

IMPACTS OF WHITE-TAILED DEER ON FOREST REGENERATION IN NORTHWESTERN PENNSYLVANIA

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Abstract: Browsing by white-tailed deer (*Odocoileus virginianus*) is a major cause of regeneration failure in Allegheny hardwood forests of northwestern Pennsylvania. I examined the impact of deer at 5 different densities (0, 10, 20, 40, and 80 deer /259 ha) on tree seedlings, woody shrubs, and herbaceous plants in large enclosures over 5 years. I examined 3 silvicultural treatments (clearcut, thinning, and uncut) at each density. After 5 years, tree seedlings in the clearcuts at the lowest deer densities were nearly twice as tall as those at the highest deer densities. Browsing at high deer densities also reduced the diversity of tree seedlings, resulting in nearly pure black cherry (*Prunus serotina*) regeneration. Fern cover increased with increasing deer densities and blackberry cover (*Rubus* spp.) decreased. I suggest deer populations should be maintained at ≤ 18 deer/259 ha to ensure tree regeneration and desired tree species composition.

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Dense white-tailed deer populations in forested regions can alter forest stand development and reduce wildlife habitat by reducing or eliminating young tree seedlings, shrubs, and herbaceous plants (Tierson et al. 1966, Jordan 1967, Marquis 1981a). Since 1930 in the Allegheny hardwood forests of northwestern and north-central Pennsylvania, deer densities have been high (Frontz 1930, Bramble and English 1948), but the role deer play in forest regeneration in Allegheny hardwood forests has been demonstrated only recently (Bennett 1957, Marquis 1981a, Marquis and Brenneman 1981).

Allegheny hardwood forests are essentially even-aged, resulting from widespread clearcutting that occurred from about 1890 to 1930 (Marquis 1975). Many stands are approaching maturity, but forest landowners hesitate to harvest them because they will not regenerate to desired species without a monetary investment. Guidelines based on surveys of overstory and understory conditions have been developed to help determine which silvicultural options (e.g., type of harvest cut and need for investments in fencing, herbiciding, and fertilizing) are necessary in these stands (Marquis et al. 1984). One of the major factors that enters in the decision process is density of deer populations. My objective was to determine the maximum deer population that will allow natural regeneration of Allegheny hardwood forests. Specifically, I was interested in differences in stocking, plant

species composition, or height growth of new stems as deer densities increased. I also looked for changes in ground cover by herbaceous plants, especially those species that interfere with the development of Allegheny hardwood regeneration (Horsley 1977, Horsley and Marquis 1983).

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STUDY AREAS

I located 4 study sites on the Allegheny Plateau in northwestern and north-central Pennsylvania at elevations ranging from 550 to 700 m. All were in 60-70-year-old Allegheny hardwood stands dominated by black cherry, red maple (*Acer rubrum*), and sugar maple (*A. saccharum*). Two sites (Fool's Creek and Deadman Corners) were located on the Allegheny National Forest, 1 on State Game Land 30, and 1 (Wildwood Tower) on Elk State Forest and land belonging to the National Fuel Gas Company (Fig. 1).

Sites were established in stands with similar

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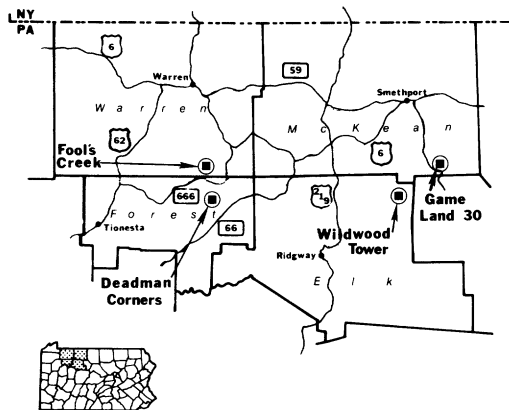


Fig. 1. Location of study areas in northwestern Pennsylvania.

overstories, but with understories of tree seedlings that represented different potentials to regenerate after clearcutting. The 4 sites represented the range in understory conditions on the Allegheny Plateau. The Deadman Corners site was well stocked with advance regeneration (Table 1) and was predicted to regenerate successfully after clearcutting even at fairly high deer populations (Marquis et al. 1984). The Fool's Creek site had less advance regeneration (Table 1) and an intermediate potential to regenerate after harvest cutting. The other 2 study sites had less advance regeneration, more interfering plants such as ferns, grasses, striped maple (*Acer pensylvanicum*), or American beech (*Fagus grandifolia*), and were not predicted to regenerate successfully after clearcutting, especially with high deer densities (Table 1).

METHODS

At each site, a 65-ha enclosure was constructed of 2.4-m woven wire fencing and subdivided into 4 subenclosures: 1 26 ha and 3 13 ha (Fig.

2). Two of these enclosures were completed in 1979 and 2 in 1980. Captive-raised yearling white-tailed females were used to stock the enclosures with 1 deer in the 26-ha pen and 1, 2, and 4 deer in each of the 13-ha pens to simulate 10, 20, 40, and 80 deer/259 ha, respectively. Five fenced plots (radius = 4.5 m) were randomly located in each cutting treatment in all 4 deer densities to represent the no-deer treatment. Each deer was equipped with a radio transmitter with a mortality switch to aid in relocation and verification of deer densities. Each subenclosure was treated with 3 different cutting treatments: 10% was clearcut, 30% was thinned (to 60% residual relative density), and the rest was left uncut. This cutting scheme was selected to simulate the relative amount of cutting that would take place every 10 years on an intensively managed forest.

Each enclosure was visited biweekly to maintain the fences and to verify the deer densities. When dead deer were found, bone marrows were checked to determine nutritional status (Cheatum 1949). When deer died or escaped, I replaced them to maintain densities. The only exception was when deer died in the winter; they were not replaced until after vegetation green-up in the spring. In the early years of this study, we found that deer placed in these areas in midwinter did not survive. Actual deer densities were calculated for each calendar year based on the number of deer-days for each enclosure (Table 2).

Systematically spaced 0.004-ha (radius = 1.1 m) vegetation sample plots were established throughout each subenclosure, with 25 in the clearcut, 15 in the thinning, and 20 in the uncut portion. Sampling intensity was greatest in the clearcuts because successful regeneration of Allegheny hardwood stands was the primary study

Table 1. Percent of 0.004-ha vegetation plots at each of 4 study sites meeting certain understory criteria prior to installation of enclosures, northwestern Pennsylvania, 1979.

Criteria	Deadman Corners	Fool's Creek	Wildwood Tower	Game Land 30
>25 black cherry seedlings ^a	94	55	28	16
>100 desirable seedlings ^a	80	29	5	7
>30% grass or fern cover ^b	12	8	17	54
>8 stems of beech or striped maple ^b	14	11	60	43

^a Advance regeneration is adequate if $\geq 70\%$ of the vegetation plots in a stand are stocked with >25 black cherry seedlings or >100 desirable seedlings (Marquis et al. 1984). In this region, desirable species of tree seedlings for timber production include black cherry, sugar maple, red maple, white ash, yellow-poplar, cucumbertree, and northern red oak.

^b These understory plants may interfere with natural regeneration of a stand if $\geq 70\%$ of the sample plots are stocked with these amounts of potentially interfering plants in a proposed clearcut or if $\geq 30\%$ of the plots are stocked with these plants in a proposed shelterwood cut (Marquis et al. 1984).

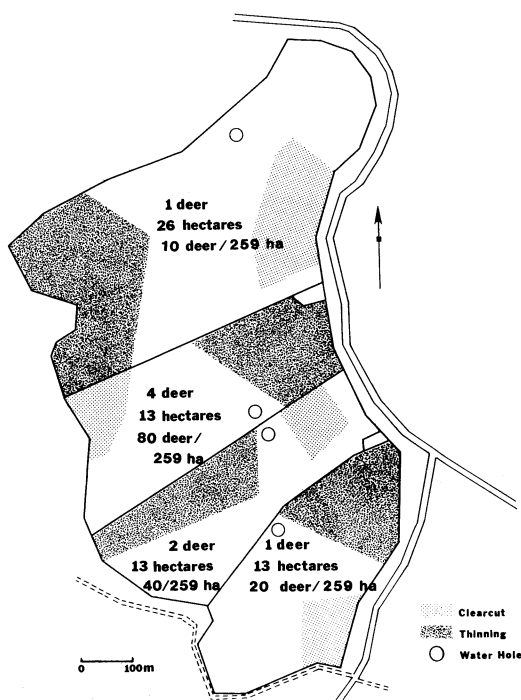


Fig. 2. Example of enclosure layout for deer density experiments, northwestern Pennsylvania, 1979–84.

objective. Vegetation was measured in late summer prior to deer stocking, and thereafter at years 3 and 5. Tree seedlings were tallied by species and height class, and the height of the tallest seedlings of black cherry, sugar maple, red maple, white ash (*Fraxinus americana*), other desirable (yellow-poplar [*Liriodendron tulipifera*], cucumbertree [*Magnolia acuminata*], and northern red oak [*Quercus rubra*]), and other commercial timber species (American beech, yellow birch [*Betula alleghaniensis*], sweet birch [*B. lenta*], eastern hemlock [*Tsuga canadensis*], bigtooth aspen [*Populus grandidentata*], and quaking aspen [*P. tremuloides*])

Table 2. Estimated deer density in each subenclosure at each study site in northwestern Pennsylvania during the first 5 growing seasons after introduction of deer (Deadman Corners and Fool's Creek = 1979–83; Wildwood Tower and Game Land 30 = 1980–84).

Target density/259 ha	Deadman Corners	Fool's Creek	Wildwood Tower	Game Land 30
10	9.4	9.2	10.1	10.2
20	21.2	18.8	20.2	19.9
40	40.6	36.6	36.2	40.3
80	72.5	70.0	66.7	68.5

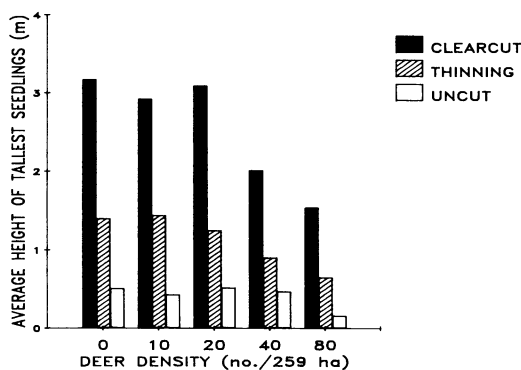


Fig. 3. Mean height (m) of dominant tree seedlings growing in clearcut, thinned, and uncut Allegheny hardwood stands in northwestern Pennsylvania and subjected to 5 different deer densities, 1979–84.

were recorded. The height of the tallest stem of commercial or noncommercial species was recorded for each plot (also referred to as dominant). Percent ground cover was estimated for each of the herbaceous plant species on each plot.

Effects of the various deer densities and cutting treatments were examined by analysis of variance with a split-plot design. Deer densities constituted the main plots and cutting treatments the subplots, with sites as blocks. Duncan's multiple-range test was used to separate significant means. Significance was established when $P \leq 0.05$.

RESULTS

Differences Due to Deer Density

After 5 years there were differences in the height growth, density, and species composition of regeneration. There were marked differences in the ground cover for certain herbaceous species. Differences in the vegetation of the various deer densities were greatest in the clearcuts where rapid seedling growth occurred and least in the uncut areas where seedling development was slow because of low light intensity.

The most obvious difference was in the mean height of the tallest woody stems on the sample plots (Fig. 3). These stems were stump sprouts or seedlings of any tree species, commercial or noncommercial. In the clearcuts with lowest deer density, the mean height of these tallest stems was about 3 m; approximately 5% of these stems were stump sprouts. In the clearcuts with highest deer density, the tallest stems were almost entirely of seedling origin and were significantly

Table 3. Mean density of tree seedlings ($\times 1,000/\text{ha}$) by browsing sensitivity, commercial value, and height class in clearcuts of different deer densities, northwestern Pennsylvania, 1979–84.

Sensitivity ^a —Value Ht class	Deer density/259 ha				
	0	10	20	40	80
Sensitive—Commercial^b					
Total	37.1	33.4	33.9	29.9	84.0 ^c
>0.9 m	4.0	4.9	4.0	2.5	0.1
>1.5 m	3.0A ^d	2.0AB	1.7AB	1.0BC	0C
Sensitive—Noncommercial^e					
Total	29.4A	20.3A	25.7A	2.7B	3.2B
>0.9 m	26.4A	19.0A	23.5A	2.0B	1.2B
>1.5 m	20.3A	14.6A	19.3A	1.5B	0.7B
Less sensitive—Commercial^f					
Total	70.4	63.0	52.6	82.8	88.2
>0.9 m	21.5	26.7	19.5	30.6	20.8
>1.5 m	8.9	14.3	8.6	13.3	8.9
Less sensitive—Noncommercial^g					
Total	3.0	6.2	3.2	4.9	2.2
>0.9 m	1.2	3.7	1.2	2.0	0.7
>1.5 m	0.7	2.2	0.5	1.0	0.1

^a Tree species were designated as sensitive or less sensitive to browsing based on studies of deer browsing in Allegheny hardwood stands (Marquis 1981a, 1983; Marquis and Brenneman 1981).

^b Sugar maple, red maple, white ash, yellow birch, and sweet birch.

^c Includes an abundance of tiny birch seedlings in 1 pen that germinated after good seed production.

^d Means within rows followed by different capital letters were different ($P < 0.05$).

^e Pin cherry.

^f Black cherry and American beech.

^g Striped maple.

shorter ($\bar{x} = 1.6$ m, $F = 14.32$, $P = 0.00016$). In the clearcuts with highest deer density, sprouts and seedlings were eliminated except where protected by slash. In the thinned areas, the tallest stems in the lowest deer densities were twice as tall as those in the highest deer densities ($F = 3.28$, $P = 0.049$) (Fig. 3).

Important differences also occurred in seedling numbers. Many seedlings became established in all treatments, and deer density had little effect on the total numbers established. But the number of seedlings that developed into the larger size classes was strongly affected by deer density, especially for those species more sensitive to browsing in the cutting treatments that permitted rapid seedling growth.

In the clearcuts (Table 3), the number of stems of noncommercial species sensitive to browsing, such as pin cherry, were significantly ($P = 0.008$) and dramatically reduced at the 2 highest deer densities. Likewise, the number of stems of commercial species sensitive to browsing, such as sugar maple, red maple, white ash, and birch, in the >1.5 m tall size class were significantly reduced at high deer densities ($P = 0.036$); a similar trend occurred in the >0.9 m size class for these species ($P = 0.076$).

In the thinnings, similar trends were evident, although the differences were not statistically significant (Table 4). Nevertheless, there were substantially fewer seedlings of browse-sensitive species in the larger size classes at very high deer densities. There were no significant differences in seedling numbers in the uncut portions of the enclosures (Table 5).

Species composition of tree regeneration was significantly different between the high and low deer densities. There were fewer tree seedling species in the high deer-density treatments than in any of the other densities. These differences are best demonstrated for the larger height classes, which varied among the different cutting treatments (Fig. 4). In the clearcuts, species diversity of seedlings >1.5 m tall was significantly reduced in the highest density pen ($P = 0.0017$). Only 2 species, usually black cherry and striped maple, escaped deer browsing to grow into this height class at these deer densities. Occasionally, stems of 1 of the more browse-sensitive species grew out of the reach of deer (>1.5 m) in the clearcuts, but such seedlings were surrounded by logging slash and thus were protected from browsing. In the thinnings, species diversities of seedlings >0.9 m at the 2 highest

Table 4. Mean density of tree seedlings ($\times 1,000/\text{ha}$) by browsing sensitivity, commercial value, and height class in thinnings of different deer densities, northwestern Pennsylvania, 1979–84.

Sensitivity ^a —Value Ht class	Deer density/259 ha				
	0	10	20	40	80
Sensitive—Commercial^b					
Total	51.1	40.8	33.1	86.4	29.7
>0.3 m	5.4	7.9	8.0	8.7	2.9
>0.9 m	1.5	1.3	2.0	1.0	0
Sensitive—Noncommercial^c					
Total	1.2	1.0	0.7	1.0	1.7
>0.3 m	0.5	0.2	0	0.2	0.2
>0.9 m	1.7	2.2	1.2	0.1	1.5
Less sensitive—Commercial^d					
Total	146.5	164.6	183.4	200.4	201.4
>0.3 m	19.8	16.3	11.6	18.3	44.7
>0.9 m	1.2	2.7	1.2	0.4	1.5
Less sensitive—Noncommercial^e					
Total	7.9	11.9	8.9	8.6	8.9
>0.3 m	6.4	8.9	7.2	5.9	6.4
>0.9 m	4.0	4.2	3.2	1.5	1.5

^a Tree species were designated as sensitive or less sensitive to browsing based on studies of deer browsing in Allegheny hardwood stands (Marquis 1981a, 1983; Marquis and Brenneman 1981).

^b Sugar maple, red maple, white ash, yellow birch, and sweet birch.

^c Pin cherry.

^d Black cherry and American beech.

^e Striped maple.

deer densities were significantly less than at the lowest deer density ($P = 0.0001$). In the uncut areas, the number of tree seedling species >0.3 m tall in the highest deer density was reduced to a single species ($P = 0.052$).

The increased dominance of black cherry in the new growth at the higher deer densities was most apparent in the clearcuts. In the clearcuts with highest deer density, 75% of the sample plots were dominated by black cherry whereas only 18% of the sample plots without deer were dominated by this species ($P = 0.0005$) (Fig. 5).

Ground cover of various herbaceous plants changed as deer density increased (Fig. 6). Blackberry cover in the highest deer-density clearcuts was significantly less than in any of the other deer densities ($P = 0.019$). A similar decrease in blackberries also was apparent in the high deer-density thinnings ($\bar{x} = 38\%$ cover in thinnings of the 10 deer/259 ha treatments vs. 3.5% cover in the 80 deer/259 ha treatments) ($P = 0.0014$). Hay-scented fern (*Dennstaedtia punctilobula*) and New York fern (*Thelypteris noveboracensis*) increased in the clearcuts with high deer density ($P = 0.0009$) (Fig. 6).

In addition to these common herbaceous

Table 5. Mean density of tree seedlings ($\times 1,000/\text{ha}$) by browsing sensitivity, commercial value, and height class in uncut areas of different deer densities, northwestern Pennsylvania, 1979–84.

Sensitivity ^a —Value Ht class	Deer density/259 ha				
	0	10	20	40	80
Sensitive—Commercial^b					
Total	34.1	22.6	39.3	25.4	10.4
>0.3 m	0.8	0.2	1.2	1.5	0
>0.9 m	0	0.1	0	0	0
Sensitive—Noncommercial^c					
Total	0.2	0.1	0.2	0.2	0
>0.3 m	0	0	0	0	0
>0.9 m	0	0	0	0	0
Less sensitive—Commercial^d					
Total	135.7	97.1	104.0	74.1	69.7
>0.3 m	8.9	2.5	3.2	2.2	0.6
>0.9 m	0.2	0.1	0	0.2	0
Less sensitive—Noncommercial^e					
Total	10.9	10.4	14.1	10.1	3.7
>0.3 m	5.9	3.7	5.2	4.7	0.5
>0.9 m	0.7	0.5	0.5	0.5	0

^a Tree species were designated as sensitive or less sensitive to browsing based on studies of deer browsing in Allegheny hardwood stands (Marquis 1981a, 1983; Marquis and Brenneman 1981).

^b Sugar maple, red maple, white ash, yellow birch, and sweet birch.

^c Pin cherry.

^d Black cherry and American beech.

^e Striped maple.

species, 45 other herbaceous plants were found on the sample plots. The mean percent cover by each of these species was generally small (<1% for most species) and therefore significant differences in cover among the different deer densities were not detectable.

Winter Mortality of Deer

From 1980 to 1985, 57% of the deer in the 80 deer/259 ha treatments died during the winter from starvation and exposure; 33% of the deer in the 40 deer/259 ha treatments died during these winters. Only 1 deer in the 20 deer/259 ha treatment died of starvation and none died in the lowest deer density. Most of these deaths occurred in February and March when the deer had used up their winter fat reserves and new woody growth was not available.

These mortality figures are heavily influenced by the study design, which artificially forced the deer to stay on the plateau top throughout the winter. Thus, study deer were exposed to far more extreme conditions than free-ranging deer that seek out sheltered lower slopes and conifer stands during harsh winter weather.

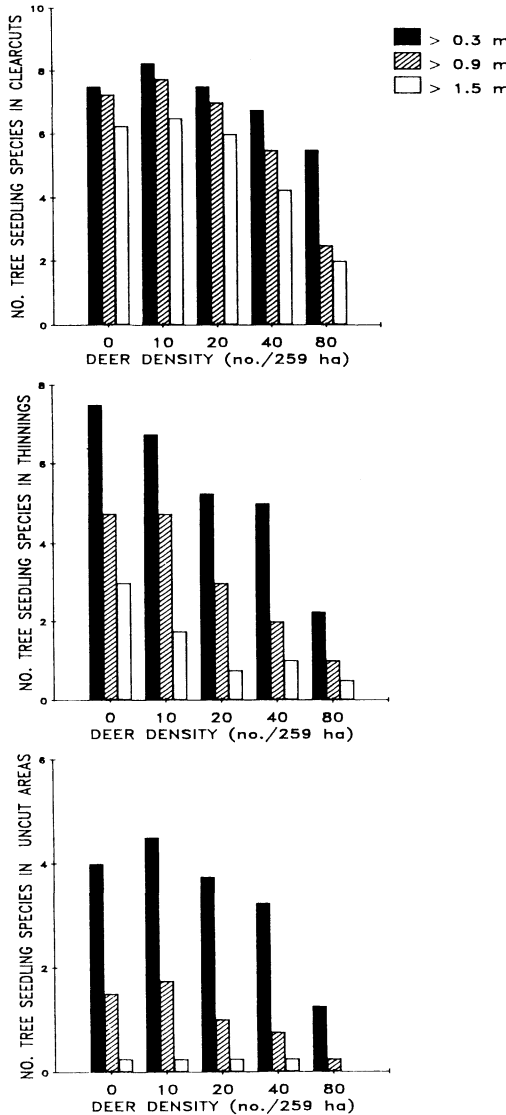


Fig. 4. Species diversity of 3 size classes of tree seedlings growing in clearcut, thinned, and uncut Allegheny hardwood stands in northwestern Pennsylvania and subjected to 5 different deer densities, 1979–84.

Thus, I do not consider these mortality rates to be representative of the mortality that might occur among free-ranging deer at the same densities.

DISCUSSION

The results of this study demonstrate that high densities of white-tailed deer (40 and 80 deer/259 ha treatments) have a detrimental impact on species composition and development of regeneration in thinned and clearcut stands. In

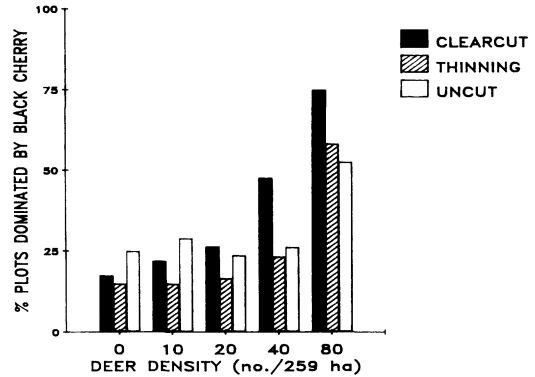


Fig. 5. Black cherry dominance among tree seedlings growing in clearcut, thinned, and uncut Allegheny hardwood stands in northwestern Pennsylvania and subjected to 5 different deer densities, 1979–84.

uncut stands, the impact of deer browsing was evident only in the 80 deer/259 ha treatment. Loss of seedling height growth at these high deer densities confirms findings reported from numerous exclosure studies (Curtis and Rushmore 1958; Graham 1958; Farnsworth and Barrett 1966; Tierson et al. 1966; Jordan 1967; Marquis 1974, 1981a; Marquis and Grisez 1978). Marquis (1981a) estimated that delays in establishment of new stands and reduced stocking levels in the heavily browsed Allegheny hardwood stands of northwestern Pennsylvania cost forest landowners about \$2,656/ha or \$33/ha/year, a reduction in yield of about 50%.

To make it easier to see the impact of deer in changing plant species composition, I grouped species into 2 groups: those sensitive to browsing, and those that were not. Those species most sensitive to browsing in northwestern Pennsylvania (e.g., pin cherry, sugar maple, white ash, yellow birch, and yellow-poplar) (Marquis 1983) disappeared as the deer density increased, whereas less sensitive species such as black cherry, striped maple, and American beech survived. In some Allegheny hardwood stands, dense striped maple and beech understories have prevented the establishment of more desirable tree seedling species (Horsley 1983). Black cherry ranks somewhere in the middle of the range of tree species' sensitivity to browsing (Marquis 1983), but because black cherry grows rapidly in full sunlight, many of the seedlings were able to survive under intense browsing pressure.

The nearly pure stands of black cherry that resulted from intense deer browsing are not altogether desirable even though cherry is a prime

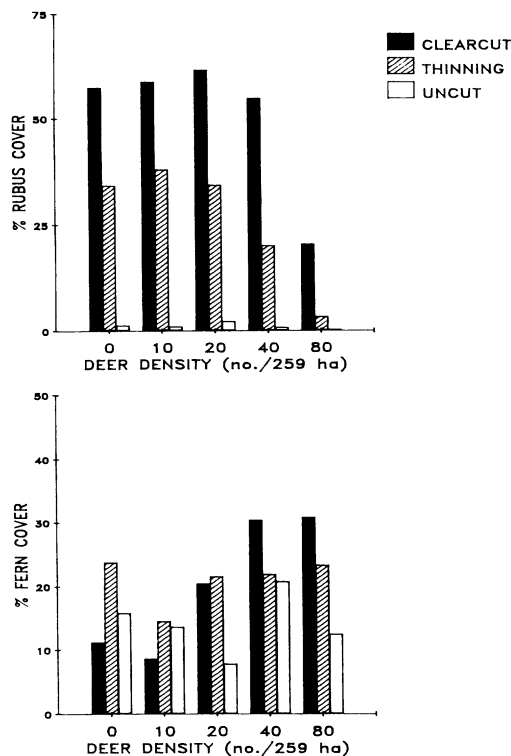


Fig. 6. Herbaceous ground cover in clearcut, thinned, and uncut Allegheny hardwood stands in northwestern Pennsylvania. These stands were subjected to 5 different deer densities, 1979–84.

timber species. A reduction in tree species diversity would severely affect local industries that use species other than black cherry (e.g., white ash for baseball bats and tool handles, red and sugar maple for furniture). Also, if vast areas of pure black cherry stands were to develop throughout this region, the potential threat from an outbreak of an insect or disease epidemic would be great. There is some concern that insects like the cherry scallop-shell moth (*Hydria prunivorata*), which periodically defoliates black cherry trees, could become a major cause of mortality.

The shift to near-monocultures of black cherry in areas of high deer populations also would affect wildlife habitat. A decrease in the diversity of overstory trees would result in a decrease in the diversity of wildlife foods available (fruits, seeds, browse, and insects). White-tailed deer have trouble surviving the rigors of winter when fed a diet of a single species (Dahlberg and Guettinger 1956:76, Banasiak 1961), so a cherry monoculture could eventually lead to poor deer

nutrition even in areas of cherry seedling abundance. Black cherry, as opposed to sugar maple, does not readily decay or form natural cavities (Rexrode and Auchmoody 1982), and is rarely used by primary and secondary cavity-nesters (Carey 1983).

The changes in herbaceous cover also affect the regeneration potentials of these stands. Low deer-density areas generally had little fern cover in the clearcuts and an abundance of blackberries in clearcuts and thinnings, whereas the high deer-density areas had scattered patches of dense fern cover and few blackberries. Horsley and Marquis (1983) demonstrated that seedlings grown in the presence of ferns had significantly lower survival and growth rates than seedlings grown without ferns. Previous studies (Marquis and Grisez 1978, Horsley and Marquis 1983) have also shown that blackberries interfere with ferns and can lead to a decline in their coverage. Deer not only have a direct effect on forest regeneration by browsing on seedlings, but also can indirectly affect the development of regeneration by changing the composition of the herbaceous vegetation, which, in turn, affects the growth and survival of seedlings.

MANAGEMENT IMPLICATIONS

Deer density has a major impact on tree regeneration and herbaceous plant cover in Allegheny hardwood forests. Deer densities of 40 and 80 deer/259 ha will result in a delay in tree regeneration and a reduction in tree species diversity. The maximum year-round deer density permitting desirable tree regeneration in this forested region of Pennsylvania is around 30 deer/259 ha (range = 20–40 deer/259 ha).

However, 30 deer/259 ha cannot be assumed as a carrying capacity in establishing deer management goals in this part of Pennsylvania for several reasons. First, population estimates used by the Pennsylvania Game Commission in their deer management efforts are overwinter values, whereas those used in this study were year-round values. Secondly, the Commission's population estimates are based on county-wide estimates from change-in-ratio procedures (Shope 1978), and are not directly comparable to the actual deer numbers of this experiment. Finally, the Commission estimates of carrying capacity are based on surveys of actual forest conditions in each county, whereas this study provides estimates for a forest managed at theoretically ideal cutting levels.

Assuming that 30 deer/259 ha under conditions of this experiment represents the maximum population that will produce fully satisfactory tree regeneration, I have applied a series of adjustments to this value to yield a deer population goal that would be comparable to current deer management figures for this region of Pennsylvania and consistent with the typical forest management practices in the region, rather than the ideal ones used in this experiment.

Because mean year-round deer populations are always higher than their corresponding overwinter populations, I adjusted the 30 deer/259 ha figure, using Pennsylvania Game Commission data for the 4-county area of the study that shows summer (post-breeding) populations range from 1.2 to $1.6 \times (\bar{x} = 1.4)$ the overwinter densities (W. K. Shope, Pa. Game Comm., unpubl. data). Because each season represents approximately half the year, year-round densities can be expected to be $1.2 \times$ higher than overwinter densities. Thus, 30 deer/259 ha year-round is equivalent to an overwinter density of 25 deer/259 ha.

The next adjustment was intended to bring the study estimate of overwinter carrying capacity (25 deer/259 ha) into line with the reduced amount of deer food available under usual management conditions, where there is only about half as much clearcutting and thinning as in the experiment. Data developed by Marquis (1981b) were used to calculate deer food production in Allegheny hardwood forests that had 10% clearcutting and 30% thinning (as in the study enclosures), or 5% clearcutting and 15% thinning every 10 years (a more realistic pattern outside). These calculations indicated the present level of cutting outside would produce 21% less browse than the cutting level used in this study. Thus the carrying capacity estimate was further reduced by 21% to 20 deer/259 ha.

The final adjustment for differences between the change-in-ratio estimates of deer density and actual deer numbers in the study was based upon a pellet-group survey conducted in the spring of 1986. Pellet groups were counted along 8 km of line-transects in a watershed immediately adjacent to 1 study enclosure to yield a deer-density estimate for the period from mid-October to April. These line-transect estimates were calibrated by conducting similar counts inside the enclosure in areas where the overwinter deer densities were known. We found that the county-wide change-in-ratio estimate

was about 22% lower than the estimate from the pellet-group procedure. So, the overwinter deer-density value was reduced by 22% (from 20 deer/259 ha to 15 deer/259 ha) to make study density values comparable to the Pennsylvania Game Commission figures.

This estimate is slightly lower than the 18 deer/259 ha goal for this part of Pennsylvania ($\bar{x}$ goals for 4 counties, range = 17–19). Obviously, my adjustments and assumptions are approximations only, and I would not consider this evidence that the current goals for carrying capacity need to be lowered. Until more precise data are available, the Pennsylvania Game Commission goal of 18 deer/259 ha seems reasonable for the region. I think that lowering deer populations to that level and maintaining them there for several years would allow the forests to develop an understory with a variety of seedlings, shrubs, and herbaceous plants that, in turn, would allow forest regeneration and assure habitat for forest wildlife species, including white-tailed deer.

LITERATURE CITED

- BANASIAK, C. F. 1961. Deer in Maine. Me. Dep. of Inland Fish. and Game, Game Div. Bull. 6. 159pp.
- BENNETT, A. L. 1957. Deer mismanagement—a threat to sustained yield forestry in Pennsylvania. Proc. Soc. Am. For. 1957:101–104.
- BRAMBLE, W. C., AND P. F. ENGLISH. 1948. The forest grazing problem created by deer in eastern forests. Proc. Soc. Am. For. 1948:257–263.
- CAREY, A. B. 1983. Cavities in trees in hardwood forests. Pages 167–184 in J. W. Davis, G. A. Goodwin, and R. A. Ockenfels, tech. coords. Snag habitat management: proc. of the symp. U.S. For. Serv. Gen. Tech. Rep. RM-99.
- CHEATUM, E. L. 1949. Bone marrow as an index of malnutrition in deer. N.Y. State Conserv. 3: 19–22.
- CURTIS, R. O., AND F. M. RUSHMORE. 1958. Some effects of stand density and deer browsing on reproduction in an Adirondack hardwood stand. J. For. 56:116–121.
- DAHLBERG, D. L., AND R. C. GUETTINGER. 1956. The white-tailed deer in Wisconsin. Wisc. Conserv. Dep. Tech. Wildl. Bull. 14. 282pp.
- FARNSWORTH, C. E., AND J. W. BARRETT. 1966. Responses to silvicultural treatment: northern hardwoods type five years after logging. Proc. Sixth World For. Congr.:2338–2343.
- FRONTZ, L. 1930. Deer damage to forest trees in Pennsylvania. Pa. Dep. For. and Waters Res. Circ. 3. 10pp.
- GRAHAM, S. A. 1958. Results of deer enclosure experiments in the Ottawa National Forest. Trans. North Am. Wildl. Conf. 23:478–490.
- HORSLEY, S. B. 1977. Allelopathic interference among plants. II. Physiological modes of action.

- Pages 93–136 in H. E. Wilcox and A. Hamer, eds. Proc. fourth North American forest biology workshop. Syracuse Univ. Press, Syracuse, N.Y.
- . 1983. Interference with desirable northern hardwood regeneration by herbaceous and woody plants. Pages 81–93 in J. Finley, R. S. Cochran, and J. R. Grace, eds. Proc.: regenerating hardwood stands. Pennsylvania State Univ., University Park.
- , AND D. A. MARQUIS. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. *Can. J. For. Res.* 13:61–69.
- JORDAN, J. S. 1967. Deer browsing in northern hardwoods after clearcutting: effect on height, density, and stocking of regeneration of commercial species. U.S. For. Serv. Res. Pap. NE-57. 15pp.
- MARQUIS, D. A. 1974. The impact of deer browsing on Allegheny hardwood regeneration. U.S. For. Serv. Res. Pap. NE-308. 8pp.
- . 1975. The Allegheny hardwood forests of Pennsylvania. U.S. For. Serv. Gen. Tech. Rep. NE-15. 32pp.
- . 1981a. Effect of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. U.S. For. Serv. Res. Pap. NE-475. 10pp.
- . 1981b. Management of Allegheny hardwoods for timber and wildlife. Proc. Int. Union For. Res. Organ. World Congr. 17:369–380.
- . 1983. Regeneration of black cherry in the Alleghenies. Pages 106–119 in The hardwood resource and its utilization: where are we going? Proc. hardwood symp. of the hardwood research council. U.S. For. Serv., South. For. Exp. Stn., New Orleans, La.
- , AND R. BRENNEMAN. 1981. The impact of deer on forest vegetation in Pennsylvania. U.S. For. Serv. Gen. Tech. Rep. NE-65. 7pp.
- , R. L. ERNST, AND S. L. STOUT. 1984. Prescribing silvicultural treatments in hardwood stands of the Alleghenies. U.S. For. Serv. Gen. Tech. Rep. NE-96. 90pp.
- , AND T. J. GRISEZ. 1978. The effect of deer exclosures on the recovery of vegetation in failed clearcuts on the Allegheny Plateau. U.S. For. Serv. Res. Note NE-270. 5pp.
- REXRODE, C. O., AND L. R. AUCHMOODY. 1982. 46 years after storm glaze-damaged black cherry. *Pa. For.* 72:8–9.
- SHOPE, W. K. 1978. Estimating deer population using CIR procedures and age structure data and harvest management decision making from CIR estimates. *Trans. Northeast. Deer Stud. Group Meet.* 14:28–35.
- TIERSON, W. C., E. F. PATRIC, AND D. F. BEHREND. 1966. Influence of white-tailed deer on a northern hardwood forest. *J. For.* 64:801–805.

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