Interference to Hardwood Regeneration in Northeastern North America: Ecological Characteristics of American Beech, Striped Maple, and Hobblebush

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ABSTRACT: *Several woody species may inhibit regeneration of desirable northern hardwoods. This includes a dense understory of American beech (*Fagus grandifolia *Ehrh.) that commonly occurs in stands infected with beech bark disease. Root injuries during logging and by natural causes also promote new suckers that, along with some stump sprouts, often maintain or increase the abundance of beech saplings. Additionally, browsing deer primarily bypass beech in favor of more palatable species. Where any of these factors has resulted in a dense understory of small beech, overstory cutting will promote its development, increase ground-level shading, and lead to a site conversion to beech. Similarly, striped maple (*Acer pensylvanicum *L.) often interferes with hardwood regeneration after overstory cutting. This species persists in heavy shade, grows rapidly after release, and produces abundant seed. When dense, striped maple may interfere with the regeneration of other species. Hobblebush (*Viburnum alnifolium *Marsh.), a shrub, reproduces by rhizomes to form thickets when damaged during overstory cutting. Heavy shade by these thickets may prevent regeneration of trees. This review summarizes characteristics of these three species with respect to their interference with desirable hardwoods in northeastern North America. It highlights the limited information about striped maple and hobblebush, and the abundance of sources that deal with American beech. North. J. Appl. For. 23(1):53–61.*

Key Words: American beech, striped maple, hobblebush, understory interference, interfering plants, hardwood regeneration.

Past research and management experience indicate that species such as American beech, striped maple, and hobblebush may interfere with regeneration of more desirable tree species (Nyland et al. 2004). When at high density in the understory, they cast such a heavy shade that advance regeneration of other species may die or not develop. Cutting at any intensity without appropriate site preparation to control these woody species makes the situation worse, often leading to a regeneration failure. Yet understanding the ways that those interfering plants grow and reproduce usually helps managers to recognize situations in which some kind of direct control would enhance opportunities for more desirable species to become established.

American Beech

General Ecological Considerations

Temperature limits the northern range of American beech (Jarvis 1956). It may become abundant on a range of sites, from either cool and moist northern slopes (Fowells 1965) to warm and dry slopes and ridges (Jarvis 1956). It currently occurs throughout much of eastern North America south of the boreal forest (Tubbs and Houston 1990), and as an overstory species in 20 forest cover types. It is a major component in three: Sugar maple–beech–yellow birch; red spruce–sugar maple–beech; and beech–sugar maple (Eyre 1980). Some evidence suggests that the abundance of beech in New York and New England has decreased since pre-settlement times (Cogbill 2000). Other reports indicate that

before beech bark disease, these associations commonly remained relatively stable unless disturbed by repeated burning, recurring growing season freezing (Hough and Forbes 1943), or cutting.

Reports from different parts of its range indicate that beech has persisted and developed to large sizes at sites with soil ranging from coarse textured sands to finer textured silt and clay loams (Peters 1997), silty and sandy sediments, fine washed till, fine and coarse tills, and even compacted dry tills (Leak 1978, 1982). This may reflect regional differences in other components of the physical environment, as well as limited competition from other species, factors related to stand natural history, and effects of past management. Nevertheless, beech grows best in loamy soils and those with high humus content (Barrett et al. 1995, Peters 1997), and will often dominate mesic sites (Whitney 1991). Conversely, understory beech grows slowly where the soil may dry below rooting depth (Tubbs and Houston 1990). And although beech seedlings have a sensitivity to low soil moisture (Peters 1997), humus often mitigates that condition in the upper horizons. Compared to sugar maple (*Acer saccharum* Marsh.), beech better tolerates soils with lower content of calcium, magnesium, manganese, and nitrogen in the upper mineral layers (Kasmer et al. 1984, Boerner and Koslowsky 1989, van Breeman 1997, Long et al. 1997). Further, high calcium may increase the shade tolerance of beech suckers with an interconnected root system (Bigelow and Canham 2002).

Beech bark disease (Houston and O'Brien 1983) profoundly changed the importance of beech throughout much of its natural range. Initially, stands with many large trees became more severely infected (Gavin and Peart 1993, Houston 1997), leading to mortality primarily of stems ≥10 in. dbh (Mize and Lea 1979). Other trees with only a light infection along narrow strips of the bole became weakened, remained alive for several years, but eventually many broke off (called beech snap) (Shigo 1972). In some stands, a second scale insect has colonized young beech trees that escaped the first wave of mortality, setting the stage for their eventual infection by the *Nectria* fungi that causes the decline and mortality (McCullough et al. 2000).

Some reports suggest that beech bark disease may have resulted in an increase of understory beech density, perhaps because of the mortality gaps that formed as beech bark disease progressed (Krasny and DiGregorio 2001). Yet research has not provided experimental evidence to indicate if the disease itself induces suckering of beech trees. Also, general reports differ with respect to effects of beech bark disease on the species composition of the aftermath forest. To illustrate, levels of understory beech have reportedly remained the same in some cases and increased in other stands in New Hampshire, while sugar and red maple (*Acer rubrum* L.) density has decreased. Although the species composition of some other New England forests apparently has not shifted significantly (Leak and Smith 1997), beech stems have increased by 25% in Massachusetts since the 1930s (Twery and Patterson 1984). Similarly, infected stands in Maine have converted into dense thickets of beech sprouts (Ostrofsky and McCormick 1986). These differences may reflect variations in the degree of infestation, the effects of site conditions, or other still unrecognized factors that temper the dynamics of beech in the aftermath forest.

Seed Production and Regeneration

American beech reproduces by both sexual and vegetative means at most sites (Hamilton 1955, Held 1983), with seedlings more numerous at northern than southern latitudes (Ward 1961). Seed production varies with year, tree age, and locality. Houle (1994) noted a positive correlation between number of nuts produced and the percent of viability. Some reports indicate that bumper crops resulting in abundant seedlings occur approximately every third year, and trees do not produce large amounts until approximately 50 years of age and at least 8 in. dbh (Leak and Graber 1993). Others suggest that beechnut production does not vary much from year to year (Hughes and Fahey 1988). Costello (1992) observed that seed production decreased measurably as beech bark disease advanced in nut-bearing trees. Infected stands had only approximately two-thirds to three-fifths as many beechnuts.

Most beech seed falls close to the parent tree, limiting dispersal into new areas (Tubbs and Houston 1990), except when transported by birds and mammals (Houston and Houston 1987). They may move appreciable quantities of nuts over a considerable distance. In fact, a single blue jay may transport up to seven nuts for 6 miles (Johnson and Adkisson 1985). As with other animal caches, uneaten seeds may later germinate, introducing beech to new stands, fortifying the distribution in poorly stocked areas, or bringing new genotypes to heavily infected sites.

Beech germinates and develops best in shade (Logan 1973), where surface soil will not dry below shallow rooting depth. Seedlings may become established in large numbers under even a dense overstory canopy, at least at some sites. Further, because of its high shade tolerance, the population of small advance beech tends to remain stable through time (Forcier 1975). In addition, those small beech trees live considerably longer than competing species (Fowells 1965).

Vegetative Reproduction

Beech regenerates from root suckers, often at great densities (Hamilton 1955), and will become multi-stemmed under stress (Peters 1997). Most root suckers develop within 25 to 30 ft of the parent tree, with 99% occurring no more than 30 to 35 ft away (Jones and Raynal 1987). Number of suckers produced off a root system tends to correlate positively with size of the parent tree, but suckering lessens among old trees (Ward 1961, Forcier 1973, Jones and Raynal 1987). Some reports suggest that these root suckers may not develop into mature beech trees (Hough 1937, Forcier 1975, Poulson and Platt 1996). Others say that they help to maintain beech as a component of the main canopy at other sites (Laufersweiler 1955, Ward 1961, Roman 1980, Held 1980, 1983). In fact, isozyme genetic studies have demonstrated cloning within groups of overstory trees, suggesting that they originated as root suckers from a common source (Houston and Houston 1987).

Suckers that initiate in early spring will more likely persist, compared to ones developing in the summer and autumn (Jones and Raynal 1988). This may be due to the ready availability of carbohydrates that have accumulated in the roots during the dormant period. Many suckers that develop within clumps die by 4 years of age, but most suckers survive for approximately 9 years (Jones and Raynal 1987). They continually produce new secondary suckers that reinforce the density of a beech understory, even beneath closed stands (Forcier 1973, 1975).

At least early root sucker development seems to depend on a connection to the root system of a larger tree. Yet available information does not indicate how long beech root suckers remain connected, or when an independent root system begins to form. In some cases, the connection lasts for many years (Jones and Raynal 1988), likely enhancing sucker growth during that time (Hamilton 1955, Ward 1961). The surviving suckers also grow rapidly after release and may dominate a new cohort after overstory cutting (Marquis 1965a, Leak 1999).

Beech has a deep and extensive root system, but with many roots at the surface and within the upper 3–5 in. of soil (Braun 1936, Hamilton 1955). Commonly, suckers arise from callus at wounds along these shallow roots (Hamilton 1955, Jones and Raynal 1988, Tubbs and Houston 1990), and often by the second growing season after injury (Ward 1961, Jones 1986). Freeze-thaw actions of soil and root disturbance during logging often cause these wounds (Held 1983, Jones et al. 1989). Studies show that damage to roots during salvage cuts has promoted dense thickets of understory beech stems genetically identical to their susceptible parents (Houston 1975, Houston and Houston 1987, McCullough et al. 2000).

Suckering may occur even without these stimuli (Hamilton 1955, Jones and Raynal 1987, 1988). In fact, Held (1980) counted 700 to 900 suckers per acre in an undisturbed stand of mature beech, and Ward (1961) found that a shallow accumulation of litter and duff at such sites favored sucker production. Other observations indicate that changes in the intensity or quality of light and fluctuations of temperature may stimulate suckering (Held 1983, Jones 1986), and that greater suckering tends to occur at severe southern exposures (Ward 1961, Held 1980, Roman 1980). In addition, the advanced age of parent trees in old stands may partly explain differences in the relative abundance of suckers between and within regions (Ward 1961, Fowells 1965, Woods 1979). Yet the exact degree that tree age or vigor influence root sucker production and survival still remains unclear (Jones 1986, Houston and Houston 1987, Jones and Raynal 1987).

Houston (2001) observed more suckers around trees with a resistance to the beech bark disease, and stumps of felled resistant trees, than around diseased trees or their stumps. Significantly more suckers also developed around stumps of disease-resistant trees, than around standing resistant trees. Yet the amount of light and degree of disturbance to exposed roots significantly affected the degree of root sucker development, independent of the tree's apparent resistance.

Such evidence suggests that managers will realize only limited gains in reducing root suckering by simply cutting the beech trees from infected stands.

Stump sprouts also contribute somewhat to beech regeneration in hardwood forests (Eyre and Zillgitt 1953, Tubbs and Houston 1990), but beech stump sprouts often lack vigor (Jarvis 1956). Some dormant buds sprout from the side of stumps of young trees, but many sprouts develop from adventitious buds that arise in callus around the top of stumps (Shafer 1965, Tubbs and Houston 1990, Mallett 2002). Relatively few of the latter kind survive (Roth and Hepting 1943, Mallett 2002). Stump sprouting potential diminishes after trees reach 4 in. diameter (Hamilton 1955, Tubbs and Houston 1990). Further, sprouts from stumps of large-diameter trees usually do not live for long, and rarely grow into trees (Eyre and Zillgitt 1953, Hamilton 1955, Fowells 1965).

Initiation and elongation of stump sprouts may depend on light levels near the ground, similar to the way it affects root suckering. Generally, increased light and temperature on the stump surface help to trigger the flush of dormant buds, but heavy shading reduces early sprout growth and suppresses development in subsequent years (Maini and Horton 1966). Sprouting also depends on climatic conditions (specific to rainfall), and a limitation of soil water helps to maintain bud dormancy (Ducrey 1992).

Understory Development

Beech has a high shade tolerance, although less so in poor soil and a cold climate (Tubbs and Houston 1990). Shoot extension lasts only approximately 30 days after initiation (Marks 1975). Yet the leaves open earlier and remain later in the season on understory beech than among overstory trees. This may enhance survival in the shaded environment (Gill et al. 1998).

In persistent heavy shading, growth of beech seedlings, sprouts, and suckers surpasses that of sugar maple (Laufersweier 1955, Canham 1988, 1990, Poulson and Platt 1996, Beaudet and Messier 1998), favoring the formation of a beech understory that often increases the importance of beech through time (Forcier 1973, 1975, Tubbs and Houston 1990). Consistent with this, studies of unmanaged stands indicated that understory beech saplings had eventually grown into main canopy positions after surviving two episodes of oppression lasting 19 to 23 years, reaching overstory status at age 66 to 88 years (average dbh of 2.0–2.9 in.). By contrast, sugar maple in the same stand had lived through three episodes of oppression lasting 22 to 28 years, and did not became part of the overstory until age 110 to 126 years (dbh of 2.5–4.6 in.) (Canham 1985, 1990). The shorter duration of oppression for beech suggests that less light triggers a height growth response.

Once established, understory beech saplings will develop into larger sizes beneath openings created by tree mortality from beech bark disease (Twery and Patterson 1984, Ostrofsky and McCormack 1986, Houston 1994, DiGregorio et al. 1999, Krasny and DiGregorio 2001), some other

natural cause, or cutting (Hamilton 1955, Jarvis 1956, Forcier 1973, 1975, Canham 1988, Tubbs and Huston 1990, Poulson and Platt 1996, Houston 1997). Conditions seem particularly favorable in areas under high browsing pressure (Hamilton 1955, Jones et al. 1989), and in uneven-aged stands where the interspersion of small, intermediate, and large trees creates a horizontal and vertical distribution of foliage that casts persistent shade to the understory (Kenefic and Nyland 1996, Nyland 2002).

Some studies showed a relationship between the abundance of beech regeneration and overstory stocking, with higher numbers in stands having higher levels of residual basal area (Leak and Solomon 1975, Leak 1980). Further, Bohn (2001) and Bohn and Nyland (2003) found that when advance beech was present at moderate to high densities, it tended to inhibit the development of other species and dominated the understory within 10 years after a partial cutting treatment. Consistent with this, Crow and Metzger (1987) suggest that light partial cutting at such sites eventually leads to "almost pure stands of beech," apparently because dense beech hinders development of other species by reducing light near the ground (Poulson and Platt 1989, Kobe et al. 1995, Hane 2003).

Some evidence suggests that when both species have grown in a shaded environment for long periods, beech will likely overtop sugar maple after release by cutting or natural causes. Further, Leak (2003) reported that although understory beech saplings may develop slowly after a first partial cutting, their growth increases after a second and third release. Most likely, recruitment beneath canopy openings depends on available light (Poulson and Platt 1996), with brightness likely varying with gap size and shape, and the height of adjacent overstory trees (Marquis 1965b, Canham 1985, 1990, Nyland 2002). Sapling height at the time of release and its proximity to a gap opening also affect the rate of development after release (Twery and Patterson 1984). In general, small gaps almost always favor beech beneath them, as well as in the area adjacent to the gap boundary (Canham 1990). In large openings where the understory has at least low light continuously, sugar maple success increases (Canham 1985, 1990).

Traditionally applied single-tree selection system (e.g., leaving the basal area >75 ft^2/ac) generally creates small openings in the canopy, and favors the regeneration and development of shade-tolerant species such as beech and sugar maple (Trimble 1965, 1970, Johnson 1984, Crow and Metzger 1987, Leak et al. 1987). Within such stands (residual basal area 75–80 ft^2/ac), Donoso et al. (2000) found no significant difference in the height or age of 1-in. diameter saplings of these two species. Advance saplings that had grown for $>80\%$ of lifespan in the postcutting selection system environment reached 1 in. dbh within 26 years. Others that had grown for two-thirds of their life beneath the precutting canopy took 34 years. Height growth of saplings from both groups initially increased after release, but then slowed after 10 years as overhead shading also increased.

Heavier cutting with extended cutting cycles will reduce canopy density appreciably, leave larger canopy gaps, and

brighten the understory more and for a longer period (Nyland 2002). Yet some research has shown that openings <80 feet wide (<0.12 ac) will have no effect on the radial increment of either beech or sugar maple (DiGregorio et al. 1999). Other work indicates that gaps large enough to increase understory light by 1 to 2% have triggered a response of both species (Canham 1989). Further, sugar maple growth will exceed that of beech at intermediate light levels (Canham 1988, Poulson and Platt 1989, 1996). In brighter conditions, the two species grow similarly (Canham 1988, Poulson and Platt 1989), or beech height growth may exceed that of maple (Poulson and Platt 1996, Beaudet and Messier 1998), perhaps because of soil conditions or the source of origin (e.g., root suckers versus seedlings). Maple development may also depend on having an opening directly overhead (Canham 1985, Poulson and Platt 1996), and on its status as well-developed advance regeneration before overstory disturbance (Leak and Wilson 1958).

Changes in light levels because of overstory branch elongation ultimately affect the long-term development of these two species. Conceptually, shading increases more rapidly over openings having a narrow width relative to the height of adjacent trees, but available research has not referenced growth patterns with respect to those factors. McClure et al. (2000) did observe that advance beech grew more rapidly than newly established beech regeneration in the light beneath 150- to 180-ft-wide openings (0.4 to 0.6 ac), and continued to develop well for as long as 30 years after the release. Yet after 33 years the advance beech had a shorter average height than seedling-origin sugar maple established after the cutting. Nyland et al. (2004b) observed that in the elevated light created by shelterwood seed cutting (20 to 50% canopy cover) seedling-origin white ash (*Fraxinus americana* L.), yellow birch (*Betula alleghaniensis* Britton), and sugar maple grew faster in height than newly established beech root suckers (throughout a 30-year period).

Light also affects lateral growth of branches on understory trees. Beneath closed canopies, lateral growth of beech exceeds that of maple. At somewhat higher (but still low) light, the two species have similar branch extension (Canham 1988). Further, both oppressed and nonoppressed beech trees never have vertically oriented upper branches, or vertical growth increases only slightly with increased light (Poulson and Platt 1996). As a consequence, beech saplings underneath a closed canopy develop wide crowns that spread over smaller trees, blocking light that enters through overstory gaps. Understory cutting experiments implicate this shading as a key factor that interferes with the survival and growth of sugar maple regeneration (Hane 2003). Greenhouse trials (Hane et al. 2003) suggest that other factors, such as phytotoxicity, may contribute as well.

White-tailed deer (*Odocoileus virginianus*) also importantly influence the composition of an understory beneath northern hardwood stands. They feed heavily on desirable seedlings such as sugar maple, yellow birch, red maple, white ash, and black cherry (*Prunus serotina* Ehrh.) (Cook 1946, Grisez 1960, Healy 1971, Richards and Farnsworth

1971). Unless they do not find other species, deer rarely browse on beech (Casanova 1940, Grisez 1960, Hough 1965, Tierson et al. 1966), except for succulent sprouts in spring and some shoots in winter (Shafer 1965, Horsley et al. 2003). This reduces the abundance and height growth of nonbeech regeneration, and contributes to a buildup of understory beech in some regions (Tierson et al. 1966, Richards and Farnsworth 1971, Marquis 1974, 1981, Marquis and Brenneman 1981, Kelty 1979, Tilghman 1989, Hane 2003, Horsley et al. 2003).

Striped Maple

General Ecological Considerations

Striped maple, a small tree or large shrub, grows under small gaps and in the understory of northern hardwood forests. It commonly occurs in well-drained sandy loams on northern slopes of upland valleys, and on other mesic sites (Hibbs et al. 1980, Gabriel and Walters 1990). It occurs at the highest densities below 2,500-ft elevation and on steep slopes (Hibbs et al. 1980).

Striped maple has a high shade tolerance (Gabriel and Walters 1990). Yet some reports classify striped maple as only intermediate in shade tolerance, or even shade intolerant, when growing in an open environment (Hibbs 1978). Common associates include American beech, sugar maple, yellow birch, and hobblebush. In undisturbed stands, striped maple may comprise 10 to 53% of advance stems (Hannah 1987). These stems grow rapidly after release by overstory cutting (Hibbs and Fischer 1979).

The stem structure and large leaves of striped maple make it highly efficient for light interception, and this results in good height and biomass growth under a closed canopy (Lei and Lechowicz 1990). Trees as old as 35 to 40 years increase in height growth after cutting and other overstory disturbances brighten the understory (Hibbs 1978, Hibbs et al. 1980, Gabriel and Walters 1990). They reach a maximum height of 50 ft, and this limits striped maple to the lower canopy. Yet it may live under canopy openings for many decades (Hibbs 1978, Gabriel and Walters 1990).

Sun-damaged leaves and multiple stems of striped maple in open environments suggest poor growth at high light intensities (Hibbs 1978). Yet most evidence suggests that striped maple responds well to changing environmental conditions, with no significant reduction in overall growth on exposed sites (Sipe and Bazzaz 1995). It will shift from oppressed to vigorous growth with small changes in light intensity beneath canopy openings caused by windthrow, tree harvest, or leaf drop (Sipe and Bazzaz 1995).

Optimal development of striped maple occurs under intermediate light intensities (small openings, or under defoliated trees), particularly on cooler, higher, more northerly slopes and in mesic soils (Hibbs 1978, Hibbs et al. 1980). In small gaps (40 to 60% solar radiation), net leader extension, height change, and basal diameter growth generally exceeds that of red and sugar maple. At the center of large gaps the basal diameter growth of red maple exceeds that of striped maple (Sipe and Bazzaz 1995). Too much light (>80% solar radiation) may inhibit height growth (Wilson and

Fischer 1976), with lateral branch growth contributing most to total growth of striped maple trees (Sipe and Bazzaz 1995). However, the annual height growth of striped maple has exceeded beech or sugar maple, but not pin cherry (*Prunus pensylvanica* L. f.), in 80-ft wide clearcut strips oriented east-west (Bicknell 1982), perhaps because of the moderating effects of trees along edges of the strips.

Regeneration and Understory Development

Observations indicate that with optimal site conditions, sexual rather than vegetative reproduction dominates in striped maple (Stalter et al. 1997), but flowering and seed production seem keyed to an increase in light that follows some kind of overstory disturbance (Hibbs 1978). Seed production begins as early as age 11 (Gabriel and Walters 1990). Seeds ripen in Sept. and Oct. and disseminate in late fall (Hibbs 1978). Most fall within a 100- to 130-ft radius around parent trees, although some may be transported up to 200 ft (Hibbs and Fischer 1979). This establishes scattered populations of advance seedlings (Hibbs 1978). Quantities range from 13.75 seeds/m^2 to as low as 1.25 seeds/m^2, and decrease with distance from a parent tree (Hibbs 1978).

Seeds buried in mineral soil or humus germinate during the first year, but those under the current year's leaf litter will not germinate until the second year (Gabriel and Walters 1990). Partial overstory cutting will promote regeneration (Gabriel and Walters 1990, Hannah 1999), but germination will drop sharply with complete overstory removal (Gabriel and Walters 1990). In general, first-year survival depends more on predation, seedbed condition, and genetic variation than overstory density. Mortality decreases after age 2, but then increases after 16 to 40 years. Trees that survive beyond 20 years beneath small gaps have low rates of mortality (Hibbs 1979).

Striped maple does not develop root suckers, but it commonly reproduces vegetatively by layering or basal sprouting (Hibbs 1978, Hibbs and Fischer 1979, Gabriel and Walters 1990). The layers often occur under small canopy gaps, originating from small diameter stems laying on the ground, and off fallen branches or logging slash (Stalter et al. 1997). These sources are the primary means of reproduction under low light (Hibbs 1978, Hibbs and Fischer 1979). That was also true after both clearcutting and thinning in New York, where >45% of stems regenerated vegetatively. Yet in Massachusetts, 89% of striped maple had originated as seedlings. Numbers of sprout-origin stems exceeded those from layering, particularly after clearcutting.

In Vermont, striped maple regenerated at all sites after shelterwood cutting to a wide range of residual densities (50–120 ft^2/ac), but in greatest abundance at sites having a good viable seed source. Although preferred seedlings outnumbered the striped maple by five to one, beech and striped maple dominated 62 to 87% of plots under all residual densities, except at the lowest stocking (Hannah 1991). Further, abundance of sugar maple, beech, and striped maple 5 years after clearcutting in New Hampshire

depended on their size and frequency as advance regeneration. They also grew most rapidly when free of interference from less shade-tolerant species (Jensen 1943). Also in New Hampshire, Marquis (1965a) found abundant beech, striped maple, and pin cherry in most patches ranging in size from 75 ft to 190 ft wide (0.1 to 0.67 ac), with striped maple reaching 10 to 12 ft tall and 1 in. dbh. It had become established as advance regeneration and grew 2 to 3 ft per year in height after release. Its dominance in that case may reflect a lack of well-developed advance seedlings of more desirable species.

Leak (2003) reported that although striped maple had regenerated in abundance after patch cutting, it died or weakened by age 47. Similarly, McClure and Lee (1993) found that large gaps of recent origin had high basal areas and densities of pin cherry and striped maple. In 24-year-old gaps, their basal area increased with gap size. Among 31-year-old gaps, basal area decreased with increasing gap area. In 44-year-old gaps, striped maple stocking was low. Stocking also declined with gap size on steeper slopes, and striped maple was more abundant under partial shade than beneath a closed canopy.

Deer browsing has reduced the density of tall striped maple (>5 feet) in some clearcuts, and the height of saplings in thinned plots (Marquis 1974, 1981). Twice as many stems of this and other commonly browsed species have survived in slash piles left during logging, than in the open (Grisez 1960). Yet with deer densities <40/mi^2, striped maple, beech, and black cherry regenerated successfully in other thinned and clearcut stands in Pennsylvania (Tilghman 1989), and striped maple has filled gaps where deer eliminated seedlings of other species (Marquis and Brenneman 1981). Some studies indicate that deer show a high preference for striped maple in late fall and winter, but only moderate to low preference at other times (Horsley et al. 2003).

Hobblebush

General Ecological Considerations

Hobblebush is a sprawling shrub that may grow to 10 ft tall, but branches commonly lay prostrate along the ground. These often root where they touch the forest floor (Seiler et al. 2003). Hobblebush has shallow roots, mostly limited to the organic layers (Gould 1966). It occurs commonly underneath well-stocked forests at moist, well-drained sites, and throughout mesic forests of eastern North America (Gould 1966, Hsu and Diamond 1998). Common associates include striped maple, American beech, sugar maple, and yellow birch (Gabriel and Walters 1990).

Hobblebush leaves begin to expand earlier than both overstory trees and understory beech, and remain on the bushes into Sept. This may relate to its shade-tolerance (Gill et al. 1998). Bushes in medium shade have larger leaves than ones under heavy shade (Gould 1966).

Regeneration and Understory Development

Hobblebush begins fruiting at 3 to 8 years of age, with limited amounts in the early years (Bonner et al. 1948), or in deep shade (Gould 1966). Seeds do not germinate readily, or germination does not occur until the second year in northern latitudes (Gould 1966, Bonner et al. 1948), making seedling regeneration uncommon (Gould 1966). Rather, hobblebush reproduces readily by layering and sprouting, and probably regenerates primarily by vegetative means. Mowing will induce sprouting, particularly from stems cut close to the ground. Layering occurs commonly in logged areas, where stems bent over to the ground readily develop roots. These new plants grow rapidly in the elevated light after overstory cutting (Gould 1966).

Gould (1966) considered hobblebush a preferred food for deer, and one that they used heavily in winter. Yet the intensity of browsing seems to vary by location. In western Pennsylvania, heavy deer browsing during 20 years in an old-growth hemlock-hardwood stand reduced hobblebush vigor and eventually eliminated it. Thereafter, browsing preference shifted to less palatable beech seedlings and root suckers (Hough 1965). By contrast, Curtis and Rushmore (1958) found that although plots outside protective exclosures had few trees of desirable species, they had abundant beech and hobblebush. This suggests low use by deer, given an alternate food source, or because the animals move off the slopes into winter yards when the snow becomes deep.

Available evidence does not clearly demonstrate effects of cutting intensity on hobblebush survival or proliferation, except in the most heavily cut stands. In one study, *Rubus*, ferns, and grasses replaced formerly abundant hobblebush after clearcutting (Jensen 1943). Similarly, Leak and Solomon (1975) found that hobblebush had increased slightly by the ninth year under a range of residual densities (down to 40 ft^2/ac), but did not occur in the clearcuts. Yet when Barrett et al. (1962) made small clearcuts (132 × 198 feet wide) or reduced the overstory basal area to 70, 50, and 30 ft^2/ac, hobblebush density did not increase dramatically in any plot during the first 4 years. From his studies, Gould (1966) concluded that the environment inside large clearcuts and clearcut patches was poor for hobblebush because of the reduced humus and lower moisture within the upper soil layers. By contrast, conditions after selection cutting stimulated hobblebush, but stem numbers had declined again by approximately 15 years. Consistent with this, Oosting and Reed (1942) found only one-half as much hobblebush beneath 60- than 10-year-old stands in Maine. When dense, the thickets may interfere with regeneration of desirable tree species (Gould 1966).

Management Implications

Because of their high shade tolerance, American beech, striped maple, and hobblebush survive for long periods beneath the canopy of northern hardwood stands, often developing into a dense understory layer that heavily shades shorter trees and interferes with the regeneration of desirable hardwoods. The density of all three species often increases after partial cutting, and when other low-intensity upper canopy disturbances increase light near the forest floor. All three also regenerate vegetatively, and the new

shoots develop rapidly in partial shade. That increases understory shading by their foliage. Damage to the root systems and flattening of the stems during logging will lead to new regeneration of those species via vegetative means. The new suckers and shoots often develop rapidly, interfering with survival and growth of seedlings of other species.

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