Part II. Deer Impact and Forest Recovery

Chapter 5. The Role of White-Tailed Deer in Altering Forest Ecosystems in Pennsylvania

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Chapter 5. The Role of White-tailed Deer in Altering Forest Structure in Pennsylvania

To predict the effects of management actions on maintaining or restoring ecosystem structures and processes in Pennsylvania, it is necessary to have a hypothesis (or hypotheses) of the impact of white-tailed deer on forest structure. Adaptive resource management does not require theories to be perfect — they can be improved over time — but they must be quantitative and they must include an estimate of the uncertainty (e.g., rate of error, standard deviation) attached to any prediction. In this chapter, the scientific literature on the impacts of white-tailed deer is reviewed to provide a basis for theoretical predictions to be used in managing deer from an ecosystem perspective.

There is a near unanimous consensus among scientists that the impact of recent high deer populations on forest structure in Pennsylvania is deleterious. Nevertheless, the consensus is not 100%, so the full range of scientific views is discussed in this chapter and in Chapter 6.

Forest plants

Population densities of white-tailed deer have been high enough to cause negative direct and indirect impacts on forest vegetation in many areas of the eastern United States since at least the mid-twentieth century[1] and in some areas, including Pennsylvania, since the 1920s.[2] Effects on woody vegetation have been studied most comprehensively. Exclosure studies comparing zero deer density inside a fence with ambient deer density outside a fence have been the most common method of investigation.[3] Even more useful are enclosure studies where a fixed number of deer are placed inside fences. For example, a 10-year deer enclosure study in northwestern Pennsylvania using a gradient of known deer densities have allowed investigators to study impacts on both vegetation and birds as a function of deer density.[4]

Selective browsing is a well-known characteristic of deer and other forest ungulates (hoofed mammals with an even number of toes, e.g., moose, elk). Food preferences depend partly on what is available to eat. Food variety and availability in turn depend on current local deer density, recent trends in local deer density, availability of alternative forage, human land-use patterns, forest disturbance history, snow cover, and various other factors. Thus, preferred species frequently differ between regions in the same forest type,[5] within regions over long periods of time,[6] at different times during a growing season,[7] and at different deer densities in the same forest type.[8] Early browse preference studies were conducted to help managers foster forests that were better habitat for white-tailed deer, but, as deer numbers skyrocketed, the research focus shifted to encouraging regeneration of tree species of commercial value to the wood products industry (Table 4). Important timber trees represent less than 20% of the native tree species and about 1% of the total native vascular plant diversity in Pennsylvania's forests; however, it is clear that the majority of the state's other native plant species are just as vulnerable to severe depletion or eradication where deer numbers are high.

Over time, selective browsing by densely populated deer results in reduced species richness and altered species composition, with dominance by the few non-preferred and browsing-resilient species.[9] Once unpalatable and resilient species become abundant, they can interfere with the reestablishment of preferred and less browsing-resilient species. Competitive exclusion of some plant species by others is an indirect effect of browsing.[10] For example, non-preferred hay-scented fern and New York fern and browsing-resilient American beech and striped maple interfere strongly with the establishment of most other species.[11] Moreover, as species become scarce, their failure to replenish the seed bank (seeds lying dormant in the soil) affects vegetation dynamics long into the future,[12] another indirect effect of high deer density.

Overbrowsing by deer has eliminated the tree seedling, sapling, and shrub layer in large areas of forest in Pennsylvania. The result is a greatly simplified vertical structure. The herbaceous layer has also been stripped of much of the species diversity that was once there. By the time the density of hay-scented fern exceeds 50 stems per square meter (4.6 stems per square foot), species richness of other forest floor species is significantly reduced.[13]

A 1995 resurvey of a heavily browsed old-growth stand in northwestern Pennsylvania that had been surveyed in 1929 showed a loss of 59 to 80% of the shrub and herbaceous species.[14] A second resurvey of the site,[15] in which the original 160 one-meter-square survey plots from 1929[16] were relocated and remeasured, revealed fewer losses. As in the original survey, it also included a random search of the rest of the tract outside of the original plots, which turned up all but seven of the species tallied in the 1929 survey plots; however, most had severely dwindled in abundance. For example, hobblebush, which was present on 50% of the plots in 1929, was absent from all plots in 2000; it was found only in the wider search of the entire stand and then as small suppressed fragments. In the same timeframe, rhizomatous ferns (hay-scented and New York ferns) increased in abundance in the plots from 3 to 21% on average. Nevertheless, the presence of even small remnants of browsing-sensitive species holds out hope for restoration following future reductions in deer densities.

Native shrubs and understory trees found in Pennsylvania forests that are preferentially grazed by deer include American yew, fly-honeysuckle, hobblebush, pinxter-flower, and mountain maple.[17] Dwarf sand cherry, a plant that is classified as rare in Pennsylvania[18] has declined throughout the Great Lakes ecoregion coincident with heavy browsing by deer.[19] Dwarf sand cherry and bearberry, another low-growing shrub, disappeared from Presque Isle in northwestern Pennsylvania during the period when deer densities increased to the point where vegetation was overbrowsed.[20]

Table 4. The 116 native tree species of Pennsylvania (exclusive of subspecies, varieties, and hybrids)[21] ranked, where known, according to relative browsing preference by deer.[22] The ranking is compiled from multiple, not strictly comparable, sources and is somewhat subjective. However, it can serve as a rough guide to the relative vulnerability among the tree species known to be present at a particular site. The table in its present state is meant to be illustrative; it should be refined (e.g., split into regional tables) based on input from a range of experts. The list includes 13 species that can have either a tree or shrub growth form. An asterisk (*) after the common name indicates species of "medium" to "high" importance to the wood products industry that occur in significant numbers in harvested stands in Pennsylvania.[23] Where cells are left blank under browsing preference, no information was found.

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Abies balsamea	balsam fir		
Acer negundo	boxelder	not preferred	not preferred
Acer nigrum	black maple	low/moderate	high
Acer pensylvanicum	striped maple	low	low
Acer rubrum	red maple*	low/moderate	high
Acer saccharinum	silver maple	low/moderate	moderate
Acer saccharum	sugar maple*	low/moderate	moderate
Aesculus flava	yellow buckeye	(unknown, but toxic to cattle)	(unknown, but toxic to cattle)
Aesculus glabra	Ohio buckeye	(unknown, but toxic to cattle)	(unknown, but toxic to cattle)
Amelanchier arborea	downy serviceberry	(is browsed)	(is browsed)
Amelanchier laevis	Allegheny serviceberry	(is browsed)	(is browsed)
Aralia spinosa	devils-walkingstick	not preferred	not preferred
Asimina triloba	pawpaw	not preferred	not preferred
Betula alleghaniensis	yellow birch*	low/moderate	high (late autumn)
Betula lenta	sweet birch*	low/moderate	high (late fall)
Betula nigra	river birch	low	moderate

(Table continued on next page.)

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Betula papyrifera	paper birch	low/moderate	high (late fall)
Betula populifolia	gray birch	low/moderate	moderate
Carpinus caroliniana	American hornbeam		
Carya cordiformis	bitternut hickory*	low	low
Carya glabra	pignut hickory	low	low
Carya laciniosa	shellbark hickory	low	low
Carya ovalis	sweet pignut hickory (red hickory)	low	low
Carya ovata	shagbark hickory*	low	low
Carya tomentosa	mockernut hickory*	low	low
Castanea dentata	American chestnut		
Castanea pumila	Allegheny chinkapin		
Celtis occidentalis	hackberry	low	low
Celtis tenuifolia	Georgia hackberry (dwarf hackberry)	low	low
Cercis canadensis	eastern redbud		
Chamaecyparis thyoides	Atlantic white-cedar	low	moderate
Chionanthus virginicus	fringetree	low	low
Cornus alternifolia	alternate-leaf dogwood	moderate	high
Cornus florida	flowering dogwood	moderate	high
Crataegus brainerdii	Brainerd hawthorn	low	high
Crataegus calpodendron	pear hawthorn	low	high
Crataegus coccinea	scarlet hawthorn	low	high
Crataegus crus-galli	cockspur hawthorn	low	high

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Crataegus dilatata	broadleaf hawthorn	low	high
Crataegus flabellata	fanleaf hawthorn	low	high
Crataegus intricata	Biltmore hawthorn	low	high
Crataegus mollis	downy hawthorn	low	high
Crataegus pruinosa	frosted hawthorn	low	high
Crataegus punctata	dotted hawthorn	low	high
Crataegus rotundifolia	fireberry hawthorn	low	high
Crataegus succulenta	fleshy hawthorn	low	high
Diospyros virginiana	common persimmon		
Fagus grandifolia	American beech	low	high
Fraxinus americana	white ash*	low/moderate	high
Fraxinus nigra	black ash	low/moderate	high
Fraxinus pennsylvanica	green ash	low/moderate	high
Fraxinus profunda	pumpkin ash	not preferred	not preferred
Gleditsia triacanthos	honeylocust	(is browsed)	(is browsed)
Gymnocladus dioicus	Kentucky coffeetree		
Ilex opaca	American holly	low	low
Juglans cinerea	butternut		
Juglans nigra	black walnut	(is browsed)	(is browsed)
Juniperus virginiana	eastern redcedar	moderate	moderate
Larix laricina	tamarack		
Liquidambar styraciflua	sweetgum	low	low
Liriodendron tulipifera	yellow-poplar (tuliptree)*	high	high

(Table continued on next page.)

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Magnolia acuminata	cucumbertree	low	moderate
Magnolia tripetala	umbrella magnolia	low	low
Magnolia virginiana	sweetbay		
Malus coronaria	sweet crab apple		
Morus rubra	red mulberry		
Nyssa sylvatica	blackgum (black tupelo)*	high	high
Ostrya virginiana	eastern hophornbeam	low	low
Oxydendrum arboreum	sourwood		
Picea mariana	black spruce	not preferred	low
Picea rubens	red spruce	not preferred	low
Pinus echinata	shortleaf pine		
Pinus pungens	Table-Mountain pine		
Pinus resinosa	red pine		
Pinus rigida	pitch pine		
Pinus strobus	eastern white pine*	low	moderate
Pinus virginiana	Virginia pine		
Platanus occidentalis	American sycamore	(is browsed)	(is browsed)
Populus balsamifera	balsam poplar		
Populus deltoides	eastern cottonwood		
Populus grandidentata	bigtooth aspen	(is browsed)	low
Populus tremuloides	quaking aspen	(is browsed)	low
Prunus alleghaniensis	Allegheny plum		
Prunus americana	American plum		

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Prunus angustifolia	Chickasaw plum		
Prunus pensylvanica	pin cherry	high	high
Prunus serotina	black cherry*	low	low
Prunus virginiana	common chokecherry		
Quercus alba	white oak*	moderate	high
Quercus bicolor	swamp white oak	moderate	high
Quercus coccinea	scarlet oak*	moderate	high
Quercus falcata	southern red oak	moderate	high
Quercus imbricaria	shingle oak	moderate	high
Quercus macrocarpa	bur oak	moderate	high
Quercus marilandica	blackjack oak	moderate	high
Quercus montana	chestnut oak*	moderate	high
Quercus muhlenbergii	chinkapin oak (yellow oak)	moderate	high
Quercus palustris	pin oak	moderate	high
Quercus phellos	willow oak	moderate	high
Quercus rubra	northern red oak*	moderate	high
Quercus shumardii	Shumard oak	moderate	high
Quercus stellata	post oak	moderate	high
Quercus velutina	black oak*	moderate	high
Robinia pseudoacacia	black locust	low	low
Salix amygdaloides	peachleaf willow		
Salix caroliniana	coastal plain willow		
Salix nigra	black willow	low	moderate
Sassafras albidum	sassafras	moderate	high
Sorbus americana	American mountain-ash		

(Table continued on next page.)

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Sorbus decora	showy mountain-ash		
Tilia americana	American basswood*	(is browsed)	(is browsed)
Toxicodendron vernix	poison-sumac		
Tsuga canadensis	eastern hemlock	low	high
Ulmus americana	American elm	(is browsed)	(is browsed)
Ulmus rubra	slippery elm	(is browsed)	(is browsed)
Viburnum prunifolium	blackhaw	moderate	high

Although primarily thought of as shrub- and small tree-browsers, deer also feed extensively on most herbaceous plants and even fungi. A combination of grasses, sedges, wildflowers, and mushrooms comprised 87% of the summer diet of white-tailed deer in northern Wisconsin.[24] Lilies alone accounted for 12% of the diet by volume in early summer. In late summer asters made up 10% of the diet of deer. Grasses and wild strawberry were also among the most important foods. A study in Missouri revealed that 98 species of herbaceous flowering plants other than grasses, sedges, and rushes accounted for 44.7% of deer food in spring and summer[25] and another in Maine showed that the forest wildflowers bluebead lily and Canada mayflower (also native in Pennsylvania) constituted 50% by weight of all plants eaten by deer during late spring.[26] Overall, herbaceous flowering plants other than grasses, sedges, and rushes made up nearly three-fourth of the diet at that time of the year. Sedges and ferns were also consumed, especially during the summer, although an investigator working in Pennsylvania found that hay-scented fern was not eaten at any time of year.[27]

Other Pennsylvania-native forest herbs that deer graze on preferentially include large white trillium,[28] bluebead lily,[29] Canada mayflower,[30] turtlehead,[31] rose mandarin,[32] and numerous lilies and orchids.[33] Goldenclub, an emergent aquatic plant of shallow water around the margins of lakes in northeastern Pennsylvania, has been grazed to the point where an intact leaf is hard to find by mid-summer at some sites.[34] Wood nettle is browsed so consistently that it has been suggested as an indicator of browsing intensity.[35] Defoliation caused by repeated browsing has been shown to lead to reduction or cessation of sexual reproductive effort or eventual mortality in many plants native to Pennsylvania, including cranefly orchid,[36] turk's-cap lily,[37] glade spurge,[38] jack-in-the-pulpit,[39] Canada mayflower,[40] American yew,[41] Solomon's-plume,[42] and bellwort.[43]

Plants on Pennsylvania's endangered and threatened list that have been negatively impacted by deer browsing include glade spurge, yellow fringed-orchid, showy lady's-slipper, leafy white orchid, and white monk's-hood.[44] Golden puccoon, a state-endangered plant that also grows at Presque Isle, was threatened with extirpation in the state by severe browsing of 51 to 66% of the flowering stems per year and up to 90% reduction in seed production.[45] A deer control program at Presque Isle State Park has since reduced the browsing pressure, allowing golden puccoon to persist.

Because they never outgrow the reach of deer, forest floor wildflowers, other herbaceous species besides the unpalatable ferns, and many shrubs are continually vulnerable to deer impact. Whether a plant species is eaten or avoided by herbivores like deer can be crucial to its success or failure.

Browsing can change the balance between native and introduced species. Those few of the many plant species introduced from other parts of the world that become invasive do so largely because they are unpalatable to local herbivores or resistant to local pathogens.[46] A plant species' population size is regulated in its native range by predation and parasitism by insects and microbes that specialize on particular host plants. The enemy-release principle[47] is based on the observation that a plant introduced into a new region leaves most or all of its specialist herbivores and pathogens behind. For example, in a recent survey of 473 plant species naturalized to the United States from Europe, introduced species were infected by 84% fewer fungal pathogens and 24% fewer viruses in their naturalized ranges than in their native ranges.[48] In some cases a plant population's release enables it to become invasive. In the same study, introduced plants with the fewest pathogen species were found most likely to be listed as serious noxious weeds. Similar results were obtained in another study of the effects of root pathogens and mycorrhizal fungi on five highly invasive plants versus five rare and endangered plants in Canadian old fields and meadows.[49]

In places where deer are densely populated but the density is not so high that the forest herbaceous layer is eliminated, there is a strong potential for selectivity by deer to exacerbate the invasiveness of unpalatable introduced species. Several studies suggest that deer avoid garlic mustard, an introduced herbaceous species invading forests across the eastern United States, in favor of more palatable native species.[50] Japanese barberry, Eurasian species of honeysuckle, and ailanthus are examples of introduced, invasive shrubs and trees that are known to be unpalatable to deer.[51]

It has been shown that deer alter their foraging behavior to correspond with resource availability, nutritional needs, and energy requirements[52] (and large predator distribution and behavior, where species that prey on deer have not been eradicated). Numerous studies of deer food preferences suggest that deer avoid most non-native plants as long as a choice of foods is available.[53] However, the selectivity observed when other foods are available decreases when resources become scarce. Japanese honeysuckle, a non-native invasive plant from Eurasia, was found to be the fourth-most-frequent plant in a study of the contents of deer rumens in Ohio[54] and among the 10 most-frequent foods found in a survey of deer rumens in Indiana.[55] This and other invasive, non-native plants, including Russian-olive, burning-bush, and privets, are browsed during the winter when food resources are scarce.[56]

Studies of indirect effects of overbrowsing by deer species other than white-tails suggest their ability to alter site nutrient cycling by changing plant species composition from species with high-nitrogen, readily decomposable litter (e.g., most hardwoods) to those with low-nitrogen litter that decomposes slowly (e.g., conifers).[57] Recent research conducted in the Adirondack region of New York State documented significant differences in litter composition and rates of nitrogen mineralization between fenced and unfenced forest tracts. The study, conducted at Huntingdon Forest, involved plots inside and outside a 2-acre exclosure originally built in 1939. Significantly more litter was produced in the fenced plot. In addition litter composition differed with more white ash litter in the fenced area and more American beech leaves in the unfenced plot. Total nitrogen mineralization was 64% greater in the unfenced area over the growing season; most of the difference was accounted for by increased ammonification in the unfenced plot.[58] Another overbrowsing effect seen in some parts of the country is the alteration of forest fire regimes through changes in understory species composition from plants that favor surface fires (e.g., grasses, low shrubs) to those that provide fire "ladders," predisposing stands to crown fires (e.g., greenbriers, certain conifers).[59]

Overall, heavy browsing by deer in woody plant communities has the ability to change the trajectory of forest vegetation development. Whether these changes are permanent is a matter of current scientific debate, but it is clear that they are long lasting.[60] A study conducted on a private wildlife preserve in central Pennsylvania where hunting is prohibited compared forest gap dynamics in the preserve with an ecologically similar forest on nearby state game lands. Pellet groups were 6 to 100 times more abundant in the wildlife preserve. Overstory tree composition, stand basal area, and density of trees over 8 inches diameter (breast height) and 51 inches tall were similar at both sites. However, the density of smaller trees was 36 times less in the wildlife preserve (or 240 times less if only trees capable of becoming part of the canopy were considered). The fraction of the tree canopy in gaps was 41% greater in the wildlife preserve and the gaps were older (judged by the degree of decomposition of gap-maker trees). The authors concluded that the forest in the wildlife preserve was being destroyed from the bottom up by excessive deer browsing.[61] It also is clear that regeneration failures and altered species composition as a result of overbrowsing by deer have serious economic consequences, for example, the need to use fencing and herbicide treatments to regenerate forest stands.[62]

Forest animals

Deer have a substantial capacity for preempting limited food resources and altering habitat for other animals.[63] Though research is still limited, available findings demonstrate that deer have both direct and indirect effects on co-occurring animal species in Eastern forests.

Direct effects occur when deer compete with other species for the same limited food resource, for example, acorns and other tree nuts that fluctuate greatly from year to year, also known as mast. Mast is an important food resource for many forest mammals and some birds such as wild turkey and blue jay.[64] For example, reproduction and over-winter survival of gray squirrels[65] and white-footed mice[66] are strongly influenced by the size of the mast crop. Several studies show that competitive consumption of acorn mast by deer has a negative effect on the abundance of the mast-dependent small mammal community the following spring.[67]

Indirect effects occur when deer alter habitat features. Overbrowsing eliminates the shrub layer and greatly reduces the diversity of forest-floor plant species. With the lower layers of the forest thus impoverished, vertical diversity (herbaceous, shrub, subcanopy, and canopy) and horizontal diversity (the patchy mosaic of different plant species across the forest landscape) are greatly diminished. Subcanopy trees tend to be short-lived; where deer eat all of their seedlings, an entire layer is vulnerable to disappearing even though it is beyond the deer's reach. Where overbrowsing of seedlings and saplings halts the regeneration of canopy trees, their contribution to vertical structure diversity at various life stages is lost. Overbrowsing reduces or eliminates species required by animals that are narrowly specialized to eat only one or a few species. It reduces or eliminates critical habitat features such as oviposition sites for insects and other invertebrates. It allows greater wind speed, increases light (and thus temperature), and reduces humidity at the forest floor. These microclimatic effects are especially detrimental to snails, other forest gastropods, salamanders,[68] frogs, and other animals dependent on moist, protected environments. Few, if any, species gain from the increase in the abundance of the few fern and tree species that are unpalatable to deer.

Indirect effects ripple outward to affect animals further removed from deer and their food plants. For example, the reduction of white-footed mouse, deer mouse, chipmunk, gray squirrel, and other small mammal densities due to competition with densely populated deer for mast can lead to reductions in predator populations that feed on them,[69] including owls, hawks, and possibly fishers, martens, and other carnivores. Dense deer populations in New York reduced the density of white-footed mice, presumably by competing with them for their principal food, acorns, and reducing forest-floor cover, exposing the mice to increased predation. White-footed mice are the main predators of gypsy moths, an introduced defoliator of oaks, thus deer in high numbers can facilitate outbreaks of gypsy moths.[70] Deer are the only host of adult deer ticks, which feed on white-footed mice as larvae and transmit the spirochete that causes Lyme disease from the mice to humans. The northeastern subspecies of the white-tailed deer and the known range of the deer tick are virtually identical, and in places such as Nantucket and Martha's Vineyard, where deer were eradicated and then reintroduced, the deer tick appeared only after deer became numerous.[71] In a 3-year study conducted at three sites in southern Maine, deer pellet group density was a consistently significant predictor of adult tick abundance.[72] Even though deer are not susceptible to Lyme disease, the transmission of the disease from mice to humans depends on their presence and increases as deer populations increase.[73]

The total biomass of herbaceous plants (the weight of harvested plants after oven-drying to eliminate water content) has been measured to be three times greater inside a deer exclosure than outside.[74] When whole layers of the forest are severely depleted or lost, the species that depend on those plant strata are also affected. Unlike white-tailed deer, most insect herbivores feed on only a narrow range of species or, in many cases, just one part of a single species.[75] Thus, insect diversity in forests is heavily dependent on the species diversity of the vegetation.[76] For example, in New Hampshire deer browsing threatened a population of blue lupine, the sole larval food of the federally endangered Karner blue butterfly.[77]

Adverse effects of overbrowsing on forest bird communities have been documented repeatedly, although not in every study. In a study in southwestern Pennsylvania, changes in species composition of bird communities were found by comparing a heavily browsed and grazed preserve with the more intact surrounding area.[78] However, the study had poorly matched control stands, a small sample size, and no net changes in the number of birds or bird diversity were found to be statistically significant. A better-designed study compared fenced deer exclosures in northern Virginia with nearby unfenced sites.[79] Reduced understory density outside the exclosures was correlated with increased nest predation and lower overall bird abundance, but not species diversity.[80]

The effect of deer browsing on songbird species richness and abundance was evaluated in a 10-year study in forested enclosures containing four densities of deer — 10, 20, 38, and 64 deer per square mile — in northwestern Pennsylvania.[81] Not only does this study have randomly matched control stands and a large sample size, it looked at effects on birds at four different deer densities. At the end of the 10 years, species richness and abundance of intermediate canopy-nesting birds were, respectively, 27% and 37% lower at the highest deer density than at the lowest. At the scale of the experiment, the threshold for detectable negative effects on species richness of intermediate-canopy-nesters was between 20 and 38 deer per square mile. Abundance in intermediate canopy-nesting birds showed a steady decline from lowest to highest deer densities. Although the effect of deer density on other groups of birds had confidence limits of less than 95%, the trend was clearly the same for birds as a group as for intermediate canopy-nesters.

The few scientific studies to date that have specifically focused on deer overbrowsing and bird communities have either shown that changes in vertical structure caused by deer have a negative impact on bird abundance or diversity, or both, or failed to detect any statistically significant relationship.[82] Meager as they are, the data are consistent with ecological theory, which predicts that deer browsing should change the distribution of bird species in a forest and decrease avian abundance or species diversity by eliminating understory plant species that provide food, cover, and nesting sites.

Impacts of deer overbrowsing on invertebrates so far has been investigated even less than impacts on birds, but the limited available evidence suggests that overbrowsing may severely affect certain groups.[83] The abundance and species richness of web spiders was found to be reduced in forests with deer compared to those without. Because total numbers of insects caught on sticky traps were similar in sites with and without deer, the authors concluded that the decrease in spiders was due to the simplification of habitat structure.[84] In some situations, deer seem to be direct competitors with insect herbivores for plant biomass. However, as with birds much of the impact is likely to be indirect, resulting from changes in the structure, species composition, and quality of the vegetation. Reductions in certain insect populations indirectly affect a host of insectivorous vertebrate species, including shrews, rodents, bats, wood-warblers, flycatchers, other bird groups, frogs, toads, and salamanders. Few studies have addressed this problem in the range of white-tailed deer, but information from studies of other deer species living in temperate forests are instructive. For example, lepidoptera (butterflies, skippers, and moths) were four times more numerous in the absence of red deer browsing in a study in native pine-dominated forests in Scotland.[85] This was a far greater difference than could have been predicted by differences in total plant biomass. The disproportionate effect was attributed to competition between deer and lepidoptera for just the nutritious young growing tips of major food plants.

Deer selectively browse fast-growing, less-well-defended species, which generally produce litter (shed leaves and dead branches) that decomposes faster than litter from the unpalatable species that are left. This causes a shift in plant species composition toward slower-growing species with slower-decaying litter, which in turn affects diverse groups such as springtails (Collembola), mites (Acari), earthworms (Lumbricidae), roundworms (Nematoda), and other animals that are vital to organic matter turnover and soil development and thus influence rates of energy and nutrient flow through the forest ecosystem.[86] A small subset of inverterbrate species dependent on the vegetation that thrives in overbrowsed environments may, like their plant hosts, prosper with high deer densities; however, like understories overwhelmingly dominated by hay-scented fern, their increase would likely represent a simplification of invertebrate communities and overall loss of diversity.

Interaction of deer and silviculture

Forest disturbances, including timber harvests, have profound effects on white-tailed deer populations and vice-versa. Because of the potential for feedback effects, the relationships among these ecological factors and ecosystem management is complex.

Deer populations tend to increase in response to timber harvest or other overstory disturbance, such as large-scale wind events. They grow the fastest following disturbances that increase the abundance of woody and herbaceous vegetation less than 5 feet tall and increase mast production. Forest stands that contain an abundance of browse (buds, twigs, and leaves of woody plants) within 5 feet of the ground are highly preferred by deer. The current year's growth of most hardwood species has a high nutrient content and is among the most highly palatable items in their diet. In Pennsylvania's hardwood forests, germination, survival, and seedling growth are increased by disturbances that open the canopy and increase the amount of light reaching the forest floor, that is, where deer impacts are low enough to allow these responses to occur and where a residual of low, shade-casting plants such as ferns or shade-tolerant small trees are not left behind. Similarly, silvicultural regeneration methods or natural disturbances that remove all or most of the overstory (e.g., clearcutting, shelterwood seed cutting,[87] selection cutting of large groups,[88] windthrow that creates large openings), where advance regeneration (shade-suppressed seedlings) or a seed bank is present, will promote the development of high-density browse. As seedlings grow and a new forest enters the sapling and poletimber (small adult) stages of development, trees grow out of the reach of deer and cast sufficient shade to substantially decrease the abundance of other browse produced. Where deer population density is below some threshold near a given location's ecological carrying capacity (see box on page 16 and Chapter 11), young hardwood stands in Pennsylvania can grow out of reach of deer in 3 to 10 years, depending on the local climate, site conditions, and species composition.[89]

The abundance and diversity of herbaceous plants used as food by deer first increase and then decline after canopy removal. The growth of tree seedlings and shrubs invading a site after disturbance and advance regeneration accelerates in the increased light to form a closed canopy. This canopy substantially reduces the density and growth of herbaceous plants originally stimulated by the disturbance and associated higher light. As trees reach the sapling stage they shade and suppress shrub growth and further seedling recruitment. After closed tree canopies develop, browse production remains low for several decades until trees achieve heights greater than 50 feet. At around that stage, canopy cover generally falls somewhat below 100% due to the death of some trees, fallen branches, and irregularly shaped tree crowns, once again establishing light conditions near the ground that are favorable for woody and herbaceous plant germination, survival, and growth. This stage is referred to as "understory reinitiation".[90] However, understory browse in a forest stand dominated by mature trees is much sparser than the amount of browse available in the first decade after harvesting.

Silvicultural thinning treatments are partial harvests used to increase the diameter growth of trees selected for their mast or timber production value by removing competing trees to encourage crown expansion of the favored trees. Thinnings increase the amount of light reaching the forest floor and can stimulate the growth of understory vegetation, but typically the growth response is short-term, subsiding as the crowns of canopy trees rapidly expand to fill their new growing space. Selective browsing by deer during understory reinitiation suppresses the advance regeneration of certain tree species. At the same time, it promotes the expansion of unpalatable or resilient species, such as hay-scented fern, New York fern, and American beech or striped maple seedlings and saplings, that may slow or prevent later recolonization by trees when the stand is subjected to a harvest that would normally spur regeneration.[91] By exhausting their major food source and fostering conditions that obstruct its regrowth, deer in high numbers can cause a forest's ability to sustain a high deer population to decline, essentially reducing the local ecological carrying capacity. If there is no alternative source of food, the deer population then decreases through malnutrition or reduced recruitment, but typically remains at a high enough density to keep the understory in a depauperate state essentially in perpetuity (see discussion of alternative persistent states on pages 107 and 108).

The supply of mast from oaks and nut trees is an important contributor to the winter diets of deer and many other wildlife species. Because thinning treatments increase the crown size and vigor of residual trees, it results in the production of more seed during good seed years,[92] which serves as a source of future seedlings but also as a rich source of fat, protein and carbohydrate for wildlife.[93] However, because oak seedlings and saplings are highly preferred browse (see Table 4, pages 53-58), overbrowsing delays or even prevents oak regeneration and stand establishment.[94] Depending on the size of the deer population and the availability of other food sources, oaks can change from a dominant to a subordinate component of the newly regenerating forest or disappear altogether.

A dense white-tailed deer population impedes the practice of sustainable forestry in all forest types in Pennsylvania.[95] It also impedes recovery after natural disturbances such as windthrow or tornado damage. If disturbed areas are not fenced to exclude deer, complete regeneration failure can result,[96] especially if woody vegetation is replaced by unpalatable species such as hay-scented and New York ferns.[97] The Pennsylvania Bureau of Forestry spends two million dollars each year on fencing to exclude deer from timber harvest areas so new trees can grow. The

Bureau currently has 800 miles of fencing on state forest land.[98] The Allegheny National Forest and the Pennsylvania Game Commission fence regeneration harvest areas in regions of high deer impact as a matter of course but smaller landowners may not choose to bear the considerable added expense. The cost of fencing varied, for the Bureau of Forestry's 126 fencing projects in 2002 and 2003, from $208 to $596 per acre[99] (average $318) or $1.75 to $2.28 per lineal foot[100] (average $1.98), with the lower part of the range applying only to exclosures of over 40 acres.[101] In addition to fencing, if seed sources, seeds, or seedlings of desired species are reduced or eliminated, third-generation stands will have to be artificially replenished through planting.

Interaction of deer and unpalatable or browsing-resilient plant species

In a forest stand where deer are densely populated, the few plant species that are unpalatable to deer or resilient to deer browsing can become so plentiful that they prevent the establishment and growth of other plant species, including tree and shrub seedlings, even if the stand is later released from overbrowsing.[102] Proliferating unpalatable or resilient species may suppress other plants by producing dense shade on the forest floor,[103] by usurping space in the soil with a dense root mat, or by competing for water and nutrients; there is conflicting evidence about whether allelopathy (releasing chemicals into the soil that are toxic to other plants) might also be a factor.[104] Research on the inhibition of black cherry establishment by hay-scented fern in northwestern Pennsylvania suggests that shade is the most important of these factors.[105]

Deer overbrowsing alone may not be enough to cause non-preferred or browsing-resilient plants to increase to the point where other species can no longer become established. One recent study in central Massachusetts concluded that more than 15 years of intensive browsing following thinning were necessary for hay-scented fern to form continuous shade on the forest floor; neither thinning alone nor overbrowsing alone was sufficient to cause this level of fern proliferation.[106] It is possible that long-term deer overbrowsing alone might cause this condition, for example, if 70 years of overbrowsing caused canopy thinning by preventing the recruitment of new canopy trees. This hypothesis could be tested by quantifying fern dominance and checking timber harvest records for randomly selected sites on state forest lands, where accurate timber harvest data are available.

In overbrowsed forests in Pennsylvania, dense groundcovers of hay-scented fern and New York fern and understories of shade-tolerant striped maple and American beech often form following canopy thinning. Two very different logging practices involve canopy thinning. One is shelterwood seed cutting — removal of enough large trees to open up the canopy and stimulate the germination and establishment of tree seedlings some years prior to their release from shade by clearcutting. When a final harvest is anticipated shortly after canopy thinning or where tree seed sources may be limiting (unless successful regeneration is obtained in conjunction with the thinning), fencing must be included as part of the treatment where deer numbers are high or else most plants, including tree seedlings, will be consumed and one or a few unpalatable or browsing-resilient species will spread and block future regeneration.[107] The other canopy thinning practice is diameter-limit cutting, in which all trees above a certain size are taken. The result of this practice is that sources of tree seeds are often critically reduced due to selective removal of the largest-crowned, best seed-producing trees and thus the probability of successful regeneration declines. Where the deer population is dense, the outcome is often a regeneration failure of desired species (in silvicultural situations) and a decline in diversity. Sometimes, especially on upland sites, low-diversity "fern savannas" can result (see discussion of diameter-limit cutting on pages 82 and 83).

Of the species whose spread is linked to deer overbrowsing, hay-scented fern and New York fern have received the most attention because of their role in both declining biodiversity and dwindling regeneration of trees important to the wood products industry. Deer do not eat these ferns,[108] most likely because the fronds have high levels of defensive compounds that make them inedible to most herbivores.[109] They regenerate from spores where moist mineral soil is present, but their primary mode of spread is by repeated forking and extension of the rhizomes (underground stems). This ability to form a continuous cover over large areas distinguishes them from most native fern species, whose leaves are arranged in rosettes or tufts. In the low light of forests that have not been disturbed for a number of years, the rhizomatous ferns grow slowly. However, in stands where a portion of the overstory has been removed, rhizomes not only grow faster and fork more frequently than in undisturbed forest, but they also form many new rhizome buds.[110] These buds grow out rapidly and greatly expand the area covered by the fern plant. Overstory removal in an overbrowsed area of New Hampshire caused the frequency of hay-scented fern to increase nearly five-fold by the third year after cutting due to vegetative expansion of existing colonies.[111]

It must be noted that the practice of "blaming" ferns for precipitous declines in forest plant species diversity and tree regeneration reflects confusion between intermediate and ultimate causes. Ferns represent a significant component of forest biodiversity; Pennsylvania has 57 native fern species or 5% of the native herbaceous flora in the state,[112] 16 of which are rare and endangered.[113] Only hay-scented fern and New York fern sometimes become invasive, and solely under a narrow range of conditions involving overbrowsing by abnormally abundant deer followed by forest thinning, canopy thinning by natural disturbance, or canopy attrition due to extremely prolonged overbrowsing. In forests not exposed to deer overbrowsing these two Pennsylvania natives behave much as other native ferns and wildflowers do, growing singly or in small patches interspersed with other plant species.

Dense understories of browsing-resilient or unpalatable trees that are also shade-tolerant (in Pennsylvania mainly American beech and striped maple), also severely curtail the establishment of other plants on the forest floor including seedlings of other tree species. Even small stems of shade-tolerant species can deter seedling establishment in partially cut stands because they often develop faster than herbaceous plants and the seedlings of less shade-tolerant tree species, producing enough shade to reduce their survival. There is some evidence that interactions among plant species with different susceptibilities to deer browsing may make the relationship between high deer populations and altered tree species composition more complex than a simple, linear, inverse relationship between deer density and species diversity of tree seedlings.[114] However, the overall pattern is conclusive that the diversity of forest understory herbaceous plants, shrubs, and tree seedlings diminishes as deer densities increase from moderate to high levels, and the apparent "exceptions" represent only small bumps on a clearly downward-sloping line (see the right-hand side of Figure 1, page 68).

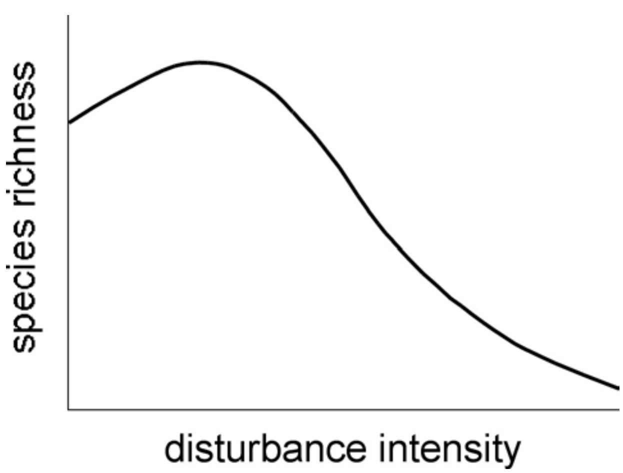
Role of alternative forage

Where white-tailed deer living in forest habitat have alternative forage available in nearby logged areas, agricultural fields, or residential areas, high deer densities can occur with less severe impacts on forest ecosystems. This is one reason that not all forests in Pennsylvania show the same impact from deer. Deer usually thrive in a mosaic of crop fields and woodlots. Forest stands interspersed with agricultural lands may not show as much loss of forest structure and species diversity due to deer overbrowsing as larger blocks of forest, which are the primary focus of this report, although forest fragmentation and "edge effects" in such landscapes have detrimental influences of their own.

Deer and diversity

Ecosystem management of deer does not mean elimination of deer. Although no one has ever

Figure 1. Hypothetical relationship between the frequency or severity of natural disturbance, such as browsing by deer, and the number of species an ecological community will support



documented a beneficial effect of deer on the diversity of plants and other animals, ecological theory does indicate that such an effect may well exist at low deer population levels. Many studies have shown catastrophic effects of white-tailed deer on forest understory plants[115] and birds,[116] however, all of this research has been conducted where deer populations are at destructively high levels. The intermediate disturbance hypothesis[117] describes a hump-shaped relationship between species diversity in an ecological community and the frequency or severity of natural disturbances such as fire, windstorm, disease outbreaks, or heavy browsing (Figure 1). The principle is that species diversity is generally maximized when there is a moderate intensity of disturbance; diversity is lower where disturbance is either less intense or more intense. Numerous studies have corroborated the hypothesis for a wide variety of ecosystems and disturbance regimes.[118]

Although the current high deer populations in Pennsylvania appear to have brought forest stands to the right-hand side of the richness curve, especially in portions of northern Pennsylvania where deer have been abundant for a very long time (see Figure 3, page 122), deer at reduced density have a role to play in functioning ecosystems in Pennsylvania. For example, in parts of northern Pennsylvania, low deer density combined with a major disturbance such as timber harvest or severe wildfire or windstorm can lead to pin cherry reducing the survival of seedlings of other species[119] and probably reducing plant diversity, at least for a few years post-disturbance.

Findings on the role of white-tailed deer in altering forest structure

(1) Virtually all of the published literature on forest structure damage in Pennsylvania suggests a major role for high densities of white-tailed deer. An abundance of experimental data supports that view in those areas where data have been collected. Alternative theories (Chapter 6) can be tested as part of adaptive resource management (Chapters 2 and 12).

(2) Deer have direct and indirect impacts on forest plants and animals. Selective browsing and grazing of preferred woody and herbaceous plants reduce species richness, plant density and biomass, height growth, and the development of vertical structure (direct effects). Loss of vertical structure and drastic reduction or elimination of many plant species lead to the decline of animal species that depend on them (indirect effects).

(3) Over time, overbrowsing-induced dominance by unpalatable and browsing-resilient species interferes with the reestablishment of species lost to browsing, even if overbrowsing stops (another indirect effect). Thus, overbrowsing can cause a persistent change in the trajectory of vegetation development. The longer overbrowsing occurs, the more difficult it becomes to restore the original vegetation, in part because seed and other propagule supplies have been greatly reduced or eliminated.

Recommendation on the role of white-tailed deer in altering forest structure

Until proven otherwise, policy makers should assume that the consensus view on the impacts of the current high densities of white-tailed deer on forest ecosystems is correct.

Endnotes

[1] Porter et al. 1994

[2] Fronz 1930; Leopold et al. 1943, 1947; Kosack 1995

[3] Hough 1949; Webb et al. 1956; Grisez 1957; Graham 1958; Grisez 1959; Shafer et al. 1961; Jordan 1967; Ross et al. 1970; Richards and Farnsworth 1971; Marquis 1974; Marquis and Grisez 1978; Anderson and Loucks 1979; Anderson and Katz 1993; Anderson 1994; Alverson and Waller 1997. Exclosure studies are invaluable in understanding the effects of deer on ecosystem processes. However, such studies must be interpreted with the knowledge that plants evolved under some level of deer browsing pressure; eliminating browsing experimentally is not intended to mimic any "natural" situation.

[4] Tilghman 1989; deCalesta 1994; Horsley et al. 2003

[5] Stiteler and Shaw 1966

[6] Hough 1965

[7] McCullough 1984; Healy 1971; Augustine and Jordan 1998

[8] Tilghman 1989; Horsley et al. 2003

[9] Lutz 1930a, 1930b; Winecoff 1930; Park 1938; McCain 1939, 1941; Leopold et al. 1943; Hough 1949; Graham 1954; Dahlberg and Guettinger 1956; Webb et al. 1956; Grisez 1957; Stoeckeler et al. 1957; Graham 1958; Grisez 1959; Beals et al. 1960; Shafer et al. 1961; Hough 1965; Jordan 1967; Behrend et al. 1970; Ross et al. 1970; Richards and Farnsworth 1971; Marquis 1974; Blewett 1976; Snyder and Janke 1976; Marquis and Grisez 1978; Anderson and Loucks 1979; Marquis and Brenneman 1981; Whitney 1984; Frelich and Lorimer 1985; Kroll et al. 1986; Risenhoover and Maass 1987; Tilghman 1989; Allison 1990a, 1990b, 1992; Strole and Anderson 1992; Anderson and Katz 1993; Anderson 1994; Balgooyen and Waller 1995; Ziegler 1995; Waller et al. 1996; Alverson and Waller 1997; deCalesta 1997; Healy 1997; Augustine and Jordan 1998; Fredericksen et al. 1998; Danell et al. 2003; Horsley et al. 2003; Boucher et al. 2004; Cote et al. 2004; Rooney et al. 2004; Whigham 2004

[10] Anderson and Loucks 1979; Horsley and Marquis 1983; de la Cretaz and Kelty 1999; George and Bazzaz 1999a, 1999b; Ristau and Horsley 1999

[11] Horsley 1977, 1993a, 1993b; Horsley and Marquis 1983; Tilghman 1989; de la Cretaz and Kelty 1999; Horsley et al. 2003

[12] Styer et al. 1997

[13] Rooney and Dress 1997a

[14] Rooney and Dress 1997b

[15] Ristau 2001

[16] Lutz 1930b

[17] Allison 1990a, 1990b, 1992; A. F. Rhoads, personal observation; Ristau 2001

[18] Department of Conservation and Natural Resources 1993

[19] Catling and Larson 1997

[20] Dr. James K. Bissell, Curator of Botany, Cleveland Museum of Natural History, personal communication, 2003

[21] Source: Rhoads and Block 2003; common names from Little 1953

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[22] Assessment by M. A. Fajvan and A. F. Rhoads based on direct observation and a review of Halls and Ripley 1961; Healy 1971; Knierim et al. 1971; West Virginia University Extension Service 1985; Horsley et al. 2003. As noted above, white-tailed deer food preferences depend partly on what is available to eat. Food variety and availability in turn depend on current local deer density, recent trends in local deer density, availability of alternative forage, human land-use patterns, forest disturbance history, snow cover, and various other factors. Thus, preferred species frequently differ between regions in the same forest type, within regions over long periods of time, at different times during a growing season, and at different deer densities in the same forest type.

[23] Commercial species representing at least 0.05% but less than 0.5% of all live trees 5 inches in diameter at breast height or larger encountered on U.S. Forest Service's Forest Inventory Analysis survey plots (Alerich 1993: pages 15-17)

[24] McCaffery et al. 1974

[25] Korschgen et al. 1980

[26] Crawford 1982

[27] Healy 1971

[28] Anderson 1994; Augustine and Frelich 1998; Knight 2004

[29] Balgooyen and Waller 1995

[30] Rooney 1997

[31] Williams et al. 2000

[32] A. F. Rhoads, personal observation

[33] Miller et al. 1992

[34] A. F. Rhoads, personal observation

[35] Augustine and Jordan 1998

[36] Whigham 1990

[37] Fletcher et al. 2001a

[38] Loeffler and Wegner 2000

[39] Ruhren and Handel 2000; Fletcher et al. 2001b

[40] Rooney 1997

[41] Allison 1990a, 1990b, 1992

[42] Fletcher et al. 2001b

[43] Fletcher et al. 2001b

[44] Loeffler and Wegner 2000; A. F. Rhoads, personal observation; Paul G. Wiegman, formerly Coordinator/Botanist, Natural Areas Program, Western Pennsylvania Conservancy, personal communication, 2003; J. M. Benner, personal observation

[45] Campbell 1993

[46] Keane and Crawley 2002

[47] Keane and Crawley 2002

[48] Mitchell and Power 2003

[49] Klironomos 2002

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[50] Anderson et al. 1996; Williams 1996

[51] Ward 2000

[52] Schmitz 1992; Vangilder et al. 1982

[53] E.g., Atwood 1941; Korschgen et al. 1980

[54] Nixon et al. 1970

[55] Sotala and Kirkpatrick 1973

[56] Conover and Kania 1988

[57] McInnes et al. 1992; Pastor and Naiman 1992; Pastor et al. 1993

[58] Didier 2003. Species basal area inside the fence was white ash 44%, American beech 22%, and sugar maple 21%. The unfenced plot had a composition of 62% beech, 25% maple, and 12% ash.

[59] Hobbs 1996

[60] Tilghman 1989; Warren 1991; Stromayer and Warren 1997; Waller and Alverson 1997; Augustine et al. 1998; Coomes et al. 2003; Horsley et al. 2003

[61] Pederson and Wallis 2004

[62] Marquis 1974; Marquis and Brenneman 1981; Horsley et al. 1994

[63] Perkins and Mautz 1987

[64] Martin et al. 1951

[65] Elliot 1978; Nixon and Hanson 1987

[66] Miller and Getz 1977; Gashwiler 1979; Ostfeld et al. 1996

[67] Brooks and Healy 1988; McShea and Rappole 1992; McShea and Schwede 1993; McShea and Rappole 1997

[68] However, one investigator in northwestern Pennsylvania found no difference in surface abundance of salamanders (amphibians) across a range of deer densities 10 years after the introduction of deer in an enclosure study (Thomas Pauley, U.S. Forest Service, Northeastern Research Station, Irvine, Pennsylvania, unpublished data).

[69] Flowerdew and Elwood 2001

[70] Ostfeld et al. 1996

[71] Spielman et al. 1985

[72] Rand et al. 2003

[73] Duffy et al. 1994. In this study, the abundance of deer tick larvae (August) and nymphs (June) was sampled in 1992 at 22 parks and natural areas — some with deer and some without — on Long Island, New York. Significant correlations were found between deer presence and the abundance of both nymphal and larval ticks. Sites without deer had, on average, 1.8% of the larval deer tick population densities and 7% or the nymphal densities found at sites with deer.

[74] Riemenschneider et al. 1995

[75] Strong et al. 1984

[76] Stewart 2001

[77] Miller et al. 1992

[78] Casey and Hein 1983

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[79] McShea and Rappole 1999

[80] Leimgruber et al. 1994

[81] deCalesta 1994

[82] MacArthur and MacArthur 1961; Karr and Roth 1971; Hooper et al. 1973; Roth 1976; DeGraaf et al. 1991a

[83] Stewart 2001

[84] Miyashita et al. 2004

[85] Baines et al. 1994

[86] Pastor et al. 1993; Stewart 2001; Tripler at al. 2002; Ayres et al. 2004; Wardle and Bardgett 2004

[87] Shelterwood cutting involves harvesting in two or more stages. The first harvest — the seed cut — increases light at the forest floor enough to allow seedlings of shade-tolerant species to become established in large numbers. The rest of the canopy is removed when the offspring of the desired tree species have grown robust root systems that allow them to tolerate drought (and, in the case of oaks, fire) and compete with the faster-growing, intolerant species.

[88] Selection cutting of large groups (also called group selection) is the complete removal of the tree canopy in multiple areas dotted across the landscape, each large enough — typically 0.5 to 2 acres — that adjacent uncut trees cannot fill in the gap by lateral growth of crown branches. At present, group selection is not a viable technique anywhere in Pennsylvania unless cut areas are fenced, because of overbrowsing by deer.

[89] Ristau and Horsley 1999

[90] Oliver and Larson 1996

[91] Horsley et al. 2003

[92] Smith et al. 1997

[93] Nutritional content of nuts ("hard mast") native to Pennsylvania forests (U.S. Department of Agriculture 2003):

	mean amounts (g) in 100 g of edible portion		
	protein (N x 5.3)	total lipid (fat)	carbohydrate
Acorns *(Quercus* spp.)	8.10	31.41	53.66
Beechnuts *(Fagus grandifolia)*	6.20	50.00	33.50
Hickory nuts (*Carya* spp.)	12.72	64.37	18.25
Walnuts, black, dried *(Juglans nigra)*	24.06	59.00	9.91
Butternuts *(Juglans cinerea)*	24.90	56.98	12.05
Hazelnuts (*Corylus* spp.)	14.95	60.75	16.70

[94] Kelty and Nyland 1981; Russell et al. 2001; Palmer et al. 2004

[95] Pennsylvania Department of Conservation and Natural Resources 2003

[96] Marquis 1974; Marquis and Grisez 1978

[97] Horsley and Marquis 1983

[98] DiBerardinis 2004

[99] Excludes outlier values for seven of the fencing projects of approximately \$180, \$989, \$878, \$851, \$725, \$674, and \$648 per acre.

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[100] Excludes an outlier value for one of the fencing projects of $2.73 per lineal foot.

[101] James Bailey, Forest Genetics/Regeneration Specialist, Silviculture Section, Bureau of Forestry, Pennsylvania Department of Conservation and Natural Resources, personal communication, 2003

[102] Horsley and Marquis 1983; Stromayer and Warren 1997; Waller and Alverson 1997

[103] de la Cretaz and Kelty 2002

[104] Horsley 1993a, 1993b

[105] Horsley 1993a

[106] de la Cretaz and Kelty 2002

[107] Marquis et al. 1975; Cody et al. 1977; Horsley and Marquis 1983; de la Cretaz and Kelty 1999; Horsley et al. 2003

[108] Healy 1971; Waller and Alverson 1997

[109] Bohm and Tryon 1967; Cody et al. 1977

[110] Horsley 1984; Hammen 1993

[111] Hughes and Fahey 1991

[112] Rhoads and Block 2003

[113] Rhoads and Block 2000

[114] For example, in parts of northern Pennsylvania, pin cherry, an early successional tree that survives in forests for 25 to 40 years, can be so abundant after complete timber removal that it slows the regeneration of canopy tree species, unless deer density exceeds about 20 deer per square mile. Above that level, deer herds browse enough pin cherry to allow trees that will eventually dominate the forest to regenerate relatively quickly. However, at the same time, deer restrict the survival of forest tree species to mainly black cherry, American beech, sweet birch, yellow birch, and, in the subcanopy, striped maple. Other components of the northern hardwood canopy and subcanopy, including sugar maple, red maple, white ash, cucumbertree, yellow-poplar, northern red oak, eastern white pine, eastern hemlock, smooth serviceberry, Allegheny serviceberry, mountain holly, and American hornbeam regenerate in significant numbers only where deer densities are considerably lower (Ristau and Horsley 1999; Horsley et al. 2003).

[115] E.g., Anderson and Loucks 1979; Marquis and Brenneman 1981; Tilghman 1989; Miller et al. 1992; Anderson and Katz 1993; Rooney and Dress 1997a; Rooney 2001; Russell et al. 2001; Horsley et al. 2003

[116] E.g., Casey and Hein 1983; deCalesta 1994; McShea and Rappole 1997

[117] Connell 1978

[118] E.g., Reynolds et al. 1993; Collins et al. 1995; Hiura 1995; Bornette and Amoros 1996; Clark 1997; Townsend et al. 1997; Floder and Sommer 1999; Molino and Sabatier 2001. A small fraction of such studies has shown a different pattern (e.g., Schwilk et al. 1997), usually decreasing diversity with increasing disturbance. Various explanations have been proposed for why the relationship between disturbance and diversity is often hump-shaped. A variety of factors may be at play in different ecosystems and at different points along the spectrum of disturbance intensity. In cases where the disturbance is browsing by an animal such as white-tailed deer, the most important factor is clearly plant-plant competition. The best competitors for light, water, and nutrients are species that grow fast and tall, but the faster and taller a plant grows, the more likely it is to be eaten. Where the most

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effective competitors are eaten disproportionately, less-competitive plant species can sustain higher population densities, which are vital to insure pollination, seed production, and long-term persistence. As plant species drop out of the picture either to the left or to the right of the highest point in the curve (see Fig. 2, animal species that depend on them are apt to decline as well. At high levels of browsing, all but a few unpalatable plants are vulnerable and many species decline precipitously or they are exterminated.

[119] Ristau and Horsley 1999; Horsley et al. 2003

Chapter 6. Factors of Human Origin in Addition to Deer Browsing that Affect Recovery of Pennsylvania's Forests

To develop a program for managing deer from an ecosystem perspective it is necessary to consider all of the major factors other than deer that affect forest structure, succession, and other processes. Consideration of these factors is also necessary to make sound predictions about recovery times following reduction in deer browsing pressure, predictions that can be used to test the theoretical understanding on which any management plan must rest. In this chapter, we consider factors pertinent to forest recovery, in addition to deer overbrowsing, that are deliberately or inadvertently influenced by human activity. As in the rest of this volume, we confine our discussion to large forested areas, leaving suburban sprawl, forest fragmentation, the farm-forest interface, and other important topics for examination elsewhere.

Acidic deposition

Acidic deposition is the transfer of strong acids and acid-forming substances from the atmosphere to the surface of the earth. The deposited material includes ions, gases, and particles derived from gaseous emissions of sulfur dioxide, nitrogen oxides, and ammonia and particulate emissions of acidifying and neutralizing compounds.[1] Although the Clean Air Act of 1990 resulted in reduction of sulfur dioxide emissions, there has been little abatement of nitrogen oxide emissions. High emissions in the Northeast result primarily from electrical power generation and heavy manufacturing. Prevailing winds from west to east cause pollutants emitted in the Midwest to be deposited eastward; Pennsylvania is particularly hard-hit. Many of the effects of acidic deposition depend on the rate at which acidifying compounds are deposited from the atmosphere compared with the rate at which acid-neutralizing capacity is generated within the ecosystem. Acid-neutralizing capacity is a measure of the ability of water or soil to neutralize inputs of strong acids. It is largely the result of terrestrial processes such as mineral weathering, cation exchange, and immobilization of sulfur dioxide and nitrogen.[2]

The observation of elevated concentrations of chemically active inorganic aluminum in surface waters has provided strong evidence of soil responses to acidic deposition.[3] Recent studies have shown that deposited material has changed the chemical composition of soils by (1) depleting the availability of cations required by plants in large quantities (calcium, magnesium, potassium), (2) increasing the mobility and chemical activity of aluminum and manganese, and (3) increasing sulfur and nitrogen content. Acidic deposition has increased the concentrations of hydrogen ions and strongly acidic anions (sulfate and nitrate) in the soils of the northeastern United States, which has led to increased rates of leaching of base cations and to the associated acidification of soils.[4] Where the supply of base cations is sufficient, the acidity of the soil water is effectively neutralized. However, where base saturation (exchangeable base cation concentration expressed as a percentage of total cation exchange capacity) is below 20%, atmospheric deposition of strong acids results in the mobilization and leaching of aluminum, and hydrogen ion neutralization is incomplete.[5] About 30% of the soils in Pennsylvania have been classified as sensitive to acidification; these are found primarily in the northern-tier counties, portions of the Ridge and Valley physiographic province, and the extreme southeastern portion of the state.[6] One study, which attempted to duplicate the methods used in earlier studies of northern Pennsylvania sites in order to evaluate change over time, determined that there has been a decrease in base cation concentrations in some soils over the past 20 to 40 years.[7] Attempts to use tree-ring chemistry to evaluate long-term environmental change have been only partially successful. This is because most tree species do not sequester ions solely in the current annual ring; only Japanese larch and, to a limited extent, black cherry have so far shown promise of preserving a chronological record of past soil changes in annual growth rings.[8]

The mechanisms by which acidic deposition can cause stress to trees are only partially understood, but they generally involve interference with calcium and magnesium nutrition and the physiological processes that depend on these elements. The depletion of calcium and magnesium in forest soils raises questions about the health and productivity of northeastern forests, particularly for those containing high base cation-demanding species. Progress on understanding the effects of acidic deposition on trees has been limited by the long response time of trees to environmental stresses, the difficulty in isolating possible effects of acidic deposition from other natural and anthropogenic stresses, and the insufficiency of information on how acidic deposition has changed soils.

To date, investigation of the possible effects of acidic deposition on trees in the Northeast has focused almost exclusively on red spruce and sugar maple. There is evidence that acidic deposition causes dieback of red spruce by decreasing cold tolerance.[9] Where it is an important forest-canopy component in northeastern Pennsylvania, red spruce so far appears to be unaffected, at least superficially,[10] although none of the relevant research has been conducted in the state. Acidic deposition may contribute to episodic dieback of sugar maple by causing depletion of nutrient cations from soils where cation concentrations are already low because of the type of bedrock (parent material) from which the soil is derived. An experimental addition of dolomitic limestone to base-cation-poor soils in north-central Pennsylvania increased calcium and magnesium cation concentration in the soil, decreased the availability of aluminum and manganese, and resulted in significant increases in sugar maple survival, crown vigor, diameter and basal-area growth, and flower and seed production compared with untreated trees.[11] Moreover, strong links have been found between low foliar magnesium, high foliar manganese, insect defoliation stress, and dieback of sugar maple in northwestern and north-central Pennsylvania and southwestern New York.[12]

A dispute has arisen in Pennsylvania over the relative importance of acid rain and deer overbrowsing in altering forests. Disputes of this type about forest dynamics can easily be accommodated within the framework of A.R.M. (see Chapter 2). We return to this issue later in this chapter in the section titled “Impacts of deer and other factors on forest ecosystems — accommodating different views.”

Fire suppression in oak-dominated forests

In the cool, moist northern hardwood areas of the Northeast and Great Lakes states, including northern Pennsylvania, fires have historically been infrequent. Wind was the most important disturbance factor.[13] However, in warmer, drier areas occupied by oak forests, including most of the southern two-thirds of Pennsylvania, surface fires occurred relatively frequently, even before the arrival of European settlers.[14] The association of fire with the successful regeneration of oaks has been known for many years. The advent of fire suppression programs in the 1930s and 1940s coincided with the beginning of widespread oak regeneration problems.

Oaks have a different pattern of growth than most of the species with which they compete. Seedlings of northern red oak and white oak, for example, divert most photosynthetic production into root growth at the expense of shoot development.[15] Competitors, including maples, yellow-poplar, birches, and black cherry, favor early shoot growth and relatively little root growth. Over time, these species develop a significant height advantage over the oaks, steadily increasing in both size and number until a multi-storied layer of vegetation develops, including a nearly continuous subcanopy.[16] The added layers of foliage beneath the overstory intercept so much light that often less than 1% of full sunlight reaches the seedling layer, resulting in a negative carbon balance (i.e., metabolism outpaces photosynthesis) for oak seedlings growing under a heavy canopy.[17] In deep shade, oak seedlings often die once acorn reserves are exhausted and, among the survivors, a vigorous root system fails to develop.[18] Even vigorous, nursery-grown northern red oak seedlings survive poorly when planted in mature undisturbed forests on mesic sites (those with moist, loamy soils) and dry-mesic sites. Thus, the presence of a dense understory of competitors often is sufficient to prevent the development of vigorous oak advance regeneration whether or not other limiting factors are present. By contrast, on xeric sites (those with dry, sandy or rocky soils), conditions usually are less hospitable for oak competitors and oak seedlings may persist for 30 to 50 years, developing a strong root system and often a tall shoot.[19] Development of vigorous oak seedlings on mesic sites is feasible, but it has been demonstrated only in cases where understory vegetation has been removed before or at the time of overstory harvest.[20] The bottleneck in developing successful oak regeneration appears to be the need for a low-competition environment in which oak seedlings can develop.

On mesic sites, which include a majority of Pennsylvania forestlands, the presence of frequent surface fires is a key factor promoting oak regeneration.[21] Most oak species have biological traits that suggest adaptation to periodic fire. These include the positioning of resprout buds below the ground surface at the root collar and thick, insulating bark. Such traits protect oaks against fire and allow them to survive even late spring or early summer burns, which are typically high in intensity.[22] In addition, the large oak root with its ample carbohydrate reserves can resprout multiple times. While some oak competitors also can resprout after fire, the rate of resprouting for oaks is higher than that of their more fire-sensitive competitors.[23] Fire has additional benefits for oaks and other nut trees, including hickories: it discourages insect predators of acorns, nuts, and seedlings; exposes the humus or mineral soil layers to drying, which does more harm to seedlings with less-robust root systems than oaks and hickories; improves germination conditions by consuming leaf litter and other forest floor organic matter; and kills seedlings of most other tree species, whose resprouting buds are at or just above the ground surface, allowing oaks to dominate the advance regeneration pool.[24] Thus, where fires occur repeatedly, oaks tend to increase in dominance over competitors.

Recently, the combination of shelterwood cutting to increase light followed in a few years by burning to reduce fire-sensitive oak competitors has been tested and found effective for regenerating oaks.[25] Early results of trials in Pennsylvania appear promising (but only where fencing has been erected to exclude deer).[26]

Silviculture and unsustainable tree harvesting

Impacts of logging on forest understory plant species diversity

There have been surprisingly few studies of the impacts of silviculture and of timber harvesting in general on species diversity in eastern North American forests. Most studies have been relatively short-term in nature (< 20 years). All longer-term studies have taken the chronosequence approach, that is, surveying multiple forest stands of a range of known ages since logging to infer the changes that a single stand might undergo over time. Stands to be compared must be in close proximity to one another, of the same forest type, and with similar soils, slope, aspect, hydrology, and other factors that may influence species composition and the pace of recovery. An experimental approach to questions about logging impacts on diversity is preferable,[27] but because of the great longevity and slow response times of trees, shrubs, and many forest understory herbaceous plants, determining long-term effects would take many decades. A potential pitfall of the chronosequence method is that the observer exerts no control over treatments. As a result, different logging practices or other unknown factors coincidentally confounded with age since logging may lead to a false inference that age caused the differences, or they may obscure the effect of age since logging, resulting in the failure to find differences actually caused by age. Another limitation is shared with most large-scale ecological studies whether they are experimental or observational; the sample size is usually small, which means only large differences can be verified as statistically significant.

A chronosequence study in the southern Appalachians focused on cover and species richness in herbaceous understories of nine old-growth forest stands and nine comparable tracts that had been clearcut 45 to 87 years earlier.[28] The previously logged stands had less herbaceous species diversity compared to nearby uncut stands. Similar results emerged from a study of clearcut, selectively cut, and uncut forest stands in North Carolina.[29] According to a later review,[30] "because of methodological problems, the accuracy of the results have been questioned.[31] Replies to these criticisms[32] and further work[33] by these authors failed to resolve the problems." However, publication of this work did serve to heighten efforts to evaluate the effects of forest management activities on the forest herb layer.

By contrast, a study of four watersheds in the Allegheny Mountains of West Virginia[34] showed little variation in herbaceous species composition or diversity[35] in the herbaceous layers of sites 22 years after clearcutting compared to sites where selective logging had occurred 70 or more years earlier. However, data on the composition of the herbaceous layer (important species were reported as wood nettle, violets, greenbrier, blackberry, seedlings of striped maple and black cherry, and several ferns) make it clear that the forests they worked in were severely depauperate at the ground level, most likely as a result of overbrowsing by deer. In yet another chronosequence study, little difference was found in the spring and summer herbaceous flora of nine forest stands in northern Georgia,[36] encompassing three sites in each of three age categories: 15, 25, and 50 years after clearcutting; no old growth stands were included for comparison. All stands were cove forests with a total of 69 herbaceous species recorded.

In northern hardwood stands in New Hampshire, a team of investigators compared the herbaceous species composition of three 25-year-old clearcuts, three 60-year-old clearcuts, and old (ca. 90 to 120 years) secondary stands adjacent to each former clearcut.[37] Based on differences in abundance between the 25-year-old clearcuts and adjacent old forest stands, they classified species as *insensitive* (7 species showing little difference between clearcuts and adjacent uncut forest); *sensitive* (6 species with lower densities in clearcuts than adjacent uncut forest); *enhanced* (4 species with greater densities in clearcuts than adjacent uncut forest); and *edge-enhanced* (6 species with greatest densities near clearcut edges, decreasing with distance into the clearcut). Interestingly, species found to be sensitive to clearcutting also are sensitive to deer browsing (blue-bead lily, Canada mayflower, Indian cucumber-root, shining clubmoss, rose mandarin, and painted trillium) and clearcut-enhanced species included those that are most deer-resistant (hay-scented fern, New York fern, and sedges). Species in the other categories also were mostly plants sensitive to browsing.

In a comparative study of forested ravines along the lower Susquehanna River in Pennsylvania,[38] sites with successional or highly fragmented forests were missing herbaceous species that were present in older, less-disturbed stands. Herbaceous forest species such as declined trillium and squirrel-corn were notably absent from younger stands even when a closed canopy was present.

While none of the studies cited above are definitive or even directly comparable, they raise questions that require more study. Chronosequence studies in the southern Appalachians suggest that large white trillium, purple trillium, Dutchman's-breeches, dwarf ginseng, Fraser's sedge, black snakeroot, blue cohosh, and hepatica (all species native to Pennsylvania) are slow to recover after logging and members of the lily (Liliaceae), orchid (Orchidaceae), and fumitory (Fumariaceae) families are especially vulnerable to disturbance.[39] A survey of parks and conservation areas throughout the United States documenting instances of deer damage to herbaceous plants found greater sensitivity to browsing, as well, among plants in the lily and orchid families.[40]

Clearly, the relationships among understory plant diversity, anthropogenic disturbances such as logging, and overbrowsing by densely populated deer are not well understood and have only recently begun to be explored in detail.[41]

Impacts of non-sustainable harvesting on forest tree species diversity

Beginning in the 1970s, harvesting became the most widespread disturbance affecting second-generation deciduous forests in Pennsylvania and other Eastern states.[42] On public land, sustainable harvesting — in the form of silvicultural treatments aimed at changing stand development and species composition — usually results in stand regeneration by tree species of commercial value. However, sustainable harvesting frequently is not being practiced on private land,[43] which comprises about 70% of Pennsylvania's forestland ownership.[44] Non-sustainable harvesting practices consist of high-grading, that is, removing all trees with significant commercial value in a single cut without regard for regeneration and future stand condition; trees with little or no commercial value are left standing. One of the most common practices is diameter-limit cutting, in which all canopy trees greater than a certain diameter are removed.[45] Because the smaller trees in a stand are mainly shade-tolerant species, diameter-limit cuts typically are species removals that disproportionately extract the shade-intolerant species while failing to provide conditions suitable for their regeneration.[46]

The accelerated rate of non-sustainable harvesting of second-growth forests on non-industrial private land has concerned scientists and managers in Pennsylvania and nearby states. A series of surveys conducted in response to these concerns unanimously confirmed that diameter-limit harvesting was practiced on the majority of ownerships.[47]

The detrimental effects of diameter-limit harvesting are exacerbated where deer populations are dense. The remaining trees after high-grading typically include species that deer do not prefer or that are resilient to repeated browsing such as striped maple and American beech. With sustained overbrowsing they form a dense understory (along with hay-scented fern and New York fern) that shades the forest floor and hinders the regeneration of trees and most shrubs and herbaceous plants, even if later released from overbrowsing. Because striped maple is a short-lived (about 40 years) understory tree and American beech is currently undergoing an epidemic of beech bark disease, the interaction of diameter-limit cutting and deer overbrowsing may be placing the future forests of Pennsylvania in jeopardy. The development of third-generation forests in the eastern United States almost certainly will deviate from established post-disturbance forest development models.[48] The unprecedented combination of overbrowsing by deer and targeted removal of high-value species that prevails today precludes any definitive predictions of future stand composition.

Introduced pests

Most outbreaks of insect herbivores or diseases in Pennsylvania's forests involve organisms inadvertently introduced to North America from Eurasia. In many cases, the natural enemies of these organisms are absent in their new home and populations of native plants have not had time to develop resistance. In some cases, such outbreaks have caused catastrophic mortality of important species, the most notable example being chestnut blight, a Eurasian fungus that reduced what may have been Pennsylvania's most abundant forest tree, American chestnut, to a sickly understory species in less than a decade.

Insects

Insect infestations occasionally are severe enough to prevent the regeneration of individual tree species, but under most conditions they are just one among a myriad of factors reducing the number of seedlings that become established. Native insect herbivores that undergo outbreak population cycles such as elm spanworm, eastern tent caterpillar, and forest tent caterpillar generally do not cause heavy mortality or major shifts in species composition. The following species were unintentionally introduced.

Cherry scallopshell moth outbreaks occur at about 10-year intervals on the Allegheny Plateau.[49] Outbreaks usually last for 2 or 3 years, repeatedly defoliating large black cherry trees.

While primarily overstory trees are affected, seedlings sometimes are defoliated and killed and seed production may be diminished for several years after defoliation.

Pear thrips are sucking insects whose damage is usually confined to fruit orchards.[50] Since its positive identification in forest environments of the northeastern United States in 1980, pear thrips have occasionally caused damage to overstory trees and seedlings of several species. Wounds of sugar maple seedlings caused by pear thrips have become infected by maple anthracnose, which subsequently has caused seedling mortality.[51] Pear thrips and maple anthracnose do not necessarily occur in synchrony; it is not clear how often these agents are important to sugar maple seedling survival.

The hemlock wooly adelgid, a small insect related to aphids, has caused serious mortality of eastern hemlock trees in southeastern Pennsylvania since about 1995. Saplings and seedlings appear to be less susceptible than larger trees. Even in dense infestations, smaller trees are infested last, appear to recover more quickly, and exhibit lower rates of mortality. This is most apparent along edges where declining trees larger than about six inches in diameter are subtended by vigorous sapling thickets. Reduced seed production in infested areas probably constitutes the major impact on regeneration. Hemlock woolly adelgid infestation has moved slowly from the southeast towards the northwest in Pennsylvania and recently an outlier population appeared in Centre County.[52]

The gypsy moth has become a well-established defoliator of oaks and some other forest, shade, and fruit trees since its accidental introduction into Massachusetts from Europe in the late 1860s. Gypsy moth expansion was slowed by domestic quarantine for many years; the first heavy defoliations did not occur in Pennsylvania until 1969.[53] White oak and chestnut oak appear to be most susceptible.[54] Large numbers of trees (often exceeding 50% of the overstory, with greater percentages in understory trees) are killed when the insect first moves into an area. Subsequent defoliations are episodic with fewer trees killed.

Gypsy moth defoliation can affect the natural regeneration of oak-mixed hardwood stands in several ways.[55] Defoliation significantly reduces acorn production; individual oak trees respond by aborting undeveloped seeds and reducing flower crops in subsequent years.[56] Mortality of oak trees of seed-bearing size also reduces the production of acorns in the long term across entire stands. Defoliation of oak seedlings results in dieback and resprouting and increased mortality, stunting the development of a cohort of seedlings and rendering them less competitive when released from shade.[57] There is also increased interference from other plants, including disturbance opportunists (early-successional species) that respond quickly to the increased light and nutrients present in defoliated stands.[58] Species such as hay-scented fern that are unpalatable to deer increase in density in defoliated stands that are subjected to heavy deer browsing. The growth responses of shade-tolerant tree and shrub species present before defoliation and intolerant species that become established in areas of heavy mortality typically result in a change in species composition of tree seedlings to a mixture with fewer oaks and more red maple, sweet birch, and black cherry.[59] The mortality or reduced vigor of overstory oaks from defoliation results in reduced stump sprouting or none.[60] The net effect is that some oak-dominated stands regenerate to a mix of other tree species that are more resistant to gypsy moth defoliation.

Diseases

Only a few diseases have been identified as impediments to tree regeneration in Pennsylvania forests, all accidentally imported from Eurasia.

Beech bark disease complex, also known as beech scale-nectria canker, is an insect-fungus complex consisting of beech scale (a European insect) and either of two species of canker fungi in the genus *Nectria*, one introduced and one native.[61] Feeding holes made by the scale are colonized by the fungus, which kills cambial tissue (the living, growing, outer layer of wood). Over time, dead cambial patches coalesce, killing the tree. Weakened and dying trees produce abundant root suckers, which form thickets. Dense shade from the highly shade-tolerant beech root suckers interferes strongly with the growth of other plant species, including tree seedlings.

Cherry leaf spot fungus, also known as cherry shot hole fungus, can hamper the regeneration of black cherry.[62] Young seedlings up to about six inches tall are the most affected. Fungal spores are transmitted in rain splash, so the probability of infection is increased when seedlings are closely spaced. In dense stands of young, recently germinated seedlings, whole cohorts sometimes are killed.

Maple anthracnose is a late spring defoliator of sugar maple and red maple, particularly under cool, moist conditions.[63] Maple anthracnose is best known for infecting and killing overstory trees, but it also is active on small seedlings and may contribute to the loss of sugar maple regeneration.

Sudden oak death is a catastrophic disease of oaks caused by a fungus introduced from Eurasia that some experts believe may pose a grave threat to forests in eastern North America.[64] Sudden oak death was first identified in California in 1994. In addition to oaks, it has been found on western North American species of buckeye, maple, and members of the heath family (including rhododendrons, azaleas, blueberries, and huckleberries) but on these hosts the pathogen has not been lethal. Researchers at the University of California at Davis recently reported that seedlings of at least two oak species native in Pennsylvania, northern red oak and pin oak, developed stem cankers after inoculations with the sudden oak death fungus.[65] It is still not known whether mature trees of these or any other Eastern oaks are susceptible.

Presently, efforts are focused on preventing the spread of this pathogen. Quarantines on movement of plant parts of oaks and other host species have been instituted in California.

Restrictions on importing ornamental rhododendrons are still being debated. The ease of spread of this pathogen on shoes or car and bicycle tires means it will be difficult to contain. A recent jump in the range of the disease from California to southern Oregon in an area remote from development, roads, or trails is particularly alarming. Not enough is known about the pathogen to say whether it could survive and spread in Eastern forests. A recent, unpublished risk assessment of Eastern oak forests places the mixed oak forest in the southern two-thirds of Pennsylvania at moderate risk, should the disease arrive in the East.[66] Given the abundance of oaks in many of Pennsylvania's forests, the pathogen could be a serious threat in the future.

Climate change

Global warming also is a potentially severe threat to eastern North American forests. However, so little is known about the likely impacts at a regional scale that only speculative statements can be made about the effects of climate change on forests in Pennsylvania. Across all of eastern North America, forests are projected to "expand under the more moderate scenarios, but decline under more severe climate scenarios."[67] Shifts in species composition and abundance are forecast for particular regions in eastern North America[68] but we did not find any specific predictions in the literature for Pennsylvania. Migration of entire biomes is predicted, but the projected rates depend on uncertain parameters.[69] Forest fragmentation, which is severe across much of the East, is an impediment to migration. Some authors argue that migration will not be fast enough and some forests may be extirpated.[70] Increased fire frequency is predicted to result from an increase in the frequency and duration of droughts,[71] which could positively affect the regeneration of oaks.

Of particular interest are studies that consider herbivory. Some investigators predict climatic effects on some insect and mammalian herbivores and an array of ensuing impacts on biodiversity, outdoor recreation, property values, the wood products industry, and water quality.[72] In their scenario, warmer winter temperatures decrease the food requirements of deer, reducing their per capita impact on forest vegetation. However, because deer population size is governed by winter survival, their populations would most likely increase as a result of warmer winter temperatures, intensifying their collective impact on forests.

In sum, the current state of knowledge gives no reason to expect climate change to mitigate current adverse effects of deer nor to have an overall beneficial effect on the recovery of Pennsylvania's forest ecosystem structure and processes.

Impacts of deer and other factors on forest ecosystems — accommodating different views

The views of forest dynamics presented in the report are based on our review of the literature and thus represent a consensus scientific perspective. Minority or intermediate views are always possible in science. Theories on the effects of silviculture or acid rain can be incorporated into the A.R.M. program that we propose, as long as the proponents are willing to make quantitative predictions, complete with error estimates.

An alternative theory that could be tested as part of A.R.M. is the hypothesis that the effects of deer on forests in Pennsylvania are minor compared to the impacts of acid rain. William Sharpe and Joy Drohan at Penn State University have written, “The controlling factor in the extent of seedling damage is not deer browsing, but the degree of acidification stress and the susceptibility of the particular tree species in question to this stress. Regeneration plans that consider the elimination of only one stress, e.g., deer herbivory, will not successfully regenerate relatively acid-sensitive species such as sugar maple and northern red oak.”[73]

If correct, such a view would imply that reductions in deer densities will not assist forests to recover under ordinary soil conditions. This theory goes beyond the null hypothesis discussed in Chapter 2 by predicting that recovery will be good where soil chemistry is favorable or lime is added in the “right” amounts. According to Sharpe and Drohan, “Because root systems on low calcium to aluminum ratio soils [acidic soils] cannot deliver enough nutrients to sustain new growth after deer browsing damage, browsed seedlings do not rapidly replace lost stems and in many cases may not survive this additional stress. In the absence of deer, damage from insects and drought may result in similar consequences.”[74] It is a testable hypothesis and the proponents are enthusiastic about including it as part of an A.R.M. protocol.[75]

Another theory that could be tested in the proposed A.R.M. program considers both acid rain and deer as important. Under this theory, predictions about deer impacts would be modified according to soil fertility. According to Dr. David DeWalle at Penn State University, “Although deer browsing pressure is important, the innate fertility of the soil [e.g., acidity] hasn’t been considered sufficiently in management thinking. It is important to consider the chemical as well as physical condition of the soil, because a significant percentage of soils in Pennsylvania are poorly buffered.”[76]

Under this second theory, soil acidity might also be predicted to have its major impact on vegetation mortality and less impact than deer on regeneration failure. According to University of Göttingen botany professor Dr. Michael Runge, “forest decline always has two aspects: the dying of trees in the overstory and the failure of regeneration. In nearly all cases, the discussion of possible causes focuses on … soil acidification, defoliation, and especially with regard to regeneration failure, browsing by deer and competition by light and nutrients with a dense herbaceous vegetation, particularly the hay-scented fern. ... The negative effect of deer browsing is obvious and can be avoided only by reducing the deer population or by fencing."[77]

As we discuss in the next section, both of these alternate views on acid rain can be incorporated into one heuristic equation, where the dispute is channeled into determining values of a few coefficients. The same process could apply to a dispute about any other factor that influences forest dynamics.

Combining multiple stresses and responses into one equation

A useful way to think about the major theories — (1) deer overbrowsing, (2) other factors, and (3) deer-other factor interactions — is to think of both the stress on, and response of, a component of the forest ecosystem as a summation of four terms:

$$\textit{stress} = S_0 + A \times \textit{deer density} + B \times \textit{other factor level} + C \times \textit{deer density} \times \textit{other factor level} \qquad \text{Eq. 1}$$

where S_0 is the background stress, and A, B, and C are parameters. The last term, the interaction term, is a product of deer density and the level of a second factor, for example, acidic deposition or intensity of forest overstory thinning. The interaction term gets very large when both deer density and the level of the second factor are high.[78]

The actual measurable response of a forest tree, shrub, or herbaceous plant species to the above hypothetical combination of stresses would be some as yet undetermined function of Equation 1 over time. For some ranges of deer density and levels of another factor, the response would be linear. For instance, if deer overbrowsing and acidic deposition are taken as the factors of interest in forest degradation, the biomass of a particular plant species in a stand might be expressed as:

$$\textit{biomass} = B_0 - A_2 \times \textit{deer density} - B_2 \times \textit{acidity level} - C_2 \times \textit{deer density} \times \textit{acidity level} \qquad \text{Eq. 2}$$

In Equation 2, the deer-dominance theory is equivalent to the A-coefficients being much larger than all the others; the acid-rain dominance theory says that the B-coefficients are larger,[79] and the interaction theory says that the C-coefficients are larger.[80]

In some areas of Pennsylvania and for some species it may be possible to show, based on the results of exclosure or enclosure studies and other data, that one or more of the coefficients is near enough to zero that it can be omitted. On the other hand, data might show that all three coefficients are large enough to play an important role in some areas and for some species. The advantage of thinking of ecosystem stresses and responses in this way is that it keeps us from excluding the middle ground. All three theories might have some corner of the truth and be useful in some parts of the state and for some species.

Note that only in the case where the B-coefficients dominate can one discount the effect of deer as an ecosystem stress. Both the deer-dominance theory and the interaction theory predict deer impacts. If the interaction theory is correct, then control of deer is even more urgent in those areas where acid rain may have increased soil acidity.

Findings on other factors affecting forest recovery

(1) Forest recovery in Pennsylvania's remaining large forest blocks is affected by a variety of factors deliberately or inadvertently influenced by human activity. These include deer overbrowsing, acidic deposition from air pollution, logging practices, outbreaks of introduced insects and diseases, the incidence and severity of fire, and climate change. The most important of these is deer browsing. Fire often is required for the release of oak seedlings from competitors.

(2) Pennsylvania receives relatively high levels of acidic deposition. Over time, acidic deposition has decreased soil pH, accelerated losses from soil of the base cations calcium, magnesium, and potassium, and increased the mobilization of chemically active aluminum and manganese. Present evidence shows that one high-base-cation-demanding tree species, sugar maple, responds positively to lime application. There is evidence that some moderate- and low-base-cation-demanding species do not respond to liming.

(3) Non-sustainable timber harvesting methods (such as diameter-limit cutting), which do not ensure the reestablishment of a diverse forest, are in widespread use in Pennsylvania, particularly on forestlands in non-industrial private ownership. Non-sustainable harvesting interacts with deer browsing in ways that severely endanger the long-term health and productivity of Pennsylvania's forests.

(4) The impact of climate change as a result of global warming is uncertain. Research on the topic that pertains specifically to Pennsylvania so far is almost nonexistent.

Recommendations on factors affecting forest recovery

(1) Deer management should focus on managing the ecosystems of which deer are a part. Deer densities in Pennsylvania's major forested areas should be brought down to levels that will allow the restoration of full forest structure, diversity, ecological processes, and ecosystem function.

(2) Serious efforts should be made by Pennsylvania officials to further limit nitrate and sulfate emissions that affect Pennsylvania forests. The role of acidic deposition on forest health and growth should receive increased study.

(3) There should be an increased effort to educate non-industrial private landowners concerning the negative impacts of non-sustainable harvesting methods on the future health and productivity of their own lands and all of Pennsylvania's forestlands. Governmental bodies should take steps to curtail the use of non-sustainable harvesting methods on public lands.

Endnotes

[1] Driscoll et al. 2001

[2] Charles 1991

[3] Driscoll et al. 1980; Cronan and Schofield 1990

[4] Driscoll et al. 2001

[5] Cronan and Schofield 1990

[6] Levine and Ciolkosz 1988

[7] Drohan and Sharpe 1997

[8] DeWalle et al. 1999a, 1999b

[9] Craig and Friedland 1991; Shortle et al. 1997

[10] R. E. Latham, personal observation

[11] Long et al. 1997

[12] Horsley et al. 2000; Drohan et al. 2002

[13] Marquis 1975

[14] Tome 1854; Abrams 1992; Lorimer 1993; Brose et al. 2001

[15] Crow 1988; Dickson 1991

[16] Lorimer 1984

[17] Hanson 1986; Pubanz and Lorimer 1992

[18] Crow 1988

[19] Liming and Johnson 1944; Sander 1972

[20] Johnson and Jacobs 1981; Johnson et al. 1989; Lorimer 1989; Loftis 1990; Nowacki et al. 1990

[21] Nowacki et al. 1990; Lorimer 1993; Brose et al. 2001

[22] Brose and Van Lear 2004

[23] Lorimer 1993

[24] Van Lear and Watt 1993

[25] Brose and Van Lear 1998; Brose et al. 1999; Lanham et al. 2002

[26] Deer Management Forum, personal observation (see Appendix C)

[27] E.g., Hughes and Fahey 1991

[28] Duffy and Meier 1992

[29] Meier et al. 1995

[30] Gilliam and Roberts 2003

[31] Elliott and Loftis 1993; Johnson et al. 1993

[32] Duffy 1993a, 1993b; Bratton 1994

[33] Meier et al. 1995

[34] Gilliam et al. 1995

[35] The study used the Shannon-Wiener index of diversity, which increases both with species richness and with evenness among the species in the number of individuals present.

[36] Ford et al. 2000

[37] Ruben et al. 1999

Endnotes

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[71] He et al. 2002; Ayres and Lombardero 2000

[72] Ayres and Lombardero 2000

[73] Sharpe and Drohan 1999: p. 200

[74] Sharpe and Drohan 1999: p. 200

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[77] Runge 1999: p. 144

[78] If the interaction term is very large, then the coefficient *C* must be positive. If, on the other hand, the interaction term is less than the sum of the other two terms, then *C* could be negative, indicating a saturation effect.

[79] Actually, based on the discussion of the acid-rain-dominance theory, there is an allowance for an interaction term as well.

[80] This equation is meant to be illustrative. From a statistical research perspective, one might add terms involving the square of deer density and the square of the acidity level to account for possible nonlinear effects. One might also add terms involving a third measurable stressor, e.g., tree-harvest intensity.

Chapter 7. Recovery of Pennsylvania's Forest Ecosystems from Deer Overbrowsing

A forest is more than trees

Trees are certainly the most conspicuous part of the web of life that comprises a forest ecosystem. But, whereas trees may dominate the structure of a forest, they are intricately linked to the many other living and non-living components. All green plants, from canopy trees to the diminutive mosses on the forest floor, contribute to total primary productivity through photosynthesis, the means by which energy enters the system.

Mycorrhizal fungi, which live on the roots of most plants and have a mutually beneficial relationship with their hosts, increase the uptake of mineral nutrients and water by trees. Squirrels "plant" the seeds of oak, beech, and hickory trees when they cache the nuts and fail to return.[1] Birds are also important in distributing seeds of many species.

Trees such as yellow-poplar, cucumbertree, and flowering dogwood are dependent on insects to pollinate their flowers. Uncounted species of invertebrates, fungi, and bacteria help to decompose organic matter that accumulates on the forest floor, building soil and releasing minerals for recycling. Insects that are predators or parasites of plant-eating insects also contribute to the balance of productivity and herbivory in forests. The adult form of many insect parasitoids, which as larvae help keep populations of destructive insects in check, feed on nectar and pollen produced mainly by herbaceous plants.

Birds feed on insects, helping to keep leaf damage to a minimum and thereby stimulating the growth of trees.[2] Some birds, such as ovenbirds and eastern towhees, nest and feed in the ground layer. Reduced cover in this forest stratum increases nest predation and decreases the ability of birds to raise their young successfully.[3] Other species, such as eastern wood-pewee, indigo bunting, and black-and-white warbler, which use the intermediate layers of the forest, have declined in heavily browsed forests.[4]

All the layers of the forest intercept rainfall, reducing erosion and facilitating percolation and groundwater recharge. Herbaceous plants on the forest floor help to hold soil in place, further reducing erosion. Erosion leads to losses of soil and nutrients from the ecosystem. Herbaceous plants also shade the soil surface, moderating temperature and moisture levels and creating microhabitat for seed germination.

Soil invertebrates, fungi, and microorganisms are also vital links in many food "chains" that make up the forest ecosystem's trophic web. As decomposers of organic debris, they control the accumulation of wastes and recycle minerals. Shifts in species composition in the above-ground vegetation affect the subterranean community by altering the nutrient content as well as the speed at which litter is broken down and thus the thickness of litter and humus accumulation.[5] These in turn affect seed-bed properties, erosion rates, and soil chemistry, including pH.

Each layer of the forest, from the canopy to the soil, provides habitat for a group of specialized plants, animals, and micro-organisms. Canopy trees link it all together, starting as seeds deposited on the forest floor, becoming seedlings in the herbaceous layer, growing into the shrub and subcanopy layers, and eventually reaching the canopy.

Overbrowsing by deer has been shown to impact tree, shrub, herbaceous, bird, and small mammal components of the forest ecosystem and cause major changes in forest structure (see Chapter 5). Although ecosystem function is harder to measure, browsing-caused changes to mineral recycling have also been documented.[6]

Values, forest integrity, and management goals

It is the value judgment of Forum members that the greatest overall benefit to the widest range of stakeholders would be served by restoring forest structure, diversity, ecological processes, and ecosystem function to a state similar to the conditions that prevailed in the relatively recent past. This is the “philosophical” basis for the management goals we outline in this report. The preponderance of scientific opinion attests that the current high densities of white-tailed deer have had highly detrimental effects on forests in Pennsylvania and much of the eastern United States. Moreover, until deer populations are reduced and maintained at lower levels, it will not be possible to restore key elements of forest health. For each of these elements, management goals include (but are not limited to):

(1) **Structure**

- bringing back the missing or impoverished subcanopy, shrub and herbaceous layers
- making it possible for tree seedlings and saplings to establish, survive, and eventually replace dead and fallen canopy trees
- reestablishing habitat for birds, mammals, and other wildlife that depend on the subcanopy, shrub, and herbaceous layers
- recovering levels of forest-floor moisture, humidity, and coarse woody debris that are beneficial to salamanders, frogs, and many other animals dependent on moist, protected environments

(2) **Diversity**

- preventing losses of entire populations of native species, particularly of plants favored as food by deer

(Box continued on next page.)

Prospects for recovery of forest ecosystems

The choice of bringing back the forest understory and ensuring the continuation of a rich overstory layer into the future is not a scientific choice but a values choice (see box above). In our judgment, the greatest overall benefit to the widest range of stakeholders would be served by restoring forest structure, diversity, ecological processes, and ecosystem function to a state similar to the conditions that prevailed in the relatively recent past.

(Box continued from previous page.)

- bringing species that are imperiled by vegetation overbrowsing back from the brink of disappearing
- preserving genetic diversity within individual species, which is essential for them to adjust and survive in the face of changing conditions, by fostering robust, rather than marginal, population numbers
- sustaining the full variety of indigenous forest types

(3) **Ecological processes**

- reestablishing seed sources and replenishing the seed bank
- curtailment of competitive exclusion of seedlings by the few plant species that have proliferated because they are unpalatable to deer or resilient to overbrowsing
- cutting back competition by deer for acorns and nuts that other wildlife species depend on for food, including, indirectly, the predators that feed on mast-consuming animals
- restoration of plant species required by animals whose food or habitat requirements are narrowly specialized
- abatement of probable indirect effects of high deer density, such as heightened severity of gypsy moth outbreaks and Lyme disease infection rates

(4) ***Ecosystem function***

- rebuilding "ecosystem services" adversely affected by vegetation losses, including erosion control, soil development, sediment retention, nutrient assimilation, habitat for other wildlife species, and opportunities for nature appreciation, education, and research

It is not clear how quickly restoration of full forest structure, species diversity, and function can be achieved once deer numbers are reduced to appropriate levels; it certainly will not happen quickly. Nor is it clear how low deer numbers will need to be to achieve recovery of the forest ecosystem. Results of the 10-year enclosure study carried out by the U.S. Forest Service's North-eastern Research Station at Irvine, Pennsylvania, indicated that trees, brambles, and birds exhibited statistically significant increases in either abundance or diversity in reduced-deer-density plots after 10 years.[7] One study in Pennsylvania addressed recovery rate of witch-hazel in fenced exclosures.[8] Another study carried out in West Virginia tracked the recovery of two populations of showy lady's-slipper after exclosures were erected. At one site where deer had removed major portions from 65% to 95% of the stems over 3 years, recovery of pre-herbivory stem heights took 9 to 10 years and recovery of flower production and leaf area required 11 to 12 years. However, even then the number of stems was only 28.5% of the pre-herbivory population size. At the second site where deer had grazed 9% to 46% of the stems over 3 years, flowering ceased for one year and pre-herbivory mean stem height, leaf area, and flower production were restored after only 2 years.[9]

A more-detailed study of the recovery of over-grazed woodlands in Britain involved fenced plots maintained as grazed (one fallow deer per 2.5 acres) and ungrazed (zero deer) treatments.[10] Vegetation in the plots was measured at 6, 14, and 22 years. By 6 years after the fences were installed, there were clear differences between the treatments; in the ungrazed plot the browse line had nearly disappeared and a dense layer of *Rubus* had developed. The ground-layer vegetation in the grazed plot and surrounding forest continued to be dominated by bracken fern, grasses, and sedges. The density and diversity of the lower layer of the forest in the deer-free plot decreased by the later measuring periods as a result of shading by the vigorous layer of tree seedlings and saplings that developed in the absence of grazing. Increases in the species diversity of small mammals and selected invertebrates were detected in the ungrazed plot 20 years after initiation of the study.

The length of time that a forest has been subjected to overbrowsing and the extent to which a dense layer of unpalatable vegetation has developed are major variables that will influence recovery time. Such "legacy effects" of overbrowsing also include declining seed availability and reduced root-sprouting potential. There has been little or no research on certain key biological issues such as how long various native plant species persist as live roots in the face of long-term chronic browsing or how likely such root sprouts are to succeed, if even deer densities were to decrease, especially at the low light levels of closed-canopy stands. Most research related to factors that affect the ecological succession of forest trees has focused on species and forest types of interest to the wood products industry (see Chapters 5 and 6). Thus, to make predictions of the recovery of biological diversity and ecosystem processes, it is fruitful in some cases to draw analogies from the silvicultural research. For example, it has been shown repeatedly that, where a tree seed source remains (adult trees and the soil seed bank), treatments such as fencing deer out to allow tree seedlings to grow above the browse line or herbicide treatment to remove competing ferns can hasten the regeneration of canopy trees.

However, fencing for 6 to 7 years, as is the current practice, does not provide long-term protection for vegetation in the lower levels of the forest. For plants that never outgrow the reach of deer, a more permanent solution to reducing deer impact is required to effect ecosystem recovery. Highly preferred shrub and herbaceous species may require extremely low deer numbers to recover their former levels of diversity and abundance. In a collaborative paper outlining a strategy for restoring old-growth forests in Pennsylvania, foresters from The Nature Conservancy and the Pennsylvania Department of Conservation and Natural Resources cite deer overabundance as one of the problems that will have to be overcome.[11] With the exception of the two studies cited above, little research is available that directly addresses the recovery of forest understory species from overbrowsing. However, research on the recovery of herbaceous components of the forest after natural disturbances or logging suggests that it can be a long, slow process (reviewed in Chapter 6 under "Impacts of logging on forest understory plant species diversity").

Slow growth rates and loss of propagules limit recovery potential

A major impediment to the recovery of the lower layers of the forest is a lack of propagules (seeds, spores, and vegetative reproductive structures such as bulblets). In areas such as northwestern Pennsylvania where overbrowsing has been a factor since the 1920s,[12] there may be few local sources of propagules remaining. Furthermore, most forest herbs do not have long-distance dispersal mechanisms.[13] In one study, at least half of 26 forest herb species investigated in eastern North America relied on vegetative reproduction and only 9 were confirmed to reproduce primarily by seed.[14] The study noted that many deciduous forest herbs lack any specialized seed dispersal mechanisms; many seeds land where the senescing stem falls. Another investigation of seed dispersal adaptations of herbaceous plants in West Virginia forests showed that ant-dispersed species constituted 30% of the herbaceous flora and included some of the most common forest herbs such as spring-beauty, wild-ginger, sharp-lobed hepatica, twinleaf, bloodroot, large white trillium, and perfoliate-leaved bellwort.[15] These species also are all members of Pennsylvania's forest flora.

Slow growth rates

Most forest-floor plants that spread primarily by vegetative means do so through the growth of horizontal underground stems (rhizomes), often at rates that are slow enough to severely limit their recovery potential. A study of the structure and rate of growth of the rhizomes of 412 species of forest herbs and dwarf shrubs in the New Brunswick-Nova Scotia border region revealed that annual growth increments ranged from barely detectable to more than 3 feet.[16] Measurements of rhizome elongation in 11 species of forest herbs in the central and southern Appalachians showed annual rates ranging from 0.06 inch in large white trillium to 3.25 inches in may-apple.[17]

Reduced seed production

In addition to limited seed dispersal mechanisms, rates of seed production are often affected in deer-impacted forests. In one study the forest herbs jack-in-the-pulpit, showy orchis, Solomon's-seal, and bellwort were found to have higher rates of seed production when protected from browsing pressure in exclosures[18] because deer often selectively remove the flowering or fruiting stem even when they do not destroy the entire plant. Reduced sexual reproduction in browsed plants has also been documented in studies of large white trillium,[19] American yew,[20] glade spurge,[21] and Canada mayflower,[22] and has been observed in yellow fringed-orchid, hobblebush, and nodding trillium.[23]

Propagule dispersal from refugia

Local refugia may be an important source of propagules to initiate the recovery of forest-floor species. Boulder tops, cliffs, rock outcrops, and other inaccessible areas such as boulder fields support small patches of plants out of the reach of deer and serve as islands of diversity in an otherwise depleted landscape.[24]

Seed production and dispersal by canopy trees

Propagules come from a variety of sources, including new seed dispersed from overstory trees, seed lying dormant in the forest floor, root suckers, and stump sprouts. Periodicity of seed production by overstory trees varies greatly among species.[25] Sugar maple has good seed crops at 7 to 8-year intervals in the unglaciated northern Allegheny Plateau region of Pennsylvania, compared with 2 to 3-year intervals in New England and the Great Lakes states. Seed supply can be an important barrier to sugar maple regeneration. Yellow-poplar has good seed crops almost annually, but seed viability is seldom more than 5%. American beech has a good seed crop about 1 year in 6, white ash at intervals of 5 or more years, sweet birch and yellow birch at 1 to 3-year intervals, black cherry and red maple at 2 to 3-year intervals, eastern hemlock at 1 to 2-year intervals,[26] and eastern white pine[27] and oaks at 3 to 5-year intervals. However, bumper crops of acorns (called mast years) occur irregularly and may be as infrequent as 10 years apart. It is commonly believed that significant quantities of oak seedlings originate only in mast years, when quantities in excess of those consumed by mammal and insect predators are produced.[28] These seedlings are generally from acorns cached but not retrieved by small mammals. Hickories have good seed crops at 1 to 3-year intervals and are influenced by the same factors as oaks.[29]

Losses to seed predation

Seeds are an important dietary component of various species of mammals, birds, and insects living in Pennsylvania's forests. A large fraction of many plant species' seed production is regularly lost to predation. In fact, seed predation is thought to be the agent of selection that resulted in episodic, synchronous masting by oaks and certain other species.[30] By interspersing several years of low production between each bumper crop, the trees keep populations of animals that specialize on acorns relatively low.

The majority of tests of the effects of seed and seedling predation have been conducted in old fields.[31] These studies show that small mammals have distinct preferences in food choice[32] and predation risk often rises with increased seed size.[33]

Among forest plant seeds, oak acorn predation has been well studied because of the importance of acorns as food for a variety of small mammals, deer, turkeys and other birds.[34] Losses of 90% of a year's seed crop to insects and other animals is typical.[35] Such evidence suggests that destruction of acorns by animals potentially can be a limiting factor for regeneration of oaks in some locations.[36] However, several animal species also benefit the trees in their role as scatter-hoarders. By burying acorns in well-distributed caches, small mammals and blue jays facilitate seed germination.[37] A review of many studies over a large geographic area suggested that a lack of oak seedlings might occur locally in some years, but the lack of seedlings was not the most important factor limiting oak regeneration in a more global sense.[38]

Acorn-infesting insects are the most important and most studied group of pests affecting oak regeneration.[39] One or more of the 22 acorn weevil species in the genus *Curculio* recorded in the United States[40] affects virtually all of Pennsylvania's oak species. Larvae hatching from eggs laid in niches beneath the shell may consume most of the nut within a few weeks. Embryos in infested acorns that escape damage may germinate, but seedlings grow slower than those from uninfested acorns.[41] The rate of infestation is variable, but has exceeded 90% in some northern red oak collections.[42] Infestation rates of filbertworm are much lower than acorn weevils, but filbertworms have been responsible for large losses in low-production years;[43] damage is caused by larval feeding and is usually lethal to infested acorns. The pip gall wasp and stony gall wasp also infest and kill intact acorns.[44] Damaged acorns also may be invaded by other insects; the best known with this mode of action are *Conotrachelus* acorn weevils and the acorn moth.[45] These insects attack otherwise healthy germinating acorns.

Seed banks

Seeds that drop to the forest floor and become buried in decomposing leaves and upper soil layers (collectively called the seed bank) are an important source of regeneration. Seed longevity in the soil varies considerably among species. Most of our knowledge about seed longevity comes from silvicultural research. For example, black cherry, white ash, and yellow-poplar seeds survive in the seed bank for 3 to 5 years. Red maple, sweet birch, yellow birch, cucumbertree, and eastern hemlock seeds live for 1 or 2 years. Sugar maple and American beech seeds have no storage life; the seeds are shed in the fall and either germinate the following spring or not at all. Lack of seed survival in the seed bank beyond the first winter is common to all oaks and hickories. Flowering dogwood, blackgum, and mountain-laurel have little or no storage life. Most species with long-lived seeds are early-successional plants that rarely persist beneath a forest canopy, for example, pin cherry, whose seeds remain viable in the forest floor for periods of 30 to 50 years or more.[46] Almost nothing is known about seed longevity of the majority of Pennsylvania's 103 native tree species, 176 native shrub species, or the rest of the 2,151 kinds of vascular plants native to the state.

The seed bank — live seed that remains dormant in the soil for varying amounts of time — has a potential role in the revegetation of deer-damaged forests. However, studies of the seed bank composition in a temperate, deciduous old-growth forest in Quebec revealed that vernal herbs (spring wildflowers that complete the entire aboveground portion of their life cycle in April and May) were not represented.[47] The most frequent seeds were those of sedges, brambles, white snakeroot, and bush-honeysuckle, all common plants of Pennsylvania forests. Overall, woody species dominated the seed bank in areas with a closed canopy; herbaceous species were more prominent in more open parts of the forest.

In a chronosequence study of the recovery patterns of understory herbaceous plants following 10, 20, and 35 years of forest restoration on former cottage and road sites in southern Ontario, where many years of human use had completely eliminated native understory herbs, native summer and fall-blooming species with wind or vertebrate-dispersed seeds dominated the restored sites.[48] Although total plant species diversity of restored and reference sites was similar, many spring-flowering forest herbs with ant- or gravity-dispersed seeds remained absent from disturbed sites even after 35 years. All but one of the restoration sites in this study were within 65 feet of intact forest. In another comparative study in central New York State, 30 of 39 forest herb species were less frequent in successional forests on abandoned agricultural sites than in adjoining undisturbed forest, and, for several species, frequency declined with distance from a mature forest source area.[49] It is clear that seed dispersal, not seed banking, is the main source of propagules in forests where adult forest-floor plants have been absent or greatly reduced for prolonged periods.

A comprehensive review of the scientific evidence regarding the presence of forest herbs in forest seed banks in eastern North America concluded that they are very rare or completely lacking.[50] Only one study of those reviewed showed any forest herbs to be present in the seed bank and those were species that were present as adults in the immediate vicinity of the samples and thus may not have been long-term components of the seed bank.

Root and stump sprouting

Some tree species, notably American beech, quaking aspen, and bigtooth aspen, reproduce abundantly from root suckers. A few native tree species can reproduce from seedling sprouts and stump sprouts when stems are cut or top-killed.[51] For example, red maple, some oaks, and American chestnut are well known as prolific sprouters, sweet birch and yellow birch seldom have successful stump sprouts, and yellow-poplar is a poor sprouter. Stumps of small trees less than about four inches in diameter sprout more frequently than stumps of larger-diameter trees. The proportion of stumps that sprout decreases as stump diameter increases and is variable among species. For example, among oak saplings, the percentage of sprouting stumps is 100% for chestnut oak, scarlet oak, and northern red oak, 85% for black oak, and 80% for white oak.[52] Because of the oaks' strong sprouting ability, oak seedlings and saplings can survive browsing, breakage, drought, and fire. Top dieback and resprouting of seedlings typically occurs a number of times. Each successive seedling sprout is taller and the root system is stronger. When oak regeneration is successful, seedling sprouts and stump sprouts usually form much of the new stand.

Little research has focused on the dynamics of root and stump sprouting in forest understory shrubs as they recover from disturbance. Shrubs of some species are killed outright by heavy browsing but others may persist for varying lengths of time as roots with gradually declining potential to regrow viable stems and leaves. The study on witch-hazel mentioned earlier is the only one published to date that has addressed this issue for a shrub.[53] In a northern hardwood stand in northeastern Pennsylvania exhibiting regeneration failure of all woody species due to heavy deer browsing, witch-hazel roots sustained their ability to produce viable sprouts after as many as 6 years with no live stems.

Role of infrequent long-distance dispersal events

Although the limited dispersal range of most forest herbs is well documented, occasional exceptions have been found. In a study of a common forest herb, wild-ginger, the mean distance ants (the principal seed-dispersal agent) moved seeds was 5 feet.[54] Given that annual rate of movement, wild-ginger could have moved only 15 miles since the beginning 16,000 years ago of the last glacial maximum from its southern refugia. Even using the single longest seed carry observed in the study (115 feet) as a basis for calculation, the maximum distance that could be accounted for was only around 350 miles. However, the range of wild-ginger today extends 800 miles north of its glacial-era refugia. Infrequent long-distance seed dispersal events that created a steppingstone-like pathway of movement are the most plausible key to this puzzle. Another investigator who created a similar model for tree migration has stressed the importance of the sparse “tail” of the seed shadow, rather than calculated average rates of movement, to account for apparent migration rates.[55]

Infrequent long-distance dispersal events may play a small role in restoring diversity in recovering forests. However this influence is more likely to be felt in large areas and over long time spans than in small isolated sites or short time spans due to the randomness of the effect and the time required to exert its impact.

Site quality limitations on growth rates

The rate of forest recovery depends partly on the rates of survival and growth of the constituent plants. Abiotic environmental stresses limit these rates. In Pennsylvania such stresses include shade, droughty soils, prolonged soil saturation, shallow or rocky soils, low soil-nutrient availability, fire, frost pockets, wind exposure, short growing season, flooding, and ice-scour. These stresses slow the growth and curb the reproductive output of all plants that they fail to kill outright. Many of Pennsylvania's 2,151 kinds of native vascular plants[56] are adapted to survive particular kinds of stress. However, there is a trade-off. Adaptation to stress is normally coupled with inherently slow growth rates.[57] Although stress-adapted plants nearly always grow best in favorable, low-stress sites, they are invariably outcompeted in such sites by faster-growing (but stess-sensitive) species.

The amount of light at the forest floor is one of the most important factors limiting regeneration and recovery rates. The ability to continue photosynthesis at low light levels, termed shade tolerance, determines in what kind of light environments a species is likely to become established.[58] Most herbaceous plants and shrubs adapted to live in forests are moderately to highly shade-tolerant; the same is true of understory trees such as striped maple, flowering dogwood, downy serviceberry, Allegheny serviceberry, American hornbeam, and eastern hophornbeam. Among native trees, eastern hemlock, American beech, and sugar maple are among the most shade-tolerant species and can become established in the low light of uncut stands, if intermediate- and ground-level vegetation are sufficiently sparse or patchy. Red maple, sweet birch, yellow birch, cucumbertree, eastern white pine, oaks, and hickories are examples of tree species that are intermediate in shade tolerance; they tend not to become established or persist where understory plants provide another layer of shade beneath the canopy. Black cherry, white ash, and yellow-poplar are examples of shade-intolerant tree species. They germinate in uncut stands but survive no longer than a few years unless additional light is supplied, so turnover (mortality and new germination) is high in the absence of canopy disturbance.

The seedbed or forest floor condition at the time of germination has an important influence on the ability of seedlings of some species to become established. Most early-successional herbaceous and shrub species and some trees, for example, red maple, white ash, sweet birch, yellow birch, and eastern hemlock, benefit from forest floor disturbance. Over their evolutionary history such species regenerated best in the mineral soil exposed by fallen trees, landslides, scouring by floods, excavations by animals, and fires severe enough to burn away organic soil layers. Many larger-seeded plants are relatively indifferent to seedbed disturbance, establishing nearly as well on disturbed or undisturbed seedbeds as long as surface soil moisture is high. This category includes shrubs such as American hazelnut, beaked hazelnut, dwarf chinkapin oak, and scrub oak, and trees such as black cherry, sugar maple, American beech, eastern white pine, black walnut, butternut, hickories, and oaks. The strong radicle (embryonic root) of these large-seeded species is capable of penetrating soil organic layers to reach mineral soil. However, acorns, nuts, and other seeds on the soil surface are a favored food of a variety of insects, small mammals, wild turkey, other birds, and deer. Most oak and hickory seedlings originate from seeds that are buried by small mammals and not retrieved,[59] often because of the death of the individual that cached them.

Despite the potential importance of soil chemical properties in limiting forest recovery, nutrition of forest plants, including tree seedlings, has received relatively little study.[60] This perhaps is due to the relatively large effects of herbivory, light, and moisture compared with those of nutrition; for example, there presently are no published cases of outright regeneration failure of any eastern North American tree species due to naturally occurring soil chemical properties. Although optimum nutrient requirements are not known for most Eastern forest species, including trees,[61] several observational studies of the distributions of tree and shrub species suggest the relative positions of species along a continuum of soil nutrient status. Sugar maple, white ash, American basswood, flowering dogwood, and hobblebush tend to occupy sites with relatively high levels of exchangeable calcium and magnesium and relatively low levels of aluminum and manganese.[62] Yellow-poplar, yellow birch, eastern hemlock, and American yew occupy sites with moderate calcium and magnesium concentrations. Red maple, northern red oak, white oak, American beech, black cherry, sweet birch, eastern white pine, and striped maple tend to be more abundant on sites with low levels of these two base cations.[63]

Fertilizer studies have been used to evaluate possible deficiencies of soil nutrients on the premise that a response will be obtained only if a nutrient is scarce enough to limit growth. Fertilization will not increase productivity when there are no nutrient deficiencies or when growth is limited by other factors, usually sunlight or moisture availability. Nitrogen, phosphorus, and potassium (the nutrients required by plants in greatest quantity) have been the most widely tested soil nutrient amendments, followed by magnesium and calcium.[64] These studies suggest that nitrogen is by far the primary growth-limiting nutrient in eastern North American forests, but response from phosphorus frequently occurs after the nitrogen deficiency is overcome. For example, fertilization of black cherry with nitrogen and phosphorus resulted in large increases in height of seedlings (4 to 6 feet in the first year) and diameter and basal area growth of dominant and co-dominant overstory trees.[65] Addition of nitrogen increased the survival of eastern hemlock seedlings, but decreased the survival of red maple and eastern white pine.[66] Nitrogen addition reduced the diameter and basal area growth of sugar maple.[67] Few responses to potassium have been found, except in areas of Ontario and Quebec where bedrock levels of calcium and magnesium are very high, creating ionic competition for potassium uptake at the root surface.[68]

Forest liming (addition of calcium and, in some cases, magnesium) has been used to address a variety of nutritional constraints on tree growth and health and to accelerate stand growth.[69] Lime treatments often have been included to moderate soil acidity (thereby reducing chemical activity of potentially toxic aluminum and manganese) or augment supplies of calcium and magnesium.[70] Application rates have ranged from 0.09 to 10 tons per acre, usually of dolomitic limestone (which is high in both calcium and magnesium), and have been evaluated over time periods from 6 weeks to 15 years after treatment. Significant differences in the nutritional status of soils and foliage have been reported following lime application, though reports of positive tree growth responses are less frequent and highly species-specific.[71] For example, in a study in northwestern Pennsylvania, sugar maple survival, crown vigor, diameter and basal area growth, and flower and seed production had significant responses to the addition of 10 tons per acre of dolomitic limestone 8 and 10 years after treatment compared with unlimed trees, but there was no response by black cherry and American beech.[72] In the same study, sugar maple seedlings survived better, but height growth was not significantly improved by lime 10 years after treatment and there were no differences in basal area of black cherry, pin cherry, American beech, striped maple, or sweet birch saplings in the 1- to 4-inch-diameter class compared with unlimed areas 15 years after liming.[73] Significant increases in germination of pin cherry, black cherry, *Rubus*, grasses, and sedges were observed on limed plots in the first growing season,[74] but the response was attributed, in part, to increased production of nitrate nitrogen from organic matter involving calcium- or magnesium-limited microorganisms.[75] Liming of planted and indigenous northern red oak seedlings gave mixed results; liming did not improve survival or height growth of planted seedlings 3 years after treatment.[76] Addition of dolomitic limestone to indigenous northern red oak seedlings on fenced and unfenced plots resulted in increases in seedling height 2 years after treatment on limed plots, however the best treatment (fence + lime) resulted in only 1.6 inches of additional height growth, on average.[77]

Other elements of the forest ecosystem

Forest structure

Another aspect of forest ecosystem recovery, in addition to the restoration of native species diversity, is the reestablishment of a healthy size-class distribution in shade-tolerant canopy trees. Forests that have been reduced to mature canopy trees and a ground layer of herbaceous species that are not preferred by deer are common throughout Pennsylvania and other areas long subjected to heavy browsing. These forests lack the shrub, tree seedling and sapling, and subcanopy components that are important structurally and also provide the replacement trees for the canopy. In a study in northern Wisconsin, it took an estimated 27 years of protection from heavy browsing to reestablish a normal population structure in eastern hemlock.[78] The researchers warned that in areas subjected to longer periods of overbrowsing, where older size classes were missing, recovery could take as long as 70 years before normal population structure was reestablished.

Birds

Alterations in bird species and abundance have been documented in heavily browsed forests.[79] The results of several enclosure and exclosure studies have linked the composition of forest bird communities to structural changes in forest habitat caused by high-density deer populations. In a study comparing enclosures with deer densities of 10, 20, 38, and 64 deer per square mile in northwestern Pennsylvania, species richness of forest understory birds increased in the plots with the lowest deer density within 10 years.

In a study of breeding bird populations at eight sites in Virginia,[80] 5-acre plots were established at each site; half were fenced and half remained unfenced. Vegetation measurements were made three times over a 9-year period; bird population data were collected by mist netting annually in June. Deer density in the region was in excess of 10 deer per square mile throughout the study. Fenced plots responded quickly to deer exclusion by developing increased density in the understory as the grasses that initially dominated the forest floor were replaced by brambles and tree saplings. By as little as 1 to 2 years into the study, bird species composition in the exclosures had shifted from birds such as chipping sparrows that prefer more open understory to indigo buntings, hooded warblers, and ovenbirds, all of which benefit from denser shrub and understory layers. Recovery may have been faster at these sites because they lacked the dense layer of hay-scented fern and New York fern frequently present in stands subjected to canopy thinning and overbrowsing in Pennsylvania.

Amphibians

Among vertebrates, amphibians rival birds and mammals in their importance in forest ecosystems. The biomass of salamanders alone in a northern hardwood forest in New Hampshire was twice that of resident birds during the breeding season and almost equal to that of small mammals.[81] Salamander abundance and species richness increase southward toward the world's center of salamander diversity, the southern Appalachians, where the average salamander biomass per acre is comparable to, or larger than, that of all other vertebrates combined.[82] Amphibians play a key role in ecosystems by exploiting prey that are too small for larger vertebrates, thereby converting large quantities of biomass and energy from small invertebrates into a prey size available to reptiles, birds, and mammals.[83] Because their larval stage is aquatic, they also exploit the high productivity of temporary pools and other wetlands and provide an energy pathway to terrestrial animals and other organisms. Amphibians have attracted much interest as sensitive indicators for monitoring ecosystem integrity in the face of disturbance.[84]

A comprehensive review in 1995 of 18 studies that examined the effects of forest disturbance (clearcutting) on amphibians showed drastic short-term declines in every case, with a median loss of nearly three-quarters of total abundance.[85] The results are more varied among studies of long-term effects. Research in the southern Appalachians demonstrated that recovery times depend in part on temperature and moisture availability. Comparison of salamander abundance in wet, high-elevation forests showed significant effects of forest age since clearcutting up to about 60 years[86] but in dryer, warmer, lower-elevation forests effects of age on both abundance and diversity were significant up to 120 to 200 years.[87] Limited results from studies in the Northeast are consistent with the high-elevation results from farther south; studies in New York,[88] New Hampshire,[89] and southern Quebec[90] suggested recovery times of between 30 and 60 years.

The literature on amphibian recovery from deer overbrowsing is nonexistent.[91] However, one conclusion from studies on post-clearcutting forest succession is highly pertinent to the question of how and to what extent deer overbrowsing affects amphibians. Salamander recovery times varied, not with forest age directly, but with changes in microhabitats that are associated with forest succession.[92] As the forest regrows, there are increases in coarse woody debris, foliage height diversity, amount of canopy cover, and litter depth — all of which tend to foster and stabilize the cool, moist conditions that are essential for all terrestrial amphibians. Deer overbrowsing adversely affects most, if not all, of these elements of forest structure (see Chapter 5).

Other factors that may affect recovery of forest ecosystems

Are nineteenth and twentieth century forest removal and other large-scale disturbances responsible for some or all of the changes in the forests?

Given research reports describing long recovery times following severe disturbance[93] it is necessary to ask to what extent the depauperate condition of much of Pennsylvania's forest might be due to long-term effects of the complete forest removals that occurred in the state around the end of the nineteenth century. One possibility is that the absence of some species is due to the successional status of the forests. Little old growth exists and the bulk of the forests are 70 to 110 years old. It is to be expected that the abundance of species for which old-growth forests are the principal habitat (e.g., certain beetles,[94] fungi,[95] lichens,[96] mosses, and liverworts[97]) would be reduced or species assemblages that are characteristic of long-undisturbed forests (e.g., vascular plants[98] and salamanders[99]) would seldom occur together or in high population numbers.

Although of theoretical interest for some species, the residual impact of the forest removals of the late nineteenth and early twentieth centuries cannot explain the overall trends in forest changes described in this report. Exclosures clearly show that many species that have essentially disappeared from large areas of the forest can be found where deer have been excluded. A one-acre exclosure built in the 1940s on State Game Land 30 in McKean County, Pennsylvania, and maintained through the present[100] provides a vivid contrast with the surrounding browsed forest. Species such as red-berried elder, alternate-leaved dogwood, purple trillium, Solomon's-plume, rose mandarin, white baneberry, ginseng, violets, Canada mayflower, and brambles are abundant within the fence[101] providing evidence that 60 years ago these species existed in the forest in abundance, in contrast to their present-day, extremely sparse distributions. Scattered refugia such as large boulders in the Allegheny National Forest just south of Sheffield, Pennsylvania, and cliffs, rock outcrops, and boulder fields in northeastern Pennsylvania similarly demonstrate the potential for increased plant diversity where deer can't reach. These "rock gardens" contain numerous blooming plants of bluebead lily, Solomon's-plume, fly-honeysuckle, wood fern, mountain maple, wild currants, and American yew, which decades ago practically disappeared from the forest floor.[102]

Has fern dominance created alternative persistent states?

It has been suggested that long-term overbrowsing may create alternative persistent states in forest ecosystems that are to some degree self-perpetuating.[103] The development of a dense cover of unpalatable species such as hay-scented fern, New York fern, striped maple, and root sprouts of American beech has occurred in areas where deer have continually removed other vegetation and the canopy density permits some light to reach the forest floor. Because of their rhizomatous growth habit, the ferns form a dense, continuous foliage layer near the ground surface that is difficult for many other species to penetrate. In such situations decreasing the deer numbers alone does not necessarily result in the recovery of other vegetation, at least not for a long time. A recent study in northern hardwood forests in the Adirondack Mountains of New York concluded that successful establishment of desired tree seedlings requires control of both deer and understory American beech.[104] In such situations, either long recovery times or additional intervention to remove the competing vegetation are required in order for other species to establish successfully.

U.S. Forest Service scientists concluded that white-tailed deer have caused substantial and long-lasting changes in the trajectory of forest vegetation development in northwestern Pennsylvania that will be difficult to reverse in some cases.[105] They cited changes in species dominance, reductions in species diversity, and lack of seed sources as contributing factors. Stands that received complete overstory removal when deer density was high are particularly resistant to recovery because they are where the densest fern layers had developed. Stands cut in a similar manner but with low deer density had low abundance of fern and higher plant species diversity.

On the other hand, the research team noted that plots in their study that received either no overstory removal or partial removal and still had a diverse seed source nearby showed potential for relatively rapid recovery if deer numbers were low enough.[106] They found that sweet birch, common blackberry, eastern hemlock, and eastern white pine were all capable of growing through the ferns. Once other species began to shade the fern layer, it thinned, allowing additional species to grow.

Penetrating and reducing the fern layer sets the stage for other species to repopulate affected areas, either from suppressed remaining fragments, local refugia, or long- or short-distance seed dispersal. However, all of this takes time. In order to decrease the recovery time for the regeneration of commercially valuable tree species, researchers at the U.S. Forest Service have developed protocols that combine canopy thinning with herbicide treatment of the fern, beech, and striped maple layers to speed the recovery process.[107] These methods, coupled with fencing to exclude deer, have made it possible to continue to harvest timber on commercial and state forest lands in many areas, but they may be prohibitively expensive for many small private landowners.

Other effects of deer browsing that may have a long-term impact are potential changes in litter decomposition rates and mineral nutrient cycling due to changes in tree species composition brought about by deer selectively foraging over very long time periods. Differences among tree species in ratios of carbon to nitrogen in leaf litter and the presence and abundance of defensive compounds are important factors affecting both palatability and the quality of soil organic matter. In at least two eastern North American forest ecosystems, changes have been documented in the quantity and chemical properties of litter due to shifts in community structure caused by selective feeding by white-tailed deer or moose.[108]

Further tests of the alternative persistent states hypothesis and other long-term implications of prolonged heavy herbivory should be undertaken to determine whether they are valid and useful models for what is occurring in Pennsylvania's heavily browsed forests.

Findings on forest recovery from heavy deer browsing

(1) Each layer of the forest, from the canopy to the soil, provides habitat for a specialized group of plants, animals, and microorganisms. Canopy trees link it all together, starting as seeds deposited on the forest floor, becoming seedlings in the herbaceous layer, growing into the shrub and understory layers, and eventually reaching a dominant position in the canopy.

(2) Overbrowsing by deer has damaged forest ecosystems in several profound ways including the widespread loss of forest structure, changes in abundance and diversity of flora and fauna, and interference with processes such as regeneration, succession, and perhaps nutrient cycling.

(3) The choice of bringing back the forest understory and ensuring the continuation of a rich overstory layer into the future is not a scientific choice but a values choice. In our judgment, the greatest overall benefit to the widest range of stakeholders would be best served by restoring forest structure, diversity, ecological processes, and ecosystem function to a state similar to the conditions that prevailed in the relatively recent past.

(4) Although there are indications that the regrowth of forest understories can occur in a few years following the reduction or exclusion of deer, full recovery of the structure and function of forest ecosystems will likely take decades and perhaps require active intervention beyond the mere reduction of deer numbers.

Endnotes

[1] Steele and Smallwood 2002

[2] Marquis and Whelan 1994

[3] Leimgruber et al. 1994; DeGraaf et al. 1991b

[4] deCalesta 1994

[5] Pastor and Naiman 1992

[6] Pastor and Naiman 1992; Didier 2003

[7] Tilghman 1989; Jones et al. 1993; Horsley et al. 2003

[8] Townsend and Meyer 2002; additional studies are underway, but not yet published, on the reduction in reproductive capacity due to browsing and rates of vegetative and reproductive recovery of several forest ground-layer species at the Lacawac Sanctuary in Wayne County, Pennsylvania, including Canada mayflower, Indian cucumber-root, two species of bellwort, Solomon’s-seal, Solomon’s-plume, starflower, teaberry, and white wood aster (Dr. Daniel Townsend, Associate Professor of Ecology, Department of Biology, University of Scranton, personal communication, 2003).

[9] Gregg 2004

[10] Putman et al. 1989

[11] Jenkins et al. 2004

[12] Fronz 1930

[13] Whigham 2004

[14] Bierzychudek 1982

[15] Beattie and Culver 1981

[16] Sobey and Barkhouse 1977

[17] Meier et al. 1995

[18] Fletcher et al. 2001a

[19] Anderson 1994; Augustine and Frelich 1998; Knight 2004

[20] Allison 1990a, 1990b

[21] Loeffler and Wegner 2000

[22] Rooney 1997

[23] A. F. Rhoads, personal observation

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[24] Hughes and Fahey 1991; Rooney 1997; A. F. Rhoads, personal observation

[25] Horsley et al. 1994

[26] Godman and Lancaster 1990

[27] Wendel and Smith 1990

[28] Lorimer 1993

[29] Bonner and Maisenhelder 1974

[30] Silvertown 1980; Crawley and Long 1995; Wolff 1996

[31] Reader and Beisner 1991; Ostfeld et al. 1997; Reader 1997

[32] Kantak 1981; Wolff et al. 1985; Bucyanayandi et al. 1990; Ostfeld and Canham 1993

[33] Smith 1972; Wolff et al. 1985; Hulme 1994; Ivan and Swihart 2000

[34] Crow 1988

[35] Arend and Scholz 1969; Marquis et al. 1976; Galford et al. 1991

[36] Lorimer 1993

[37] Thorn and Tzilkowski 1991

[38] Lorimer 1993

[39] Oak 1993

[40] Williams 1989

[41] Oliver and Larson 1996

[42] Gibson 1982

[43] Drooz 1985

[44] Gibson 1982

[45] Galford 1986

[46] Marquis 1975; Peterson and Carson 1996

[47] Leckie et al. 2000

[48] McLachlan and Bazely 2000

[49] Singleton et al. 2001

[50] Pickett and McDonnell 1989

[51] Johnson 1993

[52] Horsley et al. 1994

[53] Townsend and Meyer 2002

[54] Cain et al. 1998

[55] Clark 1998

[56] Source: Rhoads and Block 2003. Vascular plants are all trees, shrubs, vines, wildlfowers, grasses, sedges, rushes, ferns, clubmosses, and related groups. They do not include mosses, liverworts, green algae, or non-plants such as lichens, fungi, cyanobacteria ("blue-green algae"), and photosynthetic microorganisms.

[57] Chapin 1980; Chapin et al. 1993

[58] Baker 1949; Pacala et al. 1994

[59] Steele and Smallwood 2002

[60] Chapin 1980; Demchik and Sharpe 1999a, 1999b; Sharpe and Drohan 1999; Schreffler and Sharpe 2003

Endnotes

[61] Lozano and Huynh 1989; Cote et al. 1993; Cote and Camire 1995

[62] Whitney 1990, 1991; Van Breemen et al. 1997; Finzi et al. 1998; Bigelow and Canham 2002

[63] Hallett and Hornbeck 1997; Van Breemen et al. 1997; Finzi et al. 1998; Whitney 1990, 1991; Bigelow and Canham 2002

[64] Auchmoody and Filip 1973 and references therein

[65] Auchmoody 1982, 1983

[66] Catovsky and Bazzaz 2002

[67] Stanturf et al. 1989; Lea et al. 1979

[68] Ouimet and Camire 1995

[69] Auchmoody and Filip 1973; Safford 1973; Carmean and Watt 1975; Stone and Christenson 1975; Ellis 1979; Stanturf et al. 1989

[70] Mader and Thompson 1969; Leaf and Bickelhaupt 1975; Safford 1973; Czapowskyj and Safford 1979; Lea et al. 1979, 1980; Safford and Czapowskyj 1986; Kedenburg 1987; Ouimet and Fortin 1992; Kolb and McCormick 1993; Cote et al. 1995; Long et al. 1997, 1999; Demchik and Sharpe 1999a, 1999b; Swistock et al. 1999; Moore et al. 2000; Schreffler and Sharpe 2003

[71] Safford 1973; Czapowskyj and Safford 1979; Safford and Czapowskyj 1986

[72] Long et al. 1997, 1999

[73] Horsley et al. 2002

[74] Horsley et al. 2002

[75] Persson et al. 1990/1991; Duggin et al. 1991; Kreutzer 1995; Olsson and Kellner 2002

[76] Demchik and Sharpe 1999a

[77] Demchik and Sharpe 1999b; Schreffler and Sharpe 2003

[78] Anderson and Katz 1993

[79] Casey and Hein 1983; Jones et al. 1993; deCalesta 1994; McShea and Rappole 1997

[80] McShea and Rappole 2000

[81] Burton and Likens 1975

[82] Hairston 1987

[83] deMaynadier and Hunter 1995

[84] deMaynadier and Hunter 1995

[85] deMaynadier and Hunter 1995

[86] Petranka et al. 1993

[87] Petranka et al. 1994

[88] Pough et al. 1987

[89] DeGraaf and Yamasaki 1992

[90] Bonin 1991, cited in deMaynadier and Hunter 1995

[91] The only experimental study found in the preparation of this report focused on one common species exposed to four deer densities (10, 20, 38, and 64 deer per square mile) in enclosures in northwestern Pennsylvania; it

Endnotes

detected no difference among treatments in surface abundance of redback salamanders after 10 years (Thomas Pauley, U.S. Forest Service, Northeastern Research Station, Irvine, Pennsylvania, unpublished data).

[92] deMaynadier and Hunter 1995

[93] Duffy and Meier 1992; Petranka et al. 1993; Bratton and Meier 1998; Singleton et al. 2001

[94] Stork 1990; Chandler and Peck 1992; Niemelä et al. 1993; Nilsson et al. 1995; Neave 1996; Spence et al. 1996, 1997; Werner and Raffa 2000

[95] Czederpiltz 1998, 2001

[96] Selva 1994; Nilsson et al. 1995

[97] Cooper-Ellis 1998; Rambo and Muir 1998

[98] Hughes and Fahey 1991; Duffy and Meier 1992; Bratton et al. 1994; Meier et al. 1995; Ruben et al. 1999; Abrams 2003

[99] Results of 18 studies reviewed in deMaynadier and Hunter 1995

[100] Bonta 2000

[101] A. F. Rhoads, personal observation

[102] A. F. Rhoads, personal observation

[103] Augustine et al. 1998; Stromayer and Warren 1997

[104] Sage et al. 2003b

[105] Horsley et al. 2003

[106] Horsley et al. 2003

[107] Horsley 1994

[108] Pastor and Naiman 1992; Didier 2003