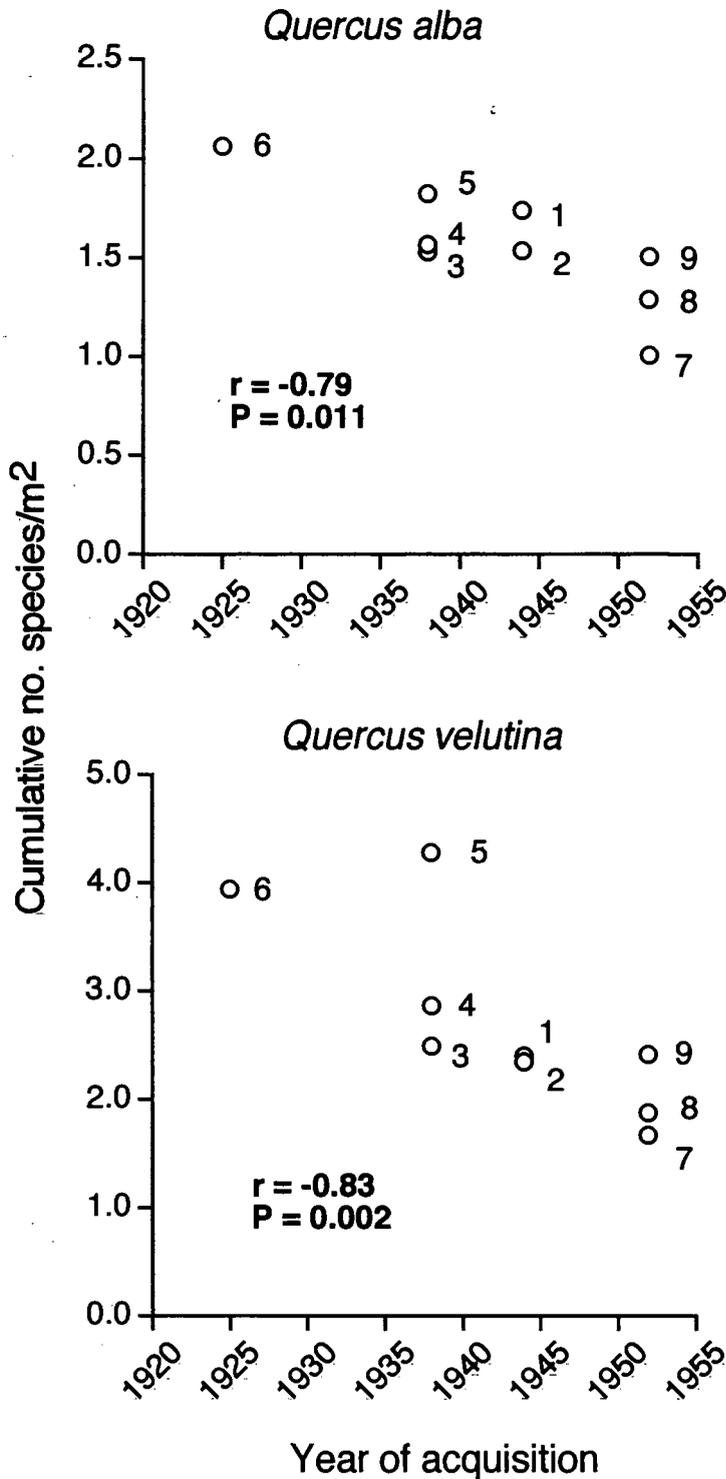


Figure 3.—Effect of time since acquisition under the auspices of the Missouri Department of Conservation on total number of species accumulated per square meter of leaf area up to the end of 2000 since the beginning of 1997 for both *Quercus alba* and *Q. velutina*. Number labels for the points are the MOFEP site numbers (see Sheriff, this proceedings).

Quercus alba

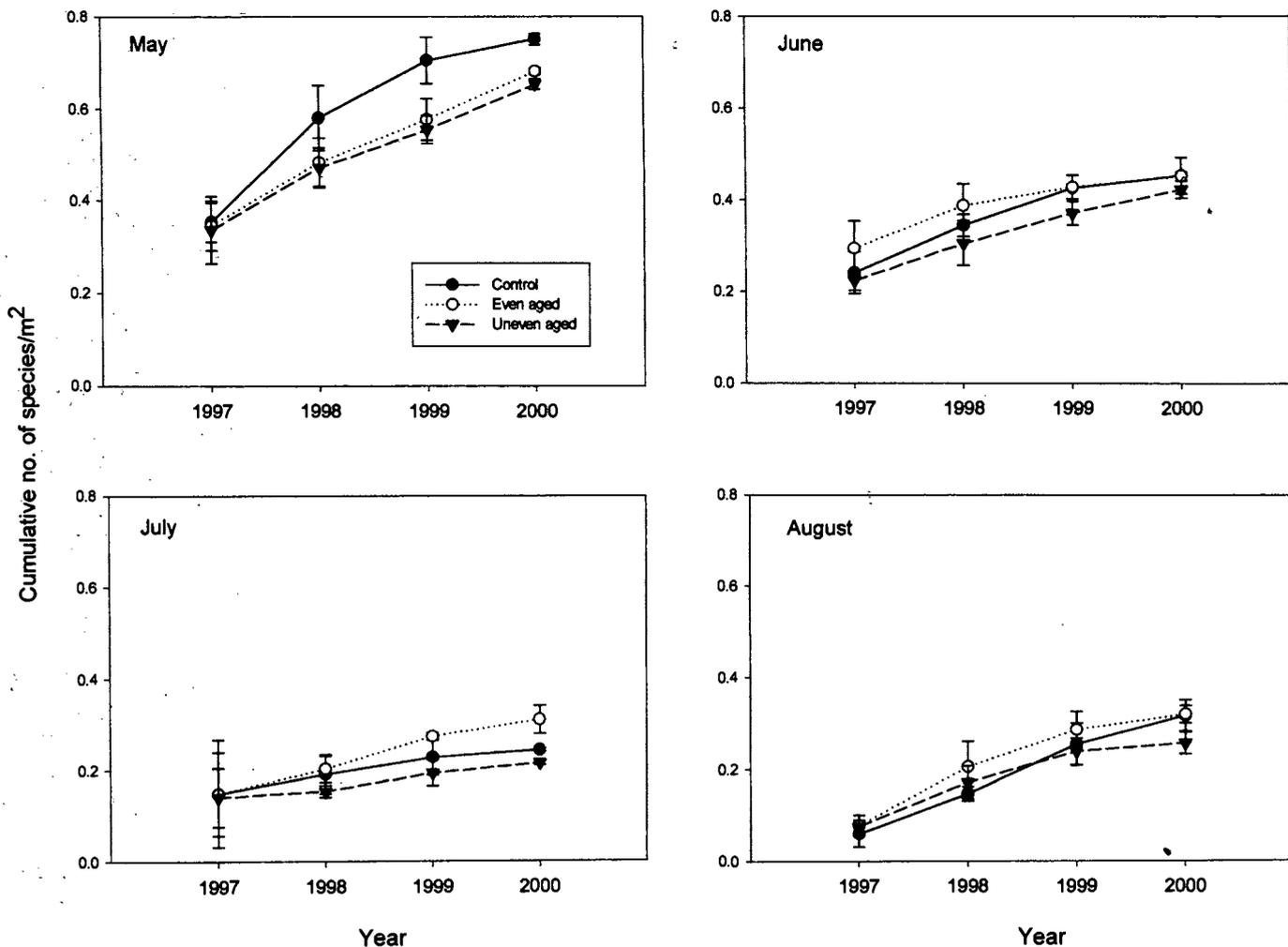


Figure 4.—Effect of treatment on species accumulation curves by individual census for *Quercus alba*. Values are the mean number of new species (\pm SE) accumulated per square meter of leaf area since the previous census.



Quercus velutina

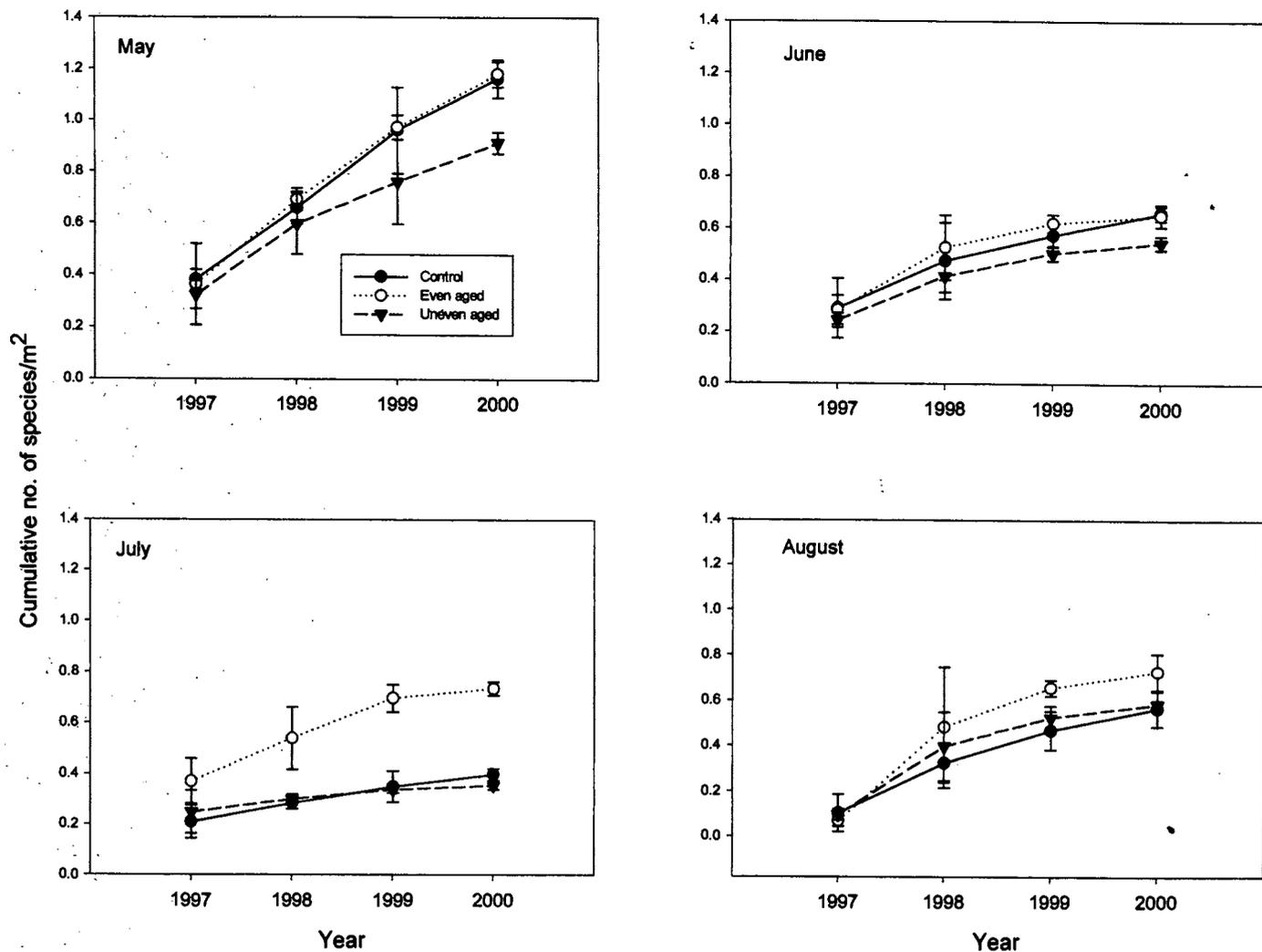


Figure 5.—Effect of treatment on species accumulation curves by individual census for *Quercus velutina*. Values are the mean number of new species (\pm SE) accumulated per square meter of leaf area since the previous census.

two censuses contributed the most to the overall pattern of species accumulation (fig. 1). May censuses continued to contribute almost twice as many new species compared to the other three censuses throughout the 4-year study period.

DISCUSSION

Species accumulation curves differed significantly by timber harvest method for *Quercus velutina* (fig. 1). For *Q. alba*, there is a trend for continued deviation in species accumulation curves over time, but the curves were not significantly different at the end of 2000. These results suggest that when a species accumulation curve for a particular harvest method and host tree species was lower than that for control sites (e.g., uneven-aged treatment on *Q. velutina*, fig. 1), harvesting reduced population size in a significant number of species such that they were no longer sampled. In turn, when a species accumulation curve in a harvest treatment was higher than that of the control (e.g., even-aged treatment on *Q. velutina*, fig. 1), we suggest that tree harvest increased the population size of a significant number of species such that they were sampled, while in control sites they were not.

Treatments did not affect species accumulation curves for *Q. velutina* immediately, as indicated by the marginally significant year effects in profile analysis (1997 vs. 1998: $P=0.13$; 1998 vs. 1999: $P=0.18$) and the very similar means in 1997. A delayed time course of block effects on species accumulation was seen for both *Q. alba* and *Q. velutina* (fig. 2), with profile analysis supporting this conclusion. The degree to which there was a real delay in treatment and block effects is not clear, as population sizes were very low in 1997 across all censuses and for both host plant species (Gram *et al.* 2001; Marquis *et al.*, in prep.). Reduced population sizes across the insect community might reduce our ability to detect treatment effects on species accumulation curves. Possible spill over effects from neighboring sites of contrasting treatments also might reduce our ability to discern treatment effects. The results of analysis of spatial effects are forthcoming in which we can test whether treatment effects are due to spill over effects from harvested areas into neighboring intact forest versus whole site effects resulting from changes in the composition and structure of the entire forest matrix.

The effects of the treatments in *Q. velutina* varied somewhat depending on census. Although there was no significant overall treatment X census interaction for either host species (table 1), there was a significant contrast between the June and July censuses in the profile analysis for *Q. velutina*. This result indicates a significant change in treatment effect across these censuses, with the greatest effect coming in June and less of an effect in July (fig. 5). Over and above the treatment effect, the May census contributed most to the overall pattern of species accumulation for both host species across the 4 years (figs. 4 and 5). This result suggests that the composition of the May fauna is more variable from year to year than is that of the later season.

The observed trend for effect of harvesting on species accumulation curves for *Quercus alba* was similar to our initial prediction, i.e., both harvesting treatments reduced the rate of species accumulation and uneven-aged treatment had the greatest effect. In contrast, the even-aged treatment actually increased the rate of species accumulation on *Q. velutina* compared to non-harvested, control sites, which were intermediate among the three treatments. Why the treatment effect was stronger in *Q. velutina* than in *Q. alba*, and why even-aged harvesting should increase the rate of species accumulation is not clear. The two tree species share a number of herbivore species, but each also has a set of unique species (34 and 14 unique species for *Q. alba* and *Q. velutina*, respectively). Perhaps the species unique to *Q. velutina* are adapted to plants growing under more open conditions, and as a result, their abundances increased with cutting. *Quercus velutina* grows on drier and more open sites than *Q. alba* does throughout its range (Fowells 1965). Spatial analysis of the treatment effects and analysis of individual insect species patterns will be necessary to resolve this question. Unfortunately, little is known at this time of the ecology of individual herbivore species in this system.

Similar to the pattern for overall abundance based on pre-treatment sampling (Marquis and Le Corff 1997), we found a significant negative relationship between the total number of species encountered in a site and the year the site was acquired by the Missouri Department of Conservation. This pattern held true for both host plant species and was found at both the



beginning and end of the post-treatment sampling period. One possible confounding factor is that through 1998, we sampled sites in the approximate order of their acquisition, oldest to most recent. This might be a problem for the spring census, for at the end of that census many species are beginning to pupate, and as a result would not be censused. However, we still see significant correlations for species accumulated for each of the individual censuses, suggesting that as these forests age, either insect species accumulate and/or population sizes increase across many or most species so that more species are sampled with increasing forest age. Block 3 (sites 7, 8, and 9) had 30 to 50 percent lower number of large *Q. alba* trees ≥ 4.5 in. d.b.h. than the other blocks (Kabrick *et al.* 1997), although the abundance of large *Q. velutina* trees does not differ by block or site. Another possible confounding factor is that sites of the same age tend to be close in proximity. To clarify the role of forest age on herbivore species richness, future sampling should include other sites of known age outside of the MOFEP design (and therefore not spatially confounded with them).

Our preliminary conclusion, based on the analysis of species accumulation curves for 4 post-treatment years, is that timber harvest affects either population size and/or the presence-absence of a number of leaf-chewing herbivore species on *Q. alba* and *Q. velutina*. These effects result in changes in species accumulation curves. Both harvesting techniques had a negative but weak effect on the number of species sampled on *Q. alba*, while even-aged management significantly increased the number of species sampled on *Q. velutina*. However, there was a strongly significant effect of the date of acquisition by the Missouri Department of Conservation on the number of observed species for both *Q. alba* and *Q. velutina*. Sites not disturbed by fire, cattle grazing, and tree harvest had more observed species. This result suggests that after additional timber harvests in the MOFEP experiment, population sizes and the number of sampled species will decline on *Q. alba* and *Q. velutina* in both even-aged and uneven-aged treatments. A corollary of this prediction would be that insect numbers and species diversity would be much lower in clearcuts than in intact forest. Comparative sampling of clearcuts and understory is underway.

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The Impact of Timber Harvest on Surface Soil Microbial Community Activity in Clearcut Missouri Ozark Forest Ecosystem Project Plots

Henry G. Spratt, Jr.¹

Abstract.—Transformations of carbon (C), sulfur (S), nitrogen (N), potassium (K), and magnesium (Mg) were determined for Oa+A- and EB-horizon soils collected from 12 permanent subplots located in MOFEP sites 1 and 3 from May 1995 to June 1999. Six of the subplots were clearcut in 1996, and six were left undisturbed. Mineralization of ¹⁴C-lignocellulose (of *Quercus alba*) was used as a measure of microbial catabolic activity in the soils. *Quercus alba* is the predominant overstory tree species on MOFEP plots. Incorporation of ³⁵SO₄ into organic sulfur compounds was used as a measure of microbial anabolic activity in the soils. Total C, N, and S (TC, TN, and TS) were determined by elemental analysis. Exchangeable K and Mg were determined using ammonium acetate extraction followed by atomic absorption spectrophotometry. After harvest, Oa+A-horizons from clearcut sites initially had higher rates of lignocellulose mineralization than controls, but these had declined by 2 years post-harvest. Organic S production rates were reduced to a large extent (by 80 to 90 percent, t-test, p<0.05) for soils from plots both high and low in the landscape. Concentrations of TC in Oa+A-horizons were lower in clearcut soils than controls on all dates beginning 1 year post-harvest (declining by as much as 35 percent compared with pre-treatment soils). Total S of both Oa+A-horizons decreased by nearly 40 percent after clearcutting, while EB-horizons tended to show an increase in TS following clearcutting (up nearly 73%). The TS content of litter falling into clearcut sites increased by nearly 50 percent 2 years post-harvest. Total N was lowest in clearcut plots. Exchangeable K concentrations in Oa+A-horizons from clearcut plots declined by nearly 75 percent 2 years post-harvest. Trends in exchangeable Mg concentrations in Oa+A-horizons were not easily determined for the clearcut plots 2 years post-harvest.

Microbial activity in forest surface soils is critical to the recycling of most elements used by plants and animals of the forest ecosystem. The predominant form of C found on the forest floor is lignocellulose. Soil microorganisms are responsible for the decomposition of lignocellulose, and they help to recycle the C, N, and S associated with this compound (Atlas and Bartha 1993, Stolp 1988). Thus, the degradation of lignocellulose in forest soils is dependent on the presence of an active community of bacteria and fungi possessing the requisite enzymes to degrade these compounds.

Microbial activity associated with degradation of lignocellulose in forest soils tends to be greater near the surface of the soil than at depth. Although soil type dependent, analyses of the distribution of saprophytic bacterial communities within forest soils suggest that both cell numbers and diversity of microbial communities decline with depth from the soil surface (Zvyagintsev *et al.* 1993). Thus, assessments of forest soil decomposition activities, and their relationships to nutrient cycling, must focus on analyses of surface soils.

Organic matter that enters forest surface soils is usually not completely degraded by microbial decomposers. Some of the more recalcitrant forms of lignin will accumulate in the soil's humus pool (Atlas and Bartha 1993). Microbial

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activity, therefore, plays an essential role in the ultimate production of soil humus.

Organic compounds present in forest soil humus may interact with other elements. The presence of ionizable carboxyl, sulfhydryl, or amino groups on soil organic matter enables this substance to serve as excellent ion exchange sites for cations and anions present in soil solution. In fact, numerous studies have documented interactions between forest soil organic sulfur and ionizable elements, such as N, Mg, K, and Ca (Homann and Harrison 1992, Mitchell *et al.* 1989, Rechcigl and Sparks 1985, Spratt 1998, Spratt 1997b, Watwood *et al.* 1993, Wiklander 1978). Thus, in addition to providing both carbon and energy sources for soil microbial communities, organic matter entering forest soils may be critical to maintaining the equilibrium of other critical potentially soluble elements found in those soils.

Disturbances that impact surface soils of forests may have major effects on soil microbial communities. In a study conducted in a clearcut pine forest, Lundgren (1982) demonstrated a 2-year increase in soil bacterial numbers in his cut plots immediately after timber harvest, followed by a reduction in bacterial numbers in comparisons with control plots. In another study where bacterial phospholipids were monitored 2 years post clearcut, soils from harvested sites demonstrated a 23 percent reduction in these indicators of bacterial biomass (Pietikainen and Fritze 1995). Pietikainen and Fritze (1995) also observed a significant reduction (by 21%) in microbial carbon 3 years post clearcut in the coniferous forest they studied. Lastly, Spratt (1997b) demonstrated that in surface soils of a Missouri forest that had been clearcut between 2 and 3 years prior to sampling, microbial incorporation of sulfate into organic matter was reduced by over 80 percent compared to control plots. These studies suggest an overall negative impact of clearcutting on soil microbial populations and processes they catalyze. So, too, might timber harvest be expected to have an impact on other critical features of the soil environment where microbes convert litter into soil humus.

Studies of surface soil C and S transformations and exchangeable bases in sample plots of MOFEP prior to experimental treatment (clearcutting) indicated dynamic seasonal changes in these elemental pools. Most notable

changes were observed for total S (TS), organic S (OS), and the exchangeable bases K and Mg (Spratt 1997a). Observed relationships between OS and concentrations of exchangeable K and Mg in forest surface soils suggest that loss of OS from forest surface soils, due to natural variation in these compounds year to year or to some type of ecosystem disturbance, may influence the concentrations of exchangeable K and Mg available in those forest surface soils. Lost OS may reflect loss of an especially reactive component of the humus, which is critical to ion exchange reactions within the soil (Spratt 1998). We are currently studying how reduced concentrations of exchangeable K and Mg may affect organisms dependent on these nutrients in the surface soils.

This report will focus on post-treatment effects on surface soils of the Missouri Ozark Forest Ecosystem Project (MOFEP) in 12 subplots located within two watersheds of MOFEP sites 1 and 3 from May 1995 to June 1999. Six of these subplots were clearcut in 1996, and the other six were left undisturbed as controls.

OBJECTIVES

The major objectives of this study are:

1. To determine the short-term effects of even-aged and non-manipulative (no-harvest) forest management practices on soil carbon and sulfur constituents in MOFEP surface soils.
2. To assess any changes in indicators of surface soil microbial activity due to even-aged and no-harvest forest management practices in MOFEP surface soils.
3. To determine any relationships that may exist between soil microbial activity and concentrations of nutrient cations (e.g., K^+ or Mg^{2+}) in MOFEP surface soils.

MATERIALS AND METHODS

Sample Sites and Collection

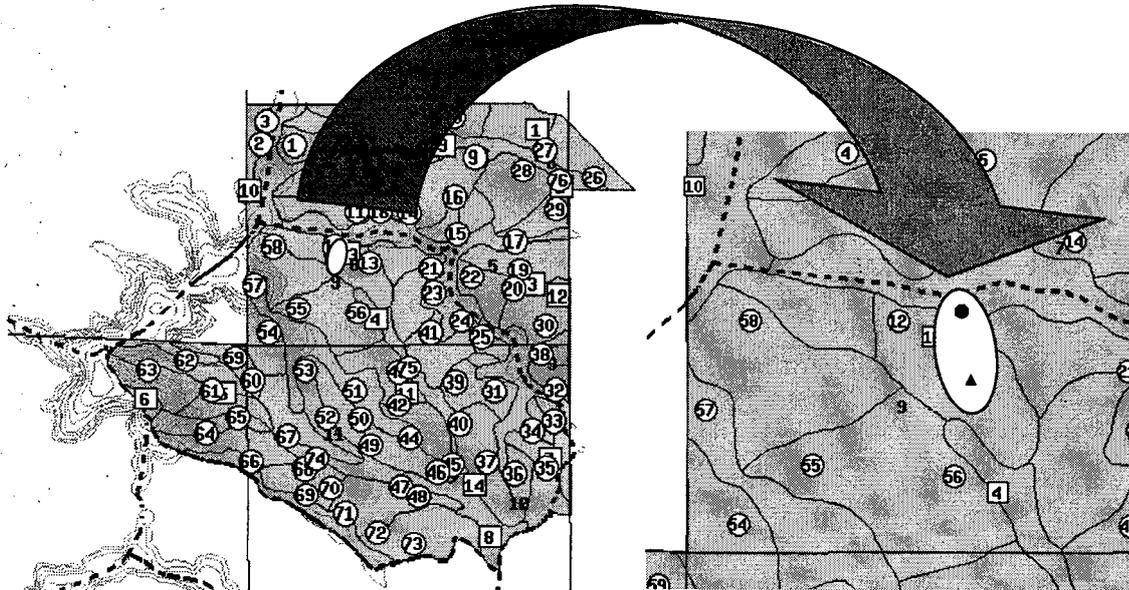
Sample site selection for this study has been described in detail by Spratt (1997a). Descriptions of the overall MOFEP design and the harvest techniques used may be found in Sheriff, this proceedings. This post-harvest study was established to observe potential



changes in surface soil nutrients (e.g., C, N, and S) and indicators of microbial activity immediately following harvest, and for a period of nearly 3 years post-harvest. The plots studied here were located in the four paired watersheds

described in the MOFEP pre-treatment document (see Spratt 1997a). These watersheds are located in MOFEP sites 1 and 3 (no-harvest and even-aged treatments, respectively, fig. 1). Of the watershed plots described (Spratt 1997a),

MOFEP Site 1 - Watershed Plots Controls



MOFEP Site 3 - Watershed Plots Clear-Cut

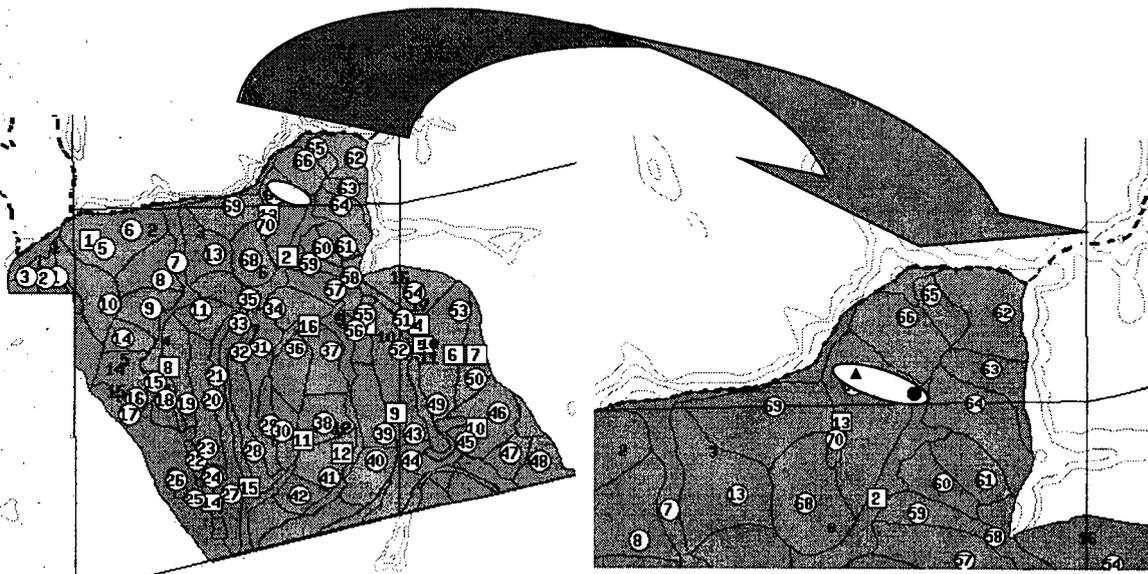


Figure 1.—Map of the MOFEP plots showing watershed plots in MOFEP site 1 (controls); watershed plots in MOFEP site 3 (clearcut). Numbers in circles indicate vegetation plots, numbers in squares indicate mast plots, remaining numbers indicate herpetofaunal arrays.

only those with north and east aspect (ELT 18) were actually clearcut. Thus, this report includes only results from clearcut and control subplots with this aspect. Additionally, within each of the two watersheds sampled, three subplots were established near the top of the slope (HI plots), and three subplots were established near the bottom of the slope (LO plots, see figure 2). Samples from sites with the uneven-aged treatment are not discussed here. Soil samples were collected from these 12 watershed subplots on the following sample dates: May 1995 (20°C), September 1995 (17°C), March 1996 (3°C), May 1996 (18°C), December 1996 (8°C), March 1997 (10°C), May 1997 (20°C), October 1997 (21°C), December 1997 (6°C), March 1998 (7°C), May 1998 (22°C), December 1998 (6°C), February 1999 (8°C), and June 1999 (23°C) [field Oa+A-horizon soil temperatures indicated in parentheses]. For the locations of the watershed plots reported here, please refer to figure 1 or the detailed maps presented in Brookshire *et al.* (1997).

Sampling in the watershed plots included collection of litter, Oa+A-horizons, and EB-horizons from all subplots. On each plot the litter was removed from the forest floor in an area of ca. 100 cm² and placed in sample bags. The Oa+A-horizons to a maximal depth of approximately 2 cm from just below the litter

were then carefully cut with a sharp spatula and placed in a sample bag. Finally, EB-horizons were collected down to a total depth of approximately 15 cm using a small trowel, carefully avoiding contamination of these soils with litter or Oa+A-horizons, and placed in a sample bag. All samples were stored in coolers on ice and transported to laboratories at the University of Tennessee at Chattanooga for processing.

Once at the laboratory, the soils and other samples were stored at 4°C and, within 3 days of collection, processed according to the chart in figure 3. To remove unwanted root material, rocks, and any other recognizable litter soils were passed through a 2-mm polyethylene sieve. The sieved samples were then subdivided into four fractions: one to measure extractable sulfate; a second percent moisture determination, elemental analysis, and determination of the exchangeable bases (K and Mg); a third to measure ³⁵S-sulfate incorporation into organic matter; and a fourth to measure ¹⁴C-lignocellulose mineralization. The exchangeable sulfate extracts were placed in sealed vials and frozen at -20°C until further processing (see below); the samples for percent moisture were weighed and then dried at 60°C until a constant weight was obtained to determine the weight of moisture lost. After the percent moisture was determined,

Soil Sampling

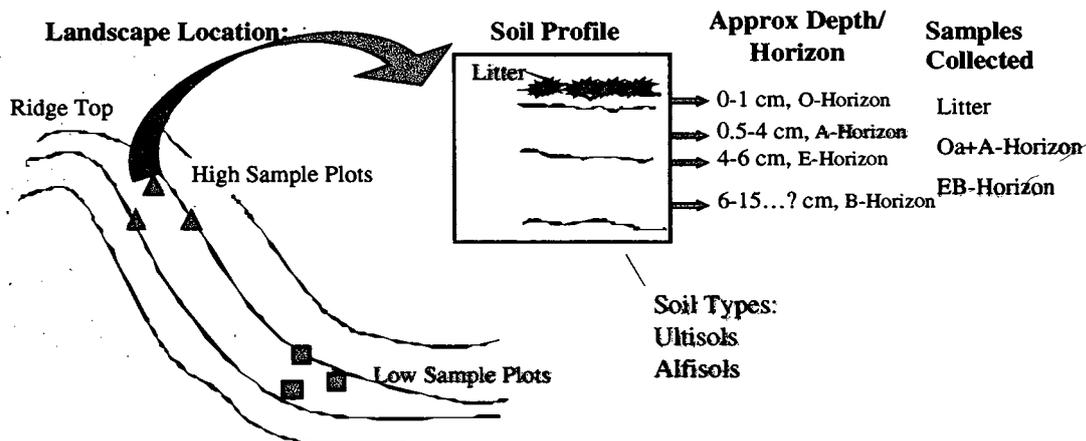


Figure 2.—Soil sampling, showing location of subplots high and low in the landscape, and approximate location of soil samples from the soil horizons found in these ultisols and alfisols.



Sample Processing

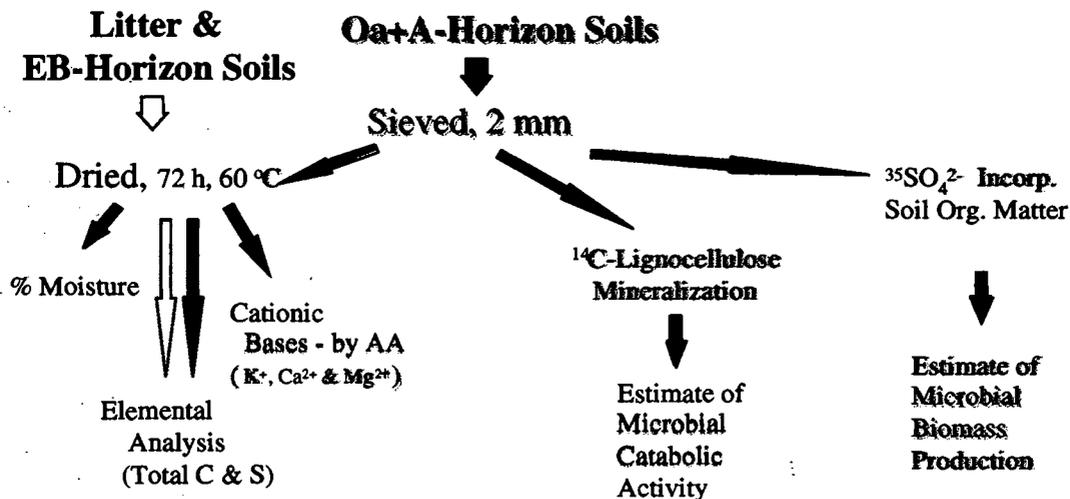


Figure 3.—Sample processing for surface soil elemental analyses and measures of microbial activity.

the dried soils were used to determine the soil TC, TN, and TS content and extractable base content (see below). Note: all data are presented on a g dry weight basis to negate changes due to different moisture content throughout the sampling period.

¹⁴C-Labeled Lignocellulose Mineralization

Published techniques to specifically label the lignin or cellulose moiety of woody plant tissue were followed (Benner *et al.* 1984, 1985; Crawford and Crawford 1976; Crawford *et al.* 1977; Hackett *et al.* 1977). White oak (*Quercus alba*) was chosen as the species to be radiolabeled, based on its distribution throughout the MOFEP sites. The process of generating the ¹⁴C-labeled lignocellulose using tree cuttings from MOFEP site 8 is described elsewhere (Spratt 1997a). Mineralization of white oak ¹⁴C-lignin and ¹⁴C-cellulose was determined using 200-ml microcosms. Suspended below stoppers inserted in the openings of the microcosm bottles was a test tube (3-ml capacity) into which 2 ml of 0.1 N NaOH was added. This NaOH served as a trap for any ¹⁴CO₂ generated during incubations. To set up the microcosms, 1 g field moist Oa+A-horizon soil was added to the bottom of each bottle. Time course experiments were initiated by addition of radiolabeled lignocellulose to soil in the bottoms of the microcosms. At

specified times the NaOH in the trapping tube was removed and replaced with fresh NaOH. Radiolabel present in the NaOH removed from the traps was quantified using liquid scintillation counting. Maximal rates of lignin or cellulose mineralization were determined by calculating the maximal change in DPM (backgrounds subtracted) recovered for different times over the time course of the incubation. Lignocellulose mineralization is used in this study as an indicator of microbial catabolic activity (fig. 4).

³⁵S-Sulfate Incorporation Experiments

Incorporation of ³⁵S-sulfate into different Oa+A-horizon soil S pools was monitored using a modification of the technique of Watwood and Fitzgerald (1988), and which is described by Spratt (1997a). Approximately 1 g sieved soil was added to 12-ml conical centrifuge tubes. ³⁵S-sulfate, as Na₂³⁵SO₄, was added (0.2 ml, ca. 1 μCi containing a total of 8 pmols sulfate) to the soil samples to initiate the incubations. The soils were incubated at field temperature, aerobically, for 48 hours in the dark. To terminate incubations, the soils were placed in a -20°C freezer. The fate of ³⁵S-sulfate added to the soils was determined by sequential extraction of the soils to quantify the radiolabel present in the water soluble and adsorbed

Measures of Soil Microbial Activity and Associated Elements

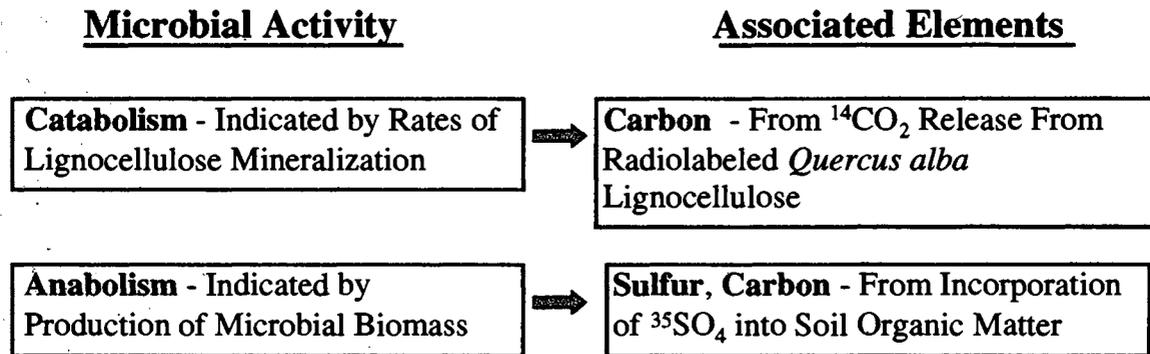


Figure 4.—Definitions of microbial activity and elements involved in microbial metabolism.

sulfate pools, and the OS fraction (Spratt 1997a, Watwood and Fitzgerald 1988). Sequential extraction with salts (1M Na_2SO_4 , 1M NaH_2PO_4 , and 1M NH_4Cl) was used to determine the amount of ^{35}S -sulfate adsorbed onto soil surfaces during the incubation. Radiolabel present in the OS fraction of the soil was determined using a strong acid/high temperature hydrolysis followed by a strong base extraction. Short-term production of OS in these soils represents microbial biomass production, and is used here as a proxy for microbial anabolic processes (fig. 4). The ^{35}S present in these fractions was determined using liquid scintillation counting.

Liquid Scintillation Counting

Quantification of the ^{14}C and ^{35}S used in all of the above experiments was made using a Wallac 1409 liquid scintillation counter. A biodegradable scintillation cocktail was used (Packard - Ultima Gold XR) for both radionuclides on all dates. Quenching of the samples was accounted for using external quench monitoring techniques (Wallac quench correction). For the ^{35}S -extraction samples specific quench curves were prepared using soils with no added ^{35}S , but extracted exactly as the radiolabeled soils. This was necessary because of the humic acids extracted from the soils along with OS compounds, which caused significant color quenching.

Determination of C, N, and S Pools

Soil TC and TS were determined for all Oa+A-horizons sampled. For some samples TN was also determined. Beginning with samples collected in March 1996, elemental analysis was conducted for Oa+A- and EB-horizons, as well as litter. A Leco CNS 2000 elemental analyzer, standardized with sulfamethazine and drift corrected using a NIS-traceable soil standard, was used for these analyses.

Exchangeable Bases

The exchangeable bases K and Mg were determined for all samples, using an ammonium acetate extraction procedure (Simard 1993, Spratt 1997a). Extracts from Oa+A- and EB-horizons were analyzed for K and Mg, using a Varian Spectr AA10 atomic adsorption spectrophotometer.

Statistical Analyses

Data presented here represent the results of a detailed study of two watersheds located within MOFEP. Due to limitations associated with potential pseudoreplication, multivariate analyses were not performed on these data. However, comparisons of the two watersheds were made using t-tests. To help demonstrate changes over



time for the treatment, compared with the controls, most data presented are normalized to control data (e.g., [experimental plot data] / [control plot data]). In this way, values greater than 1.0 represent increases in the parameter, while values less than 1.0 represent reductions in the parameter in comparison with the control plots.

RESULTS

Total C concentrations in watershed plots were either minimally affected by harvest or exhibited substantial differences from controls. For litter, minimal changes (t-test, $p < 0.05$) were observed in clearcut plots compared with controls. In clearcut plots, the total C in Oa+A-horizons from 38 to 43 mmol/g dry weight for all sample dates from March 1996 to June 1999, while in control plots, total C in Oa+A-horizons ranged from 20 to 34.5 mmol/g dwt. Changes in TC for Oa+A-horizons were most notable for clearcut plots (t-test, $p < 0.001$). A general trend towards lower TC in Oa+A-horizons from clearcut plots both high and low in the landscape began to show up in May 1997 (table 1). Total C in Oa+A-horizons of clearcut plots from low in the landscape differed from that of controls on each date sampled post-harvest. By June 1999, TC

in Oa+A-horizons of clearcut plots low in the landscape was nearly 70 percent lower than in control plots and nearly 40 percent lower than clearcut plots pre-treatment.

Total C in EB-horizons was considerably lower than that found in Oa+A-horizons, averaging 2.7 and 2.8 mmol/g dwt for EB-horizons vs. 26.0 and 27.3 mmol/g dwt for Oa+A-horizons, from control plots high and low in the landscape, respectively. Treatment effects were observed for TC in comparison of clearcut plots with control plots (t-test, $p < 0.05$). For plots high in the landscape, EB-horizons lost approximately 35 percent of the TC compared with control plots in June 1999 (table 1). Clearcut plots low in the landscape exhibited a loss of nearly 60 percent of TC in their EB-horizons compared with control plots in June 1999.

Total S from the plots studied here also varied considerably over the period sampled. Litter and Oa+A-horizons had 7 and 10 times higher TS than was found in EB-horizons (averaging 43.2 and 42.5 for litter, 43.4 and 49.0 for Oa+A-horizons, and 6.1 and 7.7 $\mu\text{mol/g}$ dwt for EB-horizons; control plots high and low in the landscape, respectively, averaged over the entire study). Litter inputs to surface soils exhibited increases in TS in the clearcut plots compared

Table 1.—Total carbon in clearcut plots (HI - high, and LO - low in the landscape), normalized to controls, May 1995 to June 1999. Mean values presented, (+/- 1 SD), $n=3$.

Sample date	Clearcut HI			Clearcut LO		
	Litter	Oa+A-horizon	EB-horizon	Litter	Oa+A-horizon	EB-horizon
May 95	—	0.71 (0.23)	—	—	0.51 (0.08)	—
Sep 95	—	0.84 (0.25)	—	—	0.59 (0.05)	—
Mar 96	0.98 (0.02)	0.92 (0.27)	0.99 (0.26)	1.00 (0.01)	0.81 (0.24)	0.76 (0.26)
May 96	1.00 (0.03)	0.76 (0.10)	0.60 (0.15)	1.00 (0.01)	0.65 (0.29)	0.89 (0.17)
Dec 96	1.04 (0.02)	0.66 (0.04)	0.77 (0.10)	0.93 (0.03)	0.75 (0.09)	0.92 (0.18)
Mar 97	0.97 (0.01)	0.72 (0.05)	1.02 (0.16)	0.96 (0.02)	0.88 (0.26)	0.82 (0.19)
May 97	0.96 (0.01)	0.47 (0.37)	0.71 (0.32)	0.96 (0.02)	0.38 (0.02)	0.62 (0.20)
Oct 97	0.84 (0.16)	0.80 (0.37)	0.55 (0.15)	0.98 (0.03)	0.31 (0.11)	1.46 (0.94)
Dec 97	1.04 (0.02)	0.57 (0.25)	0.96 (0.23)	0.93 (0.03)	0.53 (0.02)	0.70 (0.09)
Mar 98	0.95 (0.06)	0.92 (0.10)	—	0.97 (0.08)	0.54 (0.14)	0.74 (0.07)
May 98	0.94 (0.06)	0.53 (0.10)	0.93 (0.13)	0.97 (0.01)	0.31 (0.14)	0.64 (0.06)
Dec 98	—	0.68 (0.28)	—	—	0.34 (0.07)	—
Feb 99	0.99 (0.03)	0.41 (0.16)	0.73 (0.16)	0.93 (0.01)	0.23 (0.04)	0.40 (0.19)
Jun 99	0.94 (0.03)	0.62 (0.22)	0.67 (0.07)	0.93 (0.02)	0.30 (0.09)	0.39 (0.02)

with controls over the period sampled (t-test, $p < 0.001$). For Oa+A-horizons clearcutting resulted in marked loss of TS from plots both low and high in the landscape (table 2). TS in control plot Oa+A-horizons exhibited seasonal and annual variations that ranged from 25 to 72 $\mu\text{mol/g dwt}$ for plots high in the landscape and from 27 to 103 $\mu\text{mol/g dwt}$ for plots low in the landscape.

EB-horizons also exhibited changes in TS over the period sampled here. For samples from both

control and clearcut plots, the general trend in TS was for reduced levels in EB-horizons in the clearcut plots (table 2, t-test, $p < 0.05$). For soils from plots low in the landscape, the greatest loss of TS from the EB-horizons was approximately 40 percent for June 1999 samples.

Surface soil TN data were not available for samples collected earlier than May 1997 due to a malfunction in the elemental analyzer. Therefore, the data presented in table 3 are representative of only approximately two annual cycles

Table 2.—Total sulfur in clearcut plots (HI - high, and LO - low in the landscape), normalized to controls, May 1995 to June 1999. Mean values presented, (+/- 1 SD), n=3.

Sample date	Clearcut HI			Clearcut LO		
	Litter	Oa+A-horizon	EB-horizon	Litter	Oa+A-horizon	EB-horizon
May 95	—	0.60 (0.15)	—	—	0.46 (0.10)	—
Sep 95	—	0.69 (0.16)	—	—	0.57 (0.09)	—
Mar 96	0.81 (0.16)	0.91 (0.30)	0.91 (0.22)	0.86 (0.02)	0.78 (0.23)	0.76 (0.23)
May 96	0.79 (0.14)	0.72 (0.12)	0.64 (0.40)	0.64 (0.03)	0.55 (0.27)	0.77 (0.48)
Dec 96	1.15 (0.05)	0.63 (0.07)	1.15 (0.25)	1.79 (0.21)	0.58 (0.09)	1.22 (0.50)
Mar 97	1.41 (0.29)	0.82 (0.07)	0.82 (0.33)	1.16 (0.07)	1.09 (0.31)	0.69 (0.49)
May 97	1.10 (0.18)	0.46 (0.35)	0.65 (0.09)	1.10 (0.14)	0.36 (0.04)	0.64 (0.10)
Oct 97	0.74 (0.28)	0.86 (0.32)	0.60 (0.27)	1.19 (0.06)	0.32 (0.12)	1.16 (0.39)
Dec 97	1.15 (0.05)	0.60 (0.18)	1.09 (0.15)	1.80 (0.21)	0.49 (0.07)	0.55 (0.18)
Mar 98	1.31 (0.25)	0.81 (0.07)	—	1.40 (0.29)	0.42 (0.07)	0.71 (0.24)
May 98	1.20 (0.17)	0.33 (0.05)	0.84 (0.09)	1.05 (0.09)	0.36 (0.07)	0.66 (0.10)
Dec 98	—	0.74 (0.25)	—	—	0.34 (0.02)	—
Feb 99	0.94 (0.10)	0.50 (0.13)	0.94 (0.17)	1.15 (0.19)	0.26 (0.05)	0.60 (0.23)
Jun 99	1.31 (0.24)	0.66 (0.12)	0.98 (0.18)	1.17 (0.24)	0.30 (0.09)	0.59 (0.05)

Table 3.—Total nitrogen in clearcut plots (HI - high, and LO - low in the landscape), normalized to controls, May 1997 to June 1999. Mean values presented, (+/- 1 SD), n=3.

Sample date	Clearcut HI			Clearcut LO		
	Litter	Oa+A-horizon	EB-horizon	Litter	Oa+A-horizon	EB-horizon
May 97	1.22 (0.21)	—	0.92 (0.27)	1.06 (0.18)	—	0.78 (0.22)
Oct 97	0.90 (0.31)	0.84 (0.28)	0.77 (0.14)	1.23 (0.07)	0.37 (0.17)	1.68 (1.05)
Dec 97	—	0.83 (0.38)	1.33 (0.25)	—	0.62 (0.04)	0.84 (0.08)
Mar 98	1.47 (0.35)	0.91 (0.01)	—	1.40 (0.38)	0.59 (0.14)	0.71 (0.24)
May 98	1.24 (0.22)	0.63 (0.10)	1.33 (0.17)	1.14 (0.14)	0.41 (0.15)	1.10 (0.35)
Dec 98	—	1.03 (0.44)	—	—	0.38 (0.07)	—
Feb 99	0.94 (0.15)	0.64 (0.13)	1.13 (0.19)	0.93 (0.17)	0.47 (0.12)	2.15 (0.78)
Jun 99	0.65 (0.11)	0.77 (0.25)	0.72 (0.13)	1.46 (0.16)	0.36 (0.07)	0.49 (0.04)



post-harvest (from May 1997 to June 1999), with no pre-treatment data. The TN concentrations in litter and Oa+A-horizons were 8 to 10 times greater than the concentrations found in EB-horizons (averaging 938.3 and 843.4 $\mu\text{mol/g}$ dwt for litter, 806.7 and 899.0 $\mu\text{mol/g}$ dwt for Oa+A-horizons, and 93.6 and 111.9 $\mu\text{mol/g}$ dwt for EB-horizons; control plots high and low in the landscape, respectively, averaged over the entire study). Total N concentrations in litter ranged from about 700 to 1,200 $\mu\text{mol/g}$ dwt for all sample dates. For Oa+A-horizons, the control plots had greater TN concentrations than did the clearcut plots. The greatest change in TN was observed in comparisons between control and clearcut plots located low in the landscape. On each of the sample dates, TN in Oa+A-horizons was lower than that found in control soils (table 3, differing by as much as nearly 60% in December 1998). For EB-horizons, TN in clearcut soils differed little from that in control soils. However, in February 1999, one sample from clearcut plots low in the landscape had the highest TN value observed for all EB-horizons sampled over all dates (table 3). On that date, TN in this plot was more than two times greater than in the controls.

The concentration of exchangeable K was from four to five times greater in Oa+A-horizons than in EB-horizons of the plots studied, averaging 26.1 and 9.5 $\mu\text{mol/g}$ dwt, respectively, for the sampling period for soils from the two different areas. Exchangeable K in Oa+A-horizons of the plots studied here also exhibited notable change

as a result of the experimental treatment (t-test, $p < 0.05$). Variation of exchangeable K in Oa+A-horizons by up to 1.9-fold was observed for the control plots over all dates sampled (table 4, ranging from a high of 42 to a low of 16.5 $\mu\text{mol/g}$ dwt). However, comparisons of exchangeable K in Oa+A-horizons of clearcut plots high in the landscape with controls showed an initial increase immediately after harvest, followed by a decrease back to levels close to those originally found (table 4). Within surface soils from clearcut plots, variation in exchangeable K was more dramatic, dropping by as much as four-fold following treatment (from a high of 28 to a low of 7 $\mu\text{mol/g}$ dwt). In comparisons of clearcut plots located low in the landscape with controls, the same pattern as seen for soil from plots located high in the landscape was observed. Exchangeable K levels increased initially following harvest, only to drop back to near initial conditions by 2 years after harvest (table 4). Exchangeable K values in surface soils of the low plots of the clearcut treatment also exhibited a reduction in exchangeable K concentrations, dropping by 2.8-fold (22 vs. 8 $\mu\text{mol/g}$ dwt). For EB-horizons, exchangeable K from plots high in the landscape changed only a small amount compared with controls (table 4). Plots located low in the landscape generally had higher levels of exchangeable K over the period observed post-harvest.

Exchangeable Mg was as much as eight times more concentrated in Oa+A-horizons than in EB-horizons of the plots studied, averaging 41.8

Table 4.—Exchangeable potassium in clearcut plots (HI – high, and LO – low in the landscape), normalized to controls, May 1995 to May 1998. Mean values presented, (+/- 1 SD), $n=3$.

Sample date	Clearcut HI		Clearcut LO	
	Oa+A-horizon	EB-horizon	Oa+A-horizon	EB-horizon
May 95	0.56 (0.08)	—	0.45 (0.01)	—
Sep 95	0.95 (0.28)	—	0.55 (0.06)	—
Mar 96	0.96 (0.12)	—	0.92 (0.21)	—
May 96	1.21 (0.19)	—	0.64 (0.08)	—
Dec 96	1.01 (0.22)	1.09 (0.14)	0.79 (0.04)	1.27 (0.18)
Mar 97	0.58 (0.13)	1.03 (0.03)	0.79 (0.12)	0.95 (0.05)
May 97	1.87 (1.19)	0.87 (0.04)	0.62 (0.03)	1.05 (0.24)
Oct 97	0.66 (0.08)	0.84 (0.17)	0.45 (0.04)	1.24 (0.51)
Dec 97	0.65 (0.22)	0.68 (0.01)	0.50 (0.06)	0.78 (0.19)
Mar 98	—	—	—	1.14 (0.51)
May 98	0.46 (0.12)	1.49 (0.42)	0.46 (0.27)	0.97 (0.33)

and 5.5 $\mu\text{mol/g}$ dwt, respectively, for the sampling period for soils from the two different areas. Comparing exchangeable Mg from clearcut plots with controls, a slight increase in this element for Oa+A-horizons post-harvest is evident. For EB-horizons, exchangeable Mg was generally higher in all samples tested post-harvest (table 5).

Microbial catabolic activity in Oa+A-horizons from the plots studied, as evidenced by rates of lignocellulose mineralization, exhibited a marked increase in activity within 2 years post-harvest, followed by a notable reduction in activity between 2 and 3 years post-harvest. This trend was evident for samples collected from plots high and low in the landscape. Rates of cellulose mineralization peaked by December 1998 (increasing by as much as fourfold compared with controls for plots from low in the landscape, fig. 5). However, data for both February and June 1999 are not consistent with the higher rates observed in December 1998.

Lignin mineralization in surface soils of the watersheds studied followed a pattern similar to that described above for cellulose mineralization. There was a notable increase in lignin mineralization in May 1998 for Oa+A-horizons from high in the landscape (fig. 6, an increase from the controls of over sevenfold). No similar result was observed for soils from low in the landscape, however.

Microbial anabolic metabolism, as evidenced by rates of incorporation of SO_4 into soil organic matter, indicated substantial changes in the microbial communities present in clearcut Oa+A-horizons, compared with pre-treatment conditions. With variations between all plots pre-treatment ranging by no more than about 45 percent, the reductions of 82 percent and nearly 90 percent in clearcut plot soil OS production for soils from both high and low in the landscape, respectively, were significant (t-test, $p < 0.05$, fig. 7).

DISCUSSION

The data presented in this report represent a study of the relatively short-term effects of clearcutting on surface soil microbial communities and certain elemental pools in selected plots of the MOFEP study. Although the initial scope of this study was scaled down after it was determined that some pre-treatment soil sample plots were not harvested, the data presented for the north and east aspect plots in these watersheds provide some useful insights into the short-term effects of clearcutting in surface soils of these Missouri forests. This is especially true when considered in light of the earlier study conducted in south and west aspect plots in Deer Run State Forest (Spratt 1997b). Direct comparisons may not be made with results of the Deer Run study (the clearcut sites in that

Table 5.—Exchangeable magnesium in clearcut plots (HI - high, and LO - low in the landscape), normalized to controls, May 1995 to May 1998. Mean values presented, (+/- 1 SD), n=3.

Sample date	Clearcut HI				Clearcut LO			
	Oa+A-horizon		EB-horizon		Oa+A-horizon		EB-horizon	
May 95	0.79	(0.26)	—	—	1.49	(0.12)	—	—
Sep 95	1.05	(0.29)	—	—	1.43	(0.30)	—	—
Mar 96	0.99	(0.18)	—	—	2.18	(0.05)	—	—
May 96	1.23	(0.34)	—	—	1.23	(0.23)	—	—
Dec 96	0.62	(0.23)	1.34	(0.52)	1.94	(0.30)	3.93	(1.97)
Mar 97	1.09	(0.10)	1.72	(0.29)	1.93	(0.38)	0.92	(0.42)
May 97	1.23	(0.21)	1.94	(0.62)	1.40	(0.14)	1.26	(0.37)
Oct 97	0.83	(0.07)	1.28	(0.23)	0.76	(0.31)	2.11	(0.86)
Dec 97	1.20	(0.09)	1.38	(0.22)	1.68	(0.22)	1.92	(0.44)
Mar 98	—	—	—	—	—	—	0.89	(0.32)
May 98	0.89	(0.31)	2.07	(0.82)	0.95	(0.47)	0.82	(0.12)

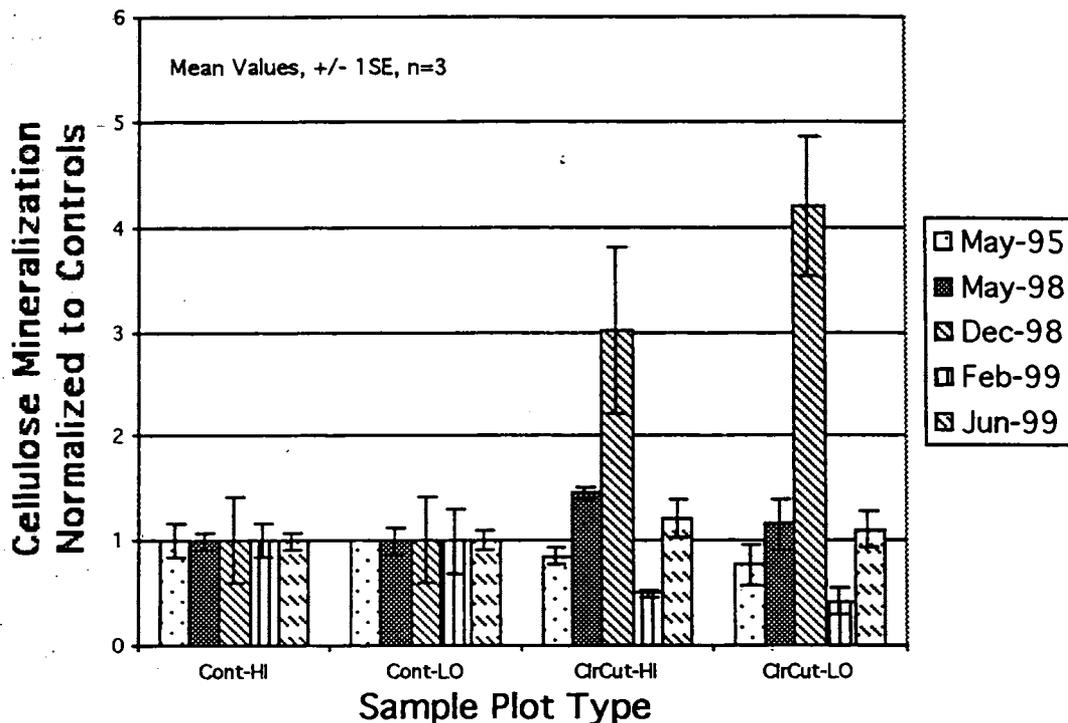


Figure 5.—Cellulose mineralization normalized to mean control cellulose mineralization for Oa+A-horizons from watershed subplots located both high (HI) and low (LO) in the landscape. Cont indicates control plots and ClrCut indicates clearcut plots.

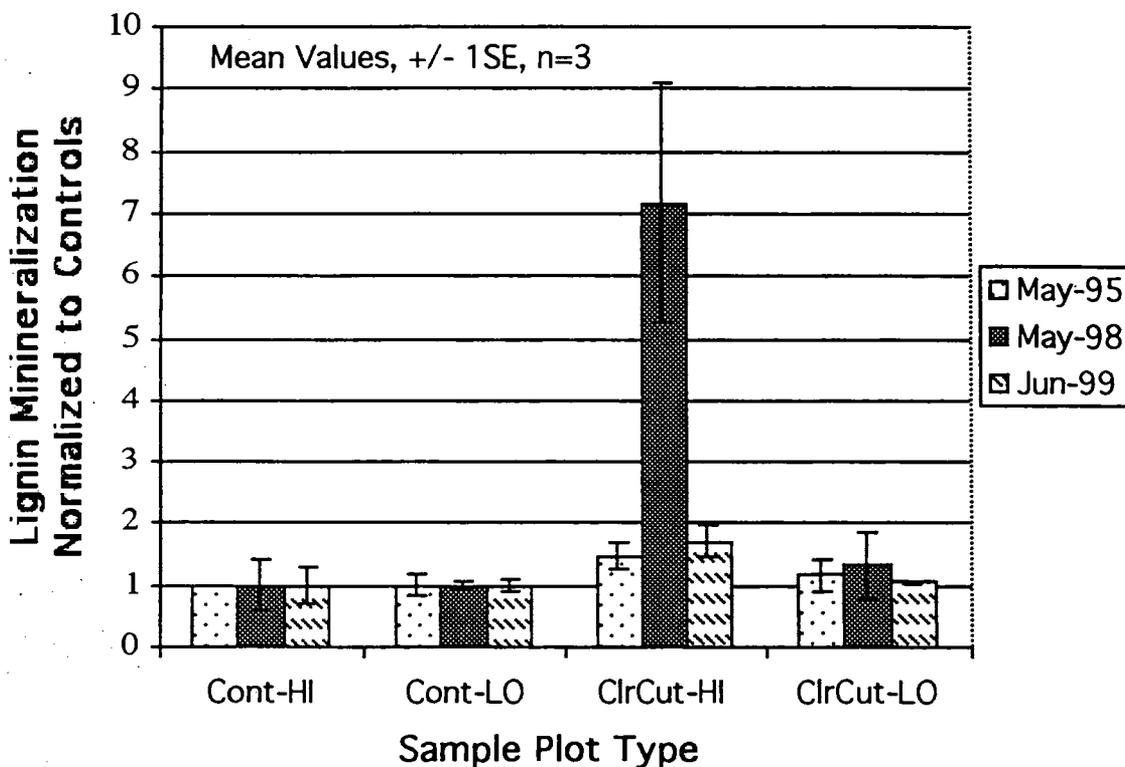


Figure 6.—Lignin mineralization normalized to mean control cellulose mineralization for Oa+A-horizons from watershed subplots located both high (HI) and low (LO) in the landscape. Cont indicates central plots and ClrCut indicates clearcut plots.

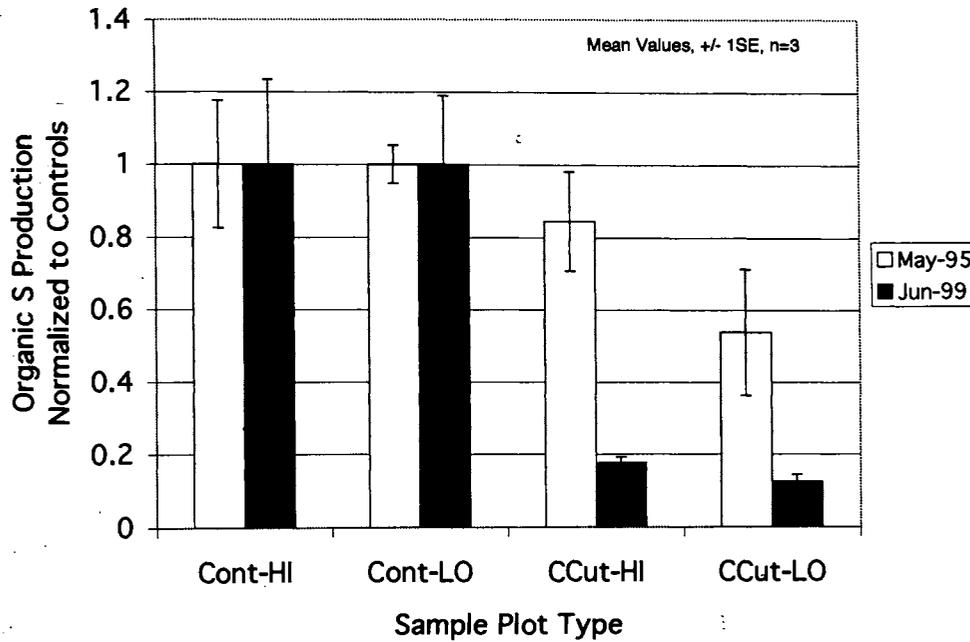


Figure 7.—Microbial OS production as an indicator of microbial anabolism. Data are normalized to mean control OS production for Oa+A-horizons from watershed subplots located both high (HI) and low (LO) in the landscape. Cont indicates control plots and C/CrCut indicates clearcut plots.

pilot study were not part of MOFEP) detailing changes in TS and OS in Oa+A-horizons (actually called A-horizon soils in Spratt 1997b, but subsequently determined to be Oa+A-horizon soils), as well as changes in exchangeable K and Mg, since all of the plots studied in the Deer Run study were located in south and west aspect habitat. However, the Deer Run study did suggest potential changes in surface soil nutrient status that might be expected within 3 years post-clearcutting in soils from other aspect plots. The basic findings of the pilot study have been supported for the north and east aspect plots studied here.

Changes in TC in surface soils from the clearcut plots 2 to 3 years post-harvest may represent initial changes in the soil habitat similar to those observed in other forest ecosystems post-harvest. Two indicators of microbial activity in soils, cell numbers and microbial biomass, were significantly reduced within 2 years post-clearcut in European forest ecosystems (Lundgren 1982, Pietikäinen and Fritze 1995). In the pilot study conducted in Deer Run State Forest, similar reductions in indicators of soil microbial activity were observed 2 to 3 years post-harvest (Spratt 1997b). In the current study, TC reductions in Oa+A-horizons from clearcut plots may indicate loss of potential

microbial carbon and energy sources. The observed reduction in TC from Oa+A-horizons (of approximately 25 percent for plots high in the landscape), if directly linked with microbial biomass, would lead to losses of microbial biomass of a similar magnitude to those observed in the European forests mentioned above (Lundgren 1982, Pietikäinen and Fritze 1995). The greater than 60 percent loss of TC for Oa+A-horizons from plots located low in the landscape may represent an even greater impact on the microbial communities in those soils.

Direct measurements of microbial activity using lignocellulose mineralization as a proxy for microbial catabolism in these soils support findings of the European studies to some degree (Lundgren 1982, Pietikäinen and Fritze 1995). For the soils studied here, mineralization activity appears to have peaked between 1 and 2 years post-harvest, and then declined. There was also, however, a large increase in microbial catabolic activity in control plot soils, presumably due to climatic effects of a seasonal nature, making this assertion more difficult to support.

Indications of microbial production in the soils studied here suggest a similar effect of clear-cutting on microbial anabolism in the Missouri



soils as has been observed for European soils post-clearcut. The OS production data presented here do provide compelling evidence for significant (t -test, $p < 0.05$) changes in microbial activity leading to the production of microbial biomass. In the 1992 Deer Run pilot study, Oa+A-horizons from south and west aspect clearcut plots 2 to 3 years post-harvest (Spratt 1997b) supported rates of microbial OS production 70 to 80 percent lower than control plots. The reductions in rates of OS production presented here, ranging from approximately 80 to 90 percent for Oa+A-horizons from north and east aspect plots, suggest that microbial communities in soils from both habitats are affected in similar ways by the disturbance of clear-cutting.

Other evidence that microbial communities of surface soils from clearcut plots may be indirectly affected by changes brought about by clearcutting may be seen in changes of nutrient concentrations in surface soils post-harvest. The TS found in Oa+A-horizons of MOFEP plots is known to be composed principally of OS (up to 98 percent of the TS, Spratt 1997a, 1997b). This is in keeping with studies of other forested ecosystems in the U.S., Canada, and Europe where OS has been found to dominate the TS of these soils (Johnson *et al.* 1986, Mitchell and Zhang 1992, Van Loon *et al.* 1987, and Zucker and Zech 1985). If the TS found in Oa+A-horizons is principally OS, and if that S represents a relatively reactive form of organic matter in the soil (e.g., either lignin or humic substances, or microbial biomass with abundant sulfhydryl groups), then the losses of TS described here for clearcut plots could indicate a potential for lost ion exchange sites within the organic fraction of these surface soils.

The TS or OS within surface soils of the plots studied here is dynamic. Interestingly, the TS data collected during March 1998 from all plots studied showed large increases in this element compared with previous sample dates (and for all later sample dates, for that matter). It is not known whether unusual weather patterns associated with the intense El Nino weather phenomenon that occurred during part of this study were responsible for these increases in TS, via increased S input in precipitation for the plots studied. Sulfur inputs to forested ecosystems via precipitation, although declining in recent years, have been important sources of this element in many eastern U.S. forests over the past 30 years (Johnson *et al.* 1986). It is

possible that such a boost in S via precipitation input might overshadow any changes that could have been occurring as a result of the MOFEP treatments during that winter. However, in subsequent samplings, the levels of TS dropped for all plots studied, indicating that the added S during March 1998 was particularly liable.

Another question of note regarding the potential indirect impact of changing elemental pools on surface soil microbial communities has to do with the origin of OS to MOFEP surface soils. Organic S from plant origin was not directly measured in either the MOFEP pre-treatment study or here, but, it may be inferred from litter TS data in this study that significant changes in the quality and quantity of plant-derived OS may have occurred on the clearcut plots post-harvest. A very large increase (20% greater than observed in control plots) in TS in litter 2 years post-harvest may represent significant changes in the sources of OS in these plots. We know that in clearcut plots of other Missouri Ozark forests shrub species tend to dominate several years post-harvest (Annand and Thompson 1997). Spratt (1998) suggested that changes in the quality of OS found in litter in clearcut areas might change post-harvest, potentially leading to the observed loss of OS in the Deer Run pilot study plots. Further study of the type of S present in litter of MOFEP and watershed plots is currently underway and may help shed light on whether the changes in TS observed here for clearcut plots might affect surface soil S pools. Other changes in surface soil nutrients observed in the Deer Run pilot study that correlated with changes in OS of Oa+A-horizons may have occurred in the plots described here.

Exchangeable K and Mg concentrations for the surface soils from north and east aspect plots studied here have changed post-harvest. While control plot exchangeable K in Oa+A-horizons exhibited variation of some 1.9 times over the period of the study, exchangeable K from clearcut plots decreased nearly fourfold post-harvest, compared with pre-treatment data. In the pilot study of Deer Run State Forest Oa+A-horizons 2 to 3 years post clearcut, Spratt (1997b) found a nearly 40 percent reduction of exchangeable K. The loss of exchangeable K from Oa+A-horizons of the clearcut plots in this study approaches 75 percent. Data for exchangeable Mg from the Oa+A-horizons of the plots studied here do not indicate a loss of the order observed for Oa+A-horizons in the pilot study (a loss of from 40 to 70%). There does

appear to have been some increased input of Mg to all soils studied here (controls and experimental) during late winter 1997. This makes the analyses more difficult to interpret. Dolomitic outcrops located throughout the MOFEP study sites (Meinert *et al.* 1997), might provide added Mg via weathering to some surface soils. However, for either exchangeable K or Mg, the potential exists for a loss of organic cation exchange sites (either purely C-based or OS-based) from surface soils of clearcut plots. The correlation between reduced exchangeable K and Mg and OS concentrations in clearcut Oa+A-horizon soils of the Deer Run State Forest pilot study was discussed previously (Spratt 1997b). Other evidence of a role for OS in the retention of exchangeable bases in forested ecosystems has been documented. A study by Watwood *et al.* (1993) suggested that ecosystem leaching of Ca, Mg, and K was positively correlated with the loss of soil organic S from the A-horizons of a wide range of forest soils. In the Missouri soils studied here, nutrient cations may also have been leached out of the surface soils, either into soil horizons deeper than 15 cm, or potentially downslope and lost to the local system. Loss of nutrient cations from forest ecosystems might have a negative effect on the productivity of those ecosystems.

The potential for loss of exchangeable bases, especially K, from the watershed surface soils studied here may have special implications for these forested ecosystems. In all cases studied in this watershed study, as well as in the MOFEP plots pre-treatment, soils sampled were classified as either alfisols or ultisols. One characteristic of alfisols and ultisols is their limited K-supplying power (Hausenbuiller 1978). In these soils, K that is available to primary producers comes primarily from exchangeable and soluble forms. As a result of the limited K-supplying power of the soils of the MOFEP plots, the predominant source of this base to the forest ecosystem must be atmospheric deposition, a noted source of K to eastern U.S. forests (Ragsdale *et al.* 1992). As the vegetation uses base cations, deciduous trees tend to accumulate exchangeable bases in surface soils (Johnson 1992). Since the soils sampled in this study were well drained and mostly lack clays, any changes that might lead to loss of ion exchange sites, especially in the surface soils, for exchangeable bases might lead to increased leaching of these nutrients. Although such deficits might not prove significant to deep-rooted overstory trees, organisms

dependent on surface soils for their nutrients might be stressed due to low levels of these bases in surface soils of clearcut plots. The potential that microbial populations responsible for nutrient cycling in the surface soils might become K limited several years post-clearcut was discussed by Spratt (1998).

Is there a minimal level of organic matter, including OS, that will retain adequate levels of K from precipitation to help keep the Missouri Ozark forest ecosystem adequately supplied with this nutrient? The Deer Run pilot study included samples from plots clearcut 8 to 10 years earlier, and exhibited levels of exchangeable K, Mg, TC, and OS much lower than those found in controls. The need for further study of relationships between forest disturbance and soil microbial processes, related to nutrient status of the ecosystem, should be evident. Further comparisons of post-treatment surface soil OS and nutrient cation data with pre-treatment baseline data may help answer this question.

FUTURE RESEARCH

To fully follow up on the results of the Deer Run State Forest pilot study will require at least one more season of sampling from the 27 MOFEP vegetation plots that were extensively studied during the pre-treatment study (see Spratt 1997a). These plots studied pre-treatment are all south and west aspect, as were the Deer Run pilot study plots. Such a followup study was recently initiated and should be completed during summer 2001. Studies of the effects of clearcutting on surface soil microbial community structure are also under consideration.

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Patterns of Mating in an Insect-Pollinated Tree Species in the Missouri Ozark Forest Ecosystem Project

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Abstract.—Contemporary gene flow is a major mechanism for the maintenance of genetic diversity. One component of gene flow is the mating system, which is a composite measure of selfing, mating with relatives, and outcrossing. Although both gene flow and mating patterns contribute to the ecological sustainability of populations, a focus of many forest management plans, these processes are often overlooked in forest management studies. As part of the Missouri Ozark Forest Ecosystem Project (MOFEP) we conducted a study of mating patterns in flowering dogwood (*Cornus florida* L), an insect-pollinated tree that is abundant and ubiquitous under story tree of upland Missouri Ozark forests. In 1998 and 1999, we collected fruit from over 200 *Cornus florida* individuals located in six compartments (MOFEP sites 1-6; ~250-500 ha each), which were subjected to one of three management treatments: even-aged, uneven-aged, and no harvest. To see whether the management treatments influenced tree density surrounding the study trees, we measured and compared tree density across treatments. Because differential germination could reflect either genetic or environmental factors affecting the mating system, we measured germination success on a per maternal tree basis. We then measured the outcrossing rate, the rate of consanguineous mating (mating with relatives), and the effective number of pollen donors for each of the six sites and tested the hypotheses that both treatment and local tree density have no influence on these aspects of mating. Furthermore, the percent germination among mothers was not significantly influenced by the application of forest treatments. Multilocus outcrossing, t_m (range 0.981-1.000), single locus outcrossing, t_s (range 0.976-0.996), and the genetic effective number of pollen donors (range 4-11) did not differ among management treatments. For 1998, mating with relatives tended to increase with local density (df=1,28, F=4.07, P=0.053, 1998 only), suggesting local familial structure at the site level. No trend in consanguineous mating was observed in the data collected in 1999. The overall results show that the first cycle of timber harvesting had little effect on insect-mediated pollen movement in *C. florida*. This lack of impact could be due to the fact that the treatments did not alter pollinator behavior. Thus, to evaluate the general impact of forest management on gene flow and mating in woody plants, we recommend ongoing monitoring as management treatments are continued and further studies on additional plant species.

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Pollen-mediated gene movement that occurs through mating patterns is crucial to the viability of plant populations in at least two important ways. First, outcrossing can promote or at least maintain genetic diversity, which is critical to the ability of populations to adapt to environmental change (Avisé 1995, Falk and Holsinger 1991, Hedrick and Miller 1992, Lande 1995, Riggs 1990). Disruption or impediments to gene movement by anthropogenic landscape change may restrict the amount of genetic variation available to succeeding generations. Second, pollen-mediated gene movement can affect the fitness of progeny through its impact on the extent of outcrossing and inbreeding. For populations with an evolutionary history of outcrossing, inbred matings often lead to inbreeding depression and lowered population fitness (Charlesworth and Charlesworth 1987) and eventually a decrease in the likelihood of local persistence (e.g., Ellstrand and Elam 1993, Gilpin and Soule 1986, Ledig 1992, Soule 1980). Thus, the mating patterns of plants are critical to the long-term sustainability of plant populations although their genetic impact may be unseen until some time in the future.

Ecological sustainability is a focus of many forest management plans (Christensen *et al.* 1996, Franklin 1996, Grumbine 1994, Kohm and Franklin 1997, United Nations 1992) and often sustainability relies on biological diversity (Lindenmayer *et al.* 2000). Ecosystem sustainability is defined in terms that identify "desired future trajectories" for a specific ecosystem (Christensen *et al.* 1996). To determine whether defined goals are being achieved, management plans must include short-term and long-term monitoring (Gram *et al.* 2001). These monitoring efforts often focus on individual species (e.g., birds, Clawson *et al.* 1997; invertebrates, Harper and Gynn 1999; leaf-chewing insects, Marquis and LeCorff 1997; toads, Johnson 1997), species diversity (e.g., Hansen *et al.* 1991, Hunter 1990, Margules *et al.* 1988, Noss and Cooperrider 1994, Pickett *et al.* 1997, Scott *et al.* 1987), as well as the maintenance of ecosystem integrity (e.g., Grumbine 1994, Likens 1992, Pickett *et al.* 1997). In the Missouri Ozark Forest Ecosystem Project (MOFEP), which is monitoring the impact of ecosystem management collectively as well as separately, some species in animal communities are increasing while others are decreasing (Gram *et al.* 2001).

Landscape change may influence mating patterns (Sork *et al.* 1999). For example, Mitton (1992) found that outcrossing rates in low-density stands were lower than those in high-density stands. He postulated that a tree's probability of receiving its own pollen is increased with fewer individuals contributing to the local pollen pool. Furthermore, Dyer and Sork (2001) found that the local forest structure, including con- and hetero-specific individuals can significantly influence pollen pool diversity in shortleaf pine, *Pinus echinata*, in the Missouri Ozarks. These results suggest that pollen movement can be impeded by increased local stand density. In terms of outcrossing rates, if timber management has created large clearings in a manner that promotes pollen movement, we predict that outcrossing will increase because each mother is sampling a larger population of pollen donors. Both Young *et al.* (1993) and Fore *et al.* (1992) analyzed fragmented populations of *Acer saccharum* and found that fragmentation may actually increase pollen-mediated gene flow. They concluded that landscape fragmentation promotes long-distance gene flow by changing wind patterns. Similarly, in a study of an animal-pollinated Sri Lankan tropical tree, *Shorea megistophylla*, Murawski *et al.* (1994) observed lower outcrossing rates in disturbed than in undisturbed populations. In contrast, in the insect-pollinated canopy tree *Spondias mombin*, Nason and Hamrick (1997) found rates of pollen immigration into small, insular forest fragments (1 to 4 adults each) to be 100 percent. Yet, both fruit set and germination rates were significantly lower in small fragments than in continuous forest populations. Their study illustrates the benefits of measuring germination rates as additional information about mating.

Less is known about the impact of landscape change on pollen pool composition. One method of gauging the influence of landscape alteration on pollen pool composition is to examine the genetic effective number of pollen donors, N_{ep} . The effective number of pollen donors is an excellent indicator of the genetic diversity of a seed crop. If the number of pollen donors is small, the progeny may be less genetically diverse than when the number of pollen donors is larger. The literature in conservation and population genetics is just starting to accumulate estimates of N_{ep} for forest tree populations. Previously, we found that the effective number

for *Quercus alba* is about eight individuals, and the average pollen movement is only about 11 m (Smouse *et al.* 2001). In a study of shortleaf pine (*Pinus echinata*) within all MOFEP sites, the estimated pollen pool structure ($\phi_{ft}=0.095$) can be translated into a value of $N_{ep}=10.5$ individuals (Dyer and Sork 2001). In contrast, a considerably smaller number of pollen donors have been reported for both sugar pine in California (*Pinus lambertiana*, $N_{ep}=1$, Westfall, in prep.) and the insect-pollinated mimosa in Georgia (*Albizia julibrissin*, $N_{ep}=1-2$, Hamrick *et al.*, in prep.). In general, pollen donor neighborhood size seems small across many of these species. If landscape alteration influences the dispersal of pollen in natural populations, then we expect to see those changes reflected in the genetic composition of sampled pollen pools.

Here, we present a case study of the impact of forest management in MOFEP on mating patterns in an insect-pollinated tree species, *Cornus florida*. MOFEP is designed to monitor the ecosystem effects of three management treatments: even-aged, uneven-aged, and no-harvest management (Brookshire and Hauser 1993, Sheriff 2001, Sheriff and He 1997). We had three specific objectives. First, we tested whether the density of con-specific adults surrounding our study trees differed across forest management treatment. Because local tree density has been shown to influence pollinator behavior, it is essential to determine whether treatments altered the density of flowering *Cornus* individuals. Our second objective was to test whether germination success differed across management treatments. Differential germination could reflect genetic processes associated with pollen movement, and it could reveal the environmental impact of management on seed quality that could influence the outcome of mating patterns. Third, we tested whether the mating system was influenced by landscape alteration. Specifically, we measured the single- and multi-locus outcrossing rates, rate of consanguineous mating (i.e., mating with relatives), and genetic effective number of pollen donors.

METHODS

Study Species

Cornus florida, flowering dogwood, is an understory, insect-pollinated, self-incompatible woody plant, ubiquitous throughout MOFEP sites. It flowers from late March through April (Radford *et al.* 1968). Numerous insect visitors have been documented for *C. florida*, primarily andrenid and halictid bees (J. Grant, personal communication), as well as beetles, flies, and butterflies (Eyde 1988). The inflorescence consists of four white or cream colored bracts subtending 15 to 35 individual, perfect flowers, each with a single ovule. A single *C. florida* inflorescence matures up to eight drupes (Apsit and Sork, personal observation) that turn bright red as they ripen during late September and October. The seeds are dispersed by birds, mammals, and gravity (McLemore 1990).

The Study Site

MOFEP is a long-term large-scale, landscape-level experiment administered by the Missouri Department of Conservation (MDC) to examine the effects of forest management practices on multiple ecosystem components, both biotic and abiotic (Brookshire *et al.* 1997). MOFEP includes study sites located across Carter, Reynolds, and Shannon Counties in southeastern Missouri. The study area has a history of anthropogenic-mediated disturbance through intensive harvesting and then burning and grazing. Since 1880, this disturbance has transformed the local forest structure from predominantly shortleaf pine (*Pinus echinata*) stands to a mixture of oak (*Quercus alba*, *Q. coccinea*, *Q. stellata*, *Q. velutina*) and hickory (*Carya tomentosa*, *C. glabra*; Cunningham and Hauser 1989). At the onset of this experiment, these counties were 84 percent forested with agricultural activity limited to bottomland streams (Xu *et al.* 1997).

The MOFEP experiment has three treatment types (no-harvest, uneven-aged management, and even-aged management) over nine experimental sites divided into three blocks (Sheriff and He 1997). The nine sites, which range in size from 266 to 527 ha, were divided among

three blocks based on spatial proximity: sites 1-3 to block 1, sites 4-6 to block 2, and sites 7-9 to block 3 (see map in Sheriff 2001). Treatments were assigned randomly to each site within a block. In this analysis, we examined only the northern sites 1-6.

The uneven-aged and even-aged treatments were initially implemented in 1991-1992 according to MDC "Forest Land Management Guidelines" (1986). These guidelines call for even-aged areas to be managed for regeneration, poletimber, and sawtimber tree size classes, while uneven-aged managed areas are to be for oak-hickory-pine regeneration and a balance of tree size classes equivalent to even-aged sites. Treatments were applied through regulated harvest of approximately 10 percent of the standing biomass per site. Ten percent per site was left as old growth forest with no timber harvest. Harvesting occurred over different spatial configurations in each treatment type. Under uneven-aged management, 5 percent of the timber harvest was single-tree selection to balance tree size classes and 5 percent was harvested as group openings (21 to 43 m in diameter depending on slope aspect) to promote regeneration. Even-aged harvesting occurred over six to nine 3- to 12-ha clearcut areas per treatment site. No timber was harvested on the no-harvest (control) sites.

Field Sampling

We sampled 252 trees across 57 locations within MOFEP sites 1-6. At each location we sampled a cluster of two to five trees, resulting in 57 clusters total. Trees within a cluster were 20-100 m apart and distance between cluster perimeters was a minimum of 75-100 m. Within every site we selected five clusters at each of two ecological landtypes (ELT): ridgetop (ELT 19) and south to southwest (SSW or ELT 17; see Meinert *et al.* 1997 for more details on ecological landtypes). Cluster location varied according to treatment. Clusters within even-aged treatments (sites 3 and 5) were located within a 50-m border of the clearcut areas at the proper ELT or aspect. Clusters within the uneven-aged treatment (sites 2 and 4) were situated within a 50-m border surrounding group cuts, as well as within the group cuts themselves. Clusters in no-harvest sites 1 and 6 were established only with respect to ELT.

In fall 1998 and 1999, we sampled sufficient fruit from the 252 study trees to ensure 25 germinants for each maternal tree. During spring 1998, we collected fresh leaf material from all adults for identification of maternal genotypes. During our field sampling, we also measured the density of neighboring adult trees by counting all con-specific individuals (d.b.h. ≥ 2.54 cm) within a 25-m radius about each tree. Local density estimates were converted into the number of flowering individuals per hectare (~ 0.405 acres).

Germination Studies

Sampled fruit was transported to the laboratory where we removed seeds from fruit and surface sterilized in 10 percent bleach solution for 10 to 15 minutes. The seeds were then planted in 96-well flats, four seeds per well. Seeds from each maternal tree were planted in consecutive wells, in columns starting with the upper left well and finishing at the lower right well for each flat. A plastic stake with the maternal tree identification number marked the beginning of each family. Seeds were cold stratified at 5°C for 120 days. Flats were moved to the University of Missouri - St. Louis Biology Department greenhouse in early spring of both years and kept at 18°C. Germination rates were calculated for each maternal tree for both 1998 and 1999 as the proportion of seeds germinated out of the total number of seeds planted per individual. We then calculated the average proportion germinated per family per cluster.

Laboratory Analysis

After the seeds germinated, we collected freshly harvested leaf material from approximately 12 to 18 germinants per maternal tree (table 1). We extracted enzymes by grinding the leaf material in 1 ml of a modified phosphate buffer (Alvarez-Buylla and Garay 1994) with mortar and pestle, absorbing the exudate onto chromatography paper wicks, and storing the wicks at -70°C . We identified four polymorphic allozyme loci (Kephart 1990, Soltis *et al.* 1983, Sork *et al.* 1993) on two gel/electrode buffer systems (table 2): fluorescent esterase (*Fe*, 3.1.1.1, 3) and triosephosphate isomerase (*Tpi*, 5.3.1.1) on a modified system 8 (Soltis *et al.* 1983); isocitrate dehydrogenase (*Idh*, 1.1.1.42) and phosphoglucosyltransferase (*Pgm*, 2.7.5.1) on morpholine citrate pH 8.0 (Soltis *et al.* 1983).

Table 1.—Number of *C. florida* seeds analyzed in 1998 and 1999

Treatment	Site	1998			1999		
		# Trees	# Seeds	per Tree	# Trees	# Seeds	per Tree
No harvest	1	18	215	12-21	115	289	7-50
No harvest	6	14	211	7-36	16	313	12-32
Uneven-aged	2	28	337	12-14	15	287	8-24
Uneven-aged	4	28	324	7-12	22	433	7-51
Even-aged	3	33	386	8-12	24	386	8-28
Even-aged	5	30	337	8-12	22	396	7-36
Totals		151	1,810		114	2,104	

Table 2.—*C. florida* adult allele frequencies by sites within each treatment type.

Allozyme name is followed by the locus number. Locus number is given when more than one locus is present for an enzyme.

Locus	Allele #	No harvest		Uneven-aged		Even-aged	
		Site 1	Site 6	Site 2	Site 4	Site 3	Site 5
Fe-3	1	0.000	0.000	0.012	0.000	0.000	0.000
	3	0.396	0.422	0.202	0.315	0.305	0.375
	5	0.604	0.578	0.786	0.684	0.683	0.625
	7	0.000	0.000	0.000	0.000	0.012	0.000
Idh	2	0.000	0.000	0.000	0.011	0.012	0.000
	3	1.000	0.988	1.000	0.978	0.988	0.938
	5	0.000	0.012	0.000	0.011	0.000	0.062
Pgm-1	1	0.017	0.000	0.012	0.011	0.037	0.000
	2	0.103	0.088	0.060	0.022	0.024	0.050
	3	0.880	0.900	0.928	0.967	0.939	0.950
	5	0.000	0.012	0.000	0.000	0.000	0.000
Tpi-1	3	0.362	0.566	0.500	0.554	0.439	0.563
	5	0.638	0.422	0.489	0.446	0.524	0.425
	7	0.000	0.012	0.011	0.000	0.037	0.012

Data Analysis

To assess whether management treatments influenced density of adult *C. florida* trees surrounding the study trees, we used a mixed-model ANOVA (Proc GLM, SAS) with three main effects—block, treatment, and ELT. In this model, ELT and treatment were fixed effects, and block was treated as a random effect. Adult density was log transformed to achieve normality. The analyses were done using average density per cluster. We calculated germination rates for each maternal tree as the proportion of seeds germinated out of the total number of

seeds planted per individual. We analyzed the effects of treatment on germination separately each year with block as a random effect (Proc GLM, SAS). The dependent variable was mean germination per cluster, which was arc sine square root transformed for the analysis to achieve normality.

Mating system parameters, which were estimated for each site using MLTR (Ritland and Jain 1981, Ritland 1990), include the following: the average adult inbreeding, F ; the average multilocus outcrossing rate, t_m ; the average single locus outcrossing rate, t_s ; the consan-

guineous mating rate, $t_m - t_s$; and the probability that a random pair of individuals within a progeny array share a father, r_p . The average effective pollen donor number per site (N_{ep}) was calculated as the reciprocal of r_p ($N_{ep} = 1/r_p$). The multilocus outcrossing rate, t_m , is often considered a better estimate of the "true" selfing rate, while the average single locus outcrossing rate, t_s , includes inbreeding through selfing and mating with relatives. Estimates of the mating system parameters used in hypothesis testing were generated from 100 bootstrapped values of the grouping procedure of the MLTR mating system program (Ritland 1990, Ritland and Jain 1981).

To test whether the mating system differed among treatments or ELT, we estimated the mating system parameters separately for each cluster. Then, using two of those parameters, mating between related individuals ($t_m - t_s$) and N_{ep} , we conducted a mixed-model ANOVA with the same model that we used for adult tree density. The estimate of ($t_m - t_s$) was arc sine square root transformed to achieve normality. In addition to the ANOVA, we performed two separate regression analyses (Proc REG, SAS Institute) for 1998 and 1999 to examine the relationship between adult tree density and mating among relatives ($t_m - t_s$). Both variables were transformed as before.

RESULTS

For the locations that we sampled, adult densities of *Cornus florida* individuals averaged over clusters among sites tended to be lowest in uneven-aged treatments (127 to 129 per ha), intermediate in no-harvest sites (135 to 151 per ha), and highest in even-aged treatments (148 to 175 per ha; fig. 1). The effect of treatment was significant although the overall model was not (table 3). Adult densities for our samples were somewhat greater in block 2 (sites 4-6) than in block 1 (sites 1-3, see fig. 1). In spite of these trends, results of the mixed-model ANOVA on adult density indicated that none of the main effects or their interactions were significant (table 3).

Germination rates were analyzed for every tree with fruit in both 1998 and 1999, regardless of whether that tree was included in the mating system analyses. Overall, there was no significant treatment effect on the germination rate in either 1998 or 1999 (table 4) although the trend in germination success increased with the degree of canopy removal adjacent to the cluster (fig. 2). With an alternate statistical design, this trend might be significant. However, with the current design, we run the risk of a type II error.

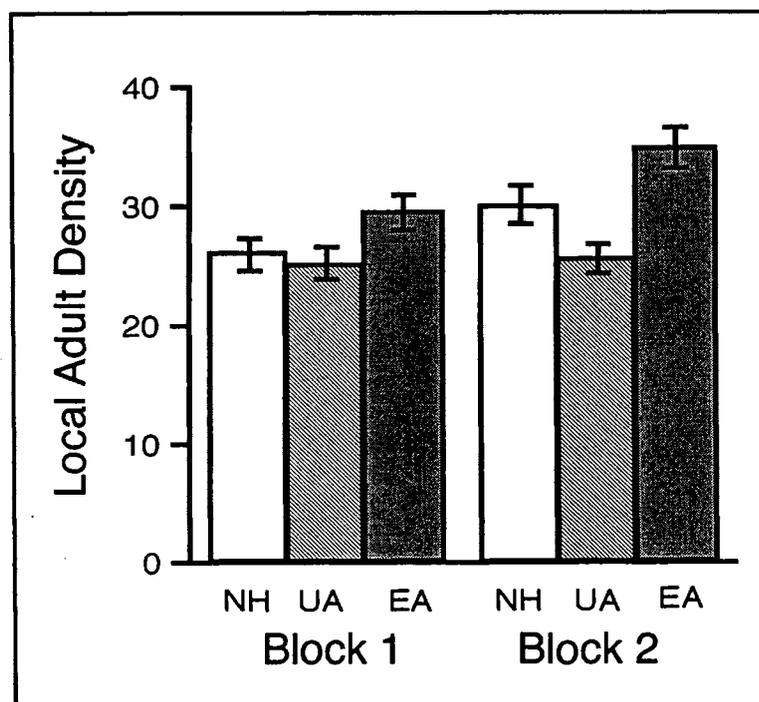


Figure 1.—Mean density of *Cornus florida* adults at sample locations of this study by management type. Block 1 consists of sites 1, 2, and 3. Block 2 consists of sites 6, 4, and 5. Vertical lines indicate 95 percent confidence intervals.



Populations at all six sites for both years showed essentially 100 percent outcrossing based on the multilocus outcrossing rate. The rates of single locus outcrossing, which includes both mating with relatives and selfing, were also quite high but always significantly less than 1.0 (table 5). Estimates of mating with relatives ($t_m - t_s$) varied between 0 and 2 percent. Values for consanguineous mating were quite low in all sites both in 1998 ($t_m - t_s$ ranged from 0.000 to 0.019) and 1999 ($t_m - t_s$ ranged from 0.004 to 0.019). Estimates of ($t_m - t_s$) were not significantly

different from zero in site 4 in 1998 and in site 6 in 1999. The outcrossing rate estimates (t_m) had very similar ranges for all sites in both 1998 (t_m ranged from 0.981 to 1.0) and 1999 (t_m ranged from 0.995 to 1.000; table 5). Estimates of t_m were not significantly different from 1.0 for one site in 1998 (site 2) and for three sites in 1999 (sites 2, 4, and 6; table 5).

The most variable mating system parameter, across sites is the correlation of paternity (r_p ; table 5). Converting r_p into the effective number

Table 3.—ANOVA results for *C. florida* adult density, averaged by cluster, using a 3-way mixed model with block as a random effect

Source	df	MS	F	P
Model	11	2.294	0.91	0.549
Block	1	0.016		
Treatment	2	0.339	22.40	0.04
Block*Treatment	2	0.015		
ELT	1	0.262	0.55	0.59
ELT*Block	1	0.479		
ELT*Treatment	2	0.999	9.89	0.09
ELT*Treatment*Block	2	0.101		
Error	23	5.287		

Table 4.—Results of mixed model ANOVA of *C. florida* germination rates in 1998 and 1999

Source	df	MS	F	P
1998				
Model	11	0.014	0.70	0.721
Block	1	0.008		
Treatment	2	0.066	5.08	0.16
Block*Treatment	2	0.013		
ELT	1	0.001	1.00	0.50
ELT*Block	1	0.001		
ELT*Treatment	2	0.002	0.04	0.96
ELT*Treatment*Block	2	0.057		
Error	19	0.383		
1999				
Model	11	0.021	0.66	0.759
Block	1	0.009		
Treatment	2	0.038	2.11	0.32
Block*Treatment	2	0.018		
ELT	1	0.056	56.00	0.08
ELT*Block	1	0.001		
ELT*Treatment	2	0.004	0.10	0.91
ELT*Treatment*Block	2	0.039		
Error	19	0.032		

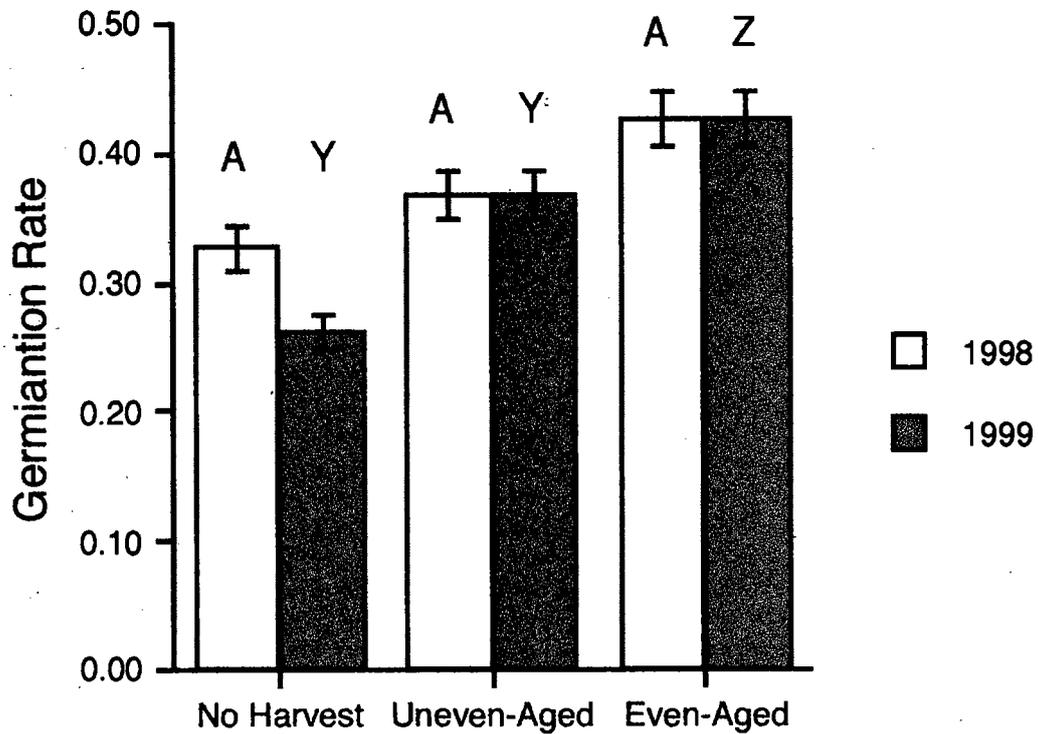


Figure 2.—Germination rates for *Cornus florida* in 1998 and 1999 by treatment type. Vertical lines indicate +/- 1 standard error.

Table 5.—Mating system parameter estimates for *C. florida* in 1998 and 1999. Numbers in parentheses are 95 percent confidence intervals based on 100 bootstrapped values of the data set.

Year	Site	Treatment	F*	t_m	t_s	$t_m - t_s$	r_p
1998	1	No harvest	0.019 (0.010, 0.028)	0.997 (0.996, 0.998)	0.978 (0.972, 0.984)	0.019 (0.013, 0.025)	0.137 (0.111, 0.163)
	6	No harvest	0.084 (0.023, 0.145)	0.999 (0.998, 1.000)	0.984 (0.983, 0.985)	0.015 (0.014, 0.016)	0.091 (0.076, 0.106)
	2	Uneven-aged	0.118 (0.060, 0.176)	0.981 (0.978, 0.985)	0.979 (0.972, 0.986)	0.002 (0.000, 0.004)	0.088 (0.083, 0.093)
	4	Uneven-aged	0.015 (0.012, 0.018)	0.996 (0.995, 0.997)	0.996 (0.995, 0.997)	0.000 (-0.001, 0.001)	0.127 (0.112, 0.142)
	3	Even-aged	0.033 (0.024, 0.042)	0.997 (0.996, 0.997)	0.989 (0.988, 0.990)	0.008 (0.007, 0.009)	0.230 (0.170, 0.236)
1999	5	Even-aged	0.048 (0.038, 0.058)	0.996 (0.995, 0.997)	0.990 (0.989, 0.991)	0.006 (0.005, 0.007)	0.197 (0.194, 0.200)
	1	No harvest	0.165 (0.077, 0.253)	0.998 (0.997, 0.999)	0.979 (0.969, 0.989)	0.019 (0.009, 0.029)	0.157 (0.140, 0.174)
	6	No harvest	0.060 (0.026, 0.094)	0.981 (0.958, 1.004)	0.981 (0.979, 0.983)	0.000 (-0.020, 0.020)	0.165 (0.145, 0.185)
	2	Uneven-aged	0.032 (0.026, 0.038)	1.000 (0.999, 1.001)	0.990 (0.989, 0.991)	0.010 (0.009, 0.011)	0.243 (0.213, 0.283)
	4	Uneven-aged	0.024 (0.021, 0.027)	0.999 (0.998, 1.000)	0.987 (0.986, 0.988)	0.012 (0.011, 0.013)	0.200 (0.170, 0.230)
3	Even-aged	0.145 (0.101, 0.189)	0.995 (0.994, 0.996)	0.976 (0.975, 0.977)	0.019 (0.018, 0.020)	0.132 (0.080, 0.184)	
5	Even-aged	0.569 (0.511, 0.627)	0.988 (0.982, 0.994)	0.984 (0.982, 0.986)	0.004 (0.000, 0.004)	0.137 (0.113, 0.161)	

*Mean adult inbreeding rate, not to be confused with the F-statistic reported in other tables.

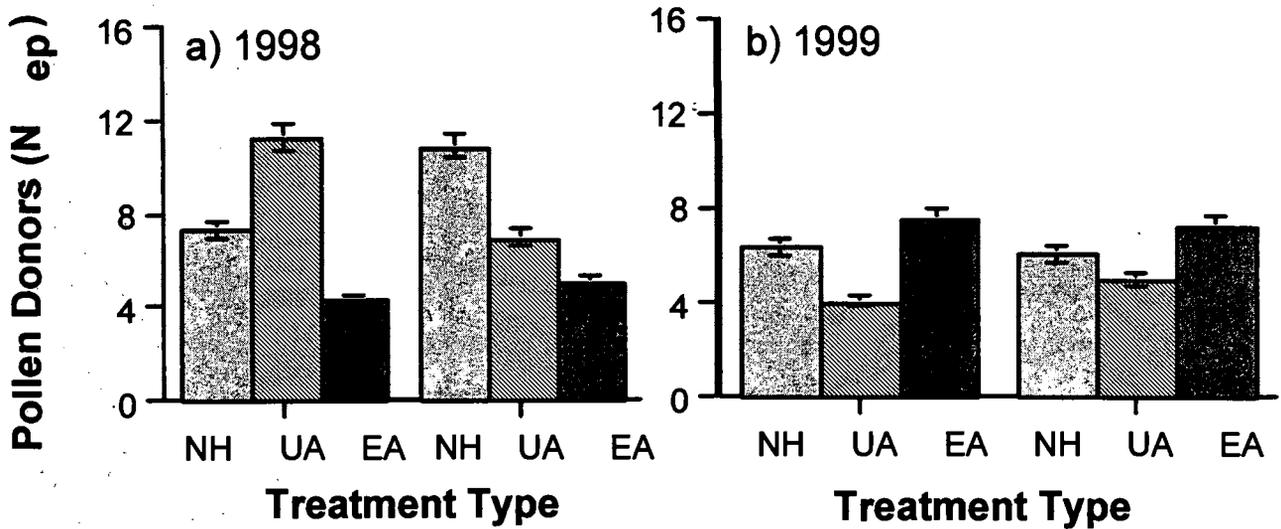


Figure 3.—Effective pollen donor number (N_{ep}) of *Cornus florida* per site by treatment type in 1998 (a) and 1999 (b). Vertical lines indicate 95 percent confidence intervals.

of pollen donors ($N_{ep} = 1/r_p$), we see that the 1998 pollen donor number (N_{ep} ranged from 4.3 to 11.4) was greater than that for 1999 (N_{ep} ranged from 4.1 to 7.6; fig. 3). These estimates are heterogeneous across treatments, blocks, and years. Site 3 (block 1) had the lowest N_{ep} (4.3) in 1998 but the highest in 1999 ($N_{ep} = 7.6$ donors). Site 2 (block 1) had the highest N_{ep} in 1998 (11.4) but the lowest in 1999 (4.1).

Our examination of mating system parameters estimated for each cluster revealed no significant pattern in consanguineous mating by treatments, blocks, or ELT (table 6). The current sampling design with blocks, treatments, and ELT, and associated interactions, caused some problems with the analysis of consanguineous

mating in 1999 (table 6). In this mixed-model design, the error terms are estimated by equating the observed Mean Square values (MS) to the expected ($E[MS]$) to provide the test statistic. Our data show that there are no significant effects in this model. We then examined the association between adult density surrounding study trees and $t_m - t_s$ in separate regressions for the 2 years. In 1998, clusters with higher adult density had higher consanguineous mating ($df=1,28$; $F=4.07$; $P=0.053$; $R^2=0.131$; fig. 4). The scatter plot demonstrates that adult densities vary a great deal within and among management treatments (fig. 4). In 1999, we found no trend toward significance for an effect of adult density on $t_m - t_s$ ($df=1,29$; $F=0.9$; $P=0.332$; $R^2=0.032$).

Table 6.—Mixed-model ANOVA results of related mating ($t_m - t_s$) in *C. florida* in 1998 and 1999

Source	1998				1999			
	df	MS	F	P	df	MS	F	P
Model		0.0058	0.88	0.57	1	0.0009	1.42	0.21
Block	1	0.0010			1	0.0019		
Treatment	2	0.0003	0.30	0.77	2	0.0006	2.00	0.33
Block*Treatment	2	0.0010			2	0.0003		
ELT	1	0.0000	0.00	0.99	1	0.0028	9.33	0.20
ELT*Block	1	0.0013			1	0.0003		
ELT*Treatment	2	0.0001	0.14	0.88	2	0.0005	0.41	0.71
ELT*Treatment*Block	2	0.0007			2	0.0012		
Error	23	0.0137			34	0.0006		

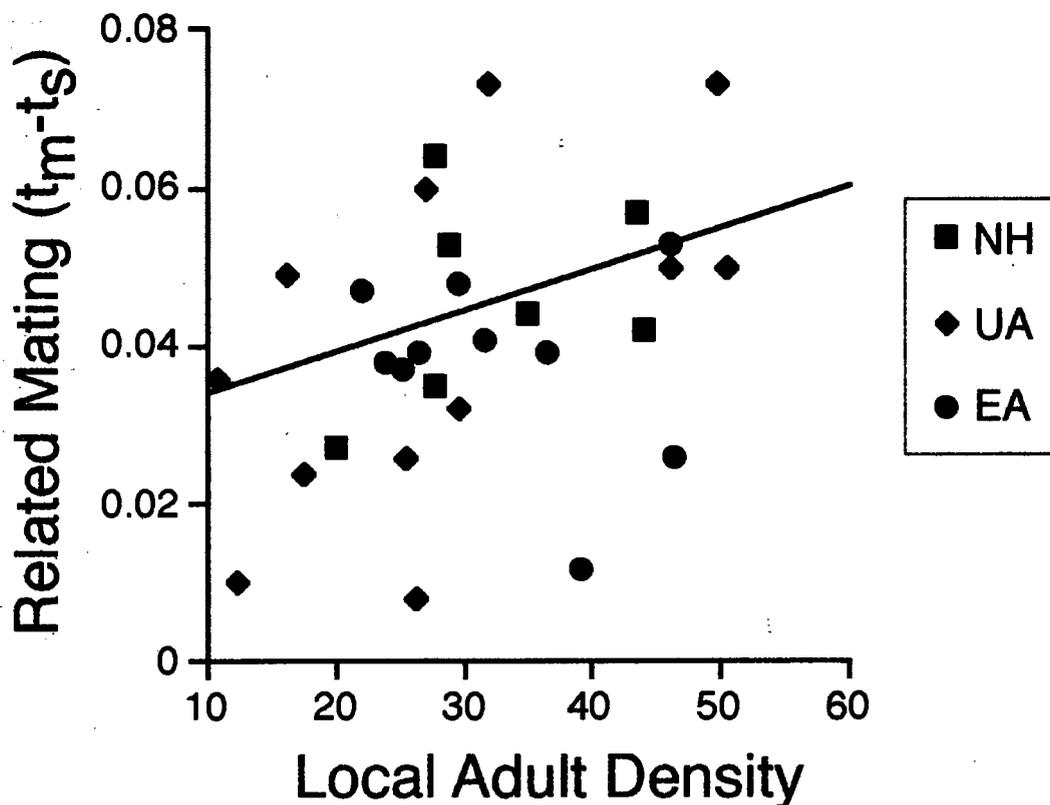


Figure 4.—Mating between related individuals ($t_m - t_s$) of *Cornus florida* per cluster and average local density of adult trees within 25 m of each adult within each cluster in 1998. (Least squares regression: $df=1,28$; $F=4.07$; $P=0.053$; $R^2=0.131$).

DISCUSSION

The foremost finding of the study is the lack of differences in mating patterns of *Cornus florida* across three types of forest management. This finding is noteworthy because this study is the first to test a hypothesis concerning the impact of landscape change on a component of gene movement. The question is whether this finding will be true for other species as well. Dogwood may have been unaffected by the first phase of MOFEP management treatments for several reasons. Because dogwood is highly abundant throughout the MOFEP area, a change in landscape may not affect the availability of trees as pollen sources or hamper the behavior of its pollinators. It is also self-incompatible, which may account for essentially 100 percent multilocus outcrossing rate and the extremely high but not especially variable single-locus outcrossing rate, which includes mating with relatives.

Having acknowledged that the abundance of *C. florida* may have buffered the mating patterns against the impact of landscape change, we should point out that the way we sampled study trees may have reduced our sensitivity in detecting an impact. One might expect that the clearcuts, group cuts, and intermediate tree thinning associated with uneven-aged and even-aged treatments could cause loss of available mates for some species in the MOFEP landscape. Instead, we observed that the local densities of *Cornus florida* adults surrounding the study trees did not differ significantly among treatments. Relative to the no-harvest treatment, the uneven-aged treatment showed slightly lower local densities and the even-aged treatments had slightly higher local densities, but these trends were not strong enough to produce an overall significant result. The lowered densities in the uneven-aged treatment are expected due to the thinning that took place throughout the sites. The slightly higher densities in the even-aged treatment are



counterintuitive except that our study trees were sampled adjacent to, not within, the forest clearings. Nonetheless, these two treatments may not have created sufficient landscape or population density changes to shape mating patterns in *C. florida*.

The effective number of pollen donors (N_{ep}) is an aspect of mating system that one might expect to be influenced by landscape change, especially if that landscape change influenced availability of mates. Although we observed a great deal of heterogeneity in N_{ep} across years and treatments, this parameter did not differ according to management treatment. The genetic effective number of pollen donors is a measure of the genetic diversity in the pollen pool and a good indicator of pollen movement (Smouse *et al.* 2001). Our estimates of N_{ep} in *C. florida* (4 to 11 individuals) are similar to those observed in MOFEP populations of white oak, *Quercus alba* (N_{ep} ~8 individuals, Smouse *et al.* 2001) and shortleaf pine, *Pinus echinata* (N_{ep} ~10 individuals, estimated from Dyer and Sork 2001). These values are much higher than that found for a savanna population of California valley oak, *Quercus lobata* (N_{ep} ~4 individuals, Sork *et al.*, in press). Other studies report N_{ep} in the one to two individual range (wind-pollinated *Pinus lambertiana*, Westfall, in prep., and insect-pollinated *Albizia julibrissin*, Hamrick *et al.*, in prep.). The high variation in estimates across studies demonstrates the need for further work on the relationship between landscape and pollen donor numbers in range of species and pollen vectors. As we suggested for the out-crossing rate result, the first cycle of landscape change may not be sufficient to influence this component of mating. So, in spite of the observation that our estimates of N_{ep} ranged from 4 to 11, management treatments do not show a consistent effect.

To support our suggestion that local tree density can be expected to influence the patterns of mating, we examined its relationship between mating system of tree clusters sampled throughout MOFEP. In general, the amount of consanguineous mating is relatively small, ranging from 1 to 9 percent across clusters. During one of the years, we found that sites with higher density showed higher levels of consanguineous mating or more inbred mating. One explanation for this trend is that in denser locations, trees are more likely to be pollinated by neighboring plants, which tend to be related in many plant populations (Bradshaw 1972).

One implication for MOFEP of the positive relationship between mating with relatives and local density is that a reduction in density should lead to decreased levels of inbreeding in *C. florida* populations and perhaps decreased inbreeding depression. If true, then as the continuation of tree thinning reduces local densities of *C. florida*, we might observe reduced inbreeding.

The first cycle of management treatment appeared to have no strong influence on germination rates. This finding is consistent with the observations that removal of canopy individuals has no influence on the probability of producing inbred offspring. If there are no differences in inbreeding in terms of multilocus selfing (table 5), consanguineous mating (table 6) or the density of local pollen donors (table 3) caused by the treatments, then the only other possible factor influencing germination would be local environmental factors. Local factors that may influence germination include light, water, and nutrient availability, which may be particularly important for an understory tree. Our results suggest that timber removal did not alter local environmental factors to such a degree that germination in *C. florida* was changed.

It is important to discuss the general applicability of our results to other woody plant species and the future of MOFEP. First, we have studied an insect-pollinated tree species in the MOFEP study sites. Wind-pollinated species may be more influenced by landscape architecture than insect-pollinated species. In the latter, the pollinators can fly to the next tree, even when forest treatment has increased the inter-tree distance. In wind-pollinated species, pollen movement can be affected by stand density. For example, Dyer and Sork (2001) found that genetic diversity in *Pinus echinata* was lower in locations with high overall tree density. In fact, Dyer and Sork (unpublished data) have found significant differences across treatments, including lower consanguineous mating in even-aged treatments and higher number of pollen donors in the uneven-aged and even-aged treatments. Thus, we know of at least one other species whose mating patterns were changed by the MOFEP experiment, and the difference may be that wind-pollinated species are more affected by changes in vegetative structure. Second, we have studied an abundant understory tree that was generally harvested only when it fell within a clearcut or group selection opening. A less abundant

species or one whose density was more affected by thinning between openings may be more sensitive to management. Third, this study was conducted after a single phase of stand treatments. We did not predict how the mating patterns of *C. florida* and other species might respond to long-term change.

In summary, the pattern of pollen movement in *Cornus florida* after the first phase of timber harvest seems to be unaffected by the MOFEP management treatments. Because it is generally feared that the consequences of landscape change are always negative, the results of our study are encouraging in that landscape change can occur without necessarily harming the genetic diversity or fitness of a plant population. It is also encouraging that the direction of results favors retention of genetic diversity and reduction of inbreeding. We cannot resolve whether the results will remain the same as timber harvest continues for another 90 years when overall adult densities are reduced. Thus, to truly understand the long-term consequence of forest management on gene flow and future genetic diversity, it will be necessary to continue monitoring pollen movement in this and other species.

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Evaluating the Effects of Ecosystem Management: A Case Study in a Missouri Ozark Forest

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Abstract.—Many federal and state management agencies have shifted from commodity-based management systems to multiple resource-based management systems that emphasize sustainable ecosystem management. Long-term sustainability of ecosystem functions and processes is at the core of ecosystem management, but a blueprint for assessing sustainability under different management strategies does not exist. Using the Missouri Ozark Forest Ecosystem Project (MOFEP) as a case study, we present one approach to evaluating the landscape-scale, short-term (1 and 2 years post-treatment) consequences of even-aged and uneven-aged forest management treatments on community-level biological diversity. We chose changes in density of ecological species groups, representing groups of species with similar resource requirements, as our response variable. Changes in density are detectable before species completely disappear from an area and these changes may be an early indicator of significant alterations to community structure and ecosystem function. Meta-analysis was used to statistically combine changes in densities across multiple species groups and assess the overall impacts of management treatments on the animal community. We also examined changes in density for each ecological species group separately. Our findings demonstrated that, in the short-term, even-aged and uneven-aged forest management treatments caused changes in animal community density in Missouri Ozark forests. Even-aged management sites showed greater changes than uneven-aged management sites after harvesting, and changes in species' densities were larger two years post-treatment (1998) than one year post-treatment (1997). Evaluation of treatment effects on individual ecological groups revealed that toads, forest interior birds, and edge/early successional birds were significantly affected by management treatments. We did not expect most species' groups to exhibit treatment effects because relatively little forest biomass was removed per experimental site (only 10%), forest cover at the regional landscape level did not change and was generally high during the study, and the time scale was relatively short. The challenges facing ecosystem management evaluation parallel the challenges of ecological science in general: identifying appropriate variables, spatial and temporal scales, and experimental/management treatments. The integrative approach demonstrated in this paper is a first step towards the analysis of the effects of management treatments on multiple organisms within an ecosystem.

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Presents the short-term effects of even-aged, uneven-aged, and no-harvest management on forest ecosystems included in the Missouri Ozark Forest Project (MOFEP). Individual papers address study design, site history, species diversity, genetic diversity, woody vegetation, ground layer vegetation, stump sprouting, tree cavities, logging disturbance, avian communities, small mammals, herpetofauna, oak herbivores, soil microbes, and synthesis across multiple ecosystem attributes.

KEY WORDS: Forest management, avian communities, small mammals, herpetofauna, cavities, ground flora, growth, species diversity, regeneration, forest soils, oak herbivores, logging damage, timber harvest, woody vegetation, genetic diversity.



Our job at the North Central Research Station is discovering and creating new knowledge and technology in the field of natural resources and conveying this information to the people who can use it. As a new generation of forests emerges in our region, managers are confronted with two unique challenges: (1) Dealing with the great diversity in composition, quality, and ownership of the forests, and (2) Reconciling the conflicting demands of the people who use them. Helping the forest manager meet these challenges while protecting the environment is what research at North Central is all about.