Ecological Applications, 13(1), 2003, pp. 98–118

WHITE-TAILED DEER IMPACT ON THE VEGETATION DYNAMICS OF A NORTHERN HARDWOOD FOREST

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Abstract. Considerable controversy has arisen over the management of white-tailed deer in eastern landscapes where there is evidence of damage to forest vegetation, crops, and wildlife habitat attributable to deer. We examined the impact of 4, 8, 15, and 25 deer/km^2 on herbaceous layer abundance and tree seedling density, height development, species composition, and diversity for 10 yr in a repeated-measures randomized-complete-block experiment at four replicate cherry–maple forest sites in northwestern Pennsylvania, USA. At each 65-ha site, deer were placed in 13- or 26-ha fenced enclosures in which the landscape composition and forage production of a forest managed on a 100-yr rotation was simulated by clear-cutting 10% of each area and thinning 30%. Vegetation was sampled 0–1, 3, 5, and 10 yr after treatment (YAT). We analyzed vegetative treatment responses separately in each silvicultural treatment.

Time was an important factor mediating responses at all deer densities. *Rubus* spp. abundance in all silvicultural treatments and the density of striped maple (STM) in clearcuts and birch (BI), American beech (AB), and red maple (RM) in thinnings showed negative trends with increasing deer density. As deer density increased, we found negative linear trends in the height of BI, RM, and AB in clearcuts; in the height of AB, RM, and STM in thinnings; and in the height of AB and RM in uncut stands. Species richness showed a negative linear trend with increasing deer density in all silvicultural treatments.

Conversely, species avoided by deer or resilient to deer browsing increased with increasing deer density. Percent cover of ferns, grasses, and sedges showed positive linear trends with deer density in clearcuts and in thinnings. The percentage of plots dominated by black cherry (BC) increased with increasing deer density in cut and uncut stands. The net result of increased deer impact was an altered trajectory of vegetation development dominated by species avoided by deer or resilient to deer browsing.

Negative effects on vegetation became significant at deer impact levels well below those observed in many eastern forests. Moreover, species not browsed or resilient to browsing may have indirect effects on vegetation development through plant–plant interactions and on wildlife habitat quality for small mammals, birds, and deer. Managing these impacts is important as pressures to harvest and fragment eastern forests accelerate.

Key words: herbivory; management; northern hardwood forest; plant–herbivore interactions; plant–plant interference; seedling density; seedling height; species diversity; succession; ungulate; vegetation trajectory; white-tailed deer.

INTRODUCTION

The population density of white-tailed deer (*Odocoileus virginianus* Zimm.) in the eastern United States increased dramatically during the 20th century compared with densities estimated during the 18th and 19th century period. Estimates of pre-European settlement deer density across the ~7.8 × 10^6 km^2 of "most favorable habitat" range from 3.1 to 7.7 deer/km^2 (Seton 1953, Severinghaus and Maguire 1955, McCabe and McCabe 1984, 1997). During the early European settlement period, commercial and private exploitation of white-tailed deer led to near extirpation in much of the eastern forest. The extensive changes in landscape patterns and values (Porter et al. 1994) of the postsettlement period created conditions for white-tailed deer recovery. Extensive forestland clearing for agriculture and timber exploitation that greatly increased forage supply, extirpation of predators, and enactment of laws to protect deer resulted in burgeoning numbers of deer. Late-20th century estimates of density range from 7.7 to 14.8 deer/km^2 in heavily forested areas (deCalesta and Stout 1997) to >60 deer/km^2 in areas with mixed forest and agricultural land (Porter et al. 1994).

Considerable controversy has arisen over the management of this abundance. The debate is rooted in values held by constituent groups. Foresters, farmers, and naturalists have presented evidence of reduced diversity or damage to tree seedlings, herbaceous plants, and crops attributed to deer (Hough 1965, Anderson and Loucks 1979, Tilghman 1989, Alverson and Waller 1997, deCalesta 1997, Augustine and Jordan 1998).

Manuscript received 20 August 2001; revised 11 March 2002; accepted 18 March 2002; final version received 17 April 2002. Corresponding Editor: R. S. Ostfeld.

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Others point to reduced diversity of wildlife communities stemming from destruction of vegetative habitat by deer (DeGraaf et al. 1991, deCalesta 1994, 1997, McShea and Rappole 1992). Conversely, some hunters believe that there are too few deer (Witmer and deCalesta 1992, Kosack 1995). Biologists are divided on the course that should be taken to manage deer; some argue that natural regulation of deer populations should be allowed to take its course, whereas others assert that postsettlement landscapes have been altered to such an extent that a natural crash in the deer population is unlikely and deer must be managed with direct removal by killing (Leopold et al. 1963, Porter 1994). Animal rights groups have entered the fray by opposing any harvest of wildlife, for any reason (Witmer and deCalesta 1992). The issue of deer management is now highly polarized; land management organizations in many states are under pressure to develop deer management programs that satisfy all constituencies (Shafer-Nolan 1997).

Policy makers and stakeholders can arrive at better solutions to deer management problems if they have information based on scientific studies of how deer affect ecosystems over time. Such studies must take into account the landscape context (food supply) in which they are conducted and must be carried out over a long time (Porter and Underwood 1999).

Most studies of ungulate effects on eastern forest ecosystems have used exclosures (Hough 1949, Webb et al. 1956, Graham 1958, Shafer et al. 1961, Jordan 1967, Ross et al. 1970, Richards and Farnsworth 1971, Marquis 1974, Marquis and Grisez 1978, Anderson and Loucks 1979, Risenhoover and Maass 1987, McInnes et al. 1992, Anderson and Katz 1993, Anderson 1994). Effects of zero animal density inside the fence are compared with the ambient animal density outside the fence, within a single disturbance level, usually undisturbed or recently harvested. When conducted over periods of time longer than ~5 yr, both the ambient animal density and the landscape context (food supply) may change. Because the impact of ungulates is dependent on both of these parameters, and deer move through a forest matrix with patches of different disturbance levels, it is difficult to interpret the long-term effects of deer on vegetation from exclosure studies, except in general terms (Taylor 1984, Brander et al. 1990). Moreover, some mechanisms of ungulate–plant interaction may be nonlinear over gradients of herbivore density. Because exclosure studies provide only two points of reference for density, nonlinear effects cannot be observed (Hobbs et al. 1996*a*, *b*).

Deer have been overabundant on the heavily forested, unglaciated Allegheny Plateau in northwestern Pennsylvania since the 1920s (Lutz 1930, Leopold et al. 1947, Hough 1949). Average densities on the Allegheny National Forest (ANF) had reached 11.6–19.2 deer/km² by the mid-1930s (McCain 1939). During this time, changes in the abundance, height, and species composition of plants within the reach of deer (<~1.5 m tall) were noted. Eastern hemlock (*Tsuga canadensis* (L.) Carr) and witch hobble (*Viburnum alnifolium* L.) virtually were eliminated from forest understories, and the abundance of seedlings >0.3 m tall of many species was greatly reduced (Lutz 1930, Park 1938, McCain 1939, Leopold et al. 1943, Whitney 1984). By contrast, seedlings and root suckers of American beech (*Fagus grandifolia* Ehrh.) and ferns (hayscented fern *Dennstaedtia punctilobula* Michx. and New York fern *Thelypteris noveboracensis* L.) increased (Hough 1965). As stands grew beyond the seedling stage (>2.5 cm diameter at 1.3 m above the ground), the forage supply dwindled as trees that had established earlier grew out of reach of deer. Several severe winters in the mid-1930s resulted in massive starvation of deer (McCain 1941, Leopold et al. 1943, 1947); density dropped to ~5.4 deer/km² by the mid-1940s (Hough 1949). In Pennsylvania, winter snow depth and exposure to wind typically are sufficiently low and winter temperatures are sufficiently mild that white-tailed deer rarely yard or display seasonal migration between defined winter and summer ranges. Instead, deer move up and down altitudinally between plateau tops and conifer-lined stream bottoms (generally a difference of ~150–300 m in elevation). Renewal of timber harvests in the early 1950s resulted in increased forage and increased deer density. By the mid-1970s, just prior to initiation of the present study, pre-fawning densities on the ANF had reached 15.6–22.6 deer/km² (Allegheny National Forest 1978).

Exclosure studies have demonstrated that ambient deer densities extant during the late-20th century are high enough to cause regeneration failure in commercially managed forests, in association with overstory removal cutting (Grisez 1957, 1959, Shafer et al. 1961, Jordan 1967, Marquis 1974, 1981, Marquis and Grisez 1978), but dose-response studies of deer impacts on the trajectory of forest vegetation development over time have not been conducted here or elsewhere in eastern forests. We conducted a 10-yr manipulative experiment at deer densities spanning the range observed from the late-19th century to the present time in the northern hardwood forest of northwestern Pennsylvania. The study used areas of managed forest with disturbance created by cutting overstory trees.

In this paper, (1) we report tests of the null hypotheses that deer densities that can be sustained over long periods on contemporary landscapes do not cause changes in understory density, seedling height growth, species composition, or woody plant diversity; and (2) we examine the implications of our results for policy debates and decisions in the eastern hardwood forest region.

METHODS

Study sites

The experiment was located at four sites in northwestern and north-central Pennsylvania within the un-

TABLE 1. Mean basal area (m^2/ha) (and one standard error of the mean) of overstory trees over all deer densities in northwest Pennsylvania hardwood stands that remained uncut vs. stands that were thinned at the beginning of the experiment prior to the introduction of deer.

Site name	Black cherry	Red maple	Sugar maple	American beech	Black and yellow birch	White ash	Yellow-poplar	Eastern hemlock	Other species†	All species
Stands that remained uncut										
Gameland 30	14.5 (0.2)	9.2 (1.6)	2.8 (1.1)	1.8 (0.5)	1.4 (<0.2)	0	0	0.2 (<0.2)	0.2 (<0.2)	30.3 (1.1)
Fools Creek	9.4 (0.7)	9.0 (1.8)	4.6 (0.5)	2.3 (0.5)	2.3 (0.5)	2.5 (0.7)	0.2 (<0.2)	0	0.2 (<0.2)	30.3 (1.8)
Deadman Corners	19.7 (2.5)	4.8 (1.8)	3.7 (0.7)	1.8 (0.5)	1.4 (0.5)	0.2 (<0.2)	0	1.6 (0.5)	<0.2 (<0.2)	33.0 (1.1)
Wildwood Tower	12.4 (1.4)	2.5 (0.5)	8.3 (0.9)	3.7 (0.7)	0.7 (0.5)	<0.2 (<0.2)	<0.2 (<0.2)	0	1.4 (<0.2)	28.9 (1.8)
Stands that were thinned										
Gameland 30	14.0 (2.5)	3.2 (1.1)	4.8 (2.1)	0.7 (<0.2)	0.2 (<0.2)	<0.2 (<0.2)	0	0	<0.2 (<0.2)	23.2 (0.9)
Fools Creek	9.9 (1.1)	4.4 (0.7)	4.4 (0.9)	1.4 (0.2)	0.5 (0.2)	1.6 (0.7)	0	<0.2 (<0.2)	<0.2 (<0.2)	22.5 (0.5)
Deadman Corners	13.1 (0.9)	2.8 (2.1)	7.8 (0.9)	0.5 (0.2)	<0.2 (<0.2)	0.2 (<0.2)	0	0	0	24.1 (1.4)
Wildwood Tower	11.5 (0.9)	2.8 (0.2)	6.0 (1.1)	0.9 (0.5)	0.7 (0.5)	0	0	0	0.9 (0.5)	22.7 (1.1)

† Other species include aspen and cucumber magnolia (*Magnolia acuminata*).

glaciated Allegheny High Plateau Section of the Appalachian Plateau Province (Harrison 1970, McNab and Avers 1994). The landscape is dominated by contiguous forest without interspersed agricultural land. Annual precipitation averages 1067 mm with 550 mm received during the growing season. The area has a humid temperate climate with an average daily temperature of 9°C, and the growing season averages 120 d (Cronce and Ciolkosz 1983, Kingsley 1985, McNab and Avers 1994). Soils are strongly acid, relatively infertile sandstones and shales; kaolinite is the dominant clay mineral and is responsible for the relatively low cation exchange properties (Ciolkosz et al. 1970). Wildwood Tower, WW (41°34′22″ N, 78°28′30″ W) is located at 710 m elevation in Elk County; Fools Creek, FC (41°38′48″ N, 79°08′11″ W) and Deadman Corners, DM (41°34′40″ N, 39°06′19″ W), both at 550 m elevation, are located in Warren and Forest County, respectively; State Game Land 30, GL (41°38′21″ N, 78°19′33″ W), at 670 m elevation, is in McKean County.

The overstory at each site (see Table 1) was dominated by black cherry (*Prunus serotina*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and birch (*Betula lenta* and *B. lutea*). In addition, small amounts of white ash (*Fraxinus americana*), yellow-poplar (*Liriodendron tulipifera* L.), eastern hemlock (*Tsuga canadensis*), cucumbertree (*Magnolia acuminata* L.), and aspen (*Populus grandidentata* Michx. and *Populus tremuloides* Michx.) were present. Black cherry (61% of all seedlings) and red maple (31% of all seedlings) dominated the seedling (<2.5 cm dbh) layer at all sites prior to treatment (Table 2). Nearly all stems, with the exception of beech and striped maple (*Acer pensylvanicum*), were <0.3 m tall; small numbers of beech (0.3–0.9 m) were present at all sites, and moderate numbers of striped maple (0.3–0.9 m) were present at GL and WW, but not FC and DM. Despite the prominence of sugar maple in the overstory, it was not represented to any extent among seedlings, due to lack of recent seed crops and other factors unrelated to deer impact (Long et al. 1997). Hayscented, New York, and wood (*Dryopteris intermedia* (Muhl.) A. Gray) fern, grasses and sedges, and blackberry (*Rubus allegheniensis* T. C. Porter) dominated the herbaceous layer. Some ecological characteristics of tree seedling and herbaceous-layer plants that were important in the experiment are shown in Table 3 (Horsley et al. 1994).

Deer density treatments

At each site (statistical block), a 65-ha enclosure was constructed using 2.4-m woven wire fencing. Enclosures were subdivided into four deer density areas, one of 26 ha and three of 13 ha each. Wild deer were driven from each deer density area twice, once after fence erection and again after logging, to insure that all wild deer were removed. No formal records were kept of the number of wild deer removed. Captive-raised yearling female deer were placed into these enclosures according to the following plan: one deer in 26 ha = 3.8 deer/km^2; one deer in 13 ha = 7.7 deer/km^2; two deer in 13 ha = 15.4 deer/km^2; four deer in 13 ha = 30.9 deer/km^2. Two of these enclosures were completed in 1979 and two in 1980. These densities spanned the range of deer present on the Allegheny Plateau in both

TABLE 2. Mean tree species density (in thousands/ha), by height class and site, during the first year of the experiment in stands that remained uncut.

Site name	Height class (m)	Black cherry	Red maple	Sugar maple	American beech	Black and yellow birch	White ash	Pin cherry	Striped maple	Cucumber	Serviceberry
Gameland 30	<0.3	641.1 (124.9)	337.0 (53.0)	0.1 (<0.1)	6.2 (0.8)	2.7 (1.1)	<0.1 (<0.1)	0.2 (0.2)	31.3 (10.7)	<0.1 (<0.1)	3.5 (2.0)
	0.3–0.9	0	1.1 (1.1)	0	1.4 (0.7)	0	0	0	10.4 (5.0)	0	0
Fools Creek	<0.3	345.0 (42.7)	304.4 (73.2)	1.0 (0.9)	3.4 (0.1)	8.1 (3.8)	35.2 (17.7)	1.7 (1.0)	1.5 (0.4)	0.1 (<0.1)	0.6 (0.2)
	0.3–0.9	0	0	0	0.2 (<0.1)	0	0	0	0.3 (0.2)	0	0
Deadman Corners	<0.3	687.8 (202.9)	263.1 (53.6)	10.0 (3.3)	14.7 (7.3)	16.9 (7.4)	<0.1 (<0.1)	1.1 (0.6)	4.5 (1.5)	0 (0)	0.9 (0.3)
	0.3–0.9	0.2 (0.2)	0	0	1.8 (0.6)	0	0	0	0.4 (0.4)	0	0
Wildwood Tower	<0.3	126.1 (11.8)	21.5 (10.1)	0.9 (0.5)	11.1 (2.3)	1.1 (0.4)	0 (0)	0.2 (<0.1)	40.6 (11.1)	6.8 (1.0)	0.1 (<0.1)
	0.3–0.9	0.1 (0.1)	0	<0.1 (<0.1)	1.8 (0.1)	<0.1 (<0.1)	0	0	18.5 (10.2)	0	0

Note: Standard errors are given in parentheses.

the presettlement and contemporary time periods (Lutz 1930, Park 1938, McCain 1939, Leopold et al. 1943, 1947, Bramble and English 1948, Hough 1949, Marquis 1975, Kosack 1995, Redding 1995). Each deer was equipped with a radio transmitter with a mortality indicator to aid in verification of deer densities once every two weeks. During the course of the study, some deer died or escaped. When this occurred in nonwinter seasons, deer were replaced immediately. However, when a deer died during the winter, it was not replaced until green-up in the spring, because experience early in the study showed that deer replaced in midwinter did not survive. On rare occasions when wildling deer penetrated the fence, they were removed. To accommodate these unplanned changes in deer densities, actual deer densities were calculated for each calendar year based on deer-days of use for each enclosure. Over the 10 yr of the study, actual deer densities averaged 3.8, 7.7, 14.7, and 24.7 deer/km²; hereafter, we refer to these densities as 4, 8, 15, and 25 deer/km².

Landscape condition

Previous research has shown that the impact of deer on forest ecosystems is influenced both by the density

TABLE 3. Regeneration strategies, deer food preferences, and shade tolerance ratings of important species particpating in vegetation dynamics.

Species	Regeneration strategies	Food preference by deer	Shade tolerance
Herbaceous			
Blackberry	seed bank and rhizomes (a, b)	high, all seasons (c)	intermediate (d)
Ferns	spores and rhizomes (e)	not preferred (c)	tolerant (e)
Grasses and sedges	seeds and rhizomes (f)	high in spring; moderate/low in other seasons (c)	intermediate to tolerant
Woody			
Black cherry	advance seedlings, seed bank, and stump sprouts (g)	low in all seasons (c)	intolerant (g)
Red maple	advance seedlings and stump sprouts (h)	moderate/low in all seasons; heavy in winter, light other seasons (c, i)	tolerant (h)
Sugar maple	advance seedlings and stump sprouts (j)	high in late fall, winter, late spring; otherwise moderate/low (c)	very tolerant (j)
Pin cherry	seed bank (k)	high in all seasons (l)	very intolerant (m)
Black and yellow birch	wind-blown seed (n, o)	high in late autumn; otherwise moderate/low (c)	intermediate (o)
American beech	root suckers, advance seedlings, and stump sprouts (p)	high in winter and late spring; low other times (c)	very tolerant (p)
Striped maple	advance seedlings, layered branches (q)	high in late fall and winter; otherwise moderate/low (c)	very tolerant (r)

Note: References are indicated by letters in parentheses: (a) Tamm 1974; (b) Jobidon 1993; (c) Healy 1971; (d) S. B. Horsley, *unpublished data*; (e) Cody et al. 1977; (f) Horsley et al. 1994; (g) Marquis 1990; (h) Walters and Yawney 1990; (i), Bramble and Goddard 1953; (j) Godman et al. 1990; (k) Marks 1974; (l) Jordan 1967; (m) Wendel 1990; (n) Baker 1949; (o), Erdmann 1990; (p) Tubbs and Houston 1990; (q) Gabriel and Walters 1990; (r) Hibbs et al. 1980.

of deer and by the forage available within the landscape used by deer (Taylor 1984, Underwood and Porter 1997, Augustine and Jordan 1998). We used timber harvesting to stimulate the production of forage (Jordan 1967, Yanai et al. 1998) at a consistent level in all study areas, creating a comparable and realistic landscape condition within each enclosure through which deer could move at will. We clear-cut 10% and thinned 30% of each area. Partial cuttings followed the guidelines of Marquis et al. (1992), but did not alter the species composition of the overstory (Table 1). The resulting landscape condition was representative of that found in a forest managed on a 100-yr rotation (Davis 1966, Marquis 1987), a common rotation length in the Allegheny Plateau region at the time.

Vegetation sampling

Vegetation was sampled periodically on permanent, systematically located 4.05 m^2 circular plots (hereafter, 4 m^2). In each deer density area, there were: 25 sample plots where the overstory was clear-cut, 15 where it was thinned, and 20 where there was no removal. Vegetation was measured during the first year of the study 0–1 yr after treatment (YAT) and thereafter in late summer 3, 5, and 10 YAT. Tree seedlings were tallied by species and height in one of four classes: 0.05–0.3 m, 0.3–1.0 m, 1.0–1.5 m, and $>$1.5 m but $<$2.5 cm diameter at 1.3 m above the ground. In addition, heights of the tallest black cherry, red maple, sugar maple, and white ash (*Fraxinus americana* L.), if present, and the height of the tallest stem of all species (dominant stem) were recorded. Heights of the tallest beech, birch, yellow-poplar, cucumbertree, aspen, and eastern hemlock were recorded only when these species were the tallest on the plot or the tallest commercial species on the plot. We collected data on herbaceous layer vegetation as percent ground cover by three groups (*Rubus* spp., ferns, grasses and sedges) that were estimated ocularly. Ground cover values of 1, 2, 5, 10, . . . , 90, 95, and 100% were used.

Statistical analysis

The study is a randomized complete-block design with four blocks (sites, df = 3) and four deer density (*impact*) treatments (df = 3). Blocks are considered random effects, and deer density treatments are fixed effects. The block × deer density interaction (df = 9) was the error term in this analysis. Dependent variables in the analysis were measures of abundance or density, height, and species composition. Percent ground cover was the measure of abundance for herbaceous plants; the number of stems, by species, in a height class or composite of height classes per 4 m^2 plot was the measure of density for tree species. Although not measured in this study, soil and environmental resource levels, particularly light, differ greatly among the cutting treatments (Marquis 1973, Horsley 1993). Thus, measures of seedling density used seedlings $\geq$1.5 m tall in stands that were clear-cut, seedlings $\geq$0.3 m tall in thinned stands, and seedlings $<$0.3 m tall in uncut stands. Height of the tallest stem, by tree species, was the dependent measure of height. There were several measures of tree species composition and diversity. In previous work, we have found that the percentage of the 4-m^2 plots dominated by a particular tree species after 10 yr (i.e., the percentage of plots in which the species was the tallest of all species) is a good predictor of future species composition (Marquis 1979, Tilghman 1989, Ristau and Horsley 1999). The number of tree species (richness) and the Shannon index (a measure based on both the number of tree species and the evenness of their distribution) also were used (Magurran 1988). In calculations of richness and the Shannon index, all stems $>$0.05 m tall were included.

The landscape condition in each enclosure represented the matrix of silvicultural treatments found in a managed forest on a 100-yr rotation. We separately analyze and report the response of vegetation in areas where the overstory was clear-cut, thinned, or left uncut. Different height classes of seedlings dominated each treatment area over time, and separate analyses allowed us to focus on dominant vegetation within each treatment area. It also allowed us to predict the results of silvicultural treatments at different deer densities individually, the way most useful to managers planning such treatments.

Bonferroni tests with 1 df were used to evaluate differences in dependent variables over the number of years since treatment. Orthogonal polynomial contrasts were used to test for linear, quadratic, and cubic trends in response means with increasing deer density (Wilkinson 1997). To achieve a reasonable compromise between the probability of a Type I error and the power of our tests, we chose a critical value of F at $\alpha = 0.10$ for all contrasts. However, we report the calculated significance of individual test statistics to allow readers to use an alternative significance level, if desired. When single contrasts are presented, we report the exact value of P (e.g., $P = 0.015$); for multiple contrasts, we report the most conservative value of P in a series of single-degree-of-freedom Bonferroni tests (e.g., if density has a nonsignificant effect on the height of several species, $P \geq 0.421$). Where data for a result are not displayed in a table or graph, we list mean values followed by the standard error in parentheses for each level of the comparison.

Because the same plots were sampled repeatedly over time, repeated-measures ANOVA with analysis of contrasts was used (Meredith and Stehman 1991, Gumpertz and Brownie 1993). The between-plot analysis tests effects averaged over all times of measurement. The within-plot analysis examines time × deer density interactions (Gumpertz and Brownie 1993). Plot-averaged data were used for all repeated-measures analyses. Normality of data was evaluated using probability plots; non-normal data were transformed using $\log_{10}$-

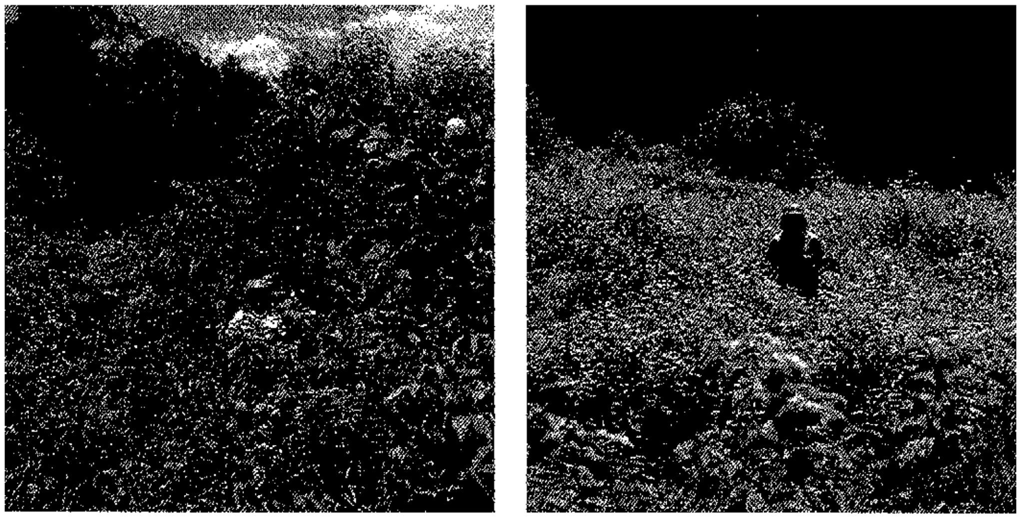

PLATE. 1. Vegetation development at the Fools Creek site in the clear-cut stand five years after treatment of 4 deer/km^2 and 25 deer/km^2. (Left photo) At 4 deer/km^2, 85% or more of the tree species composition was dominated by pin cherry (the tallest stems), black cherry, and birch. (Right photo) At 25 deer/km^2, mean height of the dominant trees was only about 20% of that at 4 deer/km^2.

or square-root transformations prior to analysis. For some models, 1 was added to each mean (mean + 1) prior to transformation, allowing us to include species that had 0 means at some deer densities. Compound symmetry of data was evaluated using the Huynh-Feldt statistic (Wilkinson 1997). Appropriate adjustments in repeated-measures analyses were made to account for unequal time intervals in single-degree-of-freedom contrasts. In cases in which the dependent variable was not equally distributed with respect to deer density at the first measurement, the first measurement was used as a covariate to adjust means of subsequent measurements prior to performing the ANOVA. Computation of statistical parameters was with SYSTAT version 7.0 (Wilkinson 1997).

RESULTS

Areas where overstory was clear-cut

General patterns of vegetation development.—During the first 10 yr after clear-cutting, herbaceous and tree vegetation developed rapidly. In the first year or two, *Rubus*, ferns, and grasses and sedges were the dominant vegetation (Fig. 1). Expansion of the ground layer continued at least through 5 yr after treatment, YAT. By 3 YAT, stems of trees had begun to emerge above the herbaceous layer (Fig. 1a); and by 10 YAT, trees had gained dominance of the site (Fig. 1b–d).

Abundance of herbaceous layer vegetation.—*Rubus* abundance increased for the first 5 YAT ($P \leq 0.006$), then decreased between years 5 and 10 ($P = 0.098$; Fig. 1b). At 5 and 10 YAT, there was a negative trend between *Rubus* abundance and deer density (linear contrast, $P \leq 0.010$; quadratic contrast, $P \leq 0.071$). By 10 YAT, the relationship between deer density and *Rubus* abundance contained only a linear trend ($P = 0.008$). Fern abundance increased with time through 5 YAT ($P \leq 0.014$), but was similar in years 5 and 10 ($P = 0.115$; Fig. 1c). In years 3 and 5 after treatment, linear ($P \leq 0.003$) and quadratic ($P \leq 0.027$) trends between deer density and fern abundance were evident; by 10 YAT, only the linear trend remained ($P = 0.002$). Grass and sedge ground cover continued to expand through 3 YAT ($P \leq 0.001$), was similar between 3 and 5 YAT ($P = 0.149$), and then decreased between 5 and 10 YAT ($P = 0.012$; Fig. 1d). By 10 YAT, there was a positive linear trend between grass and sedge abundance and deer density ($P = 0.022$).

Density of tree species.—Sixteen species of woody plants were found across the four study sites, although nearly 85% of the stems were of five species: black cherry, pin cherry, yellow and black birch, and striped maple (see Plate 1). During the first 5 YAT, trees were slower to grow above 1.5 m tall at densities of 15 and 25 deer/km^2 than at 4 or 8 deer/km^2 ($P \leq 0.011$; Fig. 1a). By 10 YAT, some self-thinning had occurred among trees at densities ≤8 deer/km^2; there were no trends in density of trees >1.5 m tall of all species combined with deer density ($P \geq 0.131$; Fig. 1a).

Black cherry was the most abundant species (Table 2). Over all deer densities, the number of black cherry trees >1.5 m tall (the threshold height considered out of the reach of deer) increased for the first 5 YAT ($P \leq 0.023$), but did not increase between 5 and 10 YAT ($P = 0.257$; Fig. 2a). For the first 5 YAT, there were no trends in black cherry abundance with deer density ($P \geq 0.152$), but by 10 YAT, there was a linear trend of *increase* in the number of black cherry stems >1.5 m tall with increasing deer density ($P = 0.005$; Fig. 2a).

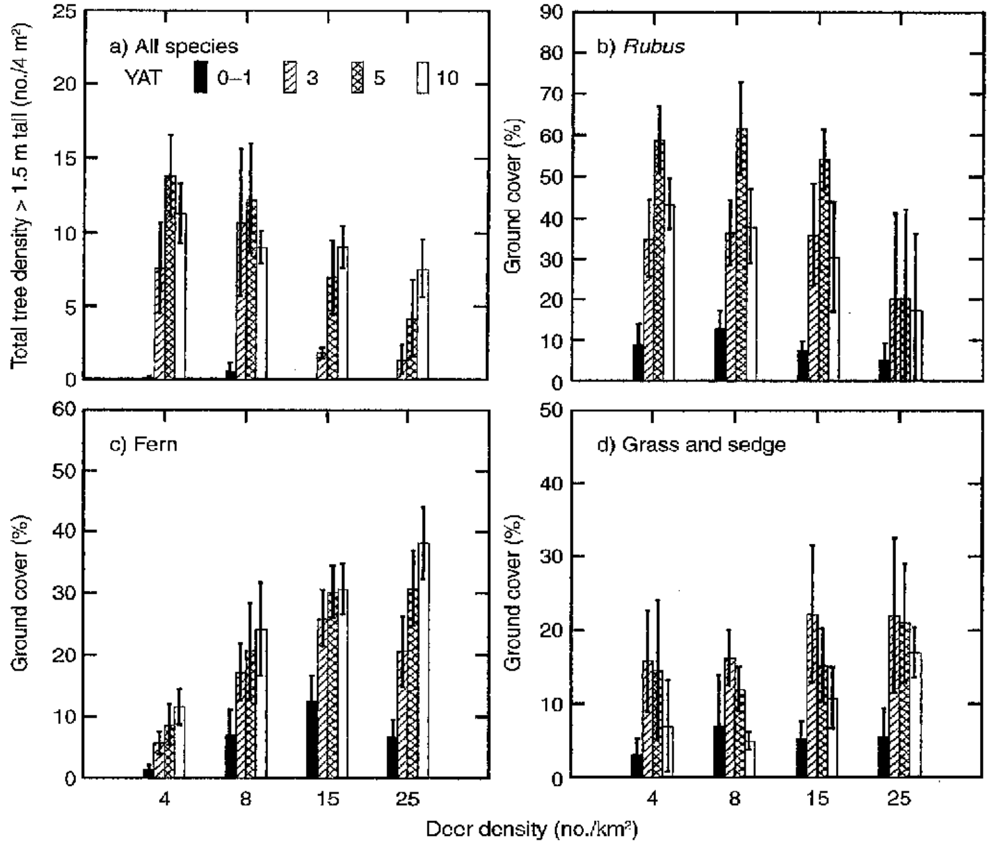

FIG. 1. Vegetation abundance 0–1, 3, 5, and 10 yr after treatment (YAT): clear-cutting at densities of 4, 8, 15, and 25 deer/km². (a) Total tree density of all species >1.5 m tall in 4-m² plots; (b) percent ground cover of *Rubus*; (c) percent ground cover of ferns; and (d) percent ground cover of grasses and sedges. All values are mean ± 1 SE.

Little pin cherry was present prior to overstory removal (Table 2); after cutting, pin cherry increased in density for the first 5 YAT ($P \leq 0.001$), then decreased between the fifth and 10th YAT ($P = 0.015$; Fig. 2b). From 3 YAT onward, there was a strong relationship between deer density and density of pin cherry; at densities of 4 and 8 deer/km², there were more pin cherry stems than at 15 and 25 deer/km² ($P \leq 0.002$).

Little birch was present prior to overstory removal (Table 2). Few seedlings >1.5 m tall were present prior to 5 YAT (Fig. 2c). There was no trend in birch density with deer density in any YAT ($P \geq 0.117$); by 10 YAT, birch density was lower at 25 deer/km² than at densities ≤15 deer/km² ($P = 0.092$).

Striped maple seedlings <0.3 m and 0.3–0.9 m were present before overstory removal (Table 2). Although the density of stems >1.5 m tall increased between 0–1 and 10 YAT ($P = 0.004$), the species did not become abundant (Fig. 2d). In years 5 ($P = 0.058$) and 10 ($P = 0.075$) after treatment, there was a linear decrease in striped maple >1.5 m tall with increasing deer density.

Red maple was second to black cherry in the density of seedlings present prior to overstory removal (Table 2), but it did not become an important species at any time after overstory removal. By 10 YAT, surviving stems of seedling origin accounted for only 10% of the red maple present; 90% originated as sprouts on cut stems. From 3 YAT onward, there were fewer red maple stems at 15 and 25 deer/km² than there were at 4 and 8 deer/km² ($P \leq 0.062$; Fig. 2e).

American beech root suckers, white ash, and sugar maple seedlings and stump sprouts were present in small numbers at most sites; small numbers precluded statistical analysis (data are not shown).

Height growth of tree species.—Height of the tallest stem increased with time, whereas it typically decreased with increasing deer density (Fig. 3a–e). There was a linear decrease in height of the tallest black cherry at 3 ($P = 0.033$) and 5 ($P = 0.056$) YAT, while black cherry still were within the reach of deer (Fig. 3a); by 10 YAT, the tallest stems were beyond the reach of deer and the trend had disappeared ($P = 0.460$). Pin cherry had grown beyond the reach of deer by 3 YAT; thus, there were no

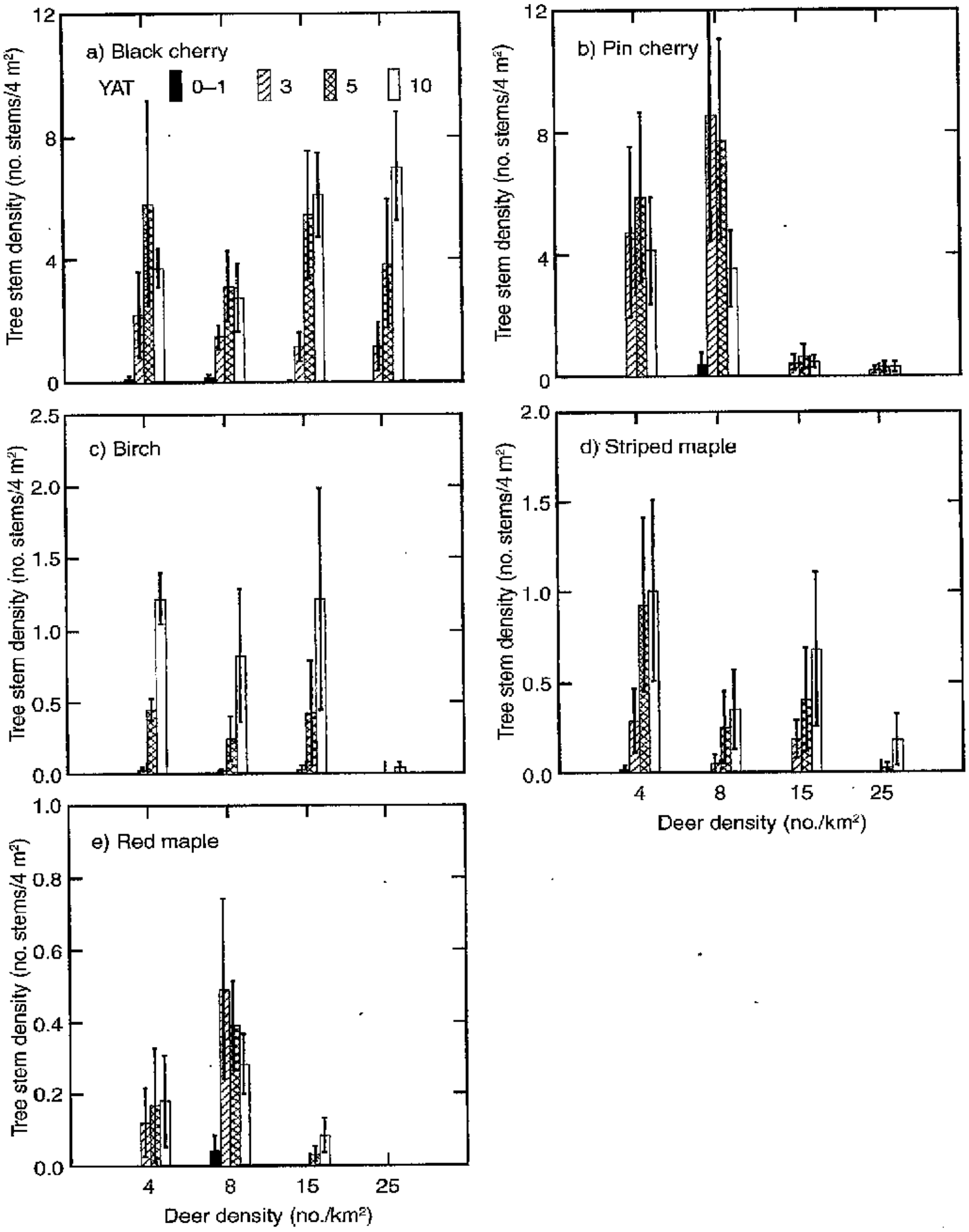

FIG. 2. Stem density (mean ± 1 SE) of tree species that were >1.5 m tall, sampled in 4-m^2 plots at 0–1, 3, 5, and 10 yr after clear-cutting (YAT) at densities of 4, 8, 15, and 25 deer/km^2. (a) Black cherry; (b) pin cherry; (c) birch (seedlings were not present in this size class until year 3 after treatment); (d) striped maple (few seedlings were present in this size class until year 3 after treatment); and (e) red maple.

trends with deer density ($P \geq 0.344$; Fig. 3b). At 15 and 25 deer/km^2, surviving pin cherry were protected by logging slash. Height of the tallest birch showed a negative linear relationship with deer density at 3, 5, and 10 YAT ($P \leq 0.010$; Fig. 3c). From 3 through 10 YAT, there were negative linear trends in height of the tallest red maple ($P \leq 0.029$; Fig. 3d) and American beech ($P \leq 0.027$) with deer density (Fig. 3e). At 10 YAT, pin cherry was the tallest of all species, followed by black cherry, birch, American beech, and red maple.

Species composition and diversity of tree species.—At 10 YAT, 85% or more of the sample plots were dominated by only three species: black cherry, pin cherry, and birch (Fig. 4a). The percentage of plots

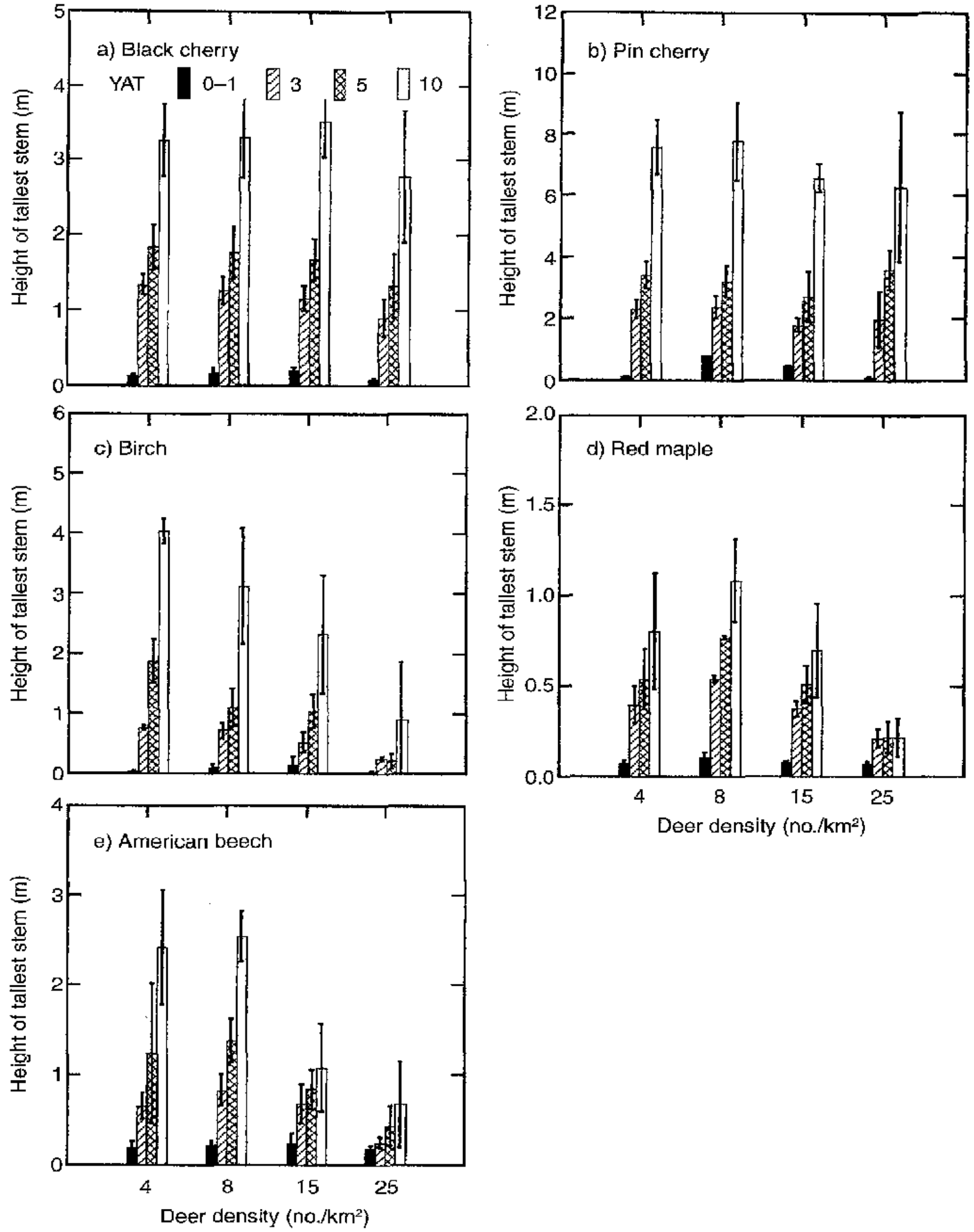

FIG. 3. Height (mean + 1 SE) of the tallest stem of tree species at 0–1, 3, 5, and 10 yr after clear-cutting (YAT) at densities of 4, 8, 15, and 25 deer/km²: (a) black cherry; (b) pin cherry; (c) birch; (d) red maple; and (e) American beech.

dominated by black cherry increased linearly with increasing deer density ($P = 0.001$). At 10 YAT, ~25% of the plots were dominated by black cherry at 4 and 8 deer/km², whereas >50% were dominated by black cherry at 15 and 25 deer/km² ($P = 0.002$). The pattern of dominance for pin cherry was the reverse of that for black cherry. The percentage of plots dominated by pin cherry decreased linearly with increasing deer density ($P = 0.034$). At 4 and 8 deer/km², ≥45% of the plots were dominated by pin cherry, whereas at 15 and 25 deer/km², pin cherry dominated ≤30% ($P = 0.038$). Birch dominated a relatively small percentage of plots compared with black cherry or pin cherry (Fig. 4a). The highest percentage of plots dominated by birch (22%) was at 4 deer/km² and decreased linearly with increasing deer density ($P = 0.047$).

Mean species richness over all deer densities was not affected by time since overstory removal (Time main

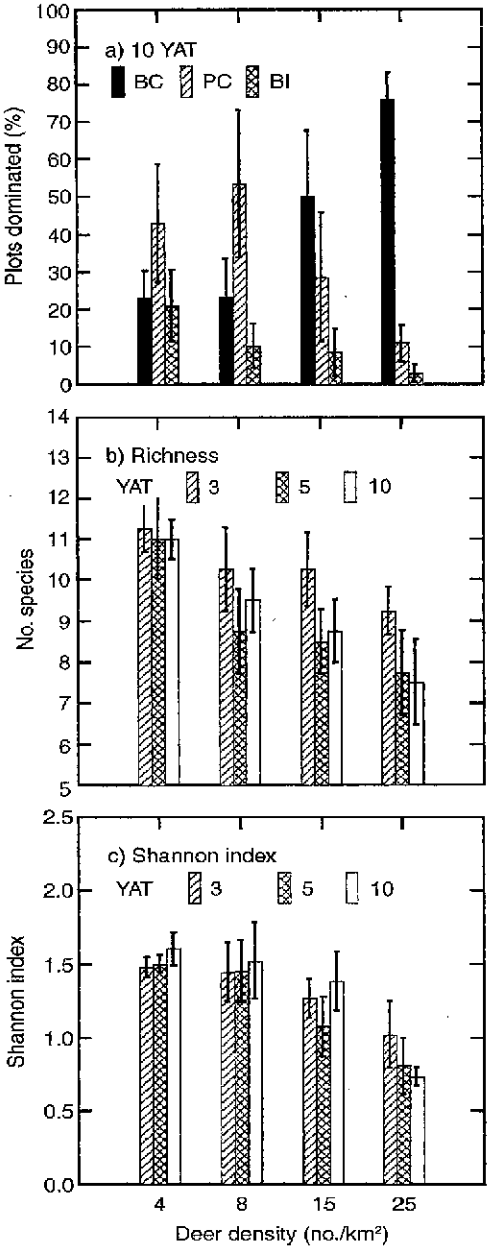

FIG. 4. Species composition and diversity of tree species 3, 5, and 10 yr after clear-cutting at densities of 4, 8, 15, and 25 deer/km². (a) Percentage of plots dominated by black cherry (BC), pin cherry (PC), and birch (BI) at 10 yr after treatment (YAT); (b) richness; and (c) Shannon index. Values in (b) and (c) for 3, 5, and 10 yr after treatment were adjusted using values in year 0–1 after treatment as a covariate. All values are mean ± 1 SE.

effect, $P = 0.449$; Time × Density interaction, $P = 0.665$), but over time, the effect of deer density on species richness increased (Fig. 4b). At 3 and 5 YAT, there was no relationship between richness and deer density ($P \geq 0.315$), but by 10 YAT, there was a negative linear trend ($P = 0.011$). Similar results were obtained for the Shannon diversity index. There was little change in the mean value of the Shannon index with time ($P \geq 0.136$), but negative linear trends with deer density were observed in years 3 ($P = 0.056$), 5 ($P = 0.012$), and 10 ($P = 0.007$; Fig. 4c).

Areas where overstory was thinned

General conditions and patterns of vegetation development.—Growth of all but the most shade-tolerant species (striped maple and American beech; see Table 3) was limited under the conditions created by thinning. During the first 5 YAT, vegetation was dominated by *Rubus*, ferns, grasses and sedges, and small tree seedlings (Fig. 5a–d, Fig. 6a–c). By 10 YAT, the abundance of some herbaceous species had declined (Fig. 5b–d) and the height of the tallest trees had increased to nearly 5 m, although some species remained within the reach of deer for the entire 10 yr of study (Fig. 7).

Abundance of herbaceous layer vegetation.—*Rubus* abundance increased for the first 3 YAT ($P < 0.001$), was similar at 3 and 5 YAT ($P = 0.286$), then decreased between years 5 and 10 ($P = 0.028$; Fig. 5b). At the FC and DM sites, which had the largest quantities of *Rubus*, abundance reached >60% ground cover in year 5 at 4 and 8 deer/km². Deer density had a strong effect on *Rubus* abundance; from year 3 onward, there was a negative linear trend between *Rubus* ground cover and deer density ($P \leq 0.005$; Fig. 5b). Abundance of ferns increased for the 10 yr of study (1–3 YAT, $P = 0.003$; 3–5 YAT, $P = 0.066$; 5–10 YAT, $P = 0.022$; Fig. 5c). A positive linear trend between fern ground cover and deer density was evident in year 10 ($P = 0.018$), but not in the three earlier time periods ($P \geq 0.401$). Abundance of grasses and sedges increased through the third year after treatment ($P = 0.001$), was similar at 3 and 5 YAT ($P = 0.256$), then decreased between years 5 and 10 ($P = 0.002$); ground cover was no more than ~10% at all times. A positive linear trend in grass and sedge abundance with deer density was apparent 10 YAT ($P = 0.036$), but not in prior measurements ($P \geq 0.238$).

Density of tree species.—More than a dozen species of seedlings were present in the <0.3 m height class at 0–1 YAT; initial density of these small seedlings was not related to the deer density treatments ($P \geq 0.372$). Five species accounted for ≥85% of the stems >0.3 m tall: black cherry > striped maple > yellow and black birch > American beech. There were no trends in the effect of deer on the density of all species combined ($P \geq 0.780$; Fig. 5a).

Black cherry (>0.3 m tall) increased through year 5 after thinning ($P \leq 0.026$), then decreased between

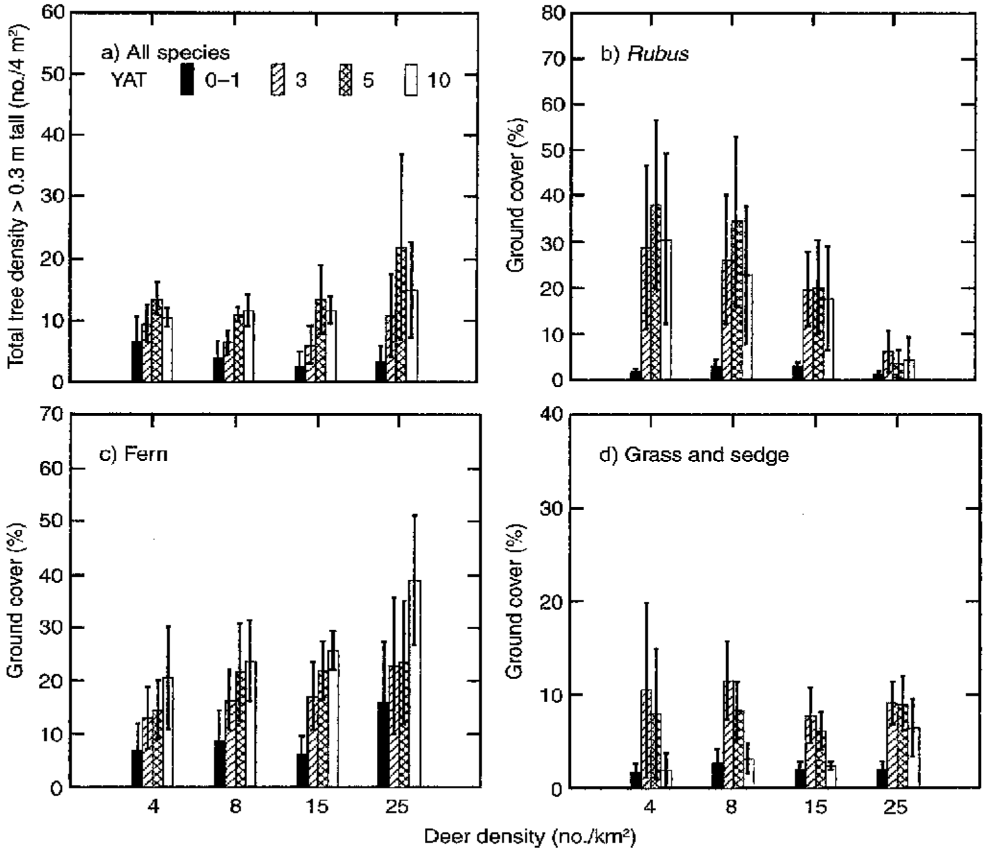

FIG. 5. Total density of all tree species >0.3 m tall and abundance of herbaceous-layer vegetation at 0–1, 3, 5, and 10 yr after overstory thinning at densities of 4, 8, 15, and 25 deer/km². (a) Total density of all tree species >0.3 m tall, sampled in 4-m² plots; (b) percent ground cover of *Rubus*; (c) percent ground cover of ferns; and (d) percent ground cover of grasses and sedges. All values are mean ± 1 SE.

years 5 and 10 (P = 0.001; Fig. 6a). There was no trend in density of black cherry with deer density ($P \geq 0.255$).

The distribution of striped maple >0.3 m tall 0–1 YAT was not equal with respect to site (Site main effect, $P < 0.001$). Nearly all of the striped maple >0.3 m tall were preexisting 0.3–0.9 m stems at the GL and WW sites (GL + WW vs. FC + DM contrast, $P \leq 0.001$; Table 2); the analysis presented is based on the GL and WW sites. Striped maple (>0.3 m tall) increased through year 5 after thinning ($P < 0.001$) and was similar in years 5 and 10 (P = 0.216). There were no trends in density of striped maple >0.3 m tall with deer density in years 3 or 5 after thinning ($P \geq 0.564$), but by year 10, there was a negative linear trend with deer density (P = 0.096).

Birch seeded in within a year or two after thinning; thus, there were no seedlings >0.3 m tall at 0–1 YAT. Abundance of birch (>0.3 m tall) increased in years 3 and 5 ($P \leq 0.037$) and was similar in years 5 and 10 (P = 0.784; Fig. 6c). There was no trend in birch abundance with deer density at 3 (P = 0.441) or 5 (P = 0.110) YAT. In year 10, there was a quadratic trend (P = 0.031).

American beech (>0.3 m tall) density increased slowly from 0–1 to 10 YAT (P = 0.022), although the number of stems was small (Fig. 6d). Beginning with year 3 after thinning, there was a negative linear trend in beech abundance with deer density (3 YAT, P = 0.086; 5 YAT, P = 0.071; 10 YAT, P = 0.011).

Despite the abundance of small red maple seedlings at the beginning of the experiment (Table 2), few grew >0.3 m tall. By 10 YAT, when red maple >0.3 m tall were most abundant, there was a negative linear trend with deer density (P = 0.045; Fig. 6e).

Pin cherry seeds present in the forest floor seed bank (Table 3) germinated during the first year or so after thinning. Few of these very shade-intolerant trees grew >0.3 m tall, and by 10 YAT, none was present (data are not shown). Small numbers of sugar maple and white ash also were present, but there were too few for statistical analysis.

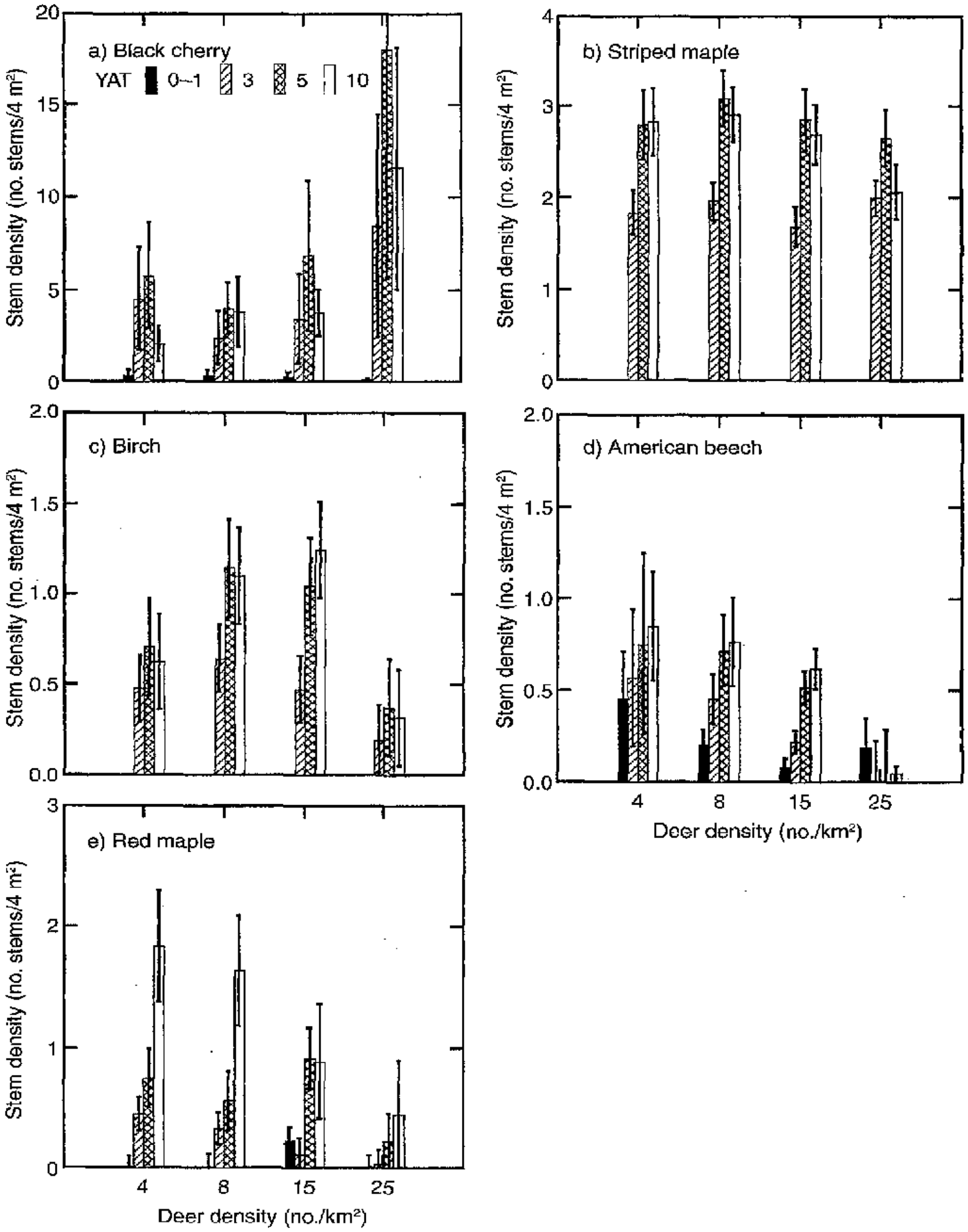

FIG. 6. Stem density (mean ± 1 SE of tree species that were >0.3 m tall, in 4-m² plots, at 0–1, 3, 5, and 10 yr after overstory thinning at densities of 4, 8, 15, and 25 deer/km²: (a) black cherry; (b) striped maple; (c) birch; (d) American beech; and (e) red maple. Values were adjusted using red maple basal area as a covariate. Values in (b) and (c) for 3, 5, and 10 yr after treatment were adjusted using values in year 0–1 after treatment as a covariate.

Height growth of tree species.—At 10 YAT, striped maple was the tallest species, followed by the birches > American beech > black cherry > red maple (Fig. 7). By 10 YAT, there was a negative linear trend in striped maple ($P = 0.067$), American beech ($P = 0.011$), and red maple height ($P = 0.015$) with deer density. No trends in birch ($P = 0.218$) or black cherry height ($P = 0.239$) with deer density were found.

Species composition and diversity of tree species.—Unequal distribution of striped maple among the four sites had important effects on species composition at 10 YAT (Fig. 8). Nearly all striped maple were at the

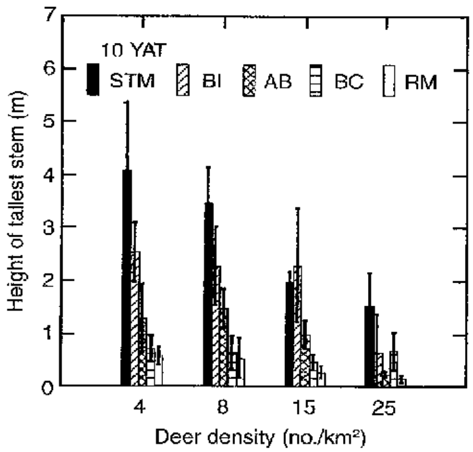

FIG. 7. Height (mean ± 1 SE) of the tallest stem of tree species 10 yr after overstory thinning at densities of 4, 8, 15, and 25 deer/km^2 for striped maple (STM), birch (BI), American beech (AB), black cherry (BC), and red maple (RM).

GL and WW sites, where 55–71% of the regeneration sample plots were dominated by striped maple; most of the remaining plots were dominated by black cherry, birch, or American beech. Despite the significant deer density effect on striped maple density and height, there were no trends in the percentage of plots dominated by striped maple during the 10 YAT at these two sites ($P \geq 0.149$; data are not shown). At the FC and DM sites, where there were few striped maple at the beginning of the study (Table 2), birch or black cherry became the dominant species, depending upon deer density: birch was dominant at deer densities ≤15 deer/km^2, whereas black cherry was dominant at 25 deer/km^2.

Across all sites, birch increased in dominance from 0–1 to 10 YAT (all values are mean ± 1 SE; at 0–1 YAT, 0.4 ± 0.8%; at 10 YAT, 23 ± 9%; $P = 0.011$). At 10 YAT, there was a quadratic trend in birch dominance with deer density (at 4, 8, 15, and 25 deer/km^2, respectively, 18 ± 9%, 25 ± 9%, 37 ± 9%, 10 ± 9%; $P = 0.083$).

Across all sites at 10 YAT, black cherry had been surpassed by either striped maple or birch at densities ≤15 deer/km^2; black cherry dominated a larger percentage of plots than birch only at 25 deer/km^2. There was a positive linear trend in the percentage of plots dominated by black cherry with deer density (at 4, 8, 15, and 25 deer/km^2, respectively, 13 ± 7%, 15 ± 7%, 15 ± 7%, 50 ± 7%; $P = 0.004$).

The percentage of plots dominated by American beech did not change with either time (at 3 YAT, 6.6 ± 3.2; at 10 YAT, 10.1 ± 4.6%; $P = 0.593$) or deer density (at 10 YAT at 4, 8, 15, and 25 deer/km^2, respectively, 6.8 ± 4.5%, 13.8 ± 4.9%, 11.8 ± 4.5%, 8.0 ± 4.9%; for linear contrast, $P = 0.895$). Red maple dominated <10% of the regeneration sample plots throughout the first 10 yr; by 10 YAT, there was a negative linear trend between the percentage of plots dominated by red maple and deer density (at densities of 4, 8, 15, and 25 deer/km^2, respectively, 2.5 ± 0.5%, 1.9 ± 0.5%, 1.7 ± 0.5%, 1.0 ± 0.5%; $P = 0.055$).

Species richness increased between 0–1 and 3 YAT ($P = 0.007$), then decreased to a level similar to that of year 0–1 by 10 YAT ($P = 0.569$; Fig. 8a). There was a negative linear trend between species richness and deer density at 3 and 5 YAT ($P \leq 0.043$), but the trend was no longer significant at 10 YAT ($P = 0.102$). Changes in the Shannon index over time were small; mean values were unchanged between 3 and 5 YAT ($P = 0.138$) and then increased between 5 and 10 YAT ($P < 0.001$). The Shannon index did not differ with deer density at 3 and 5 YAT ($P \geq 0.345$), but by 10

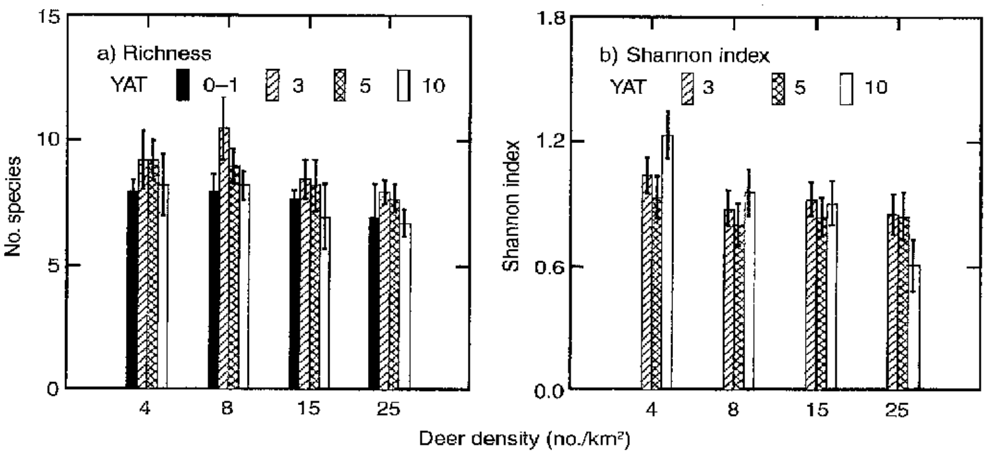

FIG. 8. Diversity of tree species 0–1, 3, 5, and 10 yr after overstory thinning at densities of 4, 8, 15, and 25 deer/km^2: (a) richness and (b) Shannon index. Values of the Shannon index for years 3, 5, and 10 after treatment were adjusted using values in year 0–1 after treatment as a covariate. All values are mean ± 1 SE.

TABLE 4. Mean abundance (percent ground cover) of the herbaceous ground layer or density (no. plants/4 m^2) of trees < 0.3 m tall in uncut stands with deer density at 10 years after treatment.

Species	Deer density (no./km^2) 4	8	15	25
Rubus	1.6 (0.7)	2.2 (0.8)	1.3 (0.3)	0.3 (0.1)
Fern	17 (4)	14 (5)	22 (4)	15 (4)
Grass and sedge	2.3 (1.0)	1.2 (0.5)	1.4 (0.6)	3.9 (1.3)
All trees	105 (15)	133 (15)	128 (15)	91 (14)
Black cherry	91 (14)	119 (14)	115 (15)	78 (14)
Red maple	9 (3)	13 (3)	11 (3)	6 (3)
Sugar maple	0.05 (0.02)	0.01 (0.02)	0.02 (0.02)	<0.01 (0.02)
Birch	0.4 (0.8)	1.2 (0.8)	1.7 (0.8)	1.2 (0.8)
American beech	0.4 (0.2)	0.4 (0.2)	0.6 (0.2)	1.2 (0.2)
Striped maple	1.5 (0.3)	2.0 (0.3)	1.6 (0.3)	2.1 (0.3)

Note: Numbers in parentheses are 1 SE.

YAT, there was a negative linear trend ($P = 0.014$; Fig. 8b).

Areas where overstory was uncut

General conditions and patterns of vegetation development.—Growth of all species and survival of some species was low in uncut stands. During the 10 yr of the study, seedlings <0.3 m tall were the most prominent vegetation. In the first YAT, 99% of the seedlings were <0.3 m tall; at 10 YAT, 96% of the seedlings were in this height range. Change in cover by herbaceous plants over time was small compared with that in thinnings or clearcuts. Density of seedlings of all species generally increased over time through 10 YAT, although the tallest stems were <1 m, well within the reach of deer. By 10 YAT, there was a negative quadratic trend between total density of tree seedlings and deer density ($P = 0.094$; Table 4).

Abundance of herbaceous ground-layer vegetation.—*Rubus* abundance was <1% ground cover at 0–1 YAT; by 10 YAT, it had reached 3% ground cover ($P = 0.019$). At 5 YAT ($P = 0.072$) and 10 YAT ($P = 0.038$), there was a negative linear trend of *Rubus* abundance with deer density (Table 4). Fern cover increased over time in uncut stands (mean ground cover: 0–1 YAT = 12 ± 3%; 10 YAT = 17 ± 3%; $P \leq 0.091$), but there were no trends with deer density (linear contrast: $P \geq 0.323$; Table 4). Grasses and sedges accounted for only ~2–4% of the ground cover in uncut stands. For the first 5 YAT, ground cover by grasses and sedges remained unchanged ($P \geq 0.696$), but by 10 YAT, grass and sedge cover had increased at 25 deer/km^2 ($P = 0.007$), resulting in a positive linear trend with deer density ($P = 0.051$; Table 4).

Density of tree species.—Black cherry (62%) and red maple (32%) accounted for 93% of the seedlings <0.3 m tall at 0–1 YAT; at 10 YAT, black cherry (88%) and red maple (8%) accounted for 96% of the small seedlings. Comparison of seedling density at 3 YAT with 10 YAT showed that black cherry was the only species that increased (at 3 YAT, 46 ± 11%; at 10 YAT, 102 ± 16%; $P < 0.001$). All other species decreased: red maple (at 3 YAT, 29 ± 8%; at 10 YAT, 10 ± 4%; $P < 0.001$), sugar maple (at 3 YAT, 0.3 ± 0.2%; at 10 YAT, 0.07 ± 0.04%; $P = 0.036$), birch (at 3 YAT, 2.6 ± 0.9%; at 10 YAT, 1.4 ± 0.5%; $P = 0.026$), striped maple (at 3 YAT, 4.4 ± 1.4%; at 10 YAT, 3.8 ± 1.2%; $P = 0.001$) or did not change in density (American beech at 3 YAT, 1.1 ± 0.2%; at 10 YAT, 1.3 ± 0.2%; $P = 0.143$). At 10 YAT, trends with deer density were apparent for black cherry (negative quadratic, $P = 0.088$) and American beech (positive linear, $P = 0.014$), but not for other species (red maple, $P \geq 0.301$; striped maple, $P \geq 0.215$; birch, $P \geq 0.208$; sugar maple, $P \geq 0.200$; Table 4).

Height growth of tree species.—Comparison of species height at 0–1 YAT with height at 10 YAT showed that all but striped maple increased: black cherry (at 0–1 YAT, 0.36 ± 0.02 m; at 10 YAT, 0.66 ± 0.12 m; $P = 0.017$), red maple (at 0–1 YAT, 0.25 ± 0.02 m; at 10 YAT, 0.42 ± 0.05 m; $P = 0.001$), birch (at 0–1 YAT, 0.26 ± 0.10 m; at 10 YAT, 2.31 ± 0.93 m; $P = 0.049$), American beech (at 0–1 YAT, 0.98 ± 0.07 m; at 10 YAT, 2.62 ± 0.44 m; $P < 0.001$), striped maple (at 0–1 YAT, 1.87 ± 0.48 m; at 10 YAT, 3.17 ± 1.07 m; $P = 0.107$). At 10 YAT, there was a negative linear trend with deer density for red maple ($P = 0.056$) but no trend for black cherry ($P = 0.319$; Table 5). Height of the tallest American beech had both negative linear ($P = 0.003$) and quadratic ($P = 0.039$) trends with deer density at 10 YAT; there was no trend for striped maple

TABLE 5. Mean height of the tallest tree, by species, in uncut stands with deer density at 10 years after treatment.

Species	Deer density (no./km^2) 4	8	15	25
Black cherry	0.72 (0.12)	0.72 (0.12)	0.62 (0.12)	0.57 (0.12)
Red maple	0.51 (0.05)	0.45 (0.05)	0.37 (0.05)	0.35 (0.05)
Birch	3.59 (1.12)	1.46 (0.93)	4.36 (1.12)	1.21 (1.14)
American beech	2.83 (0.44)	3.84 (0.44)	2.88 (0.44)	0.91 (0.44)
Striped maple	3.65 (0.70)	3.81 (1.15)	3.00 (1.15)	0.94 (1.13)

Note: Numbers in parentheses are 1 SE.

(P = 0.117) or birch (P = 0.405) height with deer density (Table 5).

Species composition and diversity of tree species.—Black cherry, striped maple, or American beech dominated most plots in uncut stands at 10 YAT. The percentage of plots dominated by black cherry did not increase over time (at 3 YAT, 32 ± 6% of plots; at 10 YAT, 30 ± 7%; P = 0.125) but from year 3 onward, there was a positive linear relationship with deer density (3 YAT, P = 0.027; 5 YAT, P = 0.025; 10 YAT, P = 0.001; Fig. 9a). At 10 YAT, black cherry dominated 19 ± 6% of the plots at 4 deer/km^2 and 55 ± 6% of the plots at 25 deer/km^2. The percentage of plots dominated by other species did not change over time: red maple (at 3 YAT, 8.8 ± 4.4%; at 10 YAT, 4.6 ± 3.3%; P = 0.549), birch (at 3 YAT, 2.8 ± 2.5%; at 10 YAT, 3.6 ± 3.1%; P = 0.721), American beech (at 3 YAT, 22 ± 4%; at 10 YAT, 27 ± 6%; P = 0.125), striped maple (at 3 YAT, 31 ± 9%; at 10 YAT, 28 ± 9%; P = 0.216). At 10 YAT, there was a linear decrease in the percentage of plots dominated by red maple as deer density increased (P = 0.088); trends with deer density were not seen for striped maple (P = 0.469), American beech (P = 0.195), or birch (P = 0.402; Fig. 9a).

Species richness decreased between 0–1 and 10 YAT (P = 0.036), although the actual differences were small. At 5 YAT, there was a negative linear relationship with deer density (P = 0.058) that continued through year 10 (P = 0.034; Fig. 9b). The Shannon index increased between 3 and 10 YAT (P = 0.028), although the differences were small, and there were no trends with deer density ($P \geq 0.253$; Fig. 9c).

DISCUSSION

Direct effects of deer density on vegetation trajectories.—Population densities of white-tailed deer have been high enough to cause negative impacts on forest vegetation in many areas of the eastern United States since at least the mid-to-late 20th century (Porter 1994) and in some areas of the eastern United States, including Pennsylvania, since the 1920s (Kosack 1995). Effects of deer on woody vegetation have received the most comprehensive investigation (Russell et al. 2001). Data derived primarily from exclosure studies suggest that deer directly impact species density (abundance, horizontal structure) and height growth (vertical structure). Over time, selective browsing by deer (or other ungulates) on species that they prefer results in reduced species richness/diversity and altered species composition dominated by unpreferred and browse-resilient species (Anderson and Loucks 1979, Frelich and Lorimer 1985, Anderson and Katz 1993, Hobbs 1996, Alverson and Waller 1997, Healy 1997, Russell et al. 2001). Threshold deer densities for these impacts have been elusive because of differences in deer density in both space and time and the two-data-point nature of exclosure data. Our study tested the null hypotheses that deer densities that can be sustained over long time

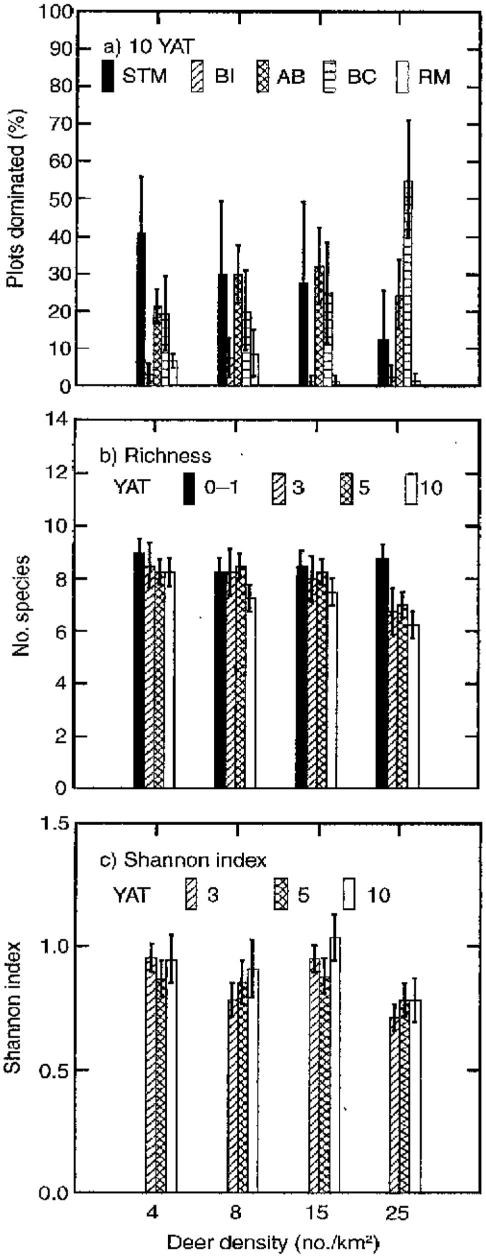

FIG. 9. Species composition and diversity of tree species in uncut stands over time after introduction of deer at densities of 4, 8, 15, and 25 individuals/km^2. (a) Percentage of plots dominated by striped maple (STM), birch (BI), American beech (AB), black cherry (BC), and red maple (RM) at 10 yr after treatment; (b) richness at 0–1, 3, 5, and 10 yr after treatment; and (c) Shannon index at 3, 5, and 10 yr after treatment, adjusted using values in year 0–1 after treatment as a covariate. All values are mean ± 1 SE.

periods on contemporary landscapes do not cause changes in understory density, seedling height growth, species composition, or woody plant diversity. Based on the experimental results presented here, we reject the null hypotheses. Deer affected species density, height development, and species diversity/composition over the 10-yr period of our experiment. With a few notable exceptions, increasing deer density led to decreasing stem density (percent ground cover for herbaceous plants) of most species over time at all levels of cutting disturbance. Exceptions to this trend were species not preferred or avoided by deer that increased in dominance (percent ground cover for herbaceous plants, percentage of plots dominated for woody species) with increasing deer density, including ferns, grasses and sedges, and black cherry. At all levels of cutting disturbance, height development of most trees decreased with increasing deer density as long as they were within the reach of deer. Over time, the net effect was a reduction in species diversity and altered species composition with increasing deer density.

Most trends between deer density and measures of species density, height, or species diversity/composition were linear. Where significant linear and quadratic components occurred in the same relationship, the linear component was always stronger and, over time, became the only significant component. Birch was the only species having significant quadratic trends with deer density.

Time was an important factor mediating relationships at all deer densities. In general, the length of time for significant relationships to develop decreased with increasing levels of overstory disturbance. In clear-cut stands, most significant relationships developed in 3–10 yr; in thinnings, 10 yr were required; and in uncut stands, only a few relationships were statistically significant in 10 yr. Relationships between *Rubus*, a highly preferred species (Table 3) and deer density developed sooner than those with other species at all levels of cutting disturbance. Significant reductions in *Rubus* density were observable as early as the first year of treatment in clearcuts, within 3 yr in thinned stands, and by 5 yr in uncut stands. Significant negative linear trends in species richness with deer density were observed within 3 yr in thinned or clear-cut stands, and within 5 yr in uncut stands. These variables may have value as early indicators of deer impact; deer browsing rate (percentage of browsed stems) on *Rubus* has been used to monitor deer impact in Europe (Morellet et al. 2001).

The threshold of deer density for negative impacts on forest vegetation under our experimental landscape condition was >~8 deer/km^2. The historic effect of 50 yr of nearly continuous high deer density (12–23 deer/km^2) prior to initiation of the experiment was to drive the vegetation toward fewer species that were of lower food preference to deer (Leopold et al. 1943, Hough 1965, Jordan 1967, Marquis 1974, 1981, Marquis and Grisez 1978, Marquis and Brenneman 1981, Whitney 1984). Black cherry was the most abundant species in both the overstory and the understory. Deer density during the experimental period determined whether the vegetation trajectory moved toward monoculture or toward restoration of a more diverse species composition. At the beginning of the experiment, the percentage of understory plots dominated by black cherry ranged from 19% to 31% over all deer densities. Ten years later, regardless of whether stands were disturbed or not, the percentage of understory plots dominated by black cherry at the highest deer density (25 deer/km^2) had increased: to 78% in clear-cut stands, to 50% in thinned stands, and to 55% in undisturbed stands. By contrast, at 4 or 8 deer/km^2 at 10 YAT, the percentage of plots dominated by black cherry ranged from 13% to 25% over all disturbance levels. In uncut stands, there were small increases in dominance by red maple, birch, and sugar maple at densities ≤8 deer/km^2. Although individually not significant, collectively, these increases seem to represent the beginning of a recovery when deer density remains low for an extended period of time. This result is particularly important in undisturbed stands that may be subject to future disturbance by cutting or natural events. Most tree species that are important in the vegetation dynamics after disturbance of northern hardwood stands in Pennsylvania (and eastern hardwoods in general) either are present before disturbance or become established shortly afterward as a result of the disturbance, e.g., pin cherry, *Rubus*, birch; see Table 3 (Grisez and Peace 1973). Thus, maintenance of low deer impact for a period of time long enough to insure the establishment of seedlings before a disturbance seems to be a prerequisite for recovery of diversity.

Overall, the qualitative impacts of deer on species density, height growth, and species composition/diversity in exclosure studies were similar to those reported here. This suggests that exclosure studies can be used with some confidence to identify situations in which deer impact is changing the direction of vegetative community development. However, information about the time required for impacts to become significant, or thresholds of deer impact, and about the shape of the response to deer density is difficult to detect or is not detectable in exclosure studies. Furthermore, such studies rarely include control over either the landscape condition or the deer density outside the exclosure, important determinants of deer impact. In other words, deer impact on vegetation depends not only on deer density, but also on the abundance of preferred food in the vicinity (Taylor 1984, deCalesta and Stout 1997, Augustine and Jordan 1998). In our study, we varied impact by holding landscape composition (percentage with various levels of disturbance) constant and by varying deer density. The numbers and diversity of seedlings that we observed at the various deer densities inside our exclosures were higher than the numbers observed at similar densities in less disturbed landscapes (*personal observation*). This probably is due to lower availability of forage in heavily forested landscapes without agricultural land, such as those where our study was conducted.

Indirect effects of deer density on vegetation trajectories.—Deer browsing can indirectly affect specific vegetation outcomes by facilitating the dominance of unpreferred and browse-resilient species over time. Once these species become established, they can minimize the reestablishment of preferred and less browse-resilient species through plant–plant interference, e.g., competition, allelopathy (Anderson and Loucks 1979, Horsley and Marquis 1983, Horsley 1993, Heitzman and Nyland 1994, de la Cretaz and Kelty 1999, George and Bazzaz 1999*a, b*, Ristau and Horsley 1999) and plant–animal interference, e.g., granivory (Brooks and Healy 1988, McShea and Rappole 1992, 1997, McShea and Schwede 1993) strategies. Vegetation outcomes in plant plant interference relationships depend not only on deer density, but also on individual species characteristics; species regeneration strategy, food preference to deer, and response to light seemed to be particularly important in our work.

Increase in fern abundance in eastern forests has caused particularly strong interference with regeneration of hardwood trees (Horsley 1977, Horsley and Marquis 1983, de la Cretaz and Kelty 1999, George and Bazzaz 1999*a, b*). Hough (1965) noted that the historic rise in fern abundance on the Allegheny Plateau in Pennsylvania was coincident with the loss of the preferred shrub, witch hobble (*Viburnum alnifolium* Marshall) at the peak of deer density in the 1930s. Our study showed that in thinned and clear-cut stands, there was a significant linear increase in fern abundance with an increase in deer density by 3 YAT. This increase was paralleled by significant decreases in the abundance of *Rubus* and tree seedlings. Studies to determine the mechanism of fern interference with black cherry seedling establishment have demonstrated that interference was due primarily to reduced light availability (Horsley 1993). Thus, once ferns become established, they can interfere with the buildup of tree seedlings and the restoration of diversity.

Stromayer and Warren (1997) have suggested that the increase in fern ground cover caused by deer in Allegheny Plateau forests represented an alternate stable state, that is, one that would persist even after the original cause, high deer density, was removed. Our data, combined with the species characteristics in Table 3, show that some of the conditions created by high deer density will be difficult to reverse. In stands that were clear-cut while deer density was high, reduced species diversity and domination by black cherry probably will be sustained where sources of windblown seed, such as birch, are too distant to increase diversity before the next harvest. Moreover, failure to replenish the seed bank of species with long-lived seeds like pin cherry (Styer et al. 1997) and *Rubus* at high deer densities probably will affect vegetation dynamics long into the future. However, where a diverse seed source remains, as in thinned and uncut areas, reductions in deer density could be associated with restoration of species diversity.

We are less sure whether clear-cut stands that regenerated to ferns under the impact of high deer density would produce a long-lasting alternate stable state if deer were removed or their density were greatly reduced. Birch, *Rubus*, white pine (*Pinus strobus* L.) (Horsley and Marquis 1983, de la Cretaz and Kelty 2002), and eastern hemlock (*personal observation*) are capable of growing through fern cover and reducing fern abundance over time, if propagules are present.

Implications for policy debates and decisions in the eastern hardwood forest region.—Our study shows that, at high densities, (1) deer make substantial changes in forests, (2) most of these effects are linear with increasing deer density, and (3) many of them accumulate over time. These results should inform policy debates and decisions throughout the eastern hardwood region. Whether an agency or landowner manages land for biological diversity, commercial production of timber or nontimber forest products, or recreation, deer affect the land manager's ability to achieve management objectives. These effects became significant in our study at densities well below levels observed in our region over time.

Agencies that manage deer abundance must recognize that, as deer density increases, so will the impact of deer on species diversity, species composition, and the abundance of plants that interfere with the restoration of diversity when deer density is reduced. Several studies have shown that competitive consumption of acorn mast by deer had a negative effect on the abundance of the mast-dependent small-mammal community in the following spring (Brooks and Healy 1988, McShea and Rappole 1992, 1997, McShea and Schwede 1993, Ostfeld et al. 1996, Healy 1997). Using data from the present study, deCalesta (1994) showed that deer caused reductions in habitat quality for songbirds. Data from this study show that where deer densities are high, forest understories become increasingly dominated by plants that are less preferred by deer, reducing the quality of deer habitat.

Although the evidence provided by our study will not resolve conflicts about deer management, it provides a strong scientific background for policy discussions. Policies that allow deer densities to increase can be expected to have specific and predictable consequences, whether those policies are implemented by deer management agencies focused on maximizing deer abundance for hunters, or by managers excluding hunting to test or allow natural regulation of deer populations.

Particularly compelling from a policy perspective is the evidence from our study that the effects of deer accumulate over time. Diversity in high deer density, uncut portions of our study areas decreased through the 10 yr of our study in ways that are mirrored by changes observed on the surrounding landscape, which has supported high deer densities for several decades. By the 10th year of our study, black cherry dominated 55% of the regeneration sample plots in uncut areas. An Allegheny National Forest (1995) survey of some 300 000 acres (121 457 ha) in 1992 (including thinned and uncut areas) found that although 28% of the overstory composition was represented by black cherry; 47% of the understory composition was represented by black cherry.

Furthermore, our study suggests that managers concerned with the effects of deer on forest ecosystems should focus on deer *impact* as well as deer *density* in making management decisions (Taylor 1984, deCalesta and Stout 1997, Augustine and Jordan 1998). Thus, 4, 8, 15, or 25 deer/km^2 have a smaller effect on forest vegetation in a stand with agricultural cropland in the vicinity than in a stand situated in a matrix of forest land. Decisions regarding deer management should consider both deer density and the composition of landscapes at relevant scales. In large blocks of contiguous forest under management on a 100-yr rotation, the conditions represented in our study, our data suggest that many tree species, as well as *Rubus* spp., will decrease at deer densities of >8 deer/km^2.

Deer impacts interact in important ways with other trends in eastern forests. Many of these forests originated from cuttings around the turn of the 19th century, or from agricultural abandonment in the first half of the 20th century. As a result, the percentage of valuable timber products such as those used for sawtimber and veneer has been increasing steadily over the last several decades as the forests mature (cf. DiGiovanni 1990, Alerich 1993, Alerich and Drake 1995). Birch (1996) found that 35% of owners who control over 60% of the private forest acreage in the northern states east of the Mississippi plan to harvest within 10 yr. Where these harvests take place in the presence of high densities of white-tailed deer, reductions in species diversity and selective removal of species preferred by deer or those not resilient to browsing essentially may be permanent, unless measures such as fencing are taken to preserve diversity.

At the same time, ownership fragmentation of the eastern forest is accelerating. Each year, ~600 000 ha of privately owned forest are split into pieces <40 ha (L. DeCoster, *personal communication*). Often, this fragmentation is associated with second home development, landscape enhancements, and reduced acreage available for public hunting. All of these forces increase the likelihood of deer attaining densities that have substantial impact, and increase the challenge for policy makers.

Overall, the results of this study provide important data for ongoing policy debates and further study. Over the 10-yr period of our experiment, increased deer impact reduced species density, height development, and species diversity/composition. The net result was an altered trajectory of vegetation development dominated by species avoided by deer and browse-resilient species. Management of white-tailed deer impact is an important dimension of sustainable ecosystem management.

ACKNOWLEDGMENTS

A study of the magnitude and duration of the one reported here cannot be the work of one or even a small group of individuals. The authors gratefully acknowledge the financial support and talents of the individuals and organizations who participated in the project. The study was a collaborative effort of the Warren, Pennsylvania, USA laboratory of the USDA Forest Service, Northeastern Research Station, and forest land management organizations including the Allegheny National Forest, the Pennsylvania Department of Conservation and Natural Resources, the Pennsylvania Game Commission, and National Fuel Gas. David A. Marquis conceived the study in the late 1970s and was the overall coordinator of the project until his retirement in 1991. Coleman Holt (1979–1981) and Nancy Tilghman (1982–1986) provided early wildlife biology expertise. Skilled technical assistance was provided by Vonley Brown, John Crossley, Virgil Flick, James Moore, James Redding, Todd Ristau, David Saf, Harry Steele, and Corinne Weldon. The authors also acknowledge with appreciation the advice of members of the Society of American Foresters Deer, Forest, Farms Committee, particularly Roe S. Cochran, Donald Dorn, Ted Grisez, Robert LaBar, and Robert Martin. Portions of this manuscript were prepared while one of us (S. B. Horsley) was on leave at the Jones Ecological Research Center, Newton, Georgia, USA; we thank the Robert W. Woodruff Foundation, Lindsay Boring, and Robert Mitchell for financial and collegial support.

LITERATURE CITED

Alerich, C. L. 1993. Forest statistics for Pennsylvania—1978 and 1989. Resource Bulletin **NE-126.** USDA Forest Service Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Alerich, C. L., and D. A. Drake. 1995. Forest statistics for New York—1980 and 1993. Resource Bulletin **NE-132.** USDA Forest Service Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Allegheny National Forest. 1978. The deer issue on the Allegheny National Forest. Environmental analysis. Allegheny National Forest. Warren, Pennsylvania, USA.

Allegheny National Forest. 1995. Management area 3. 0, 6000 plot survey report Appendix L *in* Analysis of timber harvest program capability 1995 through 2005. USDA Forest Service, Allegheny National Forest, Warren, Pennsylvania, USA.

Alverson, W. S., and D. M. Waller. 1997. Deer populations and the widespread failure of hemlock regeneration in northern forests. Pages 280–297 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Anderson, R. C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. Ecological Applications **4**:104–109.

Anderson, R. C., and A. J. Katz. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. Biological Conservation **63**:203–208.

Anderson, R. C., and O. L. Loucks. 1979. White-tailed deer

(*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. Journal of Applied Ecology **16**:855–861.

Augustine, D. J., and P. A. Jordan. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. Journal of Wildlife Management **62**:1076–1085.

Baker, F. S. 1949. A revised tolerance table. Journal of Forestry **47**:179–181.

Birch, T. W. 1996. Private forest-land owners of the northern United States, 1994. Resource Bulletin **NE-136.** USDA Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Bramble, W. C., and P. F. English. 1948. The forest grazing problem created by deer in eastern forests. Pages 257–263 *in* Proceedings of the Society of American Foresters Meeting. Society of American Foresters, Bethesda, Maryland, USA.

Bramble, W. C., and M. K. Goddard. 1953. Seasonal browsing of woody plants by white-tailed deer in the Ridge and Valley section of central Pennsylvania. Journal of Forestry **51**:815–819.

Brander, T. A., R. O. Peterson, and K. L. Risenhoover. 1990. Balsam fir on Isle Royle: effect of moose herbivory and population density. Ecology **71**:155–164.

Brooks, R. T., and W. M. Healy. 1988. Response of small mammal communities to silvicultural treatments in eastern hardwood forests of West Virginia and Massachusetts. Pages 313–318 *in* USDA Forest Service General Technical Report **RM-166.**

Ciolkosz, E. J., R. W. Ranney, G. W. Petersen, R. L. Cunningham, and R. P. Matelski. 1970. Characteristics, interpretations, and uses of Pennsylvania soils. Warren County. Progress Report 306. Pennsylvania State University, College of Agriculture, Agriculture Experiment Station, University Park, Pennsylvania, USA.

Cody, W. J., I. V. Hall, and C. W. Crompton. 1977. The biology of Canadian weeds. 26. *Dennstaedtia punctilobula* (Michx.) Moore. Canadian Journal of Plant Science **57**:1159–1168.

Cronce, R. C., and E. J. Ciolkosz. 1983. Soils of the Allegheny National Forest. Pages 8–21 *in* L. R. Auchmoody, E. Cioloosz, K. Cronce, and N. Johnson, editors. Proceedings of the Northeastern Forest Soils Conference. Warren, Pennsylvania, USA.

Davis, K. P. 1966. Forest management: regulation and valuation. McGraw-Hill, New York, New York, USA.

deCalesta, D. S. 1994. Impact of white-tailed deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management **58**:711–718.

deCalesta, D. S. 1997. Deer and ecosystem management. Pages 267–279 26 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

deCalesta, D. S., and S. L. Stout. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildlife Society Bulletin **25**:252–258.

DeGraaf, R. M., W. H. Healy, and R. T. Brooks. 1991. Effects of thinning and deer browsing on breeding birds in New England oak woodlands. Forest Ecology and Management **41**:179–191.

de la Cretaz, A. L., and M. J. Kelty. 1999. Establishment and control of hay-scented fern, a native invasive species. Biological Invasions **1**:223–236.

de la Cretaz, A. L., and M. J. Kelty. 2002. Development of tree regeneration in fern-dominated forest understories following reduction of deer browsing. Restoration Ecology **10**:416–426.

DiGiovanni, D. M. 1990. Forest statistics for West Virginia—1975 and 1989. Resource Bulletin **NE-114.** USDA Forest Service Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Erdmann, G. G. 1990. *Betula alleghaniensis* Britton Yellow birch. Pages 133–147 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2. Hardwoods. USDA Forest Service Agricultural Handbook **654.** USDA Forest Service, Washington, D.C., USA.

Frehlich, L. E., and C. G. Lorimer. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biological Conservation **34**:99–120.

Gabriel, W. J., and R. S. Walters. 1990. *Acer pensylvanicum* L. Striped maple. Pages 53–59 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2. Hardwoods. USDA Forest Service Agricultural Handbook **654.** USDA Forest Service, Washington, D.C., USA.

George, L. O., and F. A. Bazzaz. 1999*a*. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology **80**:833–845.

George, L. O., and F. A. Bazzaz. 1999*b*. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. Ecology **80**:846–856.

Godman, R. M., H. W. Yawney, and C. H. Tubbs. 1990. *Acer saccharum* Marsh. Sugar maple. Pages 78–91 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2. Hardwoods. USDA Forest Service Agricultural Handbook **654.** USDA Forest Service, Washington, D.C., USA.

Graham, S. A. 1958. Results of deer exclosure experiments in the Ottawa National Forest. Transactions of the North American Wildlife Conference **23**:478–490.

Grisez, T. 1957. Deer-browsing in the Poconos. Pennsylvania Game News. **February 1957**:7–10.

Grisez, T. J. 1959. The Hickory Run deer exclosure. USDA Forest Service Forest Research Notes **NE-87.** Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Grisez, T. J., and M. Peace. 1973. Requirements for advance reproduction in Allegheny hardwoods—an interim guide. USDA Forest Service Forest Research Notes **NE-180.** Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Gumpertz, M. L., and C. Brownie. 1993. Repeated measures in randomized block and split-plot experiments. Canadian Journal of Forest Research **23**:625–639.

Harrison, R. E. 1970. Physiographic map of the United States. *In* National atlas of the United States of America. U.S. Geological Survey, Washington, D.C., USA.

Healy, W. M. 1971. Forage preferences of tame deer in a northwest Pennsylvania clear-cutting. Journal of Wildlife Management **35**:717–723.

Healy, W. M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. Pages 249–266 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Heitzman, E., and R. D. Nyland. 1994. Influences of pin cherry (*Prunus pensylvanica* L. f.) on growth and development of young even-aged northern hardwoods. Forest Ecology and Management **67**:39–48.

Hibbs, D. E., B. F. Wilson, and B. C. Fischer. 1980. Habitat requirements and growth of striped maple (*Acer pensylvanicum* L.). Ecology **61**:490–496.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management **60**:695–713.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996*a*. Ungulate grazing in sagebrush grassland: effects of resource competition on secondary production. Ecological Applications **6**:218–227.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996*b*. Ungulate grazing in sagebrush grassland: mechanisms of resource competition. Ecological Applications **6**: 200–217.

Horsley, S. B. 1977. Allelopathic inhibition of black cherry. II. Inhibition by woodland grass, ferns, and club-moss. Canadian Journal of Forest Research **7**:515–519.

Horsley, S. B. 1993. Mechanisms of interference between hay-scented fern and black cherry. Canadian Journal of Forest Research **23**:2059–2069.

Horsley, S. B., L. R. Auchmoody, and R. S. Walters. 1994. Regeneration principles and practices. Pages 205–246 *in* D. A. Marquis,. editor. Quantitative silviculture for hardwood forests of the Alleghenies. USDA Forest Service General Technical Report **NE-183.** Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Horsley, S. B., and D. A. Marquis. 1983. Interference by deer and weeds with Allegheny hardwood reproduction. Canadian Journal of Forest Research **13**:61–69.

Hough, A. F. 1949. Deer and rabbit browsing and available winter forage in Allegheny hardwood forests. Journal of Wildlife Management **13**:135–141.

Hough, A. F. 1965. A twenty-year record of understory vegetational change in a virgin Pennsylvania forest. Ecology **46**:370–373.

Jobidon, R. 1993. Nitrate fertilization stimulates emergence of red raspberry (*Rubus idaeus* L.) under forest canopy. Fertilizer Research **36**:91–94.

Jordan, J. S. 1967. Deer browsing in northern hardwoods after clearcutting. USDA Forest Service Research Paper **NE-57.** Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Kingsley, N. P. 1985. A forester's atlas of the Northeast. USDA Forest Service General Technical Report **NE-95.** Northeastern Forest Experiment Station, Broomall, Pennsylvania, USA.

Kosack, J. 1995. The Pennsylvania Game Commission, 1895–1995: 100 years of wildlife conservation. Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA.

Leopold, A., E. F. Bean, and N. C. Fassett. 1943. Deer irruptions. Wisconsin Conservation Bulletin **8**:3–11.

Leopold, A., L. K. Sowls, and D. L. Spencer. 1947. A survey of over-populated deer ranges in the United States. Journal of Wildlife Management **11**:162–177.

Leopold, A. S., S. A. Cain, C. M. Cottam, I. N. Garielson, and T. L. Kimball. 1963. Wildlife management in the national parks. Proceedings of the 28th North American Wildlife Conference **28**:29–45.

Long, R. P., S. B. Horsley, and P. R. Lilja. 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. Canadian Journal of Forest Research **27**:1560–1573.

Lutz, H. J. 1930. Original forest composition in northwestern Pennsylvania as indicated by early land survey notes. Journal of Forestry **28**:1098–1103.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.

Marks, P. L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs **44**:73–88.

Marquis, D. A. 1973. The effect of environmental factors on advance regeneration of Allegheny hardwoods. Dissertation. Yale University, New Haven, Connecticut, USA.

Marquis, D. A. 1974. The impact of deer browsing on Allegheny hardwood regeneration. USDA Forest Service Research Paper **NE-308.** Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Marquis, D. A. 1975. The Allegheny hardwood forests of Pennsylvania. USDA Forest Service General Technical Report **NE-15.** Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Marquis, D. A. 1979. Shelterwood cutting in Allegheny hardwoods. Journal of Forestry **77**:140–144.

Marquis, D. A. 1981. Effect of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. USDA Forest Service Research Paper **NE-475.** Northeastern Forest Experiment Station, Broomall, Pennsylvania, USA.

Marquis, D. A. 1987. Silvicultural techniques for circumventing deer damage. Pages 125–136 *in* Proceedings of the Symposium: Deer, Forestry, and Agriculture: Interactions and Strategies for Management. Allegheny Society of American Foresters, Warren, Pennsylvania, USA.

Marquis, D. A. 1990. *Prunus serotina* Ehrh. Black cherry. Pages 594–604 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2. Hardwoods. USDA Forest Service Agricultural Handbook **654.** USDA Forest Service, Washington, D.C., USA.

Marquis, D. A., and R. Brenneman. 1981. The impact of deer on forest vegetation in Pennsylvania. USDA Forest Service General Technical Report **NE-65.** Northeastern Forest Experiment Station, Broomall, Pennsylvania, USA.

Marquis, D. A., R. L. Ernst, and S. L. Stout. 1992. Prescribing silvicultural treatments in hardwood stands of the Alleghenies (Revised). USDA Forest Service General Technical Report **NE-96.** Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Marquis, D. A., and T. J. Grisez. 1978. The effect of deer exclosures on the recovery of vegetation in failed clearcuts on the Allegheny Plateau. USDA Forest Service Research Note **NE-270.** Northeastern Forest Experiment Station, Broomall, Pennsylvania, USA.

McCabe, R. E., and T. R. McCabe. 1984. Of slings and arrows: an historical retrospection. Pages 19–72 *in* L. K. Hall, editor. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

McCabe, T. R., and R. E. McCabe. 1997. Recounting whitetails past. Pages 11–26 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

McCain, R. 1939. The development and use of game drives for determining whitetail deer populations on Allegheny National Forest. Transactions of the 4th North American Wildlife Conference **4**:221–230.

McCain, R. 1941. Removing surplus deer by hunting, Allegheny National Forest, Pennsylvania. Transactions of the 6th North American Wildlife Conference **6**:332–338.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litterfall of the boreal forest, Isle Royle, Michigan, USA. Ecology **73**: 2059–2075.

McNab, W. H., and P. E. Avers, compilers. 1994. Ecological subregions of the United States: section descriptions. USDA Forest Service Administrative Publication **WO-WSA-5.** USDA Forest Service, Washington, D.C., USA.

McShea, W. J., and J. H. Rappole. 1992. White-tailed deer as keystone species within forested habitats of Virginia. Virginia Journal of Science **43**:177–186.

McShea, W. J., and J. H. Rappole. 1997. Herbivores and the ecology of understory birds. Pages 298–309 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

McShea, W. J., and G. Schwede. 1993. Variable acorn crops:

responses of white-tailed deer and other mast consumers. Journal of Mammology 74:999–1006.

Meredith, M. P., and S. V. Stehman. 1991. Repeated measurements experiments in forestry: focus on analysis of response curves. Canadian Journal of Forest Research 21: 957–965.

Morellet, N., S. Champely, J.-M. Gaillard, P. Ballon, and Y. Boscardin. 2001. The browsing index: new tool uses browsing pressure to monitor deer populations. Wildlife Society Bulletin 29:1243–1252.

Ostfeld, R. S., C. G. Jones, and J. O. Wolff. 1996. Of mice and mast: ecological connections in eastern deciduous forests. BioScience 46:323–330.

Park, B. C. 1938. Deer weights and measurements on the Allegheny National Forest. Transactions of the Third North American Wildlife Conference 3:261–279.

Porter, W. F. 1994. Burgeoning ungulate populations in national parks: is intervention warranted? Pages 304–312 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier, New York, New York, USA.

Porter, W. F., M. C. Coffey, and J. Hadidian. 1994. In search of a litmus test: wildlife management on the U.S. national parks. Wildlife Society Bulletin 22:301–306.

Porter, W. F., and H. B. Underwood. 1999. Of elephants and blind men: deer management in the U.S. national parks. Ecological Applications 9:3–9.

Redding, J. 1995. History of deer population trends and forest cutting on the Allegheny National Forest. Pages 214–224 *in* K. W. Gottschalk and S. C. L. Fosbroke, editors. Proceedings of the 10th, Central Hardwood Forest Conference. USDA Forest Service General Technical Report NE-197. Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Richards, N. A., and C. E. Farnsworth. 1971. Effect of cutting level on regeneration of northern hardwoods protected from deer. Journal of Forestry 69:230–233.

Risenhoover, K. L., and S. A. Maass. 1987. The influence of moose on the composition and structure of Isle Royale forests. Canadian Journal of Forest Research 17:357–364.

Ristau, T. E., and S. B. Horsley. 1999. Pin cherry effects on Allegheny hardwood stand development. Canadian Journal of Forest Research 29:73–84.

Ross, B. A., J. R. Bray, and W. H. Marshall. 1970. Effects of long-term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. Ecology 51:1088–1093.

Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations, and communities: a review. American Midland Naturalist 146:1–26.

Seton, E. T. 1953. Whitetailed deer. Pages 229–307 *in* Lives of game animals. Volume 3, Part 1. C. T. Branford Company, Boston, Massachusetts, USA.

Severinghaus, C. W., and H. F. Maguire. 1955. Use of age composition data for determining sex ratios among adult deer. New York Fish and Game Journal 2:242–246.

Shafer, E. L., T. J. Grisez, and E. Sowa. 1961. Results of deer exclosure studies in northeastern Pennsylvania. Forest Research Notes Number 121. USDA Forest Service Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Shafer-Nolan, A. L. 1997. The science and politics of deer overabundance at Cuyahoga National Recreation Area, Ohio. Wildlife Society Bulletin 25:457–461.

Stromayer, K. A. K., and R. J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? Wildlife Society Bulletin 25:227–234.

Styer, J., W. C. Carson, and S. B. Horsley. 1997. *Prunus pennsylvanica* seed abundance following long-term deer browse. Bulletin of the Ecological Society of America, Supplement 78(4):318.

Tamm, C. O. 1974. Experiments to analyze the behavior of young spruce forests at different nutrient levels. Pages 266–272 *in* Proceedings of the First International Congress of Ecology, Structure, Functioning and Management of Ecosystems. Center for Agricultural Publication of Documents, Wageningen, The Netherlands.

Taylor, R. J. 1984. Predation. Chapman and Hall, New York, New York, USA.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management 53:524–532.

Tubbs, C. H., and D. R. Houston. 1990. *Fagus grandifolia* Ehrh. American beech. Pages 325–332 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2. Hardwoods. USDA Forest Service Agricultural Handbook 654. USDA Forest Service, Washington, D.C., USA.

Underwood, H. B., and W. F. Porter. 1997. Reconsidering paradigms of overpopulation in ungulates: white-tailed deer at Saratoga National Historical Park. Pages 185–200 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Walters, R. S., and H. W. Yawney. 1990. *Acer rubrum* L. Red maple. Pages 60–69 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2. Hardwoods. USDA Forest Service Agricultural Handbook 654. USDA Forest Service, Washington, D.C., USA.

Webb, W. L., R. T. King, and E. F. Patric. 1956. Effect of white-tailed deer on a northern hardwood forest. Journal of Forestry 54:391–398.

Wendel, G. W. 1990. *Prunus pensylvanica* L. f. Pin cherry. Pages 587–593 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2. Hardwoods. USDA Forest Service Agricultural Handbook 654. USDA Forest Service, Washington, D.C., USA.

Whitney, G. G. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock–white pine–northern hardwood stand. Ecology 65:403–408.

Wilkinson, L. 1997. SYSTAT 7. 0 for Windows. SPSS, Chicago, Illinois, USA.

Witmer, G. W., and D. S. deCalesta. 1992. The need and difficulty of bringing the Pennsylvania deer herd under control. Pages 130–137 *in* P. D. Curtis, M. J. Fargione, and J. E. Caslick, editors. Proceedings of the Fifth Eastern Wildlife Damage Control Conference, 6–9 October 1992. Cornell University, Ithaca, NewYork, USA.

Yanai, R. D., M. J. Twery, and S. L. Stout. 1998. Woody understory response to changes in overstory density: thinning in Allegheny hardwoods. Forest Ecology and Management 102:45–60.