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Forest Ecology and Management 177 (2003) 145–153

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Spatial analysis of forest gaps resulting from bark beetle colonization of red pines experiencing belowground herbivory and infection

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Received 11 February 2002; accepted 10 June 2002

Abstract

Declining red pine, *Pinus resinosa* (Aitman), plantations throughout the Great Lakes region have been associated with a complex of biotic agents. We conducted a series of measurements in 17 declining and healthy stands in Wisconsin over 3 years to determine whether tree growth and soil factors are associated with tree mortality, and to quantify the probability of tree mortality as a function of proximity to the epicenter of mortality. Plots in declining stands were established both alongside and distant from symptomatic sections. Trees in or near symptomatic regions of declining stands showed lower growth rates than trees in non-declining stands. Trees on the edge of the epicenter of mortality and 3 m into the stand had significantly lower *periodic growth ratios* than trees located 9 m from the edge of these gaps, or in non-declining stands. The distance from the edge of the mortality epicenter significantly influenced the probability of an asymptomatic tree becoming symptomatic during the course of this study. Soils were generally similar among stand conditions, although total nitrogen was significantly higher in declining than non-declining stands. Additional soil parameters varied with soil depth. Our results support the view that forest declines are due to complex interactions among multiple biotic and abiotic stresses, and exhibit particular spatial and temporal patterns.

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Keywords: Forest decline; Spatial analysis; Radial growth; Below ground herbivory; *Leptographium*; Bark beetles

1. Introduction

Declining red pine, *Pinus resinosa* (Aitman), plantations are prevalent throughout the Great Lakes region (Klepzig et al., 1991; Erbilgin and Raffa, 2002). Many of these stands are characterized by a

progressive mortality of trees that expands from an epicenter. No or very few living red pines remain in this epicenter, and the resulting gap is colonized by early succession plants. Trees adjacent to this gap often show reduced crown density and foliar discoloration, whereas trees further into the stand show no above ground symptoms.

A complex of root- and lower stem-infesting beetles and their associated fungi were observed to be more abundant in declining than healthy stands (Klepzig et al., 1991; Erbilgin and Raffa, 2002). These include four species of root colonizing weevils (Coleoptera:

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Curculionidae), two bark beetles (Scolytidae), and two species of *Leptographium* fungi. These below ground agents do not kill mature red pine, but reduce their resistance to stem colonizing *Ips* and their associated blue staining fungi, *Ophiostoma* (Klepzig et al., 1995a, 1996). Site factors associated with the onset of decline are less understood.

Erbilgin and Raffa (2002) and Klepzig et al. (1991) observed that some of the biotic agents associated with declining red pine plantations exhibit particular spatial and temporal patterns. For example, populations of root colonizing insects, particularly the weevils *Hylobius pales* (Herbst), and *Hylobius radialis* Buchanan, and the bark beetle *Hylastes porculus* Erickson, were higher in healthy stands early in the season, but higher in declining stands for the remainder of the season. In addition, root colonizing *Leptographium* spp. fungi were more prevalent in declining than healthy stands, and also more prevalent in trees at or near (6 m) the margin of mortality than more distant trees, within declining stands. Healthy stands also had higher populations of predators than declining stands, despite equivalent numbers of *Ips* trap catches among stand conditions. These results suggest that dispersal, overwintering sites, and habitat quality may contribute to spatial by temporal interactions.

Several studies have shown that tree mortality associated with forest gaps can exhibit predictable spatial variations through time (e.g., Chrismer et al., 1995; Rizzo et al., 2000). For example, Rizzo et al. (2000) concluded that conifer trees along margins of gaps are vulnerable to infection by *Heterobasidion annosum* (Fr.: Fr.) Bref. (= *Fomes annosus* (Fr.) Karst.). Similarly, Perkins et al. (1992) related gap expansion in spruce forests to winds. Pine trees in the southern US are subject to various disturbances, such as bark beetle infection, lightning, and wind, which are suggested as major causes for southern pine decline (Conner et al., 1991; Conner and Rudolph, 1995a,b; Coulson et al., 1995, 1999a,b). These spatial patterns have been quantified based on the likelihood of infection of asymptomatic trees relative to the infection margin (Chrismer et al., 1995). Similar patterns have not been quantified for red pine decline in the Great Lakes region.

We performed a series of measurements to quantify how spatial arrangement of trees, particularly distances between diseased and healthy trees on or

around the epicenter of tree mortality, influences the expansion of individual gaps. Our specific objectives were to quantify the probability of tree mortality as a function of proximity to the edge of the epicenter of tree mortality, and to evaluate tree growth and soil factors associated with the decline syndrome.

2. Materials and methods

2.1. Study site and experimental design

Seventeen study sites were established in 42–52-year old *P. resinosa* plantations throughout southwestern, south central, and west central Wisconsin, USA, as described in Erbilgin and Raffa (2002). Stands showing an actively expanding margin of dead trees or trees with foliar discoloration were designated as declining plots ($N = 9$). Two types of control plots were established: symptomatic controls, which consist of portions of declining stands that are distant from the mortality zone and do not show any symptoms of decline ($N = 4$), and asymptomatic controls, which consist of plots in stands that do not show any sign of mortality or stress ($N = 4$). Plots in stands that contain a declining section were established at the margin of tree mortality. Symptomatic control plots were established 200 m from declining plots. Asymptomatic control plots were established randomly inside non-declining stands, which averaged 500 m from declining plots.

2.2. Tree growth rate

We sampled increment cores at breast height (1.3 m) of 24 trees per plot in six declining, three symptomatic control, and four asymptomatic control plots using a 4 mm increment borer. Cores were collected from four trees each at 0, 3, and 9 m away from the plot centers in a randomly chosen cardinal direction, and its opposite direction. Distance 0 was the edge of the gaps in declining plots, and the center of the plot of healthy trees in both types of controls. Increment cores were placed in plastic drinking straws, which were then sealed at both ends with masking tape, and taken to the laboratory. Annual increments were measured using an ocular micrometer in a dissecting microscope. Periodic growth

ratios were calculated by dividing the most recent five years of growth by the five years of prior growth (Mahoney, 1978).

2.3. Spatial analysis

We conducted measurements in the nine declining sites to determine how the proximity of asymptomatic trees to symptomatic or dead trees is associated with the decline process. We mapped each epicenter of mortality as an ellipse or circle, according to its shape, and calculated its area. From each of the symptomatic or dead trees along each gap, we measured distance and direction to the nearest symptomatic and asymptomatic trees. Trees were categorized as “symptomatic” based on crown discoloration, insect boring holes, or resinous flow (Klepzig et al., 1991). “Asymptomatic” or healthy trees do not show any above ground signs or symptoms.

Maps of stands containing declining sections were digitized using AutoCad (Version 12.1). Locations of all symptomatic and asymptomatic trees were mapped based on their relative distance and direction from the epicenter.

2.4. Soil sampling

We collected soil samples in all 17 plots using the grid method of Klepzig et al. (1991). We established two 15 m × 30 m sampling grids per plot. The first grid was located inside the gap, and the second was 20 m away in a randomly chosen direction. In control stands, one grid was located within the center of the plot, and the other was 20 m away. We used an oatsfield auger to collect soil samples from 0 to 30 cm and 31 to 60 cm depth at each of 15 sampling points within each grid. Samples from similar depths were mixed to provide a composite for each depth in each grid in each plot. Thus, we had a total of four soil samples for each of 17 plots. Soil samples were stored in open waxed paper bags at room temperature until analysis. A standard forest soils analysis, that includes total nitrogen (N), exchangeable potassium (K), exchangeable calcium (Ca), exchangeable magnesium (Mg), phosphorous (P), pH, and organic matter, was performed by the University of Wisconsin-Madison Soil and Plant Analysis Laboratory (Schulte et al., 1987).

2.5. Statistical analyses

Periodic growth ratios were analyzed using analysis of variance. Log transformation of raw data in conjunction with mixed models satisfied assumptions of normality and homoscedasticity of variance (Neter et al., 1983). Site was treated as a random factor.

Soil data were analyzed using analysis of variance (Proc Mixed, SAS Institute, 1996). Graphical analysis of residuals of raw data (Neter et al., 1983) indicated that response variables had normal distributions and error terms. Analyses were conducted within and among stand conditions. The model within a stand condition was $Y_{ijk} = \text{population mean} + \text{location}_i + \text{depth}_j + (\text{location} \times \text{depth})_{ij} + \delta_{ij}$, where δ_{ijk} corresponds to plot error. The model among stand conditions was $Y_{ijk} = \text{population mean} + \text{treatment}_i + \text{location}_j + \text{depth}_k + (\text{treatment} \times \text{location})_{ij} + (\text{treatment} \times \text{depth})_{ik} + (\text{location} \times \text{depth})_{jk} + (\text{treatment} \times \text{location} \times \text{depth})_{ijk} + \delta_{ijk}$, where δ_{ijk} corresponds to plot error.

Spread of tree mortality with respect to distance from the edge of the gap was analyzed by logistic regression using Proclogist (SAS Institute, Inc., Cary, NC). We randomly selected a tree, measured the distance to the nearest neighboring tree, and continued likewise throughout each declining stand. If the two neighbor trees were of the same category (symptomatic or asymptomatic), we assigned the value of “1”. If they were of different types, we assigned a “0”. If the logistic regression analysis was significant based on a chi-square analysis with d.f. = 1 (see Table 1), we conducted additional analysis as follows. We randomly selected a symptomatic or dead tree and measured the distance to the nearest neighbor tree and continued until all diseased or dead trees were evaluated. In this analysis, we only included data from diseased–healthy or diseased–diseased pairs and excluded data from healthy–diseased pairs. We assigned “1” if both trees were diseased and “0” if the first one was diseased and the second one was healthy. Data were analyzed by logistic regression. If model parameters (intercept, slope) were significant, we used them to predict the probability of both trees being diseased in relation to distance by the following equation:

$$P = \frac{e^{b_0 + b_1 X_1}}{1 + e^{b_0 + b_1 X_1}}$$

Table 1
Number of dead trees relative to distance from the edge of the epicenter of tree mortality in declining red pine stands

Site	Distance from the edge of tree mortality epicenter (m)		Statistical analyses ^a	
	0–3	3.1–6	Chi-square ^b	P-value
Monroe 1	31	6	19.8	<0.0001
Prior to 1997	22	4		
1997–1998	2	1		
1998–1999	4	0		
1999–2000	3	1		
La Crosse 1	22	5	21.1	<0.0001
Prior to 1997	15	3		
1997–1998	3	1		
1998–1999	2	1		
1999–2000	2	0		
La Crosse 3	18	4	16.7	<0.0001
Prior to 1997	12	2		
1997–1998	2	1		
1998–1999	2	0		
1999–2000	2	1		
La Crosse 2	17	3	8.7	0.0032
Prior to 1997	12	2		
1997–1998	1	0		
1998–1999	2	1		
1999–2000	2	0		
Buffalo 2	15	3	8.9	0.0029
Prior to 1997	9	2		
1997–1998	2	0		
1998–1999	3	1		
1999–2000	1	0		
Chippewa 3	14	2	7.2	0.0071
Prior to 1997	11	2		
1997–1998	1	0		
1998–1999	2	0		
1999–2000	0	0		
Chippewa 1	10	2	2.7	0.1020
Prior to 1997	6	1		
1997–1998	1	1		
1998–1999	2	0		
1999–2000	1	0		
Chippewa 2	8	2	1.3	0.2471
Prior to 1997	5	1		
1997–1998	1	1		
1998–1999	1	0		
1999–2000	1	0		
Buffalo 1	7	2	2.6	0.1057
Prior to 1997	5	1		
1997–1998	1	0		

Table 1 (Continued)

Site	Distance from the edge of tree mortality epicenter (m)		Statistical analyses ^a	
	0–3	3.1–6	Chi-square ^b	P-value
1998–1999	1	1		
1999–2000	0	0		
Total	142	29		
Prior to 1997	97	18		
1997–1998	14	5		
1998–1999	19	4		
1999–2000	12	2		

^a Data were analyzed by logistic regression using Proclogist.

^b d.f. = 1.

where P is the probability of both neighboring trees being diseased, b_0 the intercept, b_1 the slope, and X_1 the distance between trees (m).

3. Results

3.1. Tree growth rate

Periodic growth ratios were significantly lower in declining stands than in either type of control plot (Fig. 1A). There were significant stand type by distance interactions ($F_{4,283} = 6.57$, $P < 0.0001$). Trees on the edge of the epicenter of mortality and 3 m from this zone had lower PGRs than trees located 9 m from the edge of the gap, or trees in symptomatic and asymptomatic stands (Fig. 1B). Direction of sampling within-stand type did not affect PGRs ($F_{1,283} = 0.26$, $P = 0.6113$). In control stands, distance from plot center did not affect PGR. Likewise, trees in control stands did not differ from trees 9 m from the edge of the gap in declining stands ($F_{2,292} = 10.64$, $P < 0.0001$).

3.2. Spatial analysis

A total of 171 dead or dying trees were observed, of which 67% became symptomatic during the course of this study (Table 1). Eighty three percent of the newly killed and dying trees were within 3 m of the edge of the gap. The distance from a symptomatic tree sig-

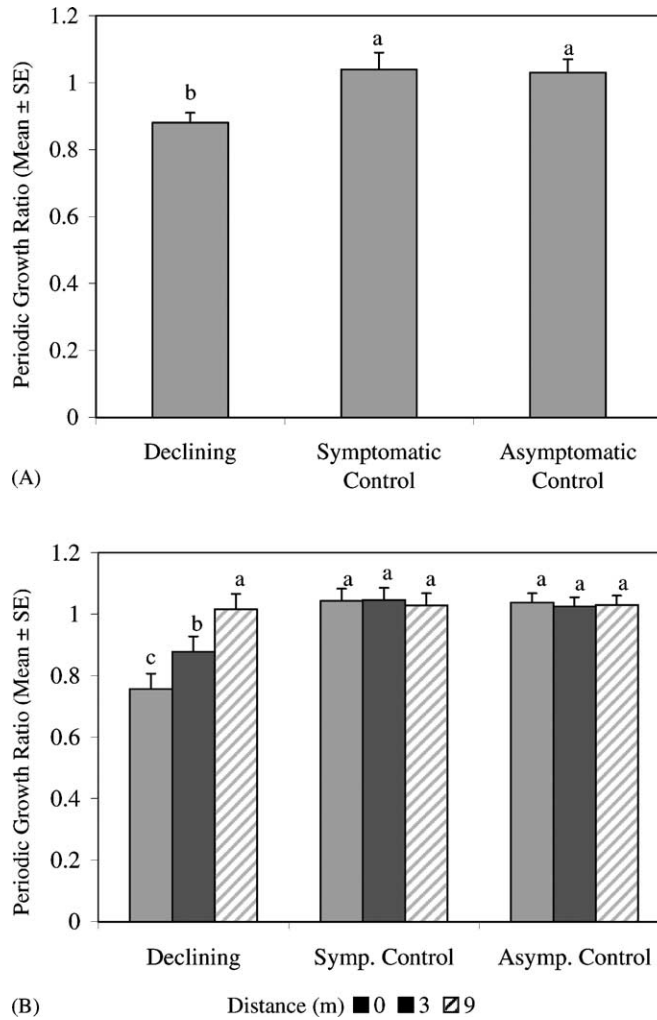


Fig. 1. Comparisons of periodic growth ratios of red pine trees in different stand conditions (A), and at various distances from the edge of the epicenter of tree mortality (or control) (B). Periodic growth ratios were computed by dividing the most recent 5 years of growth by the prior 5 years of growth. Stand types consisted of declining, symptomatic control, and asymptomatic control. Locations were 0, 3, or 9 m from the edge of the tree mortality epicenter. Results are based on the analysis of variance (Proc Mixed, SAS Institute, 1996) ($P < 0.05$). Fisher's protected LSD test ($P < 0.05$) was used for multiple comparisons of means of transformed data (log). Untransformed means are shown.

nificantly influenced the probability of an asymptomatic tree exhibiting symptoms of decline during the course of this study (Fig. 2). A logistic model provided on overall high degree of fit, and was significant for six of the nine declining sites.

3.3. Soil sampling

Among all soil parameters analyzed, only total nitrogen content varied among stand conditions

($F_{2,42} = 4.18, P = 0.038$). Total nitrogen was higher in declining than non-declining stands. Soils taken from either inside or outside the plot centers were statistically similar. All parameters except phosphorous varied with depth ($F_{1,42} = 9.35, P = 0.004$). There were significant location by stand condition interactions in pH ($F_{2,42} = 4.83, P = 0.013$) and total nitrogen ($F_{2,42} = 3.46, P = 0.04$). There were no depth by within-stand location or depth by stand condition interactions. Table 2 indicates categorical

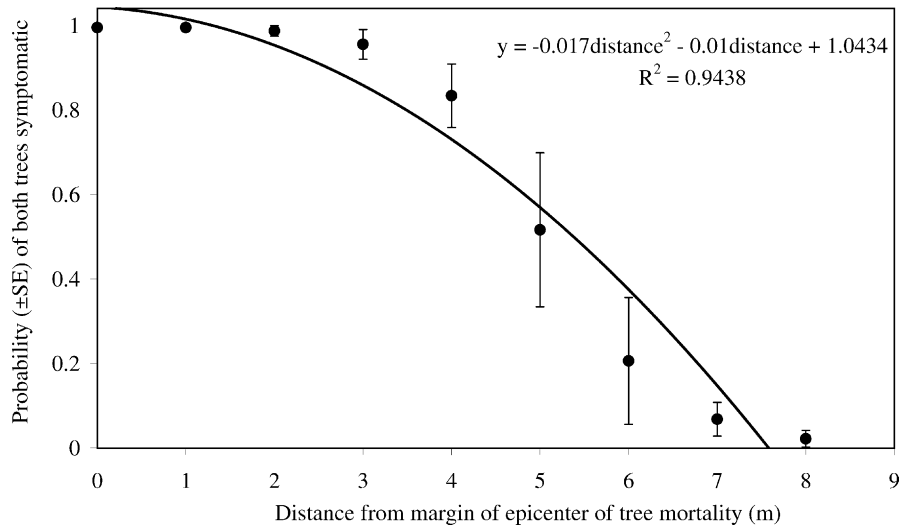


Fig. 2. Probability of healthy trees becoming symptomatic as a function of distance from the edge of the tree mortality epicenter in declining stands.

Table 2
Soil parameters in declining and asymptomatic red pine plantations in Wisconsin^a

	pH	Organic matter	Exchangeable K (kg/ha)	Exchangeable Ca (kg/ha)	Exchangeable Mg (kg/ha)	Total N
Condition						
Epicenter of mortality	—	—	—	—	—	658.6 ± 49.4 b
Symptomatic control	—	—	—	—	—	615.6 ± 65.7 b
Asymptomatic control	—	—	—	—	—	428.5 ± 86.6 a
<i>F</i> _{2,14}	—	—	—	—	—	4.18
<i>P</i>	—	—	—	—	—	0.038
Depth (cm)						
0–30	5.06 ± 0.06 b	14.6 ± 0.9 a	68.9 ± 6.3 a	722.7 ± 60.6 a	143.0 ± 12.0 a	685.4 ± 42.9 a
31–60	5.15 ± 0.06 a	10.0 ± 0.7 b	55.0 ± 4.8 b	606.6 ± 44.6 b	114.6 ± 11.3 b	449.7 ± 37.1 b
<i>F</i> _{1,42}	9.35	63.5	21.23	10.55	9.62	55.52
<i>P</i>	0.004	<0.0001	<0.0001	0.002	0.003	<0.0001
Location × treatment						
Epicenter: 0 m	4.95 ± 0.07 b	—	—	—	—	717.3 ± 54.4 a
Epicenter: 20 m	5.12 ± 0.07 a	—	—	—	—	599.8 ± 44.5 b
Symptomatic control: 0 m	5.32 ± 0.11 a	—	—	—	—	586.1 ± 62.4 b
Symptomatic control: 20 m	5.29 ± 0.07 a	—	—	—	—	645.1 ± 67.7 b
Asymptomatic control: 0 m	5.32 ± 0.07 a	—	—	—	—	442.0 ± 91.1 b
Asymptomatic control: 20 m	5.41 ± 0.11 a	—	—	—	—	414.9 ± 81.8 b
<i>F</i> _{2,42}	4.83	—	—	—	—	3.46
<i>P</i>	0.013	—	—	—	—	0.04

^a See text for descriptions of stand types. Values followed by the same letter within a column (within a heading) are not different at $P < 0.05$.

values of soil parameters when significant treatment or interaction term effects were observed. Both the symptomatic and asymptomatic regions of declining stands had higher total nitrogen content than healthy stands, and there was no difference between the gaps and symptomatic controls (Table 2). Samples within these gaps had lower mean pH than all other combinations of location and stand condition, which were equivalent (Table 2). Soil depths significantly affected all soil parameters, except phosphorous across stand types (Table 2). Surface soils had more exchangeable K, Ca, Mg, total N and organic matter than deeper soils. In contrast, pH was higher in deeper soils.

4. Discussion

Our results indicate that red pines immediately surrounding margins of killed trees show reduced growth and are at a greater risk of undergoing decline than trees farther from the margins. These spatial analyses of tree injury, combined with previous descriptions of spatial and temporal patterns of root colonizing insects, incidence and transmission of root pathogens, and bark beetle predators (Klepzig et al., 1991; Erbilgin and Raffa, 2002), support the view that a complex of predisposing and mortality factors contribute to forest declines (Manion and Lachance, 1992; Huettl and Muller-Dombois, 1993; Innes, 1993). Spatial analyses offer a method of quantifying the consequences of such complex interactions. The pattern of injury in red pine decline appears to reflect a process in which root and lower stem insects vector pathogenic fungi into trees, these root fungi grow through root grafts, and root-diseased trees become susceptible to bark beetles. Components of this process have been reported for other systems also, such as fungal vectoring by insects into roots (Harrington, 1983; Lewis and Alexander, 1986; Witcosky et al., 1986; Owen et al., 1987; Klepzig et al., 1991, 1995b; Nevill and Alexander, 1992a,b) and movement of root pathogens through grafts (Landis and Helburg, 1976; Hessburg and Hansen, 1986; Hunt and Morrison, 1986).

The spatial patterns in Figs. 1 and 2 and previous studies on the biotic agents involved (Klepzig et al., 1991, 1995a, 1996; Erbilgin and Raffa, 2002) suggest that three management applications may have promise and thus merit testing. First, mixed-block planting

may decrease the chances of spread through root grafts, and hence at least compartmentalize tree mortality. Secondly, severing root grafts by mechanical or chemical means, coupled with sanitation, may prevent expansion of this decline. Third, increased tree spacing might decrease the spread of fungal infection through root contacts between diseased and healthy trees, as has been suggested in other systems (Wagener and Mielke, 1961; Hicks et al., 1980; Hunt and Morrison, 1986). However, any thinning should be accompanied with treatments that preclude colonization of stumps by insects such as *Hylastes*, *Hylobius*, and *Dendroctonus* that would otherwise introduce additional *Leptographium* (Witcosky et al., 1986; Klepzig et al., 1995b).

Although we have an improved understanding of the expansion of this syndrome, our knowledge of why certain plantations initially become epicenters remains limited. We observed some differences in soil contents between declining and healthy stands, but such data should be treated with caution. Between site differences may simply reflect the progression of a syndrome, rather than its causation. For example, litter decomposition, nutrient availability, light, soil temperature and moisture are known to vary with features of canopy architecture and gap formation, such as are induced by these disease agents (Pickett and White, 1985). However, the probability that certain soil conditions predispose trees to initial or subsequent mortality agents cannot be dismissed, as some soil factors, e.g., moisture, have been associated with root diseases caused by *Leptographium* spp. (Leaphart and Copeland, 1957; Goheen et al., 1978). Likewise, the observation that total soil nitrogen is higher in both the asymptomatic and symptomatic sections of declining stands merits further investigation.

Acknowledgements

This study was supported by the Wisconsin Department of Natural Resources, and the University of Wisconsin-Madison College of Agricultural and Life Sciences. Dr. E. Nordheim, Statistics Department, University of Wisconsin-Madison provided valuable statistical advice throughout all phases of this study. Dr. J. Bockheim, Department of Soil Science, University of Wisconsin-Madison, assisted with protocols

of soil sampling. Field assistance by J. Syneder and A. Bojeau, Department of Entomology, University of Wisconsin-Madison, is greatly appreciated. We thank J.C. Carlson, T. Lanigan, and G. Edge of the Wisconsin Department of Natural Resources for providing study sites, and P. Crump (University of Wisconsin-Madison, CALS Statistical Services) for assistance with SAS programs.

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