

**Effects of Selective Tree Felling by *Castor canadensis* on
the Structure and Species Composition of a Northern
Hardwood-Conifer Forest**

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Effects of Selective Tree Felling by *Castor canadensis* on the Structure and Species Composition of a Northern Hardwood-Conifer Forest **Abstract**

By cutting trees, beaver, *Castor canadensis*, can alter the structure and species composition of forests. I quantified beaver selectivity according to tree species and size, as well as beaver effects on forest structure, species abundance, and regeneration, in a northern hardwood-conifer riparian forest in Hanover, NH. Beavers preferred to cut red oak, white ash, juneberry and beaked hazelnut, avoiding white pine and sugar maple. Although they cut larger trees, they preferred trees 2.5-5cm in diameter. In the study area, 72% of all stems > 2.5 cm dia. were cut, removing 12.1% of total basal area. Relative density, basal area, and importance value declined for preferred species and increased for species avoided by beavers. Regeneration capacity for preferred tree species was reduced, due to a reduction in saplings and smaller trees after beaver cutting. However, cutting increased the seedling densities of white pine and red maple and the growth rate of sugar maple seedlings. Many of the cut species stump sprouted; these sprouts grew at 2-3 times the rate of non-sprout juveniles in the same size class. Based on these data, I predict that continued beaver cutting in this forest would increase dominance of white pine and/or more shade tolerant conifers, depending on the intensity and duration of further beaver cutting. However, if beaver were to stop cutting (as they have at my study site), I predict that the forest would maintain the species composition of the original forest, with similar relative abundances.

Introduction

Large herbivores can influence the structure and dynamics of ecosystems and communities (Botkin et al. 1981; Bratton 1975; Hatton and Smart 1984; Keith et al. 1984; Lubchenco and Gaines 1981). Herbivory by moose (*Alces alces*) causes long-term stand alteration of boreal forest through changes to forest succession and nutrient cycling (Snyder and Janke 1976; Pastor et al. 1988). Sea urchins (*Stronglyocentrotus spp.*) can reduce the abundance of the dominant kelp species from the ocean floor, changing the marine community (Watanabe and Harrold 1991). Beavers, *Castor canadensis*, affect their habitat more dramatically than many other herbivores (Wright et al. 2002). Yet, to my knowledge, the impact of beavers on the structure and species composition of the forests of Northern New England has never been quantified.

The beaver is the largest rodent in North America, it occurs throughout the continent except northern Canada, Alaska and southern Mexico. Plentiful beaver attracted European colonists to New Hampshire in the late 1500's. To satisfy the demand for felted fur hats in Europe, beaver were trapped by both colonizers and Native Americans until c. 1830 when they became locally extinct (Dugmore 1914; Cronon 1983; Whitney 1994). In the 1930's beaver were reintroduced; they rapidly reoccupied their former range, and by 1955 were considered too abundant in New Hampshire. The population is now controlled by a public trapping season and the removal of "nuisance" animals (NHFGD 2006).

The national symbol of Canada, the beaver is renowned not only for its ability to fell mature trees but also to construct dams and lodges. Beavers are the quintessential ecological engineers, (although this term has been applied to species with relatively

minor effects). Beavers alter habitat structure and create new ecological communities (Gill 1972; Muller-Schwarze and Sun 2003). Two to three year old beavers leave their natal colonies, traveling up to 50 km to colonize a new site. Some live in dens dug into the banks of rivers, others build a lodge on a lake, and some create their own ponds by damming streams. Beavers can live wherever there is sufficient suitable vegetation and a year-round source of water (Howard 1982). They are generalist herbivores who eat the cambium and leaves of trees, as well as herbaceous and aquatic plants, e.g. grass and pond lilies (Northcott 1971; Nixon and Ely 1969; Jenkins 1978; Nolet et al. 1994; Wessels 1997). They need variety in their diet since no single species of plant can provide all required nutrients (Muller-Schwarze and Sun 2003). However, woody species are not used equally. Across their range, beavers have shown clear preferences (Chabreck 1958; Hall 1960; Brenner 1962, Nixon and Ely 1969; Northcott 1971; Jenkins 1979 and 1980; Belosky 1984; McGinley and Whitham 1985). Poplar (*Populus*), alder (*Alnus*), and willow (*Salix*) are generally the most preferred, followed by ash (*Fraxinus*), birch (*Betula*), cherry (*Prunus*), hazel (*Corylus*), maple (*Acer*), and oak (*Quercus*). Least preferred have been red maple (*Acer rubrum*) and conifers, e.g. pine (*Pinus*), spruce (*Picea*), fir (*Abies*), and hemlock (*Tsuga*) (Muller-Schwarze. and Sun 2003). Wessels (1997) informally observed the following preference ranking in central New England: Salicaceae (willow family including poplars), oak, ash, sugar maple (*Acer saccharum*), Rosaceae (rose family, e.g. apples (*Alus domestica*) and cherries), Betulaceae (birch family, especially muscledwood (*Carpinus caroliniana*), black birch (*Betula lenta*), and paper birch (*Betula papyrifera*)), gray birch (*Betula populifolia*), yellow birch (*Betula alleghaniensis*), speckled alder (*Alnus incana*), hophornbeam (*Ostrya virginiana*), beech

(*Fagus grandifolia*), red maple, white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*). Beavers also prefer trees with small diameters, c. 4.5 cm (Basey et al. 1988; Wessels 1997). The preference ranking varies depending on the local abundance of tree species, seasonal nutrient availabilities, and secondary metabolite concentrations (Dugmore 1914; Muller-Schwarze and Sun 2003). While in general beavers are optimal foragers, maximizing their net energy gain (Haarberg and Rosell 2006), secondary metabolites may strongly influence beaver preference, and can fluctuate due to season, growth stage (size), growth rate, and past damage. Fast growing species, small diameter trees, and trees that have not been exposed to past cutting, all tend to have less secondary metabolites and higher preference (Jenkins 1979; Basey et al. 1988). Beaver use smell and taste tests to make their choices (Jenkins 1978; Muller-Schwarze and Sun 2003). In Northern New England, beaver store branches for use in winter when ponds are frozen. A food cache is built, with less preferred species at the top, holding the preferred species under water away from surface ice (Doucet et al. 1994). Trees also supply building materials for dams and lodges.

The beavers' preference for some tree species, combined with their remarkable ability to cut large trees, can create profound changes in their habitat (Knudsen 1954; Barnes and Dibble 1988; Johnston and Naiman 1990). A single beaver in Minnesota, on average, cuts 1300 Kg/ha/year or 7% per hectare per year of the forest's biomass (Johnston and Naiman 1990). One third of this was used as food and an even smaller fraction was used for building, so beaver impact is far greater than that predicted by energetic and construction requirements alone (Johnston and Naiman 1990; Muller-Schwarze and Sun 2003). Trees left uncut are often non-preferred species of large

diameter. Beavers are classic central place foragers, reducing stem density and basal area of preferred species only in the area surrounding their lodge (Fryxell and Doucet 1993). Since beaver can cut mature trees, they tend to open the canopy, decreasing competition for light and altering the water, soil and nutrient availabilities (Wilde et al. 1950). They tend to increase the net primary productivity of remaining non-preferred woody species (Barnes and Dibble 1988; Johnston and Naiman 1990). Hence, longer-term cutting causes deciduous stands to be replaced by thicket-like zones of non-preferred species of shrubs and herbaceous plants (Johnston and Naiman 1990; Rosell et al. 2005). In boreal forest or other areas with nutrient poor soils, the loss of the preferred deciduous species also causes the loss of their nitrogen-rich leaf litter. This loss of nutrients further favors conifers, which can survive in the low soil nutrient levels maintained by their own slowly decomposing leaf litter (Bryant and Chapin 1986, Donker 1993; Rosell et al. 2005).

These large, previously mentioned, beaver effects on forested landscapes have been observed in studies located in the midwest and west of North America. However, beaver preferences and their impact on tree species abundances, forest structure, and regeneration rates have not yet been quantified in northern New England. Unlike the forest habitats examined in previous studies, the forests of northern New England do not generally have a single dominant tree species. The history of land use in this region, including burning by Native Americans, clearing for colonial farming and grazing, past beaver impacts, and modern logging activities, has created a mosaic of forest patches with different relative species abundances. These forests generally include a mix of evergreen and deciduous species, with a range of shade tolerances (Cronon 1983; Wessels 1997). The objective of my study was to determine the local tree preference

rankings and how selective felling by beaver affects the northern hardwood-conifer riparian forest, through changes in species and size class abundance, basal area, tree density, and regeneration rates. Based on previous work in western and midwestern North America, beavers in northern New England could have a similarly dramatic impact on forest structure.

Methods

Study Site

My study site was an area occupied by a beaver colony (the “Harris” colony) on a tributary of Mink Brook, 7 miles NE of the Dartmouth College campus. Beaver have been at the site for many years, and there are, *c.* 15 ponds of various ages of occupancy and abandonment along a *c.* 1 km section of the brook (Lawrence 1952). The site is in a small valley covered by northern hardwood-conifer forest. In the past, the entire area was cleared for farming (as evidenced by stone walls) and has since been logged (as evidenced by saw-cut tree stumps), similar to much of northern New England’s forest (Wessels 1997). My main study site was in the forest surrounding a pond created by beavers in 1998. The study was conducted in August and September of 2006, so beaver had been actively cutting there for 8 years. I used a second study site, similar to the first, but without any sign of recent beaver cutting, to evaluate the effects of beaver cutting on forest regeneration. This second site was 200 m away from the first, along another branch of the brook (Figure 1).

Sampling

To sample each of these areas, I established 45 m-long transects perpendicular to the pond (or stream) every 10 m along the shoreline. There were 12 transects per study site, representing a 110 m-long shoreline. All points at 10 m intervals along the transects were potential plot centers for 5 m-diameter circular plots. Thus there were 60 possible circular plots in each area. Thirty percent of these were randomly chosen, providing a sample size of 16 plots in each of the two areas. To quantify recruitment (seedling and sapling densities) and the growth rates of juvenile trees, I sampled in smaller nested plots, within the 5 m plots described above. Sapling data were collected in 4 m diameter plots and seedling data in 2 m diameter plots, in each of the plots used for tree measurements. This sampling procedure is modified from the methods of Johnston and Naiman (1990).

Measurements

Cut trees were defined as those clearly harvested by beaver, leaving a conical stump. I recorded species identity of these stumps using stump sprouts (new growth from the stump) where available, and remains of the branches and bark. All stumps could be identified to species. Size preference and size class composition changes were determined by measuring individual tree and stump diameters at a standard “stump height”, 30 cm above ground (all stumps were at least this high), giving a “diameter at stump height” (DSH). Size classes were defined for trees as pole (2.5 to 5 cm DSH), small (5-10 cm DSH), medium (10-30 cm DSH) and large (>30 cm DSH). Basal area (BA) of each tree was calculated as $\Pi (DSH/2)^2$. The species identity of each tree was also recorded. This allowed me to determine beaver species preference, and also to compare species

abundance before beaver cutting (cut stumps plus uncut standing trees) and after cutting (uncut standing trees). Only trees > 5 cm DSH were included in “before and after beaver” calculations, because it was possible for a tree < 5 cm DSH to have grown to 5cm DSH after beaver activity began (Johnston and Naiman 1990). Saplings (1-2 m tall and < 2.5 cm DSH) were identified to species and counted in the 4 m diameter plots in both study areas. Seedlings (> 1 yr old and < 1 m tall) were identified and counted in the 2 m diameter plots in both areas. For both seedlings and saplings, I measured growth rate as stem extension growth, using bud scale scars, and recorded the total extension growth over three years, 2004, 2005 and 2006. Extension growth for 2006 was complete by the time of sampling. Growth rates and seedling and sapling densities were compared between the active and inactive beaver areas as part of the regeneration component of the study. There were a few rare species in the forest which were lumped together as “other species”.

Calculations

Species preference was calculated by Jacob’s (1974) index of selectivity

$$S = \ln (r(1-p)/p(1-r))$$

where (for any given species), r is the proportion of all trees cut that are of that species, p is the proportion of individual trees (cut plus uncut) that are of that species, and $S > 0$ indicates positive preference (Jenkins 1978; Barnes and Dibble 1988). This calculation was repeated with basal area substituted for numbers of individuals. Selectivity based on basal area is more indicative of the amount of tree biomass involved in species selectivity by beavers.

Importance value (IV) of each species, an overall index of the relative contribution of that species to forest structure, was calculated as:

$$IV = (RF+RD+RB)/3$$

where RF is the relative frequency of the species (# plots where species occurred/ total # of plots X 100), RD is the relative density (# of trees of species/ total # of trees sampled X 100), and RB is the relative basal area (basal area of species/ total basal area of all species X 100) (Johnston and Naiman 1990). The densities, basal areas and importance values of each tree species were calculated for the main study area, both before and after beaver activity, and compared to evaluate changes in forest structure. Measurements of uncut trees overestimated the before-beaver basal area since uncut trees continued to grow during beaver activity; however, this bias was found to be minimal by Johnston and Naiman (1990).

Statistical tests

I conducted a G-test on the selectivity results for both numbers of trees and basal area, to determine whether beaver displayed non-random choice (preference). Seedling and sapling densities and growth rates were compared between the active and inactive beaver areas, using the Mann-Whitney Wilcoxon Rank-sum Test for nonparametric data in JMP LN 4, to determine differences in regeneration between the main study area (where beaver were active) and the second study area (no recent beaver activity).

Results

Beaver Preference

The Harris beaver colony did not cut trees (≥ 2.5 cm DSH) at random in the forest surrounding their pond, but preferred some species over others. Significant preference was found using selectivity indexes calculated both from numbers of trees and basal area (numbers $G = 91.03$, $DF = 9$, $P \leq 0.0001$; basal area per 0.5 ha $G = 740.43$, $DF = 8$, $P \leq 0.0001$). Beaver preferred to cut red oak over all other species and strongly avoided white pine (Figure 2). Beaver also had positive preferences for white ash, juneberry, and beaked hazelnut, though the ranking depended on whether number or basal area was used. They weakly avoided black cherry and sugar maple. Red maple and beech were positively preferred in terms of basal area, because these species contained some of the larger individuals cut. However, they were avoided (had negative preference) in terms of numbers, because red maple and beech individuals are abundant in the forest, compared to the number cut. The beavers showed a marked preference for pole sized trees (2.5 - 5 cm DSH) over all other size classes, including seedling and saplings, and avoided cutting large trees (≥ 30 cm DSH) (Figure 3).

Effects on Structure and Species Abundance

Over the last eight years 1998-2006, beavers cut 72% of all the stems in the forest. While this effort was focused mainly on pole sized trees (76% felled) some large diameter trees (up to 56 cm DSH) were also felled. Thus, after beaver cutting, the forest was more open, consisting mainly of larger trees of non-preferred species. Densities of the most preferred species, such as red oak and juneberry, were drastically reduced (by

88% and 50% respectively; Figure 4). Some preferred species, which were abundant before cutting, were reduced below the average density of all species; for example, red oak had 2.55 stems per 100 m² before cutting, but only 0.32 per 100 m² after (the overall average among species after cutting was 1.11 per 100 m²). The more preferred species suffered heavy cutting by basal area as well; 48% of the basal area of red oak was removed and 38% of beech (Figure 5). In total, 12.7% of the basal area of the forest was cut. This is a dramatic effect, considering that most of the basal area before beaver cutting was contributed by trees avoided by beavers, including large white pine and some large individuals of rarer species.

The results of the importance value calculations show the heavy effect of beaver selectivity on the forest (Figure 6). White ash was previously a forest dominant, but was reduced substantially in only eight years of cutting. Red maple, a close second to white ash in importance value before beaver activity, was also much reduced. White pine rose in importance value because it persisted at a similar level of abundance. It replaced the ash and maple as the most important species in the forest after beaver activity. Similar trends can be seen in the other species, with preferred species decreasing in importance, according to their selectivity values, and the avoided species increasing in importance, with the exception of black cherry which was weakly disliked but decreased in importance because it had so few trees ≥ 5 cm.

Effects on Regeneration

Beaver influenced the study site through changes in seedling and sapling densities, and change in their stem extension growth rates. Seedling densities for most tree species were higher in the cut area, with the exception of red oak and beaked hazelnut; these species had lost many of their trees of reproductive size to beavers, and do not have long-lived or widely dispersed seeds (Packham et al. 1992). Seedling densities of red maple and white pine increased significantly (mean red maple density from 1.25 to 3.4 per 20 m², $X^2 = 3.24$ DF = 1, P = 0.07; mean white pine density from 1.25 to 2.38 per 20 m², $X^2 = 2.92$, DF = 1, P = 0.09). Black cherry was the most abundant seedling species after cutting, followed by white ash, white pine, and red maple (Figure 7). Sapling densities all increased after beaver activity, except for white pine; though none of the species-level results were significant with the sample sizes obtained. Beaked hazelnut was the most abundant sapling species after cutting, followed by juneberry, beech and white ash (Figure 8).

Seedling extension growth over the last three years tended to be greater in the active beaver area (except for white pine), though this was significant only for sugar maple (median sugar maple growth 2.17 cm over three years without beaver, compared to 3.69 cm with beaver; S = 132, Z = -1.95, P = 0.05; Figure 9). Sapling extension growth tended to be higher in the active beaver area for white ash and beaked hazelnut but lower for juneberry and black cherry, though these trends were not significant. Beech sapling extension growth was marginally significantly lower (median growth over three years 23.27 cm without beaver, compared to 16.76 cm with beaver; S = 86, Z = 1.72, P = 0.09; Figure 10).

To see whether beavers preferred to cut species that regenerate rapidly, three-year growth rates were averaged across study sites (i.e. including areas where beaver were and were not active) for comparison with beaver cutting preferences (calculated using tree numbers). There was a weak positive correlation between preferred species and growth rates in seedlings, but this trend disappeared by the time the juveniles became saplings (Seedling $R = 0.73$, Sapling $R = 0.25$).

Many of the cut species were able to regenerate by stump sprouts. Seedling stump sprouts on average grew three times faster than non-sprout seedlings of the same species. Sapling sprouts grew on average twice as fast as non-sprouts. The density of these stump sprouts was high, especially in the preferred and thus heavily cut species like red maple and red oak; stump sprouts comprised a large fraction of these species' regeneration.

The size-class distributions for individual species show that seedlings were generally an order of magnitude more dense than other size classes before and after beaver activity. Across species before beaver, there was generally an "inverse j-curve" shape to the size class distribution from seedlings to large trees, typical of species that are replacing themselves in the canopy (Packham et al. 1992). This pattern was disrupted after beaver activities because sapling and pole sized trees are reduced in numbers.

Discussion

Eight years of selective beaver cutting had a dramatic effect at the Harris study site. Beaver cutting preference differed from that documented in other regions of North America (Johnston and Naiman 1990, Muller-Schwarze and Sun 2003). The forest in my study area lacked the highly preferred species of aspen, willow and alder present at other study sites. Species in the genera that were expected to be middle-ranked based on other studies, including red oak, white ash, junberry, and beech, had relatively high selectivity values at Harris. My results correspond broadly to rankings suggested based on informal observations in New England forests by Wessels (1997). The differences between my and Wessels' rankings and the other N.A. studies suggests that initial forest composition and locality have a strong influence on beaver felling preference. The high ranking of red maple in my study is interesting. Red maple is known to have greater secondary metabolite content and to provide poorer nutrition than other beaver-cut species (Muller-Schwarze. and Sun 2003), and it is normally not preferred. However, it was an abundant species at the Harris study site, comprising 22% of stems before beaver cutting. Thus, local abundance may influence its preference ranking positively. It is also the third fastest growing sapling, suggesting, that in this area it may invest less in secondary metabolites than at previously studied sites outside northern New England. However, beaver cutting preference was not correlated with faster growth in saplings overall, leading one to conclude that either faster growth is not associated with low secondary metabolite production in the species found at this study site, or beavers are not choosing trees based on secondary metabolites.

Most beaver cutting was focused on only a few species, and on pole sized trees (2.5-5 cm DSH). The resulting change in forest structure and species abundance over this short period of beaver activity (8 years) was due mainly to the reduction in these preferred species and size classes, and not to changes in regeneration that could affect forest structure in the long term. White ash, red maple, and red oak were all important species in the forest before beaver activity, but dropped in importance due to heavy beaver cutting. White pine, which is avoided by beavers, became increasingly dominant in terms of relative abundance. Currently, with many of the smaller trees removed from the understory, the “thicket effect” noted by Johnston & Naiman (1990) can be seen at my study site. Where beavers have been active, shrubs and herbaceous growth have replaced the saplings and small trees in the forest understory. This type of habitat is very productive and known for its rich diversity of plants and animals (Paine 1966).

Higher seedling densities of white pine in the beaver-cut area suggest that white pine (a light demanding species (Packham et al. 1992)) may be able to regenerate better in areas where the canopy has been opened by beaver cutting. Since white pine is avoided by beavers, they may further increase white pine juvenile abundance by removing competitors, as was seen for willow juveniles by Nolet et al. (1994). This could result in a white pine monoculture similar to those found on old farmland in the vicinity of the study site. However, because white pine is unable to regenerate in shade, more shade-tolerant non-preferred conifers, e.g. hemlock or balsam fir, could come to dominate in the heavily cut zone around the pond if the canopy were not opened enough during ongoing beaver activity (McNeel 1964). Dominance by either white pine or hemlock may be favorable

for timber production, producing a near-monospecific stand of similar aged trees (Packham et al. 1992).

However, continued beaver cutting could cause the forest to follow a somewhat different trajectory if stump sprouts of preferred species increase production of secondary metabolites, and thus, lower beavers' preference for them. This can occur when beavers cut aspen (Basey et al. 1988). In this case, preferred species could regain their original relative abundances through stump sprouting (McGinley and Whitham. 1985). But there is also evidence (including observations from this study) that stump sprouts may remain highly preferred by beavers, suggesting they may have been little if any increase in the levels of secondary metabolites. Willow and alder species do not increase metabolites to levels that change beaver preference and can be "farmed" by the beavers for many years (Ritchie 1983). If this is the case for stump sprouts at my study site, then the predicted trend toward increasing conifer domination is likely to occur once the carbon reserves in stumps have been depleted, due to repeated sprouting and beaver harvest.

In predicting the effects of beaver cutting on the New England landscapes, it is important to recognize that beaver typically move on to different sites after several years, due to food depletion and/or damage to lodges and dams by spring floods. Thus, many beaver-affected forests are abandoned after a relatively short period of beaver cutting. After beaver, the successional trajectory of the forest will depend heavily on which species were originally present, the beaver's selectivity among those species, and how depleted the preferred species had become. Regeneration at my study site for the preferred species is currently interrupted due to heavy cutting of the small trees of those species. Yet, the number of saplings and seedlings has increased in the area with recent

beaver activity and there are numerous fast growing stump sprouts present, so there is potential for regeneration if beaver activity ceases.

At my study site, the dam constructed by the beaver colony was destroyed by flooding in spring 2006, causing the beaver to move on and start cutting elsewhere. It is unlikely that the past depletion of preferred species is great enough to result in a conifer dominated forest (Muller-Schwarze. and Sun 2003); it is more likely that the preferred species will regain their original relative abundances.

Overall, the effects of beaver cutting on tree species abundances in this northern hardwood-conifer riparian forest are not as clearly predictable as in the Midwestern hardwood forest studied by Johnston and Naiman (1990). Research in the Midwest has focused on sites dominated by the highly preferred aspen species, while in the forests of northern New England, dominance tends to be shared by a number of hardwood and conifer species. Thus, there are several possible future forest scenarios in northern New England, as described above.

Future studies could build on my research by including multiple study sites and areas with varying time lengths of beaver occupation, to obtain a broader, more comprehensive assessment of beaver effects on the forest of northern New England. These forests can have vastly different species compositions. Since this affects beaver preference and the impact of beaver activities on the future forest, it is important not to generalize too broadly from one study site. Further studies should also be done over a longer time scale where the before-beaver forest structure, composition and regeneration rates are known. This would avoid the bias associated with recreating the forest (based on and the standing forest plus stumps).

Beaver are extraordinary mammals. They have the capacity to modify the environment not only by building elaborate structures and causing flooding, but also by selectively cutting much of the forest in their backyards. The information presented here may help land managers and landowners better understand the effects of beaver activities so they can decide whether this is to their disadvantage or advantage. Knowing these results will give foresters a better understanding of how species and biomass of timber stands will change with beaver activity. It may also help landscape and conservation ecologists model more accurately the effects of beavers on forest structure and composition, and thus habitat quality for other species.

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Figures



Figure 1. Aerial image of study area (south end of Harris beaver colony off Three-mile Rd in Hanover, NH). Main study site (beaver cut area) is the upper yellow rectangle. Lower rectangle is second study site (see text), used to assess regeneration in absence of beaver effects. Entire area shown is 350m by 250m.

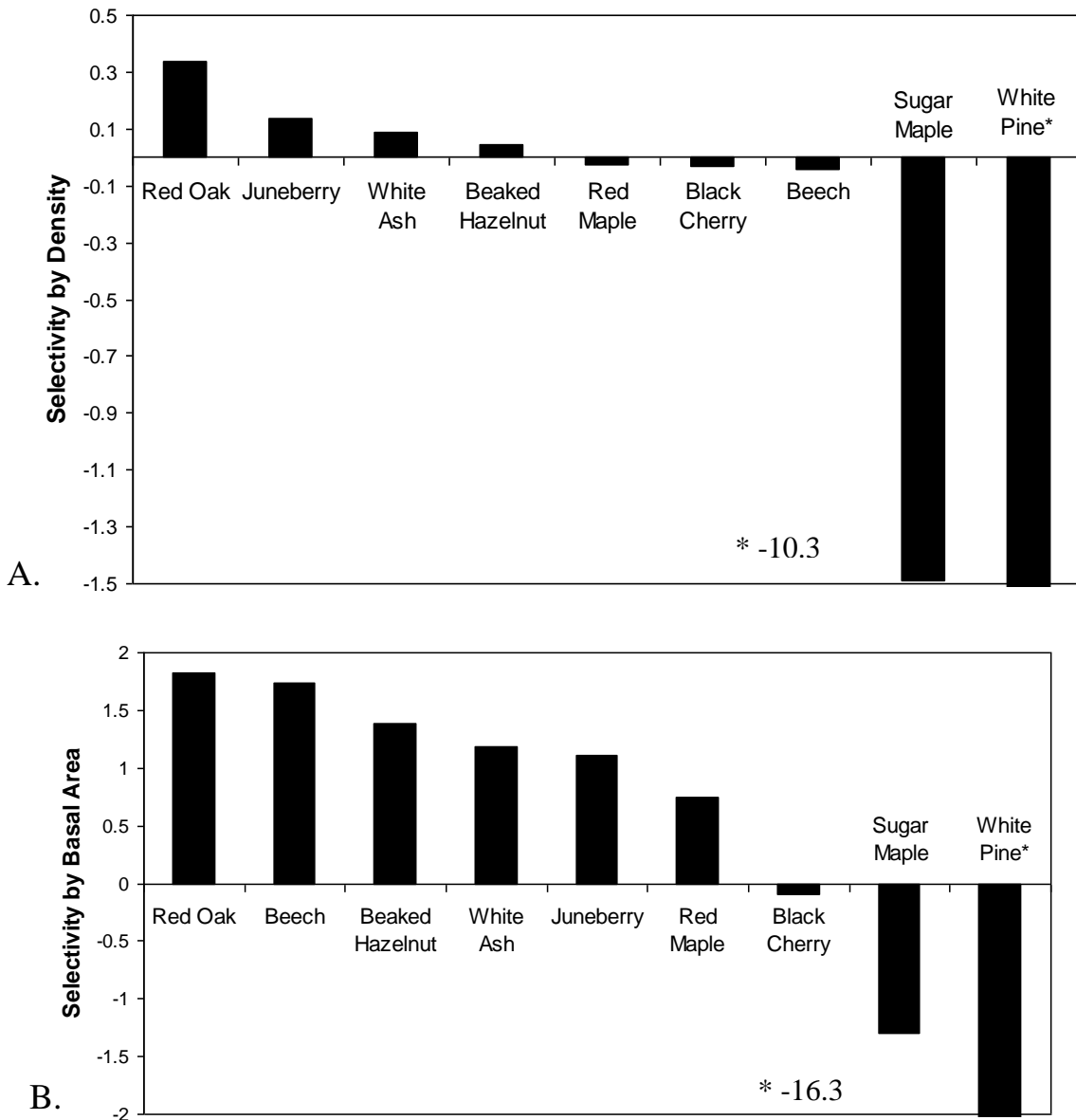


Figure 2. Jacob's Selectivity Index (S) for trees ($\geq 2.5\text{cm}$) using (a) tree density and (b) basal area. S is defined as a logarithm (see text) and zero represents neutral preference.

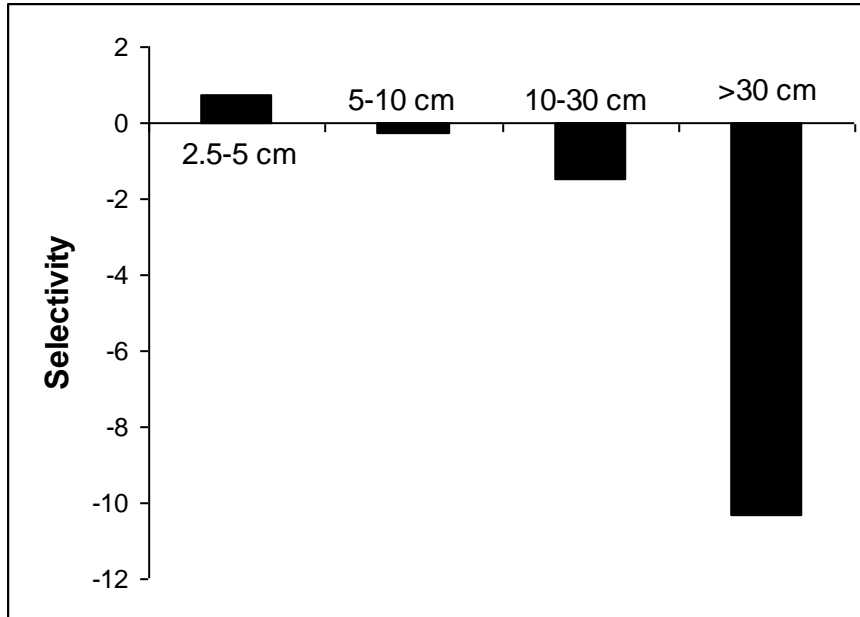


Figure 3. Jacob’s Selectivity Index for tree diameter (for trees ≥ 2.5 cm) using tree density. S is defined as a logarithm (see text) and zero represents neutral preference.

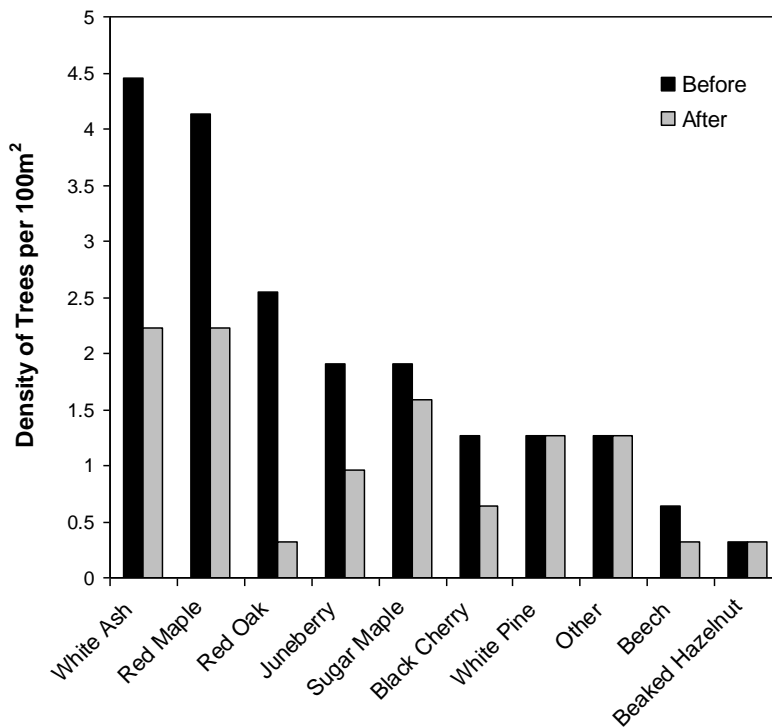


Figure 4. Density of tree species (trees ≥ 5 cm) per 100m^2 , before beaver cutting (estimated by cut plus standing trees) and after 8 years of beaver cutting.

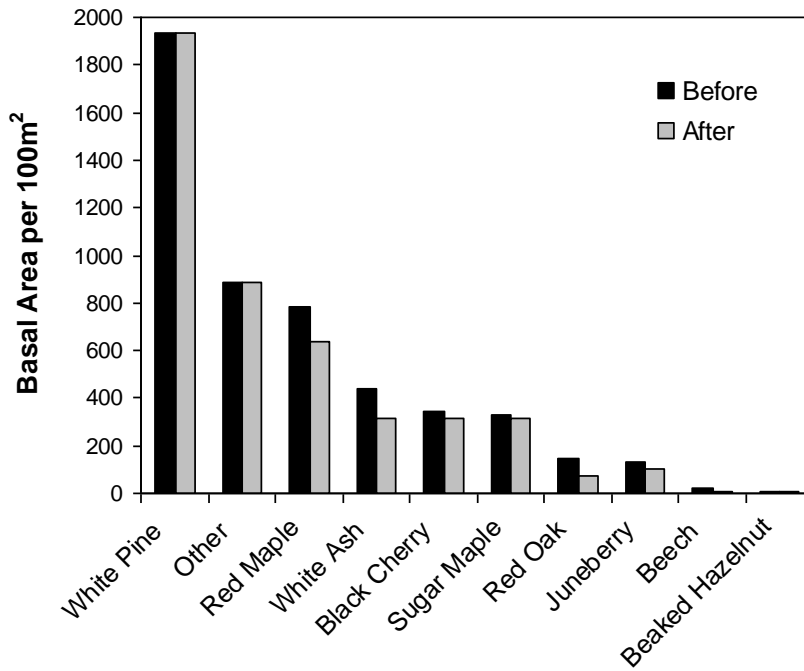


Figure 5. Basal Area of tree species (trees ≥ 5 cm) per 100m², before beaver cutting (estimated by cut plus standing trees) and after 8 years of beaver cutting.

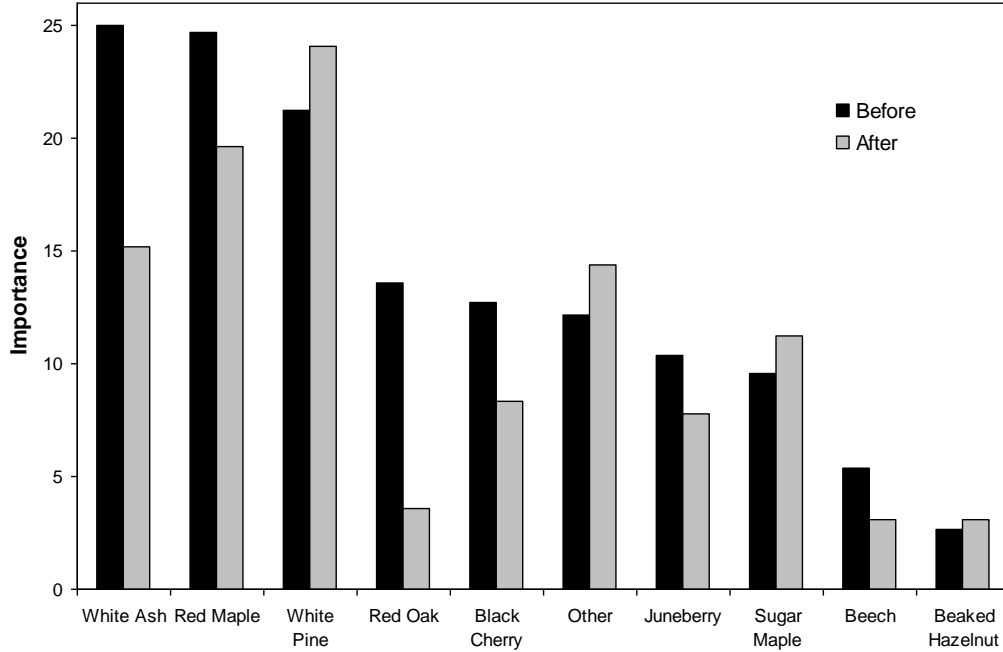


Figure 6. Importance value (see text) of tree species (trees ≥ 5 cm) per 100m², before beaver cutting (estimated by cut plus standing trees) and after 8 years of beaver cutting.

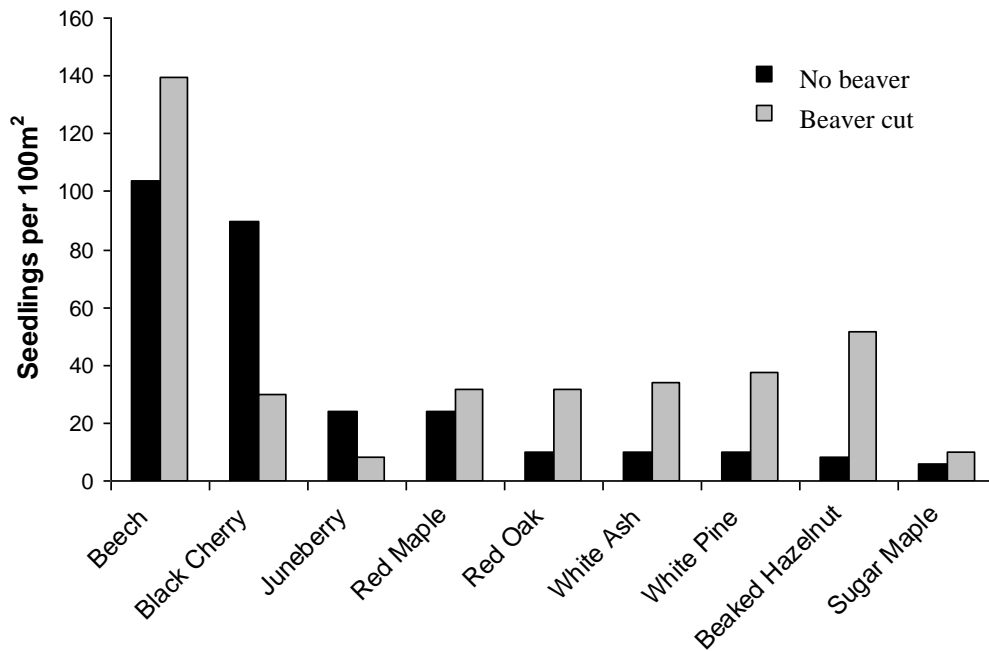


Figure 7. Densities of seedlings (>1 yr old, < 1m tall) in the area not cut by beaver (“No beaver”) compared to the area cut by beaver (“Beaver cut”).

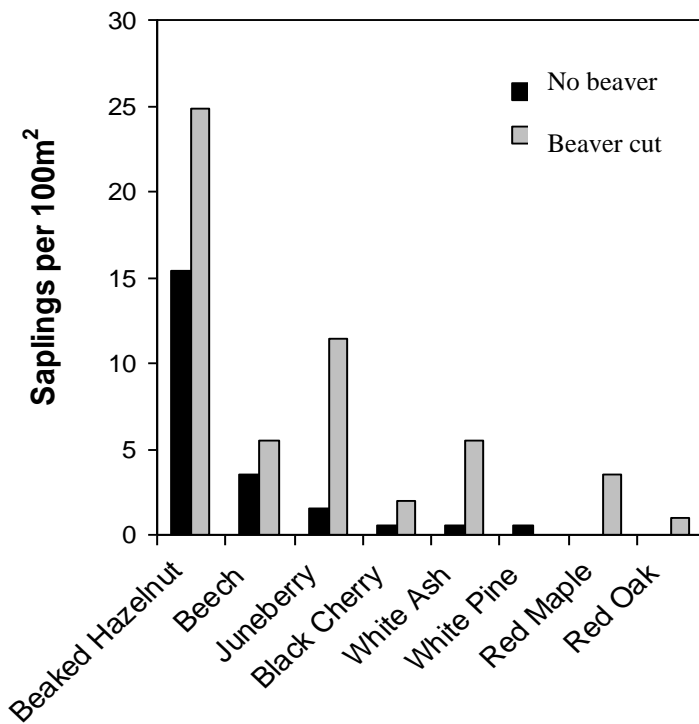


Figure 8. Densities of saplings (>1 yr old, < 1m tall) in the area not cut by beaver (“No beaver”) compared to the area cut by beaver (“Beaver cut”).

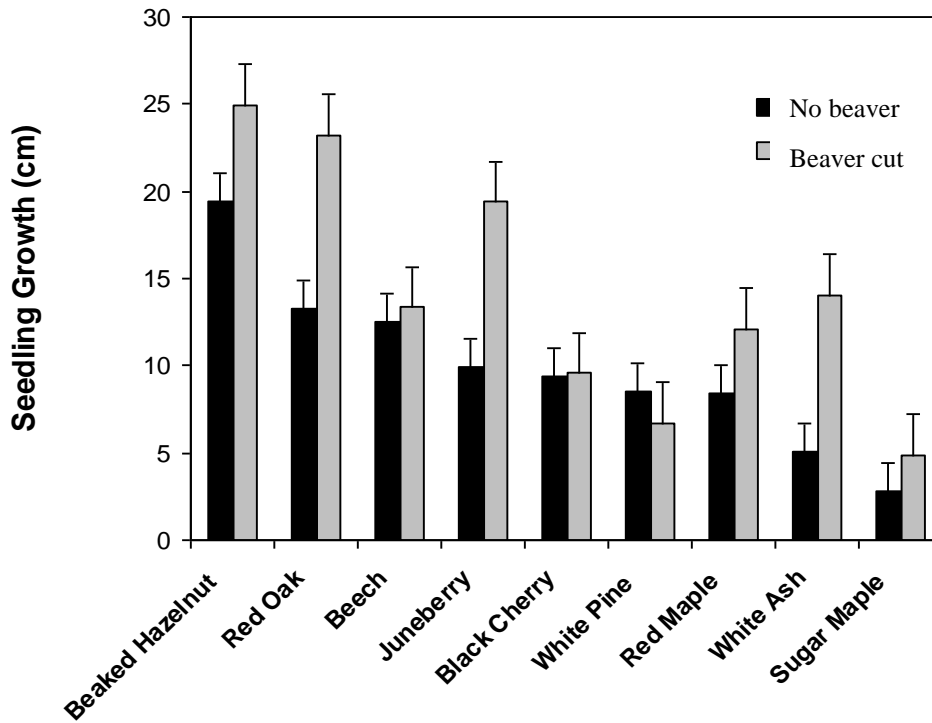


Figure 9. Stem extension growth of seedling species (<1m tall, >1 yr old) (cm) for 2004-2006 in the area not cut by beaver (“No beaver”) compared to the area cut by beaver (“Beaver cut”).

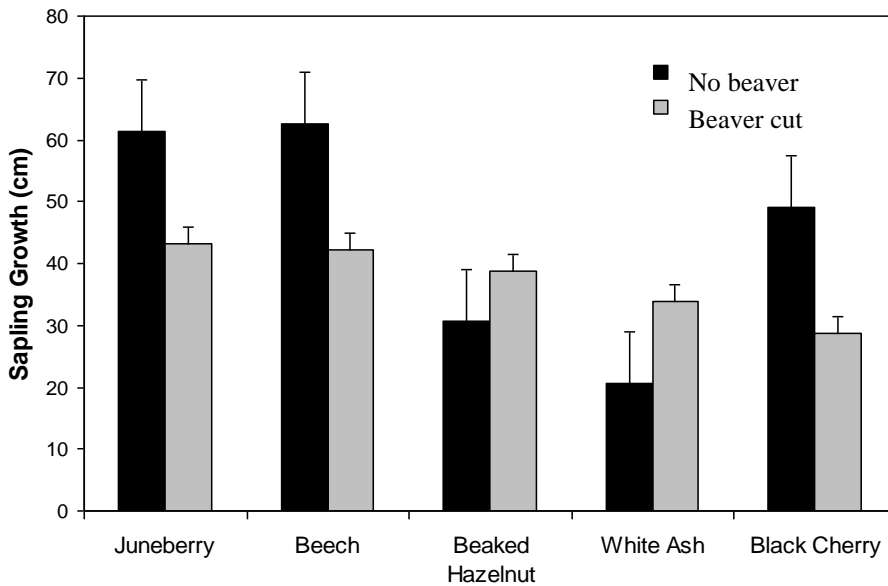


Figure 10. Stem extension growth of sapling species (1-2 m tall, <2.5 cm) (cm) for 2004-2006 in the area not cut by beaver (“No beaver”) compared to the area cut by beaver (“Beaver cut”).