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# Effects of White-Tailed Deer (Odocoileus virginianus) on Plants, Plant Populations and Communities: A Review

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# Effects of White-tailed Deer (Odocoileus virginianus) on Plants, Plant Populations and Communities: A Review

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ABSTRACT.—Large effects of white-tailed deer (*Odocoileus virginianus*) upon individual plants, plant populations and communities have been documented in a number of studies. However, well-supported experimental measures of the magnitude and geographical extent of these effects are still surprisingly scarce. Deer-caused changes in stem morphology and reductions in plant growth rates are well-documented in some parts of the North America. Furthermore, deer have been shown to affect the composition of several plant communities in the north-central and northeastern United States. There are some documented cases of deer-caused reductions in plant survival; most of these are tree seedlings and saplings. However, many studies have detected no effects on plant survival or fecundity, or have found that negative effects occur only in a fraction of years, seasons, sites or deer densities. Little is known about population-level or ecosystem-level impacts. Many regions and plant communities with large deer populations have not been studied. Whereas deer density is clearly important in determining spatial and temporal variation in the presence and magnitude of deer effects, other factors that may modify the effects of deer density are poorly understood.

## INTRODUCTION

In many parts of the eastern United States and south-eastern Canada white-tailed deer (*Odocoileus virginianus* (Boddaert)) are currently so abundant that many observers have suggested or assumed that deer are having a major impact upon the vegetation of this region (Leopold, 1950; Hough, 1965; Behrend *et al.*, 1970; Whitney, 1984; Alverson *et al.*, 1988; Michael, 1992; Strole and Anderson, 1992; Van Auken, 1993; Boerner and Brinkman, 1996; Phillips and Maun, 1996; Van Deelen *et al.*, 1996; Catling and Larson, 1997; Buckley *et al.*, 1998). Whereas substantial evidence exists that in some community types deer negatively affect the growth rate of tree seedlings and saplings, prevent adult recruitment into tree populations and alter species composition, experimental evidence for widespread (relative to the range of white-tailed deer in North America or to the geographic area over which deer populations recently have increased) substantial effects are less than frequently appears to be assumed. Here we summarize current knowledge about the nature, magnitude and spatial and temporal patterns of the effects of white-tailed deer upon individual

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plants, plant populations, plant communities and ecosystem processes and identify major gaps in our current knowledge. We also review some methodological challenges in obtaining more conclusive evidence of deer effects.

Management of deer populations is a contentious issue that has stirred emotional conflict between individuals who want to avoid the extirpation by overbrowsing of rare aesthetically pleasing or economically valuable plants and plant communities (Diamond, 1992; Diefenbach et al., 1997) and individuals who consider hunting deer to be cruel (McShea and Rappole, 1997), hunters who enjoy the abundance of deer (Diefenbach et al., 1997) and land managers who distrust human intervention in "natural" processes within wildlife refuges and preserves (Diamond, 1992). However, the effects of deer herbivory on vegetation are also of interest to ecologists examining the effects of herbivores on individual plants, plant populations and communities. By reviewing this literature we hope to provide information to aid land managers in evaluating the need to hunt deer to preserve rare or economically valuable plant species and to preserve or restore rare plant communities. In addition, we hope to enhance ecologists' understanding of the effects of herbivores on plants and the mechanisms that underlie these effects.

This review will be confined to effects of white-tailed deer, although similarly high densities of related species present similar problems elsewhere (Gill, 1988; Clutton-Brock and Albon, 1992; McInnes et al., 1992; Singer and Renkin, 1995). For brevity we will use the word 'deer' to refer to white-tailed deer. There have been a number of regional reviews of effects of white-tailed deer on plants (Neils et al., 1956; Marquis and Brenneman, 1981; Alverson et al., 1988; Witmer and deCalesta, 1992), but, to date, no wider overview of the subject.

As we will demonstrate, although there have been large increases in deer populations in many community types during the mid and late 20th century, studies that examine the effects of deer upon plant populations and communities have been conducted in a small subset of these community types (Fig. 1). Furthermore, existing studies primarily have examined deer effects upon a subset of the plant life-stages that are consumed by deer. Whereas there is sufficient evidence to conclude that deer effects can be substantial in some sites and years, we argue that how common those sites and years are remains unclear. More studies, and better designed and targeted studies, are highly desirable. In their absence, we suggest that prudent land managers and plant conservation biologists be alert for potential deer effects on plant individuals, populations and communities such as those reviewed here.

*Historical background.*—White-tailed deer occur throughout most of the United States and southern Canada east of the Rocky Mountains and are the most abundant wild ungulate on the continent (Gill, 1988). In the absence of direct data on deer abundance before European settlement, disagreement exists about whether and to what extent current deer densities exceed pre-European settlement deer densities (McCabe and McCabe, 1997). Estimates of pre-European settlement deer densities have been constructed from archeological evidence of the consumption rate of deer by native Americans, and hence rely upon assumptions concerning the demographics of native Americans and the rate at which they harvested deer, or are extrapolated from anecdotal accounts of deer abundance by early European settlers. Therefore, estimates of pre-European deer densities must be considered imprecise approximations. Nevertheless, authors have suggested that current deer densities are 2 to 4 times higher than pre-European settlement deer densities in hemlock-northern hardwoods forests (Alverson et al., 1988; Redding, 1995) and white cedar (*Thuja occidentalis*) deer yards (Van Deelen et al., 1996).

Although estimates of pre-European deer densities are imprecise, reliable accounts document a geographically widespread decline in deer populations in the late 19th Century.
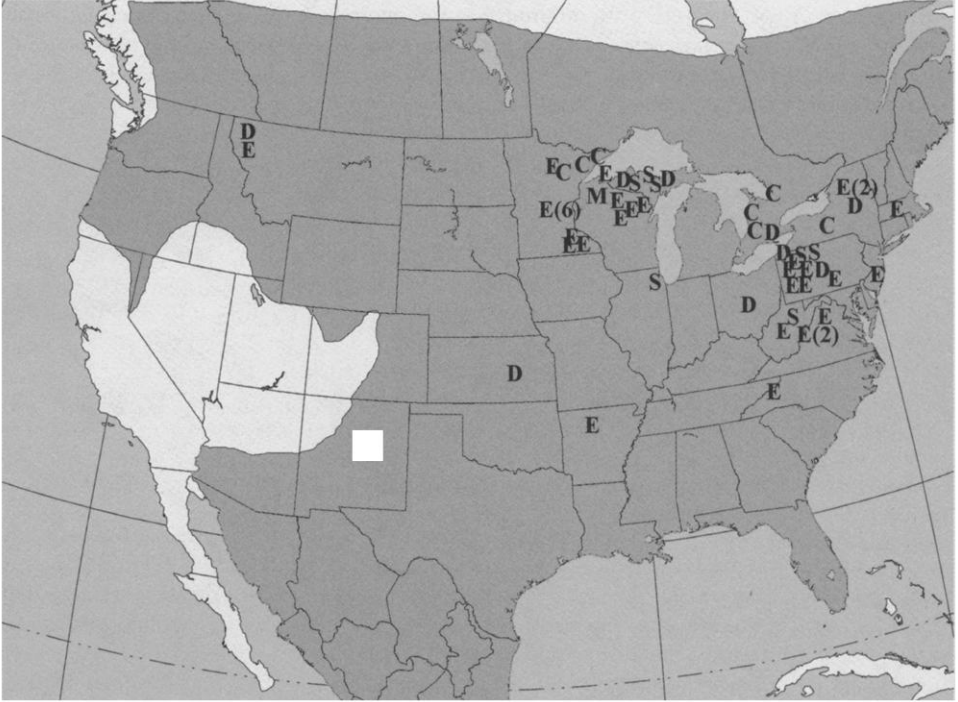
FIG. 1.—Locations of studies that have examined effects of white-tailed deer (*Odocoileus virginianus*) on individual plants, plant populations, plant communities and ecosystems. Studies of deer diets and habitat use are not included. The shaded area is the range of white-tailed deer in the United States of America and Canada. 'E' denotes studies that used deer exclosures. 'C' denotes studies that simulated deer herbivory by clipping. 'S' denotes studies that compared vegetation among sites with different deer densities. 'D' denotes descriptive studies of deer effects on vegetation other than comparisons among sites. 'M' denotes modeling studies. Sites where multiple studies of the same type have been conducted are represented by the appropriate letter followed by the number of studies in parentheses

By the early 20th Century commercial hunting had extirpated deer from much of their former range and in other areas reduced their populations (McCabe and McCabe, 1984). In the 1930s and 1940s, after establishment of strict hunting regulations and changes in land-use, deer began to increase in abundance and to expand their range (Leopold, 1943; Cook, 1945; Leopold *et al.*, 1947; Taylor and Hahn, 1947; Schorger, 1953; Hough, 1965; Behrend *et al.*, 1970; Gill, 1988). Today deer have re-occupied (or been translocated into) their entire former range and are slowly expanding their range westward (Gill, 1988).

Biologists began documenting deer population trends (particularly die-offs) (Van Volkenberg and Nicholson, 1943; Hahn, 1945; Leopold *et al.*, 1947; Leopold, 1950), diet (Hosley and Ziebarth, 1935; Petrides, 1941; Bramble and Goddard, 1943; Halloran, 1943; Hill, 1946) and habitat use (Hosley and Ziebarth, 1935; Halloran, 1943) immediately following the increase in deer populations in the late 1930s. These early studies, however, rarely addressed the response of individual plants, plant populations or plant communities to deer herbivory and those studies that did primarily presented qualitative results (Swift, 1946). Quantitative experimental and descriptive studies of plant responses to deer herbivory, including exclo-

sure experiments, appeared in the literature in the late 1950s and are most prevalent since 1970. Therefore, although scientists have been concerned with deer population sizes, diet and habitat use for at least 65 y, much of the literature that is relevant to deer effects on plants has been published in the last 35 y.

## MATERIALS AND METHODS

We searched the Agricola and Biosis electronic databases from 1985 to 2000 and 1969 to 2000, respectively, to locate articles that addressed deer effects on vegetation in North America (Table 1). Because *Journal of Wildlife Management* and *Journal of Forestry* contained many relevant articles, we searched all volumes of these journals between 1930 and the present. We did not attempt to search nonpeer reviewed literature comprehensively although we did include such documents in this review if they were referenced in peer-reviewed sources. Although we did not conduct a meta-analysis of the studies we discovered, we did consider the magnitude of treatment effects and the statistical power of studies in our subjective weighting of results.

### EVIDENCE OF DEER EFFECTS UPON INDIVIDUAL PLANTS

*Effects on plant growth rate, morphology and development.*—In theory, an herbivore might affect plant growth rate, morphology or development and yet not affect fecundity or survival. Therefore, evidence of deer effects upon plant growth does not prove that deer affect individual fitness or population growth. We discuss effects of deer upon plant growth for two reasons: information on this subject is relatively abundant and, in many cases, effects upon plant growth most likely do cause, or are concurrent with, effects upon the plant population and community.

Conclusive evidence for negative effects of deer upon plant growth exists only for certain taxa, principally tree species, in certain communities, principally mature and post timber harvest white pine-hemlock-northern hardwoods forests (Alverson and Waller, 1997) and old fields (Inouye *et al.*, 1994; Stange and Shea, 1998). The lack of evidence for widespread negative effects, in part, reflects the limited range of taxa and communities that have been studied. However, in some sites with high deer densities, experiments involving well-studied taxa and communities have found no effect of deer on plant growth rates (Jacobs, 1969) (32.6 deer/km² overwinter) or effects that are highly variable in both time and space (Inouye *et al.*, 1994) (>10.5 deer/km²). For example, in one of two old fields studied, Inouye *et al.* (1994) found that deer significantly reduced proportional rates of increase in height of *Quercus rubra* and *Pinus strobus* seedlings in only 2 and 4 of 9 y, respectively. However, these significant negative effects in a minority of years caused a significant over all negative effect of deer on growth of both species over the 9-yr study. Deer did not affect growth rates of oaks in the second old field.

Many studies have documented fewer saplings and small adult trees outside exclosures than inside them (*e.g.*, Tierson *et al.*, 1966; Harlow and Downing, 1970; Anderson and Loucks, 1979; Tilghman, 1989; Trumbull *et al.*, 1989; Healy, 1997). These differences are often interpreted as arising from deer-caused reductions in growth rates, but some of these differences may arise wholly or in part from deer-caused reductions in survival rather than in growth. (That is, deer might be killing individuals of a given size class outside the exclosure rather than slowing plants from growing into that size class, especially if the exclosure has been in place for a long time.) Studies that do not repeatedly census individuals are unable to determine conclusively whether observed changes result from reduced survival or growth and at which life-stage negative effects occur. We will review the substantial num-

TABLE 1.—Summary of studies that addressed the effects of white-tailed deer on properties of individual plants, plant populations, plant communities and ecosystems. Regional reviews, commentaries, studies of deer diets and habitat use are not included. Some studies that were not included in the text are due to methodological problems (*i.e.*, no replication) but do address effects of deer on vegetation are included in the table

| Study | Study type | Deer density (deer/km²) | Dependent variables | Results | Comments |
|---|---|---|---|---|---|
| Adams 1949 | browsing preference | 102.5 | % of saplings browsed, vol. of foliage removed | Ponderosa pine juveniles preferred over Douglas fir juveniles | |
| Aldous 1952 | clipping | no data | *Thuja*: height, dbh; hardwoods: weight, length of annual browse prod. | *Thuja*: 25% clip reduces dbh & hgt growth; hardwoods: species-specific increase or decrease with 100% clip | |
| Allison 1990 | comparison among sites, exclosure, clipping | no data | *Taxus* strobilus and seed production | strobilus & seed prod. decrease w/ increasing deer impact, higher strobilus prod. w/o deer, 100% clip reduced # of male and female strobili | |
| Alverson & Waller 1997 | exclosure | no data | hgt & survival of transplanted *Tsuga* saplings, correlation between browsing and sapling hgt | sig. taller w/o deer, no sig. diff. in survival, neg. correlation between height and browsing intensity | |
| Anderson 1994 | compare sites w/ different deer densities | high density: 22; low density 4.8 | *Trillium* height | sig. taller plants at low density sites or w/o deer | |
| Anderson & Loucks 1979 | exclosure, compare sites w/ different deer dens. | Flambeau: 50–100, Menominee: 37 | Size dist. of *Tsuga canadensis* juveniles | stems <90 mm dbh absent at Flambeau, all-aged population at Menominee | Menominee deer dens. = 5–12 10 y before study |
| Augustine & Frelich 1998 | exclosure, comparison among sites | high density (exclosure): 25–35; low density: 5–10 | comparison: size distributions, % flowering; exclosure: survival, flowering rate, leaf area | size dist. skewed to small plants and reduced flowering rate at high deer density; increased flowering rates and leaf area inside exclosure | |
| Augustine et al., 1998 | exclosure | <7 (low), 7–15 (med.), >15 (high) | # of *Laportea* stems, stems flowering status of stems | sig. reduced pop. growth rate in sites w/ high deer density and low plant density | |

TABLE 1.—Continued

| Study | Study type | Deer density (deer/km²) | Dependent variables | Results | Comments |
|---|---|---|---|---|---|
| Behrend et al., 1970 | correlation between deer densities and veg. response | 10.4 (1966), 4.6 (1969) | number of stems 3–20 ft high | temporal coincidence of increase in stems >3 ft and deer reduction | |
| Boerner & Brinkman 1996 | describe tree seedling demography | 60–70 | seedling germination, survival, species comp., browsing pressure | conclude that heavy deer browsing reduced seedling survival rate | |
| Bowers 1997 | exclosures | 12–20 | woody species richness, evenness, stem density by height (> or < 1 m) | species richness 122% higher w/o deer; stem density & evenness unaffected | |
| Bowers & Sacchi 1991 | exclosure | 12–20 | % cover of Trifolium, rate of fungal infection | w/o deer cover initially increases, then reduced below cover with deer by fungal epidemic | |
| Buckley et al., 1998 | compare transplant oak seedlings among pine Vs oak stands | no data | % seedlings browsed, survival rate, growth, # of growth flushes | higher browsing rate in pine stands, high mortality rate in pine due to deer herbivory, no effect on growth | no experimental demonstration of deer effects |
| Butterworth & Tzilkowski 1990 | exclosure | no data | size dist. of trees <5 cm dbh by commercial vs non commercial | no statistically sig. effects | claim visually apparent release w/ thinning and fencing |
| Campbell 1993 | descriptive comparison of browsed Vs unbrowsed plants | no data | growth, survival, fruit prod., stem #/indiv. | browsed plants w/ sig. lower fruit prod., browsing in two successive years increases mortality risk, no effect on growth | |
| Canham et al., 1994 | clipping | no data | sapling height, leader length, biomass of new shoots at end of exp., survival | saplings clipped for 2 summers grow sig. less, heavy clip in 2 summers increases mortality, no effect of winter clip | deer selectively browse taller, multi-stem, flowering plants |
| Catling & Larson 1997 | current distribution and historical abundance | no data | abundance of shrubs at different sites, herbarium records of abundance | temporal coincidence of decline in abundance and increased deer densities | |

TABLE 1.—Continued

| Study | Study type | Deer density (deer/km²) | Dependent variables | Results | Comments |
|---|---|---|---|---|---|
| D'Ulisse & Maun 1996 | description of herbivore damage | no data | % of plants browsed, % of capitula removed | 1993: 90% browsed, 50% capitula removed, 1994: 29% browsed, 7% removed | |
| Frelich & Lorimer 1985 | comparison among sites, modeling | 2 (inland), 10 (deer yard) | hemlock, sugar maple size and age dists.; model development of size dists. | hemlock 30 cm–1.4 m tall abundant inland and absent in yard, 60 y of heavy browsing produces unimodal, positively skewed size dist. | |
| Gedge & Maun 1992 | clipping (greenhouse) | no data | biomass, fruit prod., seed prod., seed mass | severe defoliation: sig. fewer fruits & seeds, moderate defol.: no effects | |
| Gedge & Maun 1994 | clipping, fruit removal | no data | clipping: surv., biomass prod., fruit prod.; fruit removal: flring period length, total fruit prod. | clipping reduced seed prod. in the field, reductions increase nearer anthesis; fruit removal increased fruit prod. and flring period | |
| Halls & Crawford 1960 | exclosure | no data | weight of browse and herbs for preferred, non preferred species | weight of vegetative production 2X greater in exclosures after 3 y | both deer and livestock excluded |
| Harlow & Downing 1970 | exclosure | 24.7 | # of saplings and sprouts >4.5 ft tall by species | sig. more saplings & sprouts >4.5 ft w/o deer, higher species richness of woody plants w/o deer | |
| Healy 1997 | exclosures, comparisons among sites w/ different deer densities | 3–6 (low), 10–17 (high) | size dist. of saplings (all species combined), sapling species comp. | # of saplings >100 cm sig. greater w/o deer and in stands w/ low deer density; higher sapling species richness w/ few deer | |
| Horsley & Marquis 1983 | exclosure, weeding of herbaceous layer | probably 11.2 | % cover herb species, juvenile tree size dist., growth of black cherry | deer browse *Rubus* allowing increase in fern cover which decreases juvenile tree recruitment | |
| Hough 1965 | photo record of understory changes | no data | species comp., height and dbh of tree regen. | temporal coincidence of decreased understory cover with increased deer density | |

TABLE 1.—Continued

| Study | Study type | Deer density (deer/km²) | Dependent variables | Results | Comments |
|---|---|---|---|---|---|
| Inouye et al., 1994 | exclosure | 10.5–32.4 | height growth and survival for tree juveniles | less growth w/ deer for pines, aspen, oaks in one field, oaks unaffected in second field, stem density unaffected | no replication, exclosure also affects rabbits and gophers |
| Jacobs 1969 | exclosure | 38.6 | height growth, survival and browsing damage to A. saccharum saplings | deer increase sapling mortality 6X, no sig. effect on growth | |
| Knops et al., 2000 | exclosure | 16.0 | aboveground and root biomasses, N mineralization rate, C and N content of soil | primary prod. increased over time w/o deer but not w/ deer; soil N increased w/o deer but decreased w/ deer | no replication, rabbit & deer confounded |
| Little & Somes 1965 | exclosure | no data | white cedar stem abundance, height | sig. greater reduction in # of stems outside exclosures, stems sig. shorter outside exclosures | deer effects confounded w/other properties of tip-up mounds |
| Long et al., 1998 | natural exclusion | no data | height, basal diam., density and % browsed for hemlock seedlings | mean height 3X greater, mean diam. 2X greater, mean density 6X greater w/o deer | |
| Marquis 1981 | exclosure | 11.2 | Number of stems >5 ft tall by species, total number of stems | change in species comp. of stems >5 ft, sig. less black cherry, red maple and pin cherry w/ deer | |
| Marshall et al., 1955 | clipping | no data | tree height, leader length, morphology, survival | repeated clipping reduces height and leader length in red pine, survival in white pine, increases # of plants w/ multiple leaders | |
| McShea & Schwede 1993 | exclosure | 35 | acorn consumption rates by deer, estimate mortality rate due to weevils | deer consume most acorns during mast-fall, deer cause less mortality than weevils | |
| Michael 1992 | describe correlation between deer density and tree regen. | Canaan Valley: 32.4, Freeland: 13.9, Pocahontas: 8.1 | size dist. of Balsam fir stands | stems 1–5 ft. tall very rare in all sites except Pocahontas site | |

TABLE 1.—Continued

| Study | Study type | Deer density (deer/km²) | Dependent variables | Results | Comments |
|---|---|---|---|---|---|
| Mladenoff & Stearns 1993 | modeling w/ "gap model" | no data | tree species comp. after 400 year simulation | climate change, lack of germination substrate, reduced seed source prevent *Tsuga* regen. even w/o deer | qualitative results |
| Neils *et al.*, 1956 | exclosure | 97.2 | # of seedlings, survival of transplanted saplings | sapling mortality rates higher w/ deer and seedling densities less w/deer | |
| Prachar & Samuel 1988 | exclosure | no data | height growth, survival, deer damage of aspen suckers | presence of effect on survival depends on season of browsing, reduce growth of 1st year but not 2nd year suckers | |
| Ritchie *et al.*, 1998 | exclosure | 15–30 | species comp. by functional groups, total biomass & belowground biomass, available soil N | legumes, woody plants sig. more abundant w/o deer, grasses and forbs more abundant w/ deer, total biomass >inside but belowground <inside, soil N greater inside | |
| Ritchie & Tilman 1995 | exclosure | no data | total % percent cover of legumes and by species | % legume cover sig. higher w/o deer, sig. increase in *Lathyrus* cover | |
| Rooney 1997 | natural deer exclusion | 10–12 | leaf length, plant dens., flring rate, belowground internode length | sig. longer leaves, greater shoot densities, higher flowering rates w/o deer | |
| Rooney & Dress 1997 | compare present species comp. w/ records of historical sp. comp. | 10–15 | herb and shrub species frequency, abundance, richness and evenness in 1929 and 1995 | decrease in sp. richness, rare species eliminated more often than common species, high sp. richness neg. associated w/hay-scented fern | |
| Rooney *et al.*, 2000 | compare 100 sites, path analysis w/ many envir. variables | no data | size dists. of *Tsuga canadensis* juveniles <300 cm tall | # of saplings taller than 30 cm significantly and negatively correlated with deer browsing pressure | |

TABLE 1.—Continued

| Study | Study type | Deer density (deer/km²) | Dependent variables | Results | Comments |
|---|---|---|---|---|---|
| Ross et al., 1970 | exclosure | 0–18 (temporal variation) | sapling size dists. and mean height by species | change sp. comp. of saplings >4.3 m, reduce conifer saplings avg. hgt | no replication |
| Saunders & Puettmann 1999 | clipping | no data | white pine seedling survival, hgt. & diam. growth | compensatory ability less under closed canopy than under open canopy | |
| Shelton & In-ouye 1995 | exclosure | no data | aboveground morph., height, # of seed heads, # of browsing incidents for Lactuca canadense | 7X increase in reprod. w/o deer, increase in height sig. greater w/o deer | no replication, reference plot adjacent to exclosure |
| Stange & Shea 1998 | exclosure | no data | Q. rubra seedling survival, height | sig. greater survival rate and height w/o deer | |
| Stoeckeler et al., 1957 | exclosure | 13.5–15.4 | # of saplings >4.5 ft by species | sig. increase in density of stems >4.5 ft tall w/o deer | |
| Strauss 1988 | deer foraging preference based on plant size | no data | prebrowse shoot width, presence of browsing, width of regrown shoots | prefer ramets w/ larger shoots, prefer larger shoots w/in a ramet, browsed ramets with larger new growth | |
| Switzenberg et al., 1955 | comparison of hardwood abundance, quality among sites | no data | hardwood stem density, frequency of rot and other deformities | no effect on density of hardwood regen., some increase in deformities (altered morphology) | no replication |
| Throop & Fay 1999 | descriptive comparison among sites | no data | shoot number/ramet, inflorescences/ramet | burning w/ no effect of % ramets browsed, browsed ramets w/ more shoots, inflorescences | |
| Tierson et al., 1966 | exclosure | 8.2 | number of saplings >3 ft tall by species | Deer reduce # of saplings >3 ft tall for all species except beech | sample size = 2 |
| Tilghman 1989 | deer enclosures w/ different densities | treatments = 3.7, 7.7, 14.8, 26.8; ambient = 11.2 (7.3–18.9) | size distributions of tree seedlings and saplings by tolerance type, cover of fern and Rubus | deer densities between 8–14 reduce number of saplings taller than 0.9 m, densities >14 increase black cherry dominance | |

TABLE 1.—Continued

| Study | Study type | Deer density (deer/ km²) | Dependent variables | Results | Comments |
|-------|-----------|--------------------------|---------------------|---------|----------|
| Trumbull et al., 1989 | exclosures | 8.5 | tree regen size dist., tallest sapling in different species categories, % cover ferns, *Rubus*, grass | sapling >3 ft more abundant w/o deer, tallest black cherry, sugar maple saplings sig. taller w/o deer, shift in understory species comp. | |
| Van Deelen et al., 1996 | compare past sp. comp. w/ current sp. comp. in deer yards | no data | adult tree species comp. in 1850 and 1990, age dist. of white cedar | increase in abundance of unpalatable species, decrease in palatable species; white cedars establish when deer pops. low | sample size = 2 |
| Webb et al., 1956 | exclosures | 7.2–12.7 | sapling size dist. by species, herb cover by species | sapling avg. hgt & diam less w/ deer for 2 of 7 species, change in herbaceous sp. comp. | sample size = 2 |
| Whitney 1984 | comparison of tree size dist. 1929 and 1978 | no data | tree size dist. by species | temporal coincidence between increase in deer and change of sapling species comp | |

ber of studies that document deer effects on size distributions of plant populations in the section entitled "Evidence of Population-level Effects."

Few studies have examined effects of deer upon growth of herbaceous plants. However, Augustine and Frelich (1998) suggest that deer browsing can significantly reduce the growth rate of herbs. In sugar maple-basswood forest remnants, where deer densities exceeded 25 deer/km$^2$, the mean leaf area of transplants of the long-lived, perennial herb *Trillium grandiflorum* increased 28.7% where protected from deer for 1 yr, but decreased 11.2% where unprotected. Similarly, in naturally occurring populations of *T. flexipes* and *T. cernuum*, where deer densities exceeded 25 deer/km$^2$, the mean leaf area of protected plants decreased 15.4% following a year of deer exclosure, whereas the mean leaf area of exposed plants decreased 41.1%. In forest remnants where deer densities were between 5–10 deer/km$^2$, protection from deer herbivory for one year did not significantly affect change in mean leaf area.

In both herbaceous and woody species, plants may be able to partially or, in some cases, fully regrow tissue consumed by herbivores. Such compensatory growth may limit the reduction in aboveground size caused by deer. However, compensation aboveground may reduce growth belowground. For example, clipping that simulated deer herbivory did not significantly reduce aboveground biomass of *Cirsium pitcheri* plants, but belowground biomass declined with increasing intensities and frequencies of clipping (D'Ulisse and Maun, 1996). By contrast, Rooney (1997) found no significant difference between the internodal rhizome lengths of *Maianthemum canadense* plants growing in natural refugia from deer (on top of large boulders) and those exposed to deer herbivory.

One hallmark of mammalian herbivory on plants is pronounced changes in plant morphology. The most common of these is production of abundant lateral stems in woody plants as a result of terminal meristem removal. Trees and shrubs browsed by deer often have greater stem densities than unbrowsed plants (Marshall *et al.*, 1955; Switzenberg *et al.*, 1955; Tierson *et al.*, 1966; Jacobs, 1969; Throop and Fay, 1999). Marshall *et al.* (1955) suggest that frequency of browsing is probably more important than its intensity in determining stem density. Another common effect of deer on woody plant morphology is a "browse line" below which deer have removed stems and twigs of trees (Adams, 1949; Aldous, 1952; Marshall *et al.*, 1955; Neils *et al.*, 1956; Halls and Crawford, 1960; Trumbull *et al.*, 1989). Studies rarely have addressed the effects of deer herbivory on plants' belowground morphology or relative allocation to aboveground vs. belowground structures. However, Rooney (1997) showed that the branching frequency (number of nodes between branches) of *Maianthemum canadense* rhizomes did not differ significantly between plants growing in natural refugia and those exposed to deer.

*Effects on plant survival and fecundity.*—The ultimate measure of the magnitude of effects of deer on individual plants is their impact upon average individual fitness, which is a function of stage-specific survival rate (an estimate of an individual's probability of surviving) and the stage-specific average fecundity of all stages of the life-cycle. Unfortunately, no study has yet examined effects of deer at all life-stages for any given plant species. Thus, we review studies that focused on one or a few life-stages.

Although seeds, particularly acorns, constitute a large portion of deer diets (McCaffery *et al.*, 1974; Harlow *et al.*, 1975; McCullough, 1985; Pekins and Mautz, 1987; Weckerly and Nelson, 1990), effects of deer on germination rates have not been quantified. A study of acorn removal rates in the Shenandoah Valley of Virginia suggested that removal rates by deer and rodent granivores are approximately equal, but both cause less mortality than do curculionid beetles (McShea and Schwede, 1993).

Research on effects of deer on tree survival has focused on seedlings and saplings because

a tree's entire aboveground biomass can be browsed during these life-stages. Stange and Shea (1998) show that in maple-basswood forest fragments in southern Minnesota the survival rate of *Quercus rubra* seedlings over two years was 3.2% for seedlings exposed to deer herbivory and 34.6% for seedlings protected from deer by tree shelters. Deer reduced the survival rate of *Acer saccharum* saplings by 10% over 5 y in a Wisconsin northern hardwoods forest following a partial timber cut (Jacobs, 1969). Although many saplings were browsed repeatedly, no saplings died until the fourth year of this study, suggesting that death occurred as a result of cumulative effects of deer browsing. Alverson and Waller (1997) showed that the survival rate of browsed *Tsuga canadensis* seedlings was lower than that of unbrowsed seedlings, but they did not find a significant effect of deer exclusion on seedling survival. Presumably, too few *T. canadensis* seedlings were browsed repeatedly to produce a significant treatment effect during the two year study.

Conclusive demonstrations that deer reduce survival rates of tree seedlings and saplings are rare because few studies have repeatedly censused individuals. Many studies measure seedling abundance in areas of high and low deer densities (Harlow and Downing, 1970; Trumbull *et al.*, 1989; Butterworth and Tzilkowski, 1990), but these studies do not demonstrate effects of deer on seedling and sapling survival. Differences in seedling and sapling abundance may result from different germination rates among sites due to many possible factors, including differing deer abundance or, when "seedling" and "sapling" refer to size categories, from deer effects on growth rates (Trumbull *et al.*, 1989).

Many workers have suggested that deer can substantially decrease survival rates of herbaceous plants because all aboveground tissue of these plants is accessible (Miller *et al.*, 1992; Anderson, 1994; Balgooyen and Waller, 1995). Unlike trees, herbs do not escape deer herbviory by growing above the browse line. Moreover, during spring and summer forbs often form a significant portion of deer diets (Dunkeson, 1955; Halls and Crawford, 1960; Kohn and Mooty, 1971; Crawford, 1982; Irwin, 1985; McCullough, 1985; Case and McCullough, 1987). The hypothesis that deer have large effects on survival of herbs is difficult to evaluate at this time because of a lack of studies that have repeatedly censused individual plants. In the only study we found that repeatedly censused individual plants, deer did not significantly reduce the survival rate of transplanted *Trillium grandiflorum* plants over 2 y even where deer densities exceeded 25 deer/km$^2$ (Augustine and Frelich, 1998). Although deer consumed the entire aboveground tissue of these plants, the plants re-emerged, although smaller in size, the following spring. However, because *T. grandiflorum* is long-lived relative to the 2 y duration of the study, the cumulative effects of tissue removal by deer may ultimately reduce survival rate.

The long lifespan of perennial herbs and many woody species has prevented measurement of effects of deer herbivory on the lifetime fecundity of these plants. In individual years, however, deer can reduce the proportion of plants or ramets in a population that produce reproductive structures (Rooney, 1997; Augustine and Frelich, 1998; Augustine *et al.*, 1998) and the number of reproductive structures produced per plant (Allison, 1990). *Taxus canadensis* shrubs that were protected from deer produced more male and female strobili than unprotected shrubs in the final two years of a 5 y study (Allison, 1990). Several studies have shown that deer reduce the proportion of shoots that flower in perennial forest herbs in individual years (Rooney, 1997; Augustine and Frelich, 1998; Augustine *et al.*, 1998). In maple-basswood forest fragments, where deer densities exceeded 25 deer/km$^2$, in southern Minnesota the flowering rate of protected *Trillium cernuum* and *T. flexipes* plants was 19× that of unprotected plants in the second year of protection from deer (Augustine and Frelich, 1998). In addition, in forest fragments with low densities (0.01 stems/m$^2$) of *Laportea canadensis* and high deer densities (winter deer density >15 deer/km$^2$), deer

prevented flowering by *L. canadensis* ramets entirely (Augustine *et al.*, 1998). Similarly, the proportion of *Maianthemum canadensis* plants in Allegheny northern hardwoods forests that flowered in natural refuges from deer was 39 times greater than the flowering rate of exposed plants (Rooney, 1997).

Timing of deer herbivory appears to be important in determining the magnitude of deer effects on plant survival and fecundity (Prachar and Samuel, 1988; Gedge and Maun, 1992, 1994; Canham *et al.*, 1994). For example, timing of simulated herbivory was critical in determining its effects on mortality of *Acer rubrum, Prunus serotina* and *Fraxinus americana* seedlings: winter clipping had little or no effect upon plant mortality, but summer clipping increased mortality 2× in *A. rubrum* and *P. serotina* and 5× in *F. americana* over controls (Canham *et al.*, 1994). Similarly, clipping the lakeshore dune annual, *Corispermum hyssopifolium*, reduced fecundity only late in the growing season (Gedge and Maun, 1992, 1994). In *Cakile edentula*, another dune annual, effects of clipping on plant fecundity depended on both the timing and intensity of clipping (Gedge and Maun, 1992, 1994). Reductions in fruit number were proportional to clipping intensity when clipping was performed early in the season, but reductions were much greater when clipping was performed just before anthesis. Clipping did not affect seed mass in either species, but effects on seed viability are unknown. Clearly, the interactions of factors that determine the magnitude of effects of deer, and herbivores in general, on individual plant performance are complex.

*Evidence of population-level effects.*—If deer alter survival probabilities or fecundities of individual plants in a population, they might be expected to alter the population's growth rate. However, evidence that deer affect growth rates of plant populations is scant because it rarely has been sought. In the only study to measure the effect of deer on the finite rate of increase of a plant population, deer reduced the population growth rate of *Laportea canadensis* where deer were abundant (winter deer density >15 deer/km$^2$) and *L. canadensis* was rare (0.01 stems/m$^2$). Under these conditions the finite rates of increase of protected *L. canadensis* populations were between 2.0 and 6.0, whereas unprotected populations declined slowly. Deer had no effect where they were rare (winter deer density <7 deer/km$^2$) or where *L. canadensis* was abundant (>1 stems/m$^2$) (Augustine *et al.*, 1998).

Most studies examining deer effects on plant populations describe their effects on size structures of tree populations. If deer reduce survival or growth of tree seedlings or small saplings, certain size classes may be under-represented in the population. Under-representation of sapling size classes outside deer exclosures has been described for many forest tree species, including *Tsuga canadensis* (Anderson and Loucks, 1979; Alverson *et al.*, 1988), *Acer saccharum* (Stoeckeler *et al.*, 1957) and *Betula alleghaniensis* Britt. (Stoeckeler *et al.*, 1957) in mature northern hardwoods forests, *Prunus serotina* and *A. rubrum* in old clearcuts in northern hardwoods forests (Marquis, 1981; Trumbull *et al.*, 1989), *Liriodendron tulipifera* and *Fagus grandifolia* in clear cuts in southern Appalachian cove forests (Harlow and Downing, 1970) and *Quercus rubra* in Massachusetts oak forests (Healy, 1997). For example, Stoekeler *et al.* (1957) found that deer eliminated regeneration of *Acer saccharum* trees more than 1.4 m tall on unprotected sites, whereas stems taller than 1.4 m were abundant on protected sites. In each of the studies listed above deer densities in the study sites exceeded 8.5 deer/km$^2$.

Where deer densities are consistently high at a regional scale deer may cause underrepresentation of saplings at a regional scale. Rooney *et al.* (2000) use a path analysis approach to demonstrate that under-representation of *Tsuga canadensis* saplings taller than 30 cm in forests of northern Wisconsin and the western Upper Peninsula of Michigan is strongly and positively correlated with deer density.

Several studies, however, suggest that the magnitude of deer effects on the rate of re-

cruitment of adult trees can vary greatly on a landscape scale and that deer only prevent adult recruitment in sites with high deer densities, including deer yards and thinned or clear-cut patches in forests. Tilghman (1989) found that deer significantly reduced the number of saplings taller than 0.3 m of "browse sensitive species," including *Acer saccharum, A. rubrum, Fraxinus americana, Betula alleghaniensis* and *B. lenta*, only at experimentally elevated deer densities (14.8 deer/km$^2$) that exceeded the mean deer density for the Allegheny National Forest (11.2 deer/km$^2$) and approached the maximum deer density that was recorded in a survey of 11 sites in the Alleghany National Forest in 1992 (19.0 deer/km$^2$) (Redding, 1995). At experimental densities approximating the regional mean stems taller than 0.9 m remained 77% as abundant as they were in the absence of deer. Similarly, Frelich and Lorimer (1985) showed that, whereas bell-shaped size distributions of *Tsuga canadensis* occurred in a northern Michigan deer yard (winter deer density = 10/km$^2$), *T. canadensis* populations outside the deer yard (winter deer density = 2/km$^2$) had size distributions that decreased monotonically from small to large size categories (Frelich and Lorimer, 1985).

The few studies that have examined effects of deer on size distributions of populations of herbaceous plants show that deer increase the proportion of the population in small size classes (Augustine and Frelich, 1998; Augustine *et al.*, 1998). Under conditions of high deer density (>15 deer/km$^2$) and low plant density (<0.1 stems/m$^2$), deer prevented *Laportea canadensis* ramets from exceeding 40 cm in height, but in exclosures, more than 50% of ramets exceeded 40 cm in height (Augustine *et al.*, 1998). Similarly, in forest fragments with high deer densities (>25 deer/km$^2$), size distributions of *Trillium cernuum* and *T. flexipes* populations shifted toward smaller size classes once deer began browsing plants in the spring, whereas no shift occurred in fragments with lower deer densities (<10 deer/km$^2$) (Augustine and Frelich, 1998). Lower proportional representation of large plants where deer are abundant may reflect the previously documented trend for browsing pressure to increase with plant size for plants below the browse line (Strauss, 1988; Campbell, 1993; Inouye *et al.*, 1994).

Other studies, although not describing size distributions, have shown the mean size of individuals in herbaceous plant populations to be significantly less where deer are present than where deer are absent (Rooney, 1997; Long *et al.*, 1998). For example, the mean leaf area of shoots of *Maianthemum canadense* was 23% less for shoots exposed to deer herbivory than for shoots that occurred in natural refugia (Rooney, 1997).

*Evidence of effects on mature or midsuccessional communities.*—Exclosure experiments have demonstrated that deer can decrease tree regeneration (Tilghman, 1989; Healy, 1997), change the identity of the dominant tree species in the sapling layer (which could eventually change the species composition of the canopy) (Tilghman, 1989; Healy, 1997) and decrease species richness of tree seedlings, herbs and shrubs (Tilghman, 1989; Healy, 1997; Rooney and Dress, 1997; Augustine *et al.*, 1998). The magnitude of deer effects on community composition may be very large. In old- growth hemlock-beech and hemlock forest in northwestern Pennsylvania an increase in deer densities from near zero in the early 20th Century to 7–19 deer/km$^2$ is correlated with 80.4% and 59% decreases in the number of understory herb and shrub species in hemlock-beech and hemlock forests, respectively (Rooney and Dress, 1997). Rare shrub and herbaceous species (<1% of cover in 1929) were significantly more likely to be eliminated during the 70 y of high deer densities than were abundant species (>1% of cover in 1929).

Although large effects of deer on community composition have been demonstrated, whether these effects are widespread or restricted to habitats preferred by deer remains unclear. In northern hardwoods forests of the Allegheny Plateau deer reduced the species

richness of stems taller than 0.9 m and increased dominance of *Prunus serotina* only at experimentally elevated deer densities (26.8 deer/km²) that were more than twice the mean deer density for the Alleghany National Forest (11.2 deer/km²) (Tilghman, 1989). In addition, deer reduced the density of *Laportea canadensis* in the understory of sugar maple-basswood forest fragments in Minnesota only where they were abundant (>15 deer/km²) and *L. canadensis* was rare (<1 stems/m²) (Augustine *et al.*, 1998).

In sites where deer populations are not sufficiently dense to eliminate preferred herbs from forest understories, they may increase species diversity of shrub and herbaceous layers by counteracting competitive exclusion. Webb *et al.* (1956) showed that in deer exclosures cover of *Dryopteris intermedia* increased from 25% to 45% and cover of *Viola spp.* and *Oxalis montana* decreased by 17% and 12%, respectively (Webb *et al.*, 1956).

*Effects on succession.*—Because deer prefer feeding in disturbed and early successional forest communities (Kohn and Mooty, 1971; Kearney and Gilbert, 1976), one might expect particularly pronounced effects on such communities. Whereas in some instances deer probably affect the rate and direction of succession, existing studies are insufficient to determine whether these effects are common. Furthermore, most studies have examined effects of deer on succession following logging or in old fields. Effects on other successional communities are not known.

Deer could reduce the rate of succession of old fields and clear-cuts to forest by decreasing the rate of invasion by woody species or by retarding the rate of recruitment of woody species to sapling and adult size categories. In most instances, deer appear to have little effect upon the rate of woody species invasion immediately following disturbances. For example, deer did not reduce densities of tree seedlings in old fields in Virginia (Bowers, 1997) or Minnesota (Inouye *et al.*, 1994) or in a clear-cut in a southern Appalachian forest (Harlow and Downing, 1970). In contrast, Ritchie and Tilman (1998) found that deer did reduce the density of tree seedlings and saplings in a Minnesota savanna (Ritchie *et al.*, 1998).

Because deer are known to reduce the rate of recruitment of adult trees in some sites, they may slow the rate of succession to forest in those sites. For instance, deer caused a 75% reduction in the number of stems above the browse line in a southern Appalachian clear-cut (Harlow and Downing, 1970). Other studies, however, have shown infrequent effects of deer (Inouye *et al.*, 1994) or effects only at experimentally elevated deer densities (experimental density = 14.8 deer/km², regional mean = 11.2 deer/km²); (Tilghman, 1989). In some instances the magnitude of deer effects on the rate of canopy closure following disturbance appears to be temporally and spatially variable, and therefore studies of short duration (1 to 3 y) may not detect changes in the rate of overstory regeneration.

The strongest evidence for deer effects on the direction of succession is for changes in the composition of successional forest communities. In a Virginia old field and immediately following clear-cutting in a southern Appalachian forest, deer reduced species richness of regenerating woody species (Harlow and Downing, 1970; Bowers, 1997). Because measures of species diversity consider both the number of species present (species richness) and relative abundances of the species (evenness), the reductions in species richness could have produced a reduction in the species diversity of woody regeneration. Whereas in the forest community deer also reduced species diversity of woody saplings (Harlow and Downing, 1970), in the old field deer did not affect diversity of woody saplings (Bowers, 1997).

Effects of deer on the species composition of early successional communities are not confined to woody species. Deer caused a significant reduction in percent cover of legumes in a 60-y-old, old field in Minnesota by reducing cover of *Lathyrus venosus,* one of three legume species present (Ritchie and Tilman, 1995). The negative effect of deer on legume

cover, however, was less pronounced in the old field than in a savanna that had never been cultivated. In early successional forest habitats changes in herbaceous and shrub layers may mediate indirect effects of deer on tree species composition. Following clear-cutting in Allegheny forests deer caused a decrease in cover of *Rubus* and an increase in cover by ferns and grasses (Horsley and Marquis, 1983). Growth and survival of *Prunus serotina* was lower in the presence of ferns and grass than in the presence of *Rubus*.

Local deer density and size of early successional patches probably are important in determining the magnitude of the effects of deer on the rate and direction of succession. Tilghman (1989) demonstrated that deer densities higher than the mean regional density were required to alter dominance patterns and reduce evenness of the species composition of regenerating canopy trees. In addition, Bowers (1997) suggested that the magnitude of deer effects on community properties is less in larger early successional patches because deer browsing is less concentrated.

Evidence from both early successional communities in hemlock-northern hardwoods forests of the Allegheny Plateau (Horsley and Marquis, 1983; Stromayer and Warren, 1997) and maple-basswood forest fragments of southeastern Minnesota (Augustine *et al.*, 1998) suggests that deer can cause shifts among alternate stable states in forest communities. A particular site has alternate stable states if more than one stable species composition exists for that site. An external force (such as intensive grazing or browsing) can drive the community from one stable species composition to the another. Once an alternative stable species composition has been achieved the community will not revert to its original species composition even if the external force that caused the shift is removed. For example, Stromayer and Warren (1997) suggest deer browsing of *Rubus,* which causes the understory to be dominated by ferns, forces Allegheny hemlock-northern hardwoods forests to shift to an alternate stable state in which competition from ferns will prevent tree regeneration even if deer are removed. The possibility that intense deer herbivory can push the species composition of a site from one stable state to another increases the potential risks of maintaining high deer populations. Once a shift among stable states has occurred it may be impossible to re- establish the original community.

*Evidence of ecosystem-level effects.*—Wherever deer alter species composition of a plant community a corresponding effect upon ecosystem properties and processes, such as size of nutrient pools in the soil, rate of nutrient cycling or primary productivity may occur. Deer may have large effects upon the quantity of soil nitrogen in old fields and savannas by affecting the abundance of legume species (Bowers and Sacchi, 1991; Ritchie *et al.*, 1998; Knops *et al.*, 2000). For example, Ritchie *et al.* (1998) found that decreased cover of legumes in a Minnesota savanna where deer were present corresponded to decreased total available soil nitrogen and decreased nitrogen in plant tissue. In addition, deer exclusion increased net primary productivity in the savanna, perhaps in response to greater nitrogen availability (Knops *et al.*, 2000).

In some communities negative direct effects of deer on legume abundance may be balanced or exceeded by positive indirect effects. Bowers and Sacchi (1991) documented a positive net effect of deer on cover of the legume, *Trifolium pratense.* Deer reduced the density of *T. pratense* and, thus, prevented epidemics of fungal infections that greatly reduced *T. pratense* density where deer were absent. Because legume cover increased with deer presence in this study, an increase in soil nitrogen might also be expected where deer are present. Therefore, deer effects on nitrogen availability may be more complicated than indicated by direct effects of deer (Bowers and Sacchi, 1991).

In forest ecosystems effects of deer on the relative abundance of conifer and hardwood species (*e.g.*, Ross *et al.*, 1970) could cause large changes in the rate of nutrient cycling.

Conifer litter decomposes more slowly than hardwood litter and contains fewer nutrients (MacLean and Wein, 1978; McClaugherty *et al.*, 1985). Unfortunately, effects of deer on nutrient cycling in forests that contain both conifers and hardwoods have not been studied.

## SUMMARY: WHAT IS KNOWN

The most commonly reported effect of deer upon individual plants is a change in plant morphology following removal of the terminal meristem (Marshall *et al.*, 1955; Switzenberg *et al.*, 1955; Tierson *et al.*, 1966; Jacobs, 1969; Throop and Fay, 1999). Strong evidence also exists that deer can reduce growth rates of tree seedlings and saplings (Inouye *et al.*, 1994; Alverson and Waller, 1997; Stange and Shea, 1998). Negative effects of deer on plant survival are less well documented than effects on growth, but the under-representation of saplings in some tree populations in communities where deer are abundant may reflect reductions in seedling survival as well as growth. In general, deer probably have a much larger effect on survival of seedlings and saplings than on the rate at which seeds, even acorns (McShea and Schwede, 1993), become seedlings (*i.e.*, the probability of a seed becoming a seedling, the germination rate).

In sites with high deer densities, deer can affect size distributions of populations of preferred browse species by preventing recruitment to sapling and small adult size classes (Tierson *et al.*, 1966; Harlow and Downing, 1970; Anderson and Loucks, 1979; Marquis, 1981; Tilghman, 1989; Trumbull *et al.*, 1989; Healy, 1997). All studies that documented deer-induced failure of adult recruitment were conducted in sites where deer densities exceeded 8.5 deer/km$^2$. In addition, because deer feed selectively, deer can affect the species diversity and identity of the dominant species in both herbaceous (Webb *et al.*, 1956; Horsley and Marquis, 1983; Bowers and Sacchi, 1991) and canopy layers in forest communities (Harlow and Downing, 1970; Marquis, 1981; Tilghman, 1989). These effects on populations and communities are best documented for early successional forest communities following timber harvesting. Both through direct effects on juvenile trees and through indirect effects by changes in the species composition of the herb layer, deer can slow the rate (Stoeckeler *et al.*, 1957; Harlow and Downing, 1970; Ritchie *et al.*, 1998) and alter the direction of succession in forests (Harlow and Downing, 1970; Horsley and Marquis, 1983).

Many studies reviewed here have documented large spatial (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Anderson, 1994; Inouye *et al.*, 1994; Healy, 1997; Augustine and Frelich, 1998; Augustine *et al.*, 1998; Rooney *et al.*, 2000) and temporal variation (Inouye *et al.*, 1994) in the magnitude of deer effects on vegetation. Both experimental (Tilghman, 1989; Anderson, 1994; Augustine and Frelich, 1998; Augustine *et al.*, 1998) and comparative descriptive studies (Frelich and Lorimer, 1985; Michael, 1992; Rooney *et al.*, 2000) have shown that deer density is frequently positively and significantly correlated with the magnitude of deer effects on vegetation. Deer densities may be the primary factor affecting spatial and temporal variation in deer effects. However, the density of the plant consumed by deer (Augustine *et al.*, 1998) and the availability of plant resources (particularly light) (Saunders and Puettmann, 1999) may modulate the effects of deer density. The interactions among these factors should not be discounted in formulating future research questions.

## SUMMARY: WHAT IS NOT KNOWN

(1) Most published studies have been conducted in mature and early successional white pine-hemlock-northern hardwoods forests of the Allegheny Plateau (Marquis, 1981; Horsley and Marquis, 1983; Tilghman, 1989; Trumbull *et al.*, 1989; Butterworth and Tzilkowski, 1990), the Adirondack mountains (Webb *et al.*, 1956; Stoeckeler *et al.*, 1957) or the Upper Great Lakes region (Jacobs, 1969; Ross *et al.*, 1970; Anderson and Loucks, 1979; Frelich

and Lorimer, 1985; Allison, 1990; Alverson and Waller, 1997), in maple-basswood forest fragments in southern Minnesota (Augustine and Frelich, 1998; Augustine *et al.*, 1998; Stange and Shea, 1998) and in old fields in central Minnesota (Inouye *et al.*, 1994; Ritchie and Tilman, 1995; Knops *et al.*, 2000) and western Virginia (Bowers and Sacchi, 1991; Bowers, 1997). The potential for substantial deer effects is high in many other regions of the United States and Canada. It is not known what effects deer have in these other communities and regions.

(2) Effects of deer on aboveground growth rates and stem morphology of plants have been more extensively studied than other potential effects on growth, morphology and phenology of individual plants. The effects of deer herbivory on belowground growth and aspects of aboveground morphology other than stem density require documentation. In particular, the fate of the plant may depend upon the rate at which belowground stored reserves are exhausted and upon the extent to which aboveground regrowth reduces root growth, increasing later drought mortality and decreasing belowground competitive ability.

(3) Clipping experiments suggest that timing of herbivory (*e.g.*, growing season vs. dormant periods, early in the growing season vs. near anthesis) is important in determining the magnitude of the effects of herbivory (Gedge and Maun, 1992, 1994; Canham *et al.*, 1994). However, in general, the effects of timing, frequency and intensity (amount of tissue removed) in determining the magnitude of the effects of deer herbivory are poorly understood. Studies that have examined these mechanisms using actual deer herbivory rather than clipping are especially rare.

(4) Do deer effects on plant morphology and aboveground growth, the best studied properties of individual plants, indicate effects on other individual properties, such as survival and fecundity, population growth rates and community composition? Little is known about the magnitude of deer effects on growth rates of plant populations or on plant fitness. Whereas some studies have quantified effects of deer upon survival (Jacobs, 1969; Inouye *et al.*, 1994; Alverson and Waller, 1997) and fecundity rates (Allison, 1990) of particular age or size classes, no published studies have constructed complete life-tables with and without deer and then used such data to predict deer effects on the finite rate of increase of a plant population. Such information could allow predictions of effects on plant populations and communities to be much more precise.

(5) The vulnerability of most plant communities to being pushed into an alternate stable state by intense deer herbivory is unknown. In how many communities is this potentially irreversible change possible? Can we predict which communities are likely to be pushed into an alternative stable state by intense deer herbivory?

(6) Effects of deer upon ecosystem properties and processes, such as nutrient cycling, biomass distribution and productivity, have received little study and are poorly understood.

(7) What is the magnitude of temporal and spatial variation in effects of deer upon plants? Do differences in deer densities adequately explain temporal and spatial variation in deer effects? How do the density of the plants consumed and the availability of plant resources modify the influence of deer density? Studies reviewed here clearly show that effects of deer vary substantially through time and in space (Frelich and Lorimer, 1985; Inouye *et al.*, 1994; Augustine and Frelich, 1998; Augustine *et al.*, 1998) and that differences in deer densities are important in determining when and where deer will have significant effects on vegetation. However, Augustine *et al.* (1998) also showed that for a constant deer density where the density of the plant consumed was greater, the magnitude of deer effects on the plant population was less. The interactions between deer density, plant abundance and resource availability are poorly understood.

## METHODOLOGICAL CHALLENGES AND LIMITATIONS

Experimental designs involving exclosures or enclosures, which are essential to the experimental study of deer herbivory in the field, pose several challenges that warrant discussion. Ideally, designs would be used that overcome all of the problems discussed below. In most cases, however, constraints of time and funds do not allow this. In this situation, readers may be better able to evaluate the strengths and weaknesses of a study's conclusions if they consider the consequences of the limitations of the methodology used.

(1) The great leaping ability of deer can make effective deer exclosures or enclosures difficult to construct. The necessary height of the fence will vary with the area of the site that is to be fenced and the fencing design. However, in exclosure studies scientists can monitor the area inside the fencing for evidence of deer activity, such as recent browse damage, hoof-prints or feces. Published studies that have taken these precautions and have been successful in excluding deer exist. These studies can be used as a guideline for effective fencing design. Studies in which the exclosures are not completely effective in excluding deer can still produce valuable results if the reduction in deer density is quantified.

(2) Subjective (nonrandom) placement of plots can be a serious problem in exclosure and enclosure studies. If plots are placed in areas of unusually high deer density, such as areas with evidence of recent deer browsing, and this placement is not clearly planned, reported and taken into account in the interpretation of the results, erroneous conclusions will be reached. However, if such variation (deer densities, densities of the target plant, etc.) is purposely incorporated into the design of the study and is clearly reported, this information can enhance scientists' understanding of spatial variation in the presence and magnitude of deer effects.

(3) "Fenceline effects" are another challenge of exclosure and enclosure studies. Reference plots that are placed next to exclosures may have exceptionally high rates of herbivory.

(4) Sample sizes frequently are small in exclosure and enclosure experiments because exclosures/enclosures are expensive to build. Exclosure studies reviewed here had a mean sample size of 15.9 plots (SD = 19.2, range 1–72, N = 30). Seven of the 30 exclosure studies read in preparing this review contained less than two replicates and four were unreplicated (Table 1). Small sample sizes increase the probability that real differences between manipulated plots and controls will not be detected and, hence, present the risk of detecting only deer effects that are of very large magnitude.

(5) The relationship between deer density and the total impact upon a plant, plant population or plant community is important for management. However, studying the effects of different deer densities is difficult. Whereas ambient deer density usually provides the 'control treatment' and exclosures provide complete deer absence, intermediate densities usually must by simulated by clipping. A methodological problem is that the relationship between deer density and degree of browsing damage is usually not known, so the levels of clipping appropriate for a study are unknown. Furthermore, clipping may fail to mimic effects of herbivores in other ways, such as timing and patterns of tissue removal within a plant (Strauss, 1988; Baldwin, 1990; Krause and Raffa, 1992). Instead of clipping, comparisons of vegetation among sites with different deer densities can be made, but then differences in deer densities are confounded with other variables, weakening conclusions. Conclusions from such comparative studies are much stronger if a multivariate analysis, such as path analysis, that includes potentially confounding variables in the regression model is used to explain differences in vegetation between the sites (Rooney *et al.*, 2000). A third method, small randomly located enclosures that contain different deer densities and are

sufficiently replicated avoids inadequacies of clipping and confounded independent variables, but is costly in materials and labor.

(6) Inferring or predicting effects of deer upon plant communities from the extensive literature describing deer diets is tempting. However, problems with this approach are so severe that we have excluded such data from this review. Many diet studies describe deer food intake with no corresponding data on plant abundance. Without the latter, preference cannot be determined. In some studies data on food intake or on plant abundance are problematic because, for example, only certain subsets of plants were sampled (Johnson, 1980) despite the fact that deer are known to eat a wide variety of plants. Furthermore, the relationship between preference and browsing pressure is not always strong and the relationship between browsing pressure and plant response may not be clear.

## SUMMARY: WHAT REMAINS TO BE DONE

Sufficient evidence exists to conclude that white-tailed deer can have a substantial impact upon plant morphology and, in some cases, plant growth rates, especially for tree seedlings and saplings. Strong evidence also exists that in certain cases the structure of plant populations and composition of plant communities can be altered by deer. However, this is quite different from concluding that such effects are widespread or usual. Studies conducted to date indicate that effects of deer upon plants vary substantially in both space and time. Deer density is important in determining temporal and spatial variation in deer effects on vegetation. The density of the plant consumed and plant resource availability also contribute to the observed temporal and spatial variation in deer effects. Critical future questions include 'what is the relative importance of these factors in determining when and where substantial deer effects will occur?' and 'how do these factors interact to produce substantial effects of deer on plant populations and communities?' Finally, an answer to the question 'how widespread or frequent are substantial effects of deer on vegetation?' awaits future research in many North American plant communities that have received little or no attention.

Although we fail to reject the null hypothesis that deer do not have widespread effects upon plant individuals, populations, communities and ecosystems this does not, of course, mean that deer effects are not widespread. The many aspects of plant growth, individual fitness, population and community structure and dynamics and ecosystem processes that have not been studied may be affected by deer. Where deer are affecting, for example, plant growth rates, deer probably affect population growth rates, future community composition and so on. Likewise, the absence of experiments in many regions where deer are highly abundant should not be interpreted as evidence that deer do not affect plant populations and communities in these regions.

More interesting than the scarcity of studies that address particular questions in particular communities are three possible explanations why studies that examine deer effects on vegetation may fail to find significant effects. One is that substantial effects may be limited to certain combinations of deer densities, plant densities and site characteristics. Another possibility is that some direct negative effects of browsing are obscured by indirect positive effects caused by reduced competition resulting from having neighboring plants eaten or by maintaining populations below densities at which pathogens are readily transmitted. The third possibility, which is especially strong for short-lived plants, is that many of the most dramatic changes happened in the past, so that present vegetation has already undergone most changes that deer can cause. If so, we will miss these effects because we have no baseline to serve as a reference. For example, some highly preferred species that are highly susceptible to deer browsing may now be so rare or even absent that we cannot now detect

effects upon them. The largest changes in deer density occurred in the late 19th and early 20th centuries (Hahn, 1945; Leopold *et al.*, 1947; Redding, 1995), and the greatest changes in plant communities may also have occurred at that time.

   Thus, although evidence for widespread substantial effects of white-tailed deer upon plant populations and communities is not as clear as some have assumed, substantial effects under particular sets of circumstances have been clearly demonstrated. In the face of uncertainty the usual prescription is conservative management. Given the very large, and sometimes increasing, deer populations now common in some plant communities and the worrisome possibility that effects of deer overbrowsing may be irreversible, or reversible only with complicated and expensive intervention in the future, the most prudent management option would be to attempt to keep deer populations at more moderate densities. The optimal deer density for any particular site will vary with the managment objective and the plant community, but the deer densities in studies cited in this review and the presence and magnitude of deer effects documented in these studies can provide initial guidelines (Table 1). Furthermore, land managers should be alert for readily observable deer effects, such as altered aboveground morphology or population size distributions, on plant species that are preferred by deer or are of conservation concern.

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