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Effects of Selection Cutting on Soil Chemistry, Plant Community Composition and Structural Features of Northern Hardwood Forests

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Effects of selection cutting on soil chemistry, plant community composition and structural features of northern hardwood forests

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Abstract

Selection-cutting is the preferred method of logging in northern hardwood forests, because it is thought to favor the regeneration of valuable, shade-tolerant trees, maximize long-term productivity. and increase the health, quality and economic value of residual trees. Claims have also been made for the ecological sustainability of selection cutting, in particular that it: (a) preserves soil fertility; (b) maintains natural canopy composition; (c) protects plant and animal habitat. I evaluated these claims by studying the effects of selection-cutting on several measures of soil fertility (Ca, Al, Ca/Al molar ratios, pH), canopy composition and tree regeneration, herbaceous layer composition, and structural features related to habitat quality (cavity trees, snags, coarse woody debris) in 55 stands ranging from newly cut to old-growth (not all data overlaps). I found that forest growth after selection-cutting depletes soil solution calcium and lowers soil solution Ca/Al molar ratios, posing a threat to long-term forest health and productivity, particularly at higher elevations and in sites on siliceous bedrock. I found that selection-cut stands dominated by red oak (*Quercus rubra*) are converting to sugar maple (*Acer saccharum*) stands, posing a threat to both canopy and herbaceous layer diversity. I found no lasting effects of selection-cutting on herbaceous layer composition, diversity or quality, but I found indirect threats from the conversion of red oak stands to sugar maple and from depletion of soil solution calcium. Finally, I found that current selection-cutting practices generally do not meet published targets for large trees, cavity trees, snags and coarse woody debris, but that they probably could meet those targets with minor changes to cutting practices. I conclude by discussing the implications of these results for the management of northern hardwood forests.

Résumé

La coupe sélective est la méthode privilégiée d'exploitation forestière dans les bois-francs nordiques parce qu'elle semble favoriser la regénération d'arbres d'ombre précieux, maximiser la productivité à long terme et augmenter la santé, la qualité et la valeur économique des arbres rémanants. On prétend aussi que la coupe sélective contribue à la durabilité écologique notamment en : (a) conservant la fertilisation des sols; (b) préservant la composition naturelle des couverts; (c) protègeant les habitats des espèces végétales et animales. J'ai évalué ces propositions en étudiant les effets de la coupe sélective sur plusieurs mesures de fertilisation des sols (Ca, Al, rapports molaires Ca/Al, pH), la composition des couverts et la regénération des arbres, la composition des strates herbacées et les caractéristiques structurales reliées à la qualité de l'habitat (arbres creux, chicots, débris ligneux bruts) dans 55 peuplements, des nouvelles coupures aux forêts vierges (les données ne se recoupent pas toutes). J'ai découvert que l'accroissement forestier après une coupure sélective épuise le calcium de solution du sol et abaisse la solution du sol des rapports molaires Ca/Al, menaçant la santé des forêts et la productivité à long terme, surtout aux altitudes supérieures et dans les sites sur substratum siliceux. J'ai trouvé que les peuplements à coupure sélective dominés par le chêne rouge (*Quercus rubra*) font place à aux érables à sucre (*Acer saccharum*), menaçant à la fois la diversité des couverts et celle des strates herbacées. Je n'ai pas découvert d'effets à long terme de la coupe sélective sur la composition, la diversité et la qualité des strates herbacées; par contre j'ai trouvé des dangers indirects en raison du remplacement des peuplements de chêne rouge par ceux d'érable à sucre, et par l'épuisement calcium de solution du sol. Finalement, j'ai trouvé que les pratiques actuelles de coupe sélective n'atteignent pas en général les cibles officielles pour les grands arbres, pour les arbres creux, pour les chicots et pour les débris ligneux bruts, mais qu'elles pourraient y arriver si on les modifiait quelque peu. Je conclus en discutant les conséquences de ces résultats sur la gestion des bois-francs nordiques.

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Table of Contents

List of Figures

List of Tables

List of Appendices

CHAPTER ONE

General research goal

In Eastern North America, much attention is now being given to the management of the northern hardwood forest (Larson *et al.* 1999; Perera *et al.* 2000). The range of this vast forest coincides with one of the most densely populated, and heavily industrialized regions of the continent (Braun 1964). Consequently, it is under intense pressure throughout to support multiple, often conflicting uses. Advocates of forestry, mining, and hydroelectric power place demands on the forest, while acidic precipitation and dust drift and settle over the trees and into the lakes. Recreation facilities are constructed, and even protected areas are called upon to accommodate the millions of people each year who retreat to the forest to camp, hike, canoe, ski, fish and hunt.

Forestry is probably the most controversial use of northern hardwood forests, because of its high visibility and its economic importance (Larson *et al.* 1999; Perera *et al.* 2000). Campers and hikers seeking a wilderness experience are often vocal protesters when their favorite trail enters a new clear-cut or crosses the muddy scars of a new skidder trail, while the residents of small lumber towns are often quick to point out that the "trail" may, in fact, be a logging road, and that forestry is their livelihood. Aboriginal peoples look to forestry both as a threat to traditional forest uses, such as hunting and trapping, and as a potential source of non-traditional employment and income. Non-native hunters and anglers welcome the wilderness access and game habitat that forestry provides, while naturalists worry about the spread of exotic plants and an overabundance of white-tail deer. Despite the discord, however, there is a growing consensus that forestry practices must change (Working Group on Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests 1995; Kimmins 1997a,b; Perry 1998; Larson *et al.* 1999; Aber *et al.* 2000; Euler and Epp 2000). World-wide concern for losses in natural habitat and biodiversity have increased attention on forestry in northern hardwood forests, as proponents of conservation heed the adage, "think globally and act locally" (Larson *et al.* 1999). More recognition is being given to the value of northern hardwood forests as habitat for birds, mammals, amphibians, reptiles, plants and fungi (Kitchings and Walton 1991; Haney and Schaadt 1996; Keddy and Drummond 1996; Pelton 1996; Selva 1996). Increased research has led to a greater appreciation of the complexity of forest ecosystems, the multiple ecological and natural functions that they fulfill, and the many ways that they are being degraded by human impacts (Perry 1998; Kimmins 1997a,b; Larson *et al.* 1999; Aber *et al.* 2000; Euler and Epp 2000).

With such rising public awareness of the northern hardwood forests, forestry companies and other land management agencies are facing mounting pressure to manage forests "sustainably" – sustainability, in this context, referring to ecosystem processes and functions, rather than extractable resources (Kimmins 1997a,b; Perry 1998; Aber *et al.* 2000). They have been called upon to manage forests less for the production of wood fibre, and more for the sustainment of natural landscapes, habitats and nutrient-energy cycles. A significant part of this "greening" of forestry has been a re-evaluation of current logging practices, and where appropriate, the introduction of more sustainable logging methods. These changes are occurring at different spatial and temporal scales, from the spacing and scheduling of cuts across a landscape over a period of years, to the placement of skidder trails, and the timing of harvest within a single stand and a single season (Perry 1998). Unfortunately, many "improvements" are being implemented without the necessary knowledge to predict their outcomes, and without adequate plans to monitor and evaluate their ecological effects (Kimmins 1997a,b; Perry 1998; Aber *et al.* 2000).

In northern hardwood forests, there is increasing emphasis on selection-cutting as an ecologically sustainable alternative to other logging methods (Matthews 1989). Implemented in stands of shade tolerant trees, selection-cutting (also known as improvement cutting) consists of the cutting and removal of about 1/3 of the mature trees in a stand, leaving much of the canopy intact to provide shelter for the continuous recruitment and growth of more shade-tolerant trees (Matthews 1989; Anderson *et al.* 1990). Historically, it was used by foresters to insure a steady supply of hardwood trees, particularly when stable market conditions favored long-term planning (Matthews 1989)

In recent years, however, new claims have been made about the ecological advantages of selection-cutting in both northern and southern hardwood forests, as well as temperate rainforests and even tropical forests. Among other benefits, it is said to maintain natural stand composition, protect animal and plant habitat, and preserve soil fertility (Matthews 1989). These claims have been made, however, with little scientific research on the real effects of selection-cutting.

The goal of my research is to assess some of the claims made for selection-cutting, by determining some of its effects on the northern hardwood forest. The kinds of information which could be collected on the effects of selection-cutting are practically unlimited, so it is important to focus on those properties of the forest which are most ecologically significant, and most logically related to selection-cutting. This requires a more thorough description and understanding of the ecology of the northern hardwood forest and of selection cutting.

Ecology of the Northern Hardwood Forest

Distribution

The northern hardwood forest is classified as part of the temperate deciduous forest biome (Whittaker 1975; Aber and Melillo 1991). In fact, it is actually a broad ecotone between the boreal forest and the true temperate deciduous forest (Kricher and Morrison 1988). Braun (1964) refers to it as the "Hemlock-White Pine-Northern Hardwood association. Within this area, it occupies a wide variety of terrain, from the rugged Canadian Shield and the Appalachian cordillera, to limestone and glacial outwash plains.

Soils

Northern. hardwood forests occur mainly on alfisols and spodosols[1] (Brady and Weil 1996). Both have well-developed profiles, beginning with an A horizon, a dark surface layer of mixed mineral earth and decomposed organic matter (humus). Most decomposition occurs in

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[1] In the Canadian System of Soil Classification (Agriculture Canada 1987), alfisols are equivalent to brunisols and luvisols, while spodosols are equivalent to podzols.

this horizon, making it the most fertile portion of the soil (Swift *et al.* 1979; Ulrich *et al.* 1981; Vogt *et al.* 1986; Brady and Weil 1996). Below the A horizon, the leaching of clay, iron and aluminum oxides produces a bleached E horizon. The leached clay and minerals are then deposited further down, in a slightly darker region, the B horizon. Alfisols and spodosols are differentiated mainly by the presence or absence of an O (organic) horizon above the A horizon, the thickness of the A horizon, the thickness of the E horizon, and the presence or absence of subordinate layers within the B horizon (Brady and Weil 1996).

Alfisols occur mainly in temperate to warm-temperate climates, under a variety of mesic hardwood forests (Brady and Weil 1996). Because of high rates of decomposition, they lack a pronounced O horizon, but have a thick, crumbly A horizon, very rich in humus (mull). Alfisols are not normally acidic, and rates of leaching are low, so their E and B horizons are less defined. Alfisols retain a significant cation-exchange-capacity, which, combined with good texture, makes them very fertile. They are associated with northern, hardwood forests around the Great Lakes and southern Ontario, in areas dominated by sedimentary or meta-sedimentary bedrock, or by glaciolacustrine sediments (Brady and Weil 1996; Perera *et al.* 2000).

Spodosols develop in moist regions of cold or cool-temperate climates, usually under conifers, and often on acidic bedrock (Brady and Weil 1996). Because of cool temperatures, and poor litter quality, decomposition is slow (Brady and Weil 1996). Consequently, they normally have a layer of partially decomposed organic matter (mor), an O horizon, above a thin A. Leachates from these two horizons are high in organic acids, and since the parent material is naturally low in buffering capacity, spodosols can be very acidic. This produces a very pronounced, pale E horizon, in which a naturally low cation-exchange-capacity is further reduced by adsorption of H^+ and Al^{n+} ions to exchange sites. Their B horizons are more pronounced, often with distinct, narrow layers of aluminum, iron and organic molecule deposition. Spodosols are of naturally low fertility, and are particularly sensitive to acid deposition. They are associated with northern, hardwood forests in the northern Appalachian Mountains, and areas on the Canadian Shield, such as the Frontenac Axis of Eastern Ontario (Brady and Weil 1996; Perera *et al.* 2000).

Forest soils are not static, responding to changes in forest composition and litter quality (Packham *et al.* 1992; Brady and Weil 1996). In temperate forests, for example, conversion of from conifers to hardwoods can lower C:N ratios, resulting in faster decomposition and changes in humus from mor to mull (Packham *et al.* 1992). This, in turn, can result in changes in the underlying soil layers and produce intermediate soils with properties of both alfisols and spodosols, called the semi-podzols (Packham *et al.* 1992). In addition, on the Canadian Shield, fine scale differences in geology, geography and forest composition also mean that major soil groups are often interspersed (Brady and Weil 1996).

Composition

The northern, hardwood forest is a transitional forest between the more southerly parts of the temperate deciduous forest, and the northern boreal forest. It has a significantly lower diversity than the southerly parts of the temperate deciduous forest, but contains species from both the boreal and temperate deciduous biomes (Braun 1964). Whereas parts of the temperate deciduous forest may contain up to 30 species of canopy trees, the northern hardwood forest has only 11 dominant or sub-dominant species, with only 3-4 normally dominating a single stand (Braun 1964). *Acer saccharum* (sugar maple), *Tsuga canadensis* (northern hemlock) and *Fagus grandifolia* (American beech) are widespread, while *Quercus rubra* (red oak) can locally dominate on sites with a southern aspect. *Betula allegheniensis* (yellow birch) is often abundant, and, in fact, could almost be considered a "field mark" of northern hardwood forests, due to the virtual overlap of their ranges (Kricher and Morrison 1988). *Tilia americana* (American basswood) replaces *T. heterophylla* (white basswood) of the southern forests, while three new species are added: *Pinus strobus* (white pine), *Pinus resinosa* (red pine) and *Picea rubens* (red spruce). Two boreal species, *Picea glauca* (white spruce) and *Abies balsamea* (balsam fir), may also be common at the northern edge of the region. *Q. alba* (white oak), *Juglans nigra* (black walnut), *Carya ovata* (shagbark hickory) and *C. cordiformis* (bitternut hickory) may be present in small numbers on sites with a southern aspect, but they are never dominant, while truly southern species, such as *Liriodendron tulipfera* (tuliptree), *Magnolia acuminata* (cucumber magnolia), *Aesculus octandra* (yellow buckeye) and *Nyssa sylvatica* (sourgum) are entirely absent. Early- and mid-successional tree species, such as *Populus grandidentata* (bigtooth aspen) and *Fraxinus americana* (white ash), may be mixed with classical northern hardwood species in areas of disturbance, and moisture-loving species, such as *Acer rubrum* (red maple) and *Thuja occidentalis* (northern white-cedar) may be found in low-lying, moist stands.

European settlement, population expansion and resource extraction have wrought extensive and rapid changes in the ecology of northern hardwood forests (Larson *et al.* 1999; Epp 2000; Thompson 2000). So far, these impacts have been reflected in changing composition.

rather than diversity. Many tree species have declined, though none have actually been lost. White pine and red spruce were extensively and intensively logged during the late 19th and early 20th centuries, nearly eliminating them from the northern hardwood forests (Keddy 1993; Epp 2000; Larson *et al.* 1999). Subsequent fire suppression has eliminated the ecological conditions necessary for their reestablishment (Spies and Turner 1999; Thompson 2000). Hemlock was also widely cut, primarily for the production of tannin from its bark (Frelich 1995). For a variety of reasons – perhaps grazing by white-tail deer, suppression by sugar maple, or climate change (see ch. 4) – it, too, has often failed to reestablish (Anderson and Loucks 1979; Alverson *et al.* 1988; Strole and Anderson 1992; Frelich *et al.* 1993; Mladenoff and Stearns 1993). Logging has also had an indirect effect on another species, yellow birch, by eliminating the supply of large, decaying logs on which its small seeds normally germinate and grow (Harmon *et al.* 1986; Mcgee and Birmingham 1997; Hagan and Grove 1999). Finally, introduced diseases, already responsible for largely eliminating *Castanea dentata* (American chestnut) and *Ulmus americana* (American elm) from the eastern deciduous forest, are threatening at least two northern hardwood species, American beech and butternut Hickory (Fleming *et al.* 2000).

Disturbance and gap dynamics

Where conifers historically formed a large proportion of the northern hardwood forest canopy, fire could be a major driver of forest dynamics (Heinselman 1973; Spies and Turner 1999; Li 2000). In general, however, catastrophic fires were very infrequent in the cool, moist, northern hardwoods, and have virtually disappeared since the decline of the conifers and the advent of fire suppression (Spies and Turner 1999). As a result, fire no longer plays a role in the disturbance patterns of northern hardwood forests (Runkle 1985; Spies and Turner 1999).

Individual tree mortality and windthrow are the primary agents of disturbance (Runkle 1985; Spies and Turner 1999). They are less extensive and severe than fire, creating small-to-moderate sized gaps, and leaving fallen trees in place on the forest floor (Runkle 1985; Spies and Turner 1999). Diseases, while they may entirely eliminate some species from the forest over time, attack single trees. Tornadoes and hurricanes usually cause severe damage to only small portions of a forest, and even where wind damage is extensive, the forest understory and herbaceous layers remain intact (Runkle 1985; Lorimer 1989; Peterson and Pickett 1995). Consequently, succession in temperate hardwood forests is usually characterized by gap regeneration (Lorimer 1989; Runkle 1985).

Watt, working in British beechwoods, was the pioneer of research in gap regeneration (Watt 1947). The basic concept has been reworked several times, for example as the "shifting-mosaic steady state" model (Bormann and Likens 1979), or the "patch-dynamics" model (White and Pickett 1985), but the basic principles are unchanged. A disturbance opens a gap in the forest canopy which, depending on the cause of the disturbance (disease, lightning strike, windthrow. catastrophic blowdown) may vary from 25 m^2 to over 3000 ha (Runkle 1985; Lorimer 1989). Small gaps, however, are much more frequent than large gaps, with 280-375 m^2 being about average for old-growth forests (Lorimer 1989). The environment within the gap is significantly different than the surrounding forest, with more light, higher wind speeds, lower humidity and greater fluctuations in temperature (Runkle 1985).

Regeneration of woody plants is greatly influenced by gap size. Larger gaps favor the growth of pioneer species – shade-intolerant trees, which can only germinate and grow in the open, away from the edge of the surrounding forest (Whitmore 1989). Smaller gaps, still partially shaded, favor the establishment of shade-tolerant, so-called "climax" species (Whitmore 1989). Here they retain the advantage gained by virtue of their presence in the original understory, making optimal use of intermittent and indirect light to grow and fill in the canopy, while suppressing any less-tolerant species germinating on the floor below (Whitmore 1989).

Runkle (1981) notes that shade-tolerance is not an entirely reliable predictor of which species will successfully colonize a small gap, and that moderately intolerant species, such as *Betula alleghaniensis* (yellow birch) or *Fraxinus americanus* (white ash), can sometimes persist in stands where gaps are relatively small. The timing and duration of seed production, propagule size and preferential browsing by herbivores all interact with morphological and physiological differences between tree species to maintain diversity within the temperate deciduous forest (Grubb 1977; Runkle 1981; Peterson and Pickett 1995; Canham 2000).

At a landscape scale, disturbance and succession within the temperate deciduous forest create a "shifting mosaic" of stand types (Bormann and Likens 1979). In the shifting mosaic model (Bormann and Likens 1979), severe disturbances can propel a forest stand into a reorganization phase where the previous canopy is felled or removed, the total biomass declines, evapotranspiration rates fall sharply, and water run-off, erosion and nutrient losses rise sharply. In a resilient ecosystem, however, regeneration is rapid, with new vegetation colonizing and stabilizing the new gap almost immediately. Within four or five years, the forest enters a long aggradation phase characterized by regeneration, succession and maturation of the forest.

culminating in a mature healthy stand of trees, in which biomass accumulation is at a maximum. Then, around 160 years, as trees begin to age, decay and die back, the forest enters a transition phase of declining biomass. A process of single-tree replacement begins, and the forest floor takes on a characteristic "pit and mound" topology, created by the uprooting of trees and the decay of old boles and stumps. Finally, if the stand remains undisturbed, it enters a steady state phase, where the growth and decay of the trees balance, and where replacement equals mortality. This is an old-growth forest. The entire cycle may take up to several hundred years to complete.

In the shifting-mosaic model, the proportions of the four stand types in a forest depend upon the relative rates of disturbance and succession (Bormann and Likens 1979). High disturbance rates favor the earlier phases, while low disturbance rates allow more stands to achieve a steady state. Bormann and Likens originally envisioned a dynamic equilibrium eventually being established across a forest landscape, in which the proportions of the forest in each phase would be relatively constant through time (Bormann and Likens 1979). It is now recognized that the relative proportions of stand types change through time, as the rate and severity of disturbances fluctuate (White and Pickett 1985). However the shifting mosaic model is still the most widely accepted explanation of temperate deciduous forest dynamics.

Selection-Cutting in Northern Hardwood Forests

Silvicultural advantages

Selection-cutting has become the preferred method of logging in northern hardwood forests, replacing clear-cutting and shelterwood-cutting under most conditions (Matthews 1989; Anderson *et al.* 1990). It is designed to: (a) maintain stand composition by regenerating shade-tolerant trees; (b) produce an all-age stand by retaining larger, more-mature trees; (c) increase stand productivity by maintaining the average age of trees in the range of highest growth; and (d) improve tree health and economic value, by removing poor trees and optimizing tree density and spacing to favor long, straight boles (Matthews 1989; Anderson *et al.* 1990). Ideally, logging is carefully controlled to leave the stand with a "balanced age structure." This is sometimes called the "inverse-j structure" because a density plot of residual tree diameters should show an exponential decline in stem numbers as diameter increases – like a "j" lying on its back (Matthews 1989; Anderson *et al.* 1990). Cutting cycles can be as short as 10 years, and each cut reduces the basal area of a stand by approximately 1/3 depending upon the initial basal area and stand quality (Matthews 1989; Anderson *et al.* 1990).

Uniform selection cutting removes single trees independently, in a uniform pattern across a stand (Matthews 1989; Anderson *et al.* 1990). This method favors the regeneration of only the most shade-tolerant trees, such as Sugar Maple, American Beech and Eastern Hemlock (Matthews 1989; Anderson *et al.* 1990). Group selection-cutting removes trees in clumps, leaving a more heterogeneous cover of canopy and gaps (Matthews 1989; Anderson *et al.* 1990).

This method also allows regeneration of species with intermediate shade tolerance, such as yellow birch, red oak, white ash and black cherry, particularly when complimented by site preparation (Anderson *et al.* 1990). Even in group selection-cutting, however, gaps are normally smaller than 0.2 ha (2000 m^2) to prevent the growth of shade-intolerant tree species (Anderson *et al.* 1990).

Selection-cutting must be distinguished from "selective-cutting", otherwise know as "high-grading" (Matthews 1989; Seymour and Hunter, Jr. 1999). In selective cutting, loggers remove the most valuable trees from a stand, paying little attention to residual stocking (*i.e.* the trees left behind) (Matthews 1989). Whereas selection-cutting is specifically designed to increase the productivity and value of the residual stock, selective cutting invariably reduces the future timber value of a stand (Matthews 1989; Seymour and Hunter, Jr. 1999). It may also reduce overall genetic quality of the forest by selectively culling the healthiest, most productive, most disease-resistant trees (Matthews 1989; Millar 1999).

Selection-cutting offers several potential advantages for foresters. Unlike clear-cut stands, selection-cut stands require little or no management between harvests, and both regeneration and thinning occur naturally (Matthews 1989; Anderson *et al.* 1990). While the yield per harvest is less for selection-cut stands than for clear-cut or shelterwood stands, the long-term yield is projected to be greater (Matthews 1989; Anderson *et al.* 1990). The majority of trees in selection-cut stands are between 20-60 years old – the age when their growth rate is highest. Selection-cutting, therefore, maintains stands in their most productive state, so that, in theory, they can be harvested every 10 to 25 years (Matthews 1989; Anderson *et al.* 1990). Moreover, while selection-cut stands cannot be harvested as efficiently as clear-cut stands or shelterwood-cut stands, the trees may be more economically valuable (Matthews 1989; Anderson *et al.* 1990). Some foresters believe that, by harvesting unhealthy damaged trees first, and by optimizing tree density to promote rapid, apical growth, selection-cutting can incrementally improve tree quality (Matthews 1989; Anderson *et al.* 1990). Initial cuts may produce low-quality, less-valuable timber, but with the objective of increasing the financial return on subsequent cuts (Matthews 1989; Anderson *et al.* 1990). The remaining trees are thought to be more resistant to disease, and because they should have longer, straighter boles, with fewer knots, they should produce more valuable grades of lumber (Matthews 1989; Anderson *et al.* 1990). Hence, selection-cutting is sometimes called "stand improvement cutting" (Anderson *et al.* 1990).

The Value of Selection-Cutting in Ecological Forestry

In addition to its recognized silvicultural values in northern, hardwood forests, selection-cutting is now being promoted by foresters as an environmentally friendly method of logging (Matthews 1989). In the past, foresters based their logging methods on strictly silivcultural and economic considerations (Kimmins 1997a,b). In this context, the advantages and disadvantages of selection-cutting were thought to be well-understood and balanced against those of other systems, such as plantations, clear-cutting and shelterwood cutting (Kimmins 1997a,b).

All of these forestry practices made common assumptions: (a) that forests could be regenerated, naturally or artificially, at a sufficient rate to sustain market demands; (b) that soils would continue to support forest regrowth; (c) that forests were sufficiently resilient to recover from the effects of logging; (d) that forest composition and condition could be manipulated to accommodate changing economic and market demands (Kimmins 1997b). These assumptions were untested, and they have since proved to be largely untrue (Kimmins 1997b; Perry 1998). Nonetheless, they dominated forestry management philosophy and practices in northern, hardwood forests until the 1960s (Kimmins 1997b; Perry 1998). Since then, several issues have brought northern hardwood forests to the attention of environmentalists and scientists (Aber *et al.* 2000). Acid rain, spruce and maple decline and the acidification of streams and lakes have directed attention to the impacts of air pollution (Kimmins 1997b; Aber *et al* 2000). The "rediscovery" of previously unsuspected "eastern old-growth forests" has prompted widespread demands for the conservation and protection of these stands (Davis 1996; Trombulak 1996; Zahner 1996). The resurgence of aboriginal culture, and the reinvention of ancient nature religions has even given conservation movements an aspect of spiritual legitimacy (Perlman 1996; Standing Woman and Comer 1996). At a very large scale, the application of landscape ecology to continental patterns of land-use has focused attention on roles of the "Adirondack-to-Algonquin corridor" (A2A) and the "Great Northern Forest" (of the northern United States) in the continuity and connectivity of the Appalachian, northern hardwood, and boreal forests (Noss 1992; Foreman 1992; National Audubon Society *et al.* 1996; A2A Conservation Initiative 2000). Many forestry companies have responded by embracing – in theory, if not always in practice – a variety of new principles and methods under the general heading of "ecological forestry" (Kimmins 1997a,b; Perry 1998; Seymour and Hunter, Jr. 1999).

"Ecological forestry" is the application of "ecosystem management" to forestry practices

(Kimmins 1997a,b; Perry 1998; Aber *et al.* 2000). Ecosystem management has become the operating paradigm for most of the major land and sea management agencies in North America, including the U.S. Forest Service, the U.S. Bureau of Land Management, the Canadian Forest Service, the Canadian and U.S. Parks Agencies, and it is implicit in the Environment and Development Agenda of the United Nations Environment Programme (UNEP 1992; Kimmins 1997a,b; Perry 1998). The Ecological Society of America has defined it as:

> "... management driven by explicit goals, executed by policies, protocols, and practices, and made adaptable by monitoring and research based upon our best understanding of the ecological interactions and processes necessary to sustain ecosystem structure and function" (Christensen *et al* 1996, p. 668).

Ecosystem management must include the following elements:

> "1. long-term sustainability as a fundamental value, 2. clear, operational goals, 3. sound ecological models and understanding, 4. understanding complexity and interconnectedness, 5. recognition of the dynamic character of ecosystems, 6. attention to context and scale, 7. acknowledgement of humans as ecosystem components, and 8. commitment to adaptability and accountability" (Christensen *et al.* 1996, p. 668).

In many, if not most of the world's forests, the goals of ecosystem management seem certain to include continued, even increased production of wood products (Kimmins 1997a,b;

Perry 1998; Frelich and Puettmann 1999; Aber *et al.* 2000). So long as the human population continues to grow, so will the world-wide demand for timber and wood fiber (Kimmins 1997a). Significant areas of forested landscape – including much of the northern, hardwood forests – will continue to be logged. In these "production forests" the general goal of ecosystem management will be "to maintain species and structural diversity and natural processes while simultaneously producing commodities" (Frelich and Puettmann 1999, p. 521). The requirement to produce commodities means that production forests will be subject to deliberate, direct human manipulation, in addition to any unintentional or indirect anthropogenic influences (Kimmins 1997a,b; Frelich and Puettmann 1999). The intensity, pattern and methods of this manipulation are the primary concerns of ecological forestry (Kimmins 1997a,b; Frelich and Puettmann 1999; Aber *et al.* 2000), and its guiding principle is probably best stated by Seymour and Hunter (1999): "manipulation of a forest ecosystem should work within the limits established by natural disturbance patterns prior to extensive human alteration of the landscape" (p. 29).

The focus of ecological forestry on natural disturbance patterns is based upon our current understanding of disturbance – its intensity, frequency and extent – as the primary factor in forest ecosystem dynamics (Kimmins 1997a,b; Perry 1998; Frelich and Puettmann 1999; Seymour and Hunter, Jr. 1999; Spies and Turner 1999; Aber *et al.* 2000). The hope is that, by emulating natural disturbance patterns, ecological forestry can accomplish its goals of maintaining essential forest processes, as well as structural and biological diversity (Frelich and Puettmann 1999; Seymour and Hunter, Jr. 1999; Aber *et al.* 2000).

Selection-cutting in northern hardwood forests, foresters argue, should help to maintain ecosystem processes and diversity by mimicking natural gap dynamics (Brokaw and Lent 1999;

Frelich and Puettmann 1999; Spies and Turner 1999). In doing so, it is supposed to maintain many of the characteristics of mature, northern hardwood stands: intact canopy cover, all-age or multi-cohort structure, complex vertical structure, and a patchy horizontal structure (Brokaw and Lent 1999; Spies and Turner 1999). Maintenance of these characteristics is claimed to protect natural forest processes and/or functions. The continuous presence of a broadleaf canopy above the forest floor, along with its associated root system, is supposed to protect the hydrological cycle of the stand (Matthews 1989; Waring and Running 1998). Retention of a canopy is also supposed to reduce the drastic changes in moisture and light conditions which can accompany more intensive harvesting, thus protecting forest microclimates (Matthews 1989; Waring and Running 1998). Furthermore, by maintaining the hydrological cycle and microclimates, and by providing yearly inputs of organic matter (*i.e.* leaves) to the forest floor, retention of an intact canopy is supposed to maintain essential decomposition and recycling trophic webs (Matthews 1989; Waring and Running 1998).

Selection-cutting maintains a continuous canopy cover by creating an all-age structure: below the upper forest canopy are successive sub-canopy layers of young and immature trees ready to exploit any new opening above (Matthews 1989; Brokaw and Lent 1999). This all-age composition, with its complex vertical structure, is supposed to create natural variations in vertical microclimates, by mimicking natural, vertical gradients of light and moisture (Brokaw and Lent 1999). At the same time, it is supposed to maintain the diversity of vertical habitats, by providing nesting and denning resources, growth substrates for epiphytic plants, foraging opportunities and natural cover at many different heights above the forest floor (Brokaw and Lent 1999).

Finally, the creation of gaps in the upper canopy by the harvesting of mature trees is supposed to provide a variety of regeneration niches for sub-canopy trees, shrubs and herbaceous plants (Grubb 1977; Frelick and Puettmann 1999; Palik and Engstrom 1999). These might include relatively open, warm sites in the center of newly-formed gaps, shaded, moderate sites at the edge of new gaps or under new growth in older gaps, and deeply-shaded, cool sites under the residual or regenerating canopy – hopefully the same kinds of niches that might be found in a natural forest.

Foresters claim that selection-cutting, by emulating these natural processes, effectively protects the natural properties and biodiversity of northern, hardwood forests (Matthews 1989; Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999). Maintenance of the hydrological cycle and the processes of the decomposition and recycling cycles is supposed to protect nutrient cycles and long-term soil fertility, by preventing the mass wasting of mineral and organic matter, by reducing the leaching of nutrients from the forest floor and soil, and by insuring that much of the forest's nutrient capital is protected from loss within the ecosystem's biological compartments (Matthews 1989; Waring and Running 1998). Maintenance of a complex vertical structure, offering a variety of microclimates, habitats and niches, is supposed to protect the diversity of forest plants and animals (Matthews 1989; Brokaw and Lent 1999). The creation of different regeneration niches is supposed to protect the diversity of canopy trees, and, in conjunction with maintenance of the general forest microclimate, is supposed to protect the diversity of other woody and herbaceous plants (Matthews 1989; Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999). Thus, these four criteria – soil fertility, structural diversity, canopy diversity and herbaceous diversity – are at the heart of the arguments for the ecological advantages of selection cutting (Matthews 1989).

Selection of Indicators

Effective ecosystem management requires that the claims for the ecological advantages of selection-cutting in northern hardwood forests be assessed (Christensen *et al.* 1996; Aber *et al.* 2000). Historically, forestry science has focused on improving yields and timber quality, rather than measuring ecological impacts (Kimmins 1997b; Perry 1998). Furthermore, explicit consideration of the ecological impacts of forestry is a recent phenomenon, within the last 40 years, so there has not been sufficient time to evaluate the longer-term effects of newer forestry practices (Kimmins 1997b; Perry 1998). Another obstacle has been the difficulty in choosing the appropriate measures (Woodley *et al.* 1999). There have been many attempts to develop a comprehensive suite of indicators of forest health and integrity over the past decade, with mixed success (Woodley *et al.* 1999). Although general criteria for ecological forestry have been identified, application of those criteria to individual cases has generated a daunting number of measures and norms, as well as debate about their utility (Woodley *et al.* 1999).

Some consensus has emerged from these debates. It is widely agreed that measures of forest health and integrity should be specific to each forest type (Kimmins 1997b; Woodley *et al.* 1999). That is, they should take into account differences in climate, soils, topography, natural disturbance regimes, landscape patterns and species composition (Kimmins 1997b; Waring and Running 1998). Measurements must also have appropriate spatial and temporal scales, and account for the linkages between scales (Waring and Running 1998; Seymour and Hunter, Jr. 1999; Spies and Turner 1999; Woodley *et al.* 1999). This is essential, because small-scale, local processes can produce large-scale, emergent patterns (O'Neill *et al.* 1986). Less obvious, and more contentious, is the requirement that measurements reflect management objectives for a forest stand or landscape (Aber *et al.* 2000; Kimmins 1997b; Woodley *et al.* 1999).

To assess the claims made for the sustainability of selection-cutting in northern hardwood forests, appropriate measures must be selected for each of the four criteria of concern: soil fertility, structural diversity, canopy diversity and herbaceous diversity. These measures should incorporate current understandings of northern hardwood forest ecology, as well as reflect the spatial and temporal scales of the analysis and the management objectives at those scales (Waring and Running 1998; Oliver *et al.* 1999). It must be emphasized that the scale of this research is strictly limited to the stand level, over relatively short time periods (one or more cutting cycles). This research cannot answer questions at the landscape scale, such as where to cut, how much to cut, and how much to protect (Oliver *et al.* 1999). It may, however, have implications for these questions, since it could influence such things as the length of cutting cycles and the quality of landscape corridors.

Soil fertility

The effects of logging on soil fertility have been a concern since the beginnings of scientific forestry in 19th century Germany (Pritchett 1979a; Perry 1998). Soil fertility directly effects forest productivity, and indirectly influences the productivity and diversity of plant and animal communities (Perry 1998; Hansen and Rotella 1999). There have been two broad, interrelated areas of concern: (a) soil organic matter and structure; (b) nutrient cycling, particularly the long-term protection of nutrient capital (Pritchett 1979a; Powers *et al.* 1990; Kimmins 1997a; Perry 1998; Aber *et al.* 2000). Concern for soil organic content and structure arise from the recognition that poor logging practices in general, and intensive logging in particular, can drastically increase soil erosion, volatilization of organic matter, and nutrient leaching, particularly if vegetation is not quickly reestablished (Bormann *et al.* 1974; Kimmins 1997a; Perry 1998; Aber *et al.* 2000). Consequently, foresters have developed a suite of methods and tools which, if conscientiously employed, can protect soil organic matter and structure in most harvest systems (Matthews 1989; Powers *et al.* 1990; Frelich and Puettmann 1999; Aber *et al.* 2000). Selection cutting, in particular, mitigates these effects by leaving most of the canopy and the root structure intact, thereby maintaining the hydrological cycle and binding the soil (Matthews 1989; Kimmins 1997a; Waring and Running 1998).

Most of the current concern is over the protection of nutrient capital in intensive forestry operations, such as plantation forestry or short-rotation clearcutting (Pritchett 1979a; Kimmins 1997a; Perry 1998; Aber *et al.* 2000). Historically, however, depletion of nutrient capital has not been considered an issue for northern hardwood forests, because inputs from weathering and atmospheric deposition were thought to be sufficient to replace losses from timber removal (Pritchett 1979a; Pritchett 1979b). However, some early foresters warned that depletion of nutrient capital could become a concern if short-rotation, whole-tree harvesting was introduced, such as is used in selection-cutting (Pritchett 1979a; Wells and Jorgensen 1979; Matthews 1989; Kimmins 1997a; Aber *et al.* 2000).

Traditionally, forestry has focused on nitrogen as a limiting factor in forest growth

(Kimmins 1997a; Waring and Running 1998; Aber *et al.* 2000). However, more recent research suggests that the potential for nutrient deficiencies in northern hardwood forests is greatest for calcium (Federer *et al.* 1989; Kimmins 1997a; Fisher and Binkley 2000). Calcium is the most abundant macronutrient in trees, where it has both essential structural and regulatory roles – not least of all in the formation of cell walls (McLaughlin and Wimmer 1999). It is most concentrated in bark and foliage, and is two to four times as abundant in hardwoods as in conifers (Marion 1979; Wells and Jorgensen 1979; Kimmins 1997a; Fisher and Binkley 2000). When the amounts of nutrients removed in the harvest of hardwoods are compared to stores in the soil, the largest relative loss is of calcium (Marion 1979; Kimmins 1997a; Fisher and Binkley 2000). Calcium losses are largest with whole-tree versus sawlog harvesting, and in short-rotation versus long-rotation systems (Wells and Jorgensen 1979; Kimmins 1997a; Perry 1998; Fisher and Binkley 2000).

On calcium-poor soils, short-rotations and whole-tree harvesting have the potential to reduce soil calcium capital to below the critical levels required for healthy tree growth (Voigt 1979; Johnson, *et al.* 1988; Federer *et al.* 1989; Johnson and Todd 1990; Johnson *et al.* 1992; Kimmins 1997a). The risk of calcium deficiencies is exacerbated by recent declines in atmospheric deposition of calcium and other base cations (Hedin *et al.* 1994).

Despite these concerns, the effect of selection-cutting on soil calcium in northern hardwood forests has received little attention. Most research on calcium depletion has been done in other forest types, on the effects of clear-cutting, and on the differences between whole-tree and sawlog harvesting (*e.g.* Federer *et al.* 1989; Johnson *et al.* 1997; Johnson and Todd 1998; Yanai *et al.* 1999). The potential effects of selection-cutting in northern hardwood forests on soil calcium are particularly significant when considered in the context of acid deposition (Voigt 1979; Kimmins 1997a; McLaughlin and Wimmer 1999). Acid deposition is generally high throughout the range of the northern hardwood forests, and, on poorly-buffered soils, it can lead to soil acidification (Voigt 1979; U.S. - Canada Air Quality Committee 1998). Acidification, in turn, can result in enhanced leaching of calcium and other cations (Cole *et al.* 1992; Johnson *et al.* 1992; Mitchell *et al.* 1992; Richter *et al.* 1992). It can also release aluminum ions into the soil solution, particularly at pH levels below 4.2 (Tomlinson 1983). Aluminum in soil solution may displace calcium from cation exchange sites, further aggravating the direct effects of acidification (Lawrence *et al.* 1995). Many species of aluminum are also toxic to plants, and at critical levels they can directly inhibit or damage fine roots and foliage, reducing plant health and growth (McLaughlin *et al.* 1992; Cronan 1994; McLaughlin 1996). In addition, sub-toxic concentrations of aluminum can indirectly damage plants by binding to, and blocking, cation-uptake channels on plant roots, thereby causing or aggravating deficiencies and imbalances of calcium and other cations (Cronan *et al.* 1989; McLaughlin *et al.* 1992; Cronan 1994; McLaughlin 1996).

Conversely, high levels of calcium in the soil can mitigate the toxic effects of aluminum (Cronan and Grigal 1995). The interaction of calcium and aluminum has led to speculation that Ca/Al molar ratios in soil solution may be a useful indicator of forest soil health, with ratios less than 1.0 (+/- 0.5) posing a 50% risk of damage to tree health and growth (Cronan and Grigal 1995). The likelihood of problems would be greatest in soils with low buffering capacity, a low cation exchange capacity, and a low base saturation (Cronan and Grigal 1995).

There is ample evidence from Europe, where acid deposition has been occurring at higher rates and for longer than in North America, of a general relationship between acid deposition, soil acidification and forest decline (Ulrich 1988; Van Breemen 1990). In North America, however, no conclusive evidence has yet been found of widespread problems of calcium deficiencies or aluminum toxicity in forests resulting directly from acid deposition (Hall 1994; Miller-Weeks *et al.* 1994; U.S. E.P.A. 1994; McLaughlin 1996; United States - Canada Air Quality Committee 1998). Most of these studies, however, have reported localized declines on soils that lie on acidic bedrock, are otherwise naturally low in bases, or are exposed to acid fog or clouds (Hall 1994; Miller-Weeks *et al.* 1994; U.S. E.P.A. 1994; McLaughlin 1996; United States - Canada Air Quality Committee 1998). These are factors which the ALBIOS study (Aluminum in the Biosphere), among others, has found can aggravate the effects of acid deposition on soil calcium and aluminum concentrations (Cronan 1994; McLaughlin 1996). Together with acid deposition, they could also aggravate any effects of selection cutting.

Chapter 3 examines the effects of selection-cutting on calcium, aluminum and Ca/Al ratios, while taking into account as much as possible the effects of other factors, such as geology and acid deposition.

Diversity and composition of the canopy and herbaceous layers

One consequence of harvesting trees at economic maturity is a reduction in the mean and variance of canopy gap sizes: the harvest of a 60 year old maple tree leaves a smaller gap than the death or blowdown of a 300 year old maple, particularly if the older tree also brings down other trees in its collapse (Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999). Although more variable than a regenerated clear-cut, a shelterwood-cut or a plantation stand, the gap structure and dynamics of a uniform selection-cut stand are still more homogenous than in a natural, old-growth stand. Consequently, there will be less variation in light and moisture levels in a selection-cut stand than an old-growth stand, leading to a more narrow range of regeneration niches (Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999). This can result in the exclusion of trees with intermediate shade-tolerance, such as yellow birch, basswood and white pine (Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999). In some cases, this natural process of exclusion is sometimes accompanied by deliberate attempts to "weed out" species of lesser economic value, such as hemlock (Walker 1999).

There is also good reason to expect decreased abundance and size of coarse woody debris (see below) to reduce tree diversity. A number of species, including yellow birch, rely upon decaying logs for germination and growth sites above the smothering layer of leaf duff normally found on the floors of northern hardwood forests (Harmon *et al.* 1986; McGee and Birmingham 1997; Frelich and Puettmann 1999; McComb and Lindenmayer 1999).

Together these factors can homogenize a uniform selection-cut stand, leaving little but the most shade-tolerant species, sugar maple and American beech (Seymour and Hunter, Jr. 1999; Spies and Turner 1999). Group selection-cutting should create a greater variety of gaps than uniform selection-cutting, thus providing a greater range of regeneration niches (Matthews 1989). Nonetheless, it will still result in many fewer large pieces of coarse woody debris on the forest floor than in an old-growth stand. Even in group selection-cutting, therefore, some reductions in canopy diversity can be expected.

Maintaining species richness in the forest canopy is a direct contribution to biodiversity and, therefore, a goal in itself (Palik and Engstrom 1999; Seymour and Hunter, Jr. 1999). It has, however, other advantages. It contributes to the diversity of other organisms by increasing the diversity of food sources, by contributing to structural diversity, and by providing trees of varying hardness for cavity-nesting birds (Bull 1978; Brokaw and Lent 1999; Frelich and Puettmann 1999; Palik and Engstrom 1999; Aber *et al.* 2000). It may also contribute to the overall stability of the forest ecosystem, particularly in light of the potential effect of introduced diseases and pests, such as Asian Maple Beetle and Beech Bark Disease (Perry 1998; Tilman 1999; Aber *et al.* 2000). And it may have effects on forest biogeochemistry, by increasing the ability of forest communities to exploit different soil nutrient pools (Blum *et al.* 2002).

The same factors which should reduce canopy diversity in selection-cut northern hardwood forests should also reduce the diversity of the herbaceous layer (Frelich and Puettmann 1999; Palik and Engstrom 1999). Decreased variation in gap sizes should lead to a more narrow range of regeneration niches, as should reductions in the abundance and size of coarse woody debris (Harmon *et al.* 1986; Frelich and Puettmann 1999; McComb and Lindenmayer 1999). In addition, the lack of large, "tip-up" prone trees in selection-cut forests should reduce the availability of "pits and mounds" as regeneration sites. Pits and mounds form when a tree topples, leaving a depression of exposed mineral earth where its root system was pulled from the soil (the pit), and a raised hummock where the root system came to rest (the mound) (White 1990). A number of herbaceous species show a measurable preference for pits or mounds in establishment and growth (Thompson 1980).

The diversity of herbaceous species in selection-cut northern hardwood forests may also be effected by the physical impacts of logging on forest soils (Gjedtjernet 1995; Frelich and Puettmann 1999; Aber *et al.* 2000). Logging in northern hardwood forests involves the use of heavy, powerful, wheeled machines, called "skidders" to haul cut trees out of the forest into clearings, where they are then cut into sawlogs for transportation. Skidders are known to compact forests soils, increasing their bulk density, decreasing their water-retention capacity and porosity, and making them less conducive to healthy root development (Gjedtjernet 1995; Frelich and Puettmann 1999). Repeated skidder traffic can also remove the litter and organic layers of the forest floor (Gjedtjernet 1995; Frelich and Puettmann 1999). Together, these effects have the potential to damage herbaceous layer vegetation, even species whose primary meristems are below ground.

Logging may also open up space for the introduction of weedy and/or exotic plant species (Aber *et al.* 1979; Perry 1988; Aber *et al.* 2000). Logging vehicles may actually serve as vectors for these species, carrying them into a stand on their wheels or suspension – anywhere a seed might hitch a ride. Could competition from these weedy species change the herbaceous composition of a site? If so, for how long? Some endemic forest herbs have low population growth rates, taking many years to reach reproductive age – *Panax cinquefolia* (American ginseng) being a well-known example (Nantel *et al.* 1996; Frelich and Puettmann 1999). How will they react to competition? Does selection-cutting eliminate certain species from northern hardwood forests? Does it reduce the quality of the herbaceous community – however that might be defined?

Little work has been done to answer these questions; most research has focused on clearcutting in other forest types (*e.g.* Duffy and Meier 1992). A notable exception is the work of Reader and Bricker (1992), who conducted a controlled experiment in hardwood forest, finding that declines in the richness and abundance of herbs were no greater in selection-cut stands than in control stands. Metzger and Shultz (1981, 1984) compared the vegetation of clearcut and selection-cut northern hardwood stands immediately following cutting and fifty years later, finding that selection-cut stands were slightly more diverse. There has been no work, however, on changes in herbaceous communities over a full cutting cycle, nor has there been a comparison of herbaceous communities in selection-cut stands and old-growth stands.

Chapter 4 examines the effects of selection cutting on the diversity and composition of the canopy and herbaceous layers over the cutting cycle and in comparison to old-growth stands, taking into account other variables, such as soil pH and elevation. Floristic quality was assessed using a published index specific to the region (Oldham *et al.* 1995), as were the effects of selection-cutting on uncommon or rare species.

Structural diversity

Intensive forestry methods simplify the structural diversity of forest stands, especially those methods which employ single- or double-cohort regeneration (*i.e.* one-age or two-age stands), such as plantations, clear-cutting or shelterwood-cutting (Matthews 1989; Perry 1998; Aber *et al.* 2000). Such methods reduce both vertical and horizontal diversity, by reducing the number of canopy layers and by minimizing natural gap dynamics (Brokaw and Lent 1999; Spies and Turner 1999). Many studies on the ecological effects of forestry have shown correlations between biodiversity and structural diversity (Brokaw and Lent 1999; Seymour and Hunter, Jr. 1999; Aber *et al.* 2000). The loss of biodiversity is generally more apparent at a landscape scale as a "homogenization" of the forest biota (*i.e.* *beta*-diversity or species turnover), rather than at a local scale (*i.e.* *alpha*-diversity or richness) (Kimmins 1997b; Seymour and Hunter, Jr. 1999; Spies and Turner 1999). Nonetheless, even at a stand scale, reductions in structural diversity are often accompanied by changes in the compositions of animal and plant communities (Kimmins 1997b; Perry 1998; Brokaw and Lent 1999; Aber *et al.* 2000). Specialist species may be displaced by generalist species; endemic species may be displaced by exotic species (Aber *et al.* 2000). Species richness may not change, but species with narrow niches, which require special habitat features, often decline or are lost altogether (Kimmins 1997b; Aber *et al.* 2000).

In northern hardwood forests, selection-cutting is a better silviculture method for maintaining vertical and horizontal structural diversity at the stand scale (Matthews 1989; Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999). There are, however, important differences between the structural diversity of selection-cut forests and undisturbed forests (Brokaw and Lent 1999). Selection-cutting mimics natural gap dynamics; it does not duplicate them (Perry 1998; Seymour and Hunter, Jr. 1999). In particular, the balanced design of a selection-cut forest is based on economic cycles rather than ecological cycles (Matthews 1989; Kimmins 1997a; Perry 1998; Walker 1999). Because the maturity of a tree is defined in economic terms rather than ecological terms, selection-cutting discriminates against large, old trees (Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999; Aber *et al.* 2000). These are the trees most prone to disease, accumulated damage and blowdowns (Harmon *et al.* 1986; McComb and Lindenmayer 1999). This has the effect of reducing: (a) the number of large trees which can serve as substrates for epiphytic plants (lichens, mosses) and as food sources for "mast" dependent species, such as bears, deer and (historically at least) Passenger Pigeons; (b) the number of dying and dead trees available for excavation by cavity-dependent animals; (c) the amount and size of coarse woody debris being contributed to the forest floor; and (d) the mean and variance in intra-stand gap sizes by reducing the crown size of canopy trees (Maser *et al.* 1979; Thomas *et al.* 1979; Harmon *et al.* 1986; Bucher 1992; Kimmins 1997a; Brokaw and Lent 1999; Frelich and Puettmann 1999; McComb and Lindenmayer 1999; Aber *et al.* 2000). The first three of these features have been shown in many studies to contribute to the diversity and/or abundance of plant, animal and microbial species (Bull 1978; Thomas *et al.* 1979; Harmon *et al.* 1986; Perry 1998; Brokaw and Lent 1999; McComb and Lindenmayer 1999; Aber *et al.* 2000).

A movement called "New Forestry", beginning in the 1980's, sought ways to retain or recreate these features in production forests (Kimmins 1997b; Perry 1998). In northern hardwood forests, the emphasis has been on "variable harvest retention systems", in which a certain number of older trees in each stand are retained and allowed to decay and die (Thomas 1979; Bull 1983; Perry 1998; McComb and Lindenmayer 1999; Spies and Turner 1999; Aber *et al.* 2000). Trees might be left singly, in blocks, or around sensitive areas such as watercourses or nest sites where logging would be restricted anyway . Some researchers have suggested guidelines and targets for determining the number of trees to be retained (*e.g.* Tubbs *et al.* 1987; Keddy and Drummond 1996; GFERG 1997; McGee 1999). The retention of old trees has not been systematic, however, and in most places there have been no legislated standards or targets to meet. Furthermore, some authors have argued that variable harvest retention systems are expensive to implement, significantly reducing allowable cuts (Hicks 1983; Menasco 1983; Kimmins 1997b). It is important, therefore, to determine how much of these features – large trees, dead trees, and large coarse woody debris – is being retained in selection-cut northern hardwood forests, and compare these levels to projected needs (Harmon *et al.* 1986; McComb and Lindenmayer 1999). This will be the primary objective of chapter 5.

Objectives

Chapter 5 will conclude with a summary of the conclusions regarding the ecological effects and conservation value of selection cutting in northern hardwood forests. I hope to make specific management recommendations to improve, if necessary, the sustainability of selection cutting in northern hardwood forests, in agreement with the principles of ecological forestry and ecosystem management. Finally, I will make recommendations for future research on the role and effects of selection-cutting in northern hardwood forests.

Chapter 2

Research Area, site selection, general sampling design.

I chose the Madawaska Highlands of southeastern Ontario, Canada, as my primary research area. This large, rural region has several desirable features. First, it has an almost continuous cover of forest, with a high proportion of northern hardwood forest (Perera *et al.* 2000). Second, it has a high proportion of Crown (i.e. public) land ownership, with much of the Crown land licensed for harvest by large forestry operators (Ontario Ministry of Natural Resources 1996). Third, it is mostly situated on acidic bedrock, and is subject to high levels of acid deposition – factors which may predispose northern hardwood forest to damage from logging (Perera *et al.* 2000; United States – Canada Air Quality Committee 1998).

The Madawaska Highlands are part of a geological feature called the Frontenac Axis (Perera *et al.* 2000). This is an extension of the Canadian Shield running southeast from the Algonquin Dome to the St. Lawrence River just east of Lake Ontario, where it forms a narrow link to the Laurentian mountain range (Figure 2.01) (Perera *et al.* 2000). The bedrock consists mostly of siliceous, metasedimentary rock, such as gneiss or granite, interspersed with calcareous metasediments, such as marble. The general topography is rolling hills and outcrops, cut 1.0 to 1.5 billion years B.P. by pre-Quaternary erosion of the Laurentian Mountains, and shaped by the last glacial episode, 12,000 years B.P (Perera *et al.* 2000). Surficial geology is mostly thin glacial till (ground moraine), with smaller areas of glacial outwash and end moraine.

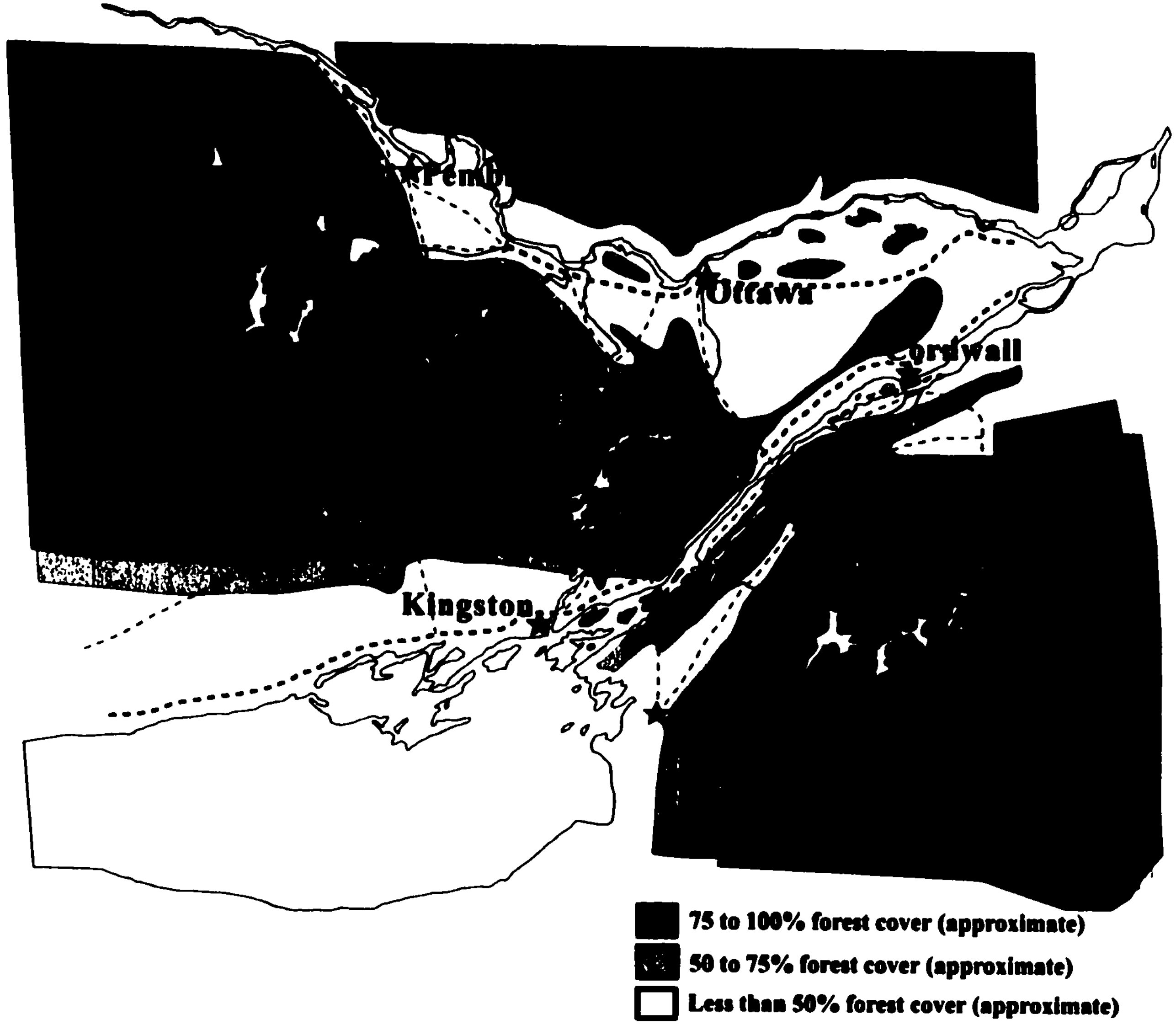


Figure 2.01. Map of the Frontenac Axis showing research sites and forest cover.

The soils are primarily humo-ferric podzols (*i.e.* spodosols), interspersed with luvisols and brunisols (*i.e.* alfisols) (Perera *et al.* 2000).

The Frontenac Axis declines from the northwest to the southeast, from approximately 500 m on the Algonquin Dome to approximately 100 m near the St. Lawrence River (Perera *et al.* 2000). Over the same range, the mean annual growing degree days (>5° C) decline from 2200 to 1600 (Perera *et al.* 2000). Precipitation, on the other hand, tends to vary more from west to east. In the area of the Madawaska Highlands, there is a distinct rainshadow effect, with mean annual precipitation declining from about 1100 mm to 650 mm from west to east across the width of the Axis (Perera *et al.* 2000).

All of this precipitation is acidic. Acid deposition on the Frontenac Axis is very high. Despite years of decline, the sulphate deposition in 1995 was still over 15 kg/ha/year, while nitrogen deposition was over 20 kg/ha/year (United States – Canada Air Quality Committee 1998). These levels are believed to significantly exceed critical values (*i.e.* the buffering capacities) of both lakes and forest soils (United States – Canada Air Quality Committee 1998).

Most of this deposition falls on wilderness. The rugged terrain of the Axis prevented extensive settlement of the area, thereby insuring that much of the land remained public (Perera *et al.* 2000). This was particularly true for the Madawaska Highlands, in the northern half of the Axis, where more than 50% of the land is crown-owned (Ontario Ministry of Natural Resources 1996). Consequently most of the land has also remained forested and available for logging under Crown licenses (Ontario Ministry of Natural Resources 1996). Forestry on this land is regulated according to provincial regulations, standards and management plans prepared by the Ontario Ministry of Natural Resources (OMNR).

Management plans are based upon the provincial Forest Resource Inventory (FRI) and OMNR guidelines for the various forest "working groups." Classic northern hardwood forest corresponds to the "shade tolerant working group" (Anderson *et al.* 1990). On FRI maps, these are stands dominated by *A. saccharum*, *F. grandifolia* or *T. canadensis* (Anderson *et al.* 1990). *T. canadensis*, though a conifer, is a shade-tolerant, climax species. The shade tolerant working group is more ubiquitous in the Madawaska Highlands now than in the past, due to cutting and lack of regeneration of conifers and red oak.

FRI maps and OMNR management plans were used to locate shade-tolerant stands with a wide range of time-since-cutting. Potential research stands had to be able to accommodate a circular plot of 45.14 m. radius, as well as a buffer zone of approximately 25 m. (in order to avoid edge effects). For practical reasons, the stand also had to be within a short hike of a passable road.

Plot layout and sampling was based largely on the OMNR's Growth and Yield (G & Y) system of permanent sample plots (PSPs), in order to make the resulting data compatible with the data set from this larger research program (Hayden *et al.* 1995; Woods 1995). The research plot was a nested design, consisting of three circular 11.28 m radius Growth Plots within a circular 45.14 m. radius Mortality Plot (Figure 2.02). Unlike the G & Y system, smaller Shrub and Regeneration Plots were not established. Instead, 25 circular 1 m^2 plots were randomly placed throughout the Mortality Plot for sampling of all herbaceous layer vegetation (Figure 2.02).

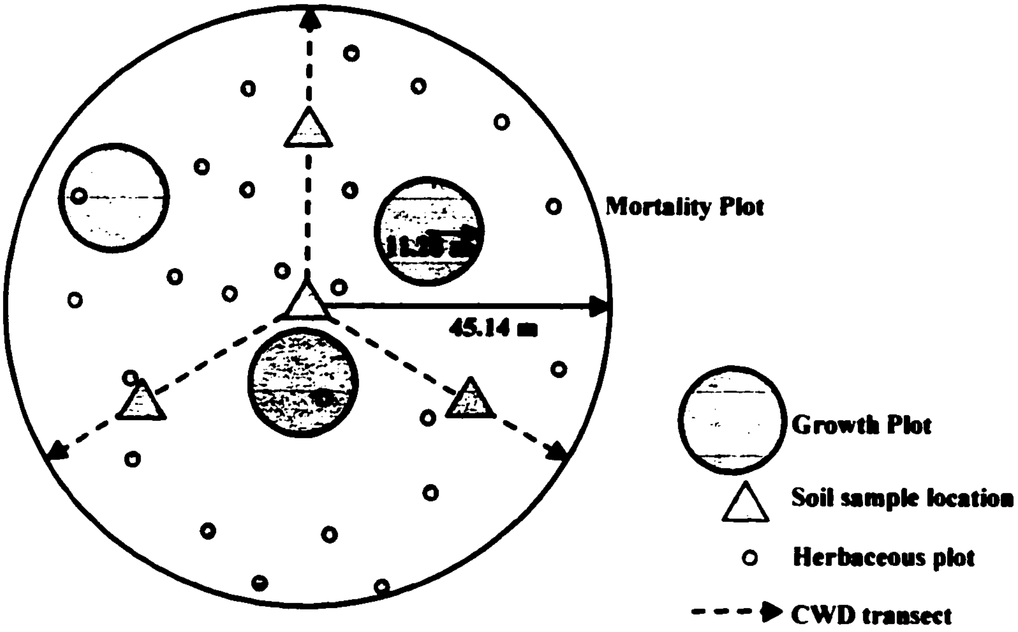


Figure 2.02. Sample Plot Layout

As in the G & Y system, three 45.14 m transects were run from the center to the edge of the Mortality Plot for sampling coarse woody debris (CWD) (Figure 2.02). Soil samples were collected at four different locations within the Mortality Plot (4 samples/location): at the center of the plot, and from three other locations at regular intervals around the plot (Figure 2.02).

Ten of the sites sampled were PSPs. In PSPs attempts were made to locate and resample the original Growth Plots and CWD transects. In some cases the plot markers could not be located, particularly in sites which had been cut since the initial sampling.

Originally, I had hoped to determine how many times each site had been cut. This proved impossible. OMNR management plans and cutting records for the Madawasca Highlands go back only to the 1960s – logging before that time having been largely unregulated (Perera *et al.* 2000) – and in most areas the licensees had changed several times. For the same reason, it was not possible to determine the exact year of logging for sites over 40 years old. In most of these stands, the mean age of the stand from the Forest Resource Inventory was used. When available, OMNR coring data was used to age older PSPs.

In addition to sites which had been previously cut, I also sought to locate and sample old-growth sites. In this study, old-growth was defined as an all-age stand with a majority of mature and over-mature canopy trees, containing trees and snags near the maximum diameter for their species, with large pieces of CWD on the forest floor, "pit and mound" topology, and no history nor sign of cutting or burning. These are commonly used characteristics for identifying old-growth, northern hardwood forest (Leverett 1996; White 1990). Few such northern hardwood forest stands are left on the

Frontenac Axis. Using an OMNR survey by White (1990), I located four old-growth stands within the Madawaska Highlands. One of these was actually an old sugar bush, but it still met the basic definition of old-growth.

In order to increase the sample size of old-growth plots, six other old-growth sites were located outside the Madawaska Highlands. With the assistance of Harvey Anderson and Jim Rice of the OMNR, three sites were located in the Swann Lake Forestry Research Reserve in Algonquin Park, Ontario. With the assistance of Jim Papereau of the Adirondack Park Authority, New York State Environmental Conservation, another three sites were located on the north side of Ampersand Mountain, in Adirondack Park, New York.

Since old-growth stands, by definition, have no records of disturbance, it was not possible to determine time since cutting for these stands. For eight of the stands, tree coring was used to assign ages. Attempts were made to obtain three intact cores from each stand, beginning with the largest dominant trees. Most trees sampled, however, had heart-rot, and it was not always practical to obtain three cores. Stands were assigned the age of the oldest intact core. Two stands could not be aged: one site was cut prior to coring, and coring was prohibited in another stand by agreement with the OMNR.

The increasing error in stand age past 40 years since cutting was an unavoidable problem. The only practical way to avoid it would have been to sample only those stands whose cutting and disturbance history was documented. Because of the lack of records, this would have reduced the sample size of stands over 40 years old – already small – to unacceptably low levels. Of necessity, therefore, I concentrated most of my analyses on the effects of logging over one cutting cycle. 10 to 25 years, where the stand ages were certain and the data density was highest.

Time since cutting was treated as a continuous variable. There is some debate (Hunter and White 1997; Leverett 1996) about whether logged stands ever return to pre-cutting, old-growth conditions, or if they forever remain categorically different from virgin forest. Based on a literature review, however, Hunter and White (1997) failed to find any clear ecological thresholds distinguishing old-growth and disturbed forests.

OMNR stand information was confirmed in all cases by ground-truthing. In several cases observations suggested that the OMNR information was wrong, and the sites were rejected. In several sites the proportions of *Q. rubra* were higher than indicated by the FRI. As long as these stands were being managed as shade tolerant stands, however, they were retained.

Almost all of the sites displayed typical shield topology: hilly, with thin soil or bare rock at high points, and pockets of deeper, more organic soil at low points. Several sites were situated on glacio-fluvial deposits of varying depths. Slope and aspect generally varied greatly within each plot. Overall, however, the majority of the sites were remarkably similar in topology and appearance. This obviously reflects the selection criteria, which were deliberately biased toward mesic conditions.

Other basic data collected for each site included bedrock and surficial geology, acid deposition, latitude and longitude, and elevation. In all cases, the precambrium geology and surficial geology of the sites were read directly from geological maps (Lumbers 1954; Isachsen and Fisher 1970; OMNR 1972a; OMNR 1972b; Lumbers 1982;

Pauk and Mannard 1987; Easton 1990; Caldwell and Pair 1991; Kettles 1992; Easton *et al.* 1995a; Easton *et al.* 1995b). The age, scale and precision of the maps varied greatly.

In view of the comparatively coarse resolution of the geological map data, quantitative or even semi-quantitative classification was unwarranted. Instead, all sites were classified as either siliceous or calcareous bedrock. Whenever possible, classifications based upon geological map information were verified by observations of exposed bedrock in the field.

No direct acid deposition data were collected. Instead, acid deposition data were provided by Environment Canada's NatChem database (Canadian National Atmospheric Chemistry Database 2000; Ro and Vet 1999). This is a central database combining and standardizing North American acid deposition data from 18 monitoring networks and 730 sampling sites in Canada and the United States for the years 1980 to 1996. From these data, Environment Canada researchers used ordinary kriging interpolation methods to produce an H^+ deposition contour map on a grid of 7.5 km by 7.5 km . Acid deposition for specific sites are taken from the closest grid values.

Cumulative H^+ deposition from 1980 to 1996 was calculated for each site. The resolution of the data was not sufficient to distinguish all sample sites; neighboring sites often had the same figures for acid deposition. In addition, preliminary analysis of the data revealed high spatial autocorrelation. The data were highly non-normal, with the sites clustered into two groups with significantly different levels of acid deposition. Because of the problems that these patterns posed for statistical analysis, acid deposition was converted to a categorical variable, with the data from the two clusters being classified as "high" and "low" deposition.

Latitude and longitude were recorded using the Universal Transect Mercator system, and were estimated to the nearest 100 meters from the Government of Canada 1:50,000 topographic map series (Canada Surveys and Mapping Branch 1950). The same maps were used to estimate elevation to the nearest 10 meters.

Sampling took place over three summers: 1996 – 1998. Logistical problems prevented complete sampling of all sites. Appendix A lists the research sites, basic site information and the data collected in each plot.

Chapter 3.

The responses of soil solution calcium and aluminum, and soil pH, to selection-cutting in northern hardwood forests.

Introduction

Selection-cutting is the preferred silvicultural method in northern hardwood forests (Matthews 1989; Anderson *et al.* 1990). As currently practiced, it calls for short harvest rotations of 10 to 40 years, with each harvest removing approximately 1/3 of the basal area of forest stand (Matthews 1989; Anderson *et al.* 1990). By doing so, it is intended to favor the regeneration of valuable, shade-tolerant species, such as *Acer saccharum* (sugar maple) and *Fagus grandifolia* (American beech), maintain the stand in its most productive state, and improve the health and economic value of the trees (Matthews 1989; Anderson *et al.* 1990).

In response to societal demands for more ecologically sustainable methods of forestry, selection-cutting has also been promoted as a method of extracting timber from forests without causing significant, adverse ecological effects (Matthews 1989; Kimmins 1997a,b). Many of the arguments in favor of selection-cutting assume that its effects on soil fertility are benign (Matthews 1989; Waring and Running 1998). Effective ecosystem management requires that this premise be tested, if it is to form a basis for sustainable resource management (Christensen *et al.* 1996; Kimmins 1997b; Perry 1998; Aber *et al.* 2000).

Historically, depletion of nutrient capital has not been considered an issue in northern hardwood forests because inputs from weathering and atmospheric deposition were thought to be sufficient to replace losses from timber removal (Pritchett 1979a; Pritchett 1979b; Anderson *et al.* 1990; Waring and Running 1998). However, there are concerns that nutrient depletion may become a problem if short-rotation, whole-tree harvesting is used (Pritchett 1979a; Wells and Jorgensen 1979; Matthews 1989; Kimmins 1997a; Aber *et al.* 2000). Unlike most agro-forestry systems, where the nutrients of primary concern are phosphorous and/or nitrogen, the greatest potential for harvest-related nutrient deficiencies in northern hardwood forests is for calcium (Kimmins 1997a; Fisher and Binkley 2000). When the amounts of nutrients removed in the harvest of hardwoods is compared to available soil nutrient capital, calcium shows the largest relative loss (Hornbeck and Kropelin 1982; Johnson *et al.* 1982; Silkworth and Grigal 1982; Federer *et al.* 1989). On acidic or highly-weathered soils, short harvest rotations are not long enough for these losses to be replenished by current inputs of calcium from weathering and atmospheric deposition (Federer *et al.* 1989). In eastern North American and European forests, in fact, these losses are superimposed upon long-term declines in calcium resulting from acid deposition (Ulrich 1988; Federer *et al.* 1989; Johnson *et al.* 1992; McLaughlin and Wimmer 1999; DeVries *et al.* 2000; Driscoll *et al.* 2001). Recent evidence shows that conifers in northern hardwood forests can partially compensate for the calcium losses by obtaining calcium from the mineral apatite, through the action of root-associated ectomycorrhizae (Blum *et al.* 2002). Nonetheless, on calcium-poor soils, and in light of declines in atmospheric deposition of calcium (Hedin *et al.* 1994), short-rotations and harvesting may have the potential to reduce soil calcium capital to below critical levels required for healthy tree growth (Voigt 1979; Johnson, *et al.* 1988; Federer *et al.* 1989; Johnson and Todd 1990; Johnson *et al.* 1992; Kimmins 1997a; Driscoll *et al.* 2001; Blum 2002).

Despite these concerns, the effect of selection-cutting on soil calcium in northern hardwood forests has received little attention. Most research on calcium depletion has been done in other forest types, on the effects of clear-cutting, and on the differences between whole-tree and sawlog harvesting (*e.g.* Federer *et al.* 1989; Johnson *et al.* 1997; Johnson and Todd 1998; Yanai *et al.* 1999).

In general, there is no evidence of widespread calcium deficiencies in northern hardwood forests (Hall 1994; Miller-Weeks *et al.* 1994; U.S. E.P.A. 1994; McLaughlin 1996; United States – Canada Air Quality Committee 1998; Yanai *et al.* 1999). Many studies, however, have found localized declines on soils that are predisposed to acidification, are naturally low in bases, or are exposed to acid fog (Hall 1994; Miller-Weeks *et al.* 1994; U.S. E.P.A. 1994; McLaughlin 1996; United States – Canada Air Quality Committee 1998; Driscoll *et al.* 2001). These are also the areas which would have the greatest potential for calcium losses from logging.

Calcium deficiencies can impair the growth and health of trees (McLaughlin and Wimmer 1999). On acidic soils, however, these effects are difficult to distinguish from aluminum toxicity. Soil aluminum levels generally increase as calcium levels and pH decline (Richter 1992, Cronan 1994; Cronan and Grigal 1995; Lawrence *et al.* 1995; Lawrence and Huntington 1998; Lyon and Sharpe 1999). In toxicity assays on Sugar Maple, aluminum in solution was found to cause changes in tissue nutrient balances at 3 ppm (100 µmol/L) and while aluminum in soils caused reduced root or shoot growth at 15 ppm (600 µmol/L) (Cronan *et al.* 1989). Conversely, high levels of soil solution calcium have been shown to mitigate the toxic effects of aluminum (Cronan and Grigal 1995). The interaction of calcium and aluminum has led to speculation that Ca/Al ratios in soil solution may be a useful indicator of forest soil health. Following an extensive literature review, Cronan and Grigal (1995) concluded that there is a 50% probability of reduced tree growth and health at Ca/Al molar ratios of 1.0 (+/- 0.5)or lower, based on measurement of inorganic aluminum. Since approximately 70% of the aluminum in the soil solutions of Ontario northern hardwood forests is inorganic, with some variation by soil layer (Lazerte 1988; Cronan 1994), the critical Ca/Al ratio based upon total aluminum would be approximately 0.7.

I sampled 41 stands of northern hardwood forest in eastern Ontario and upstate New York. 33 stands had been previously selection-cut, while 8 stands were old-growth. In each stand, I measured calcium and aluminum in soil solution in order to address two questions: (1) does selection-cutting deplete soil solution calcium in northern hardwood forests, and; (2) will northern hardwood forest soils support short-rotation harvesting? The general approach was to fit statistical models to observed variation in soil solution calcium and aluminum among a range of hardwood sites in eastern Ontario and northern New York that differed in their time since cutting. By statistically controlling for the effects of other confounding variables, I could extract the effect of time since-cutting on calcium and aluminum levels. In order to assess current risks to northern hardwood forests, I compared unadjusted soil solution aluminum concentrations and Ca/Al molar ratios to the critical values at which decreased forest health and reduced productivity can be expected: 3 ppm and 15 ppm for aluminum concentrations; 1.0 and 0.7 for Ca/Al molar ratios (see above).

In addition to measuring calcium and aluminum in soil solution, I also measured soil pH. Soil calcium and aluminum levels are normally correlated with soil pH (Cronan and Grigal 1995), and pH is a commonly-used measure of forest soil health. There is, for example, an extensive body of literature relating it to the diversity and composition of herbaceous plant communities (*e.g.* Falkengren-Grerup and Tyler 1993; Brunet *et al.* 1996; Gough *et al.* 2000). Given that soil pH can be easily measured in both the field and the laboratory, this has led to speculation that it could be used as a simple indicator of soil solution calcium and aluminum (*e.g.* Falkengren-Grerup *et al.* 1995). I sought to evaluate this possibility by examining the relationships between calcium, aluminum and pH, and comparing their responses to geology, elevation, acid deposition and time since cutting.

Methods

Selection and measurement of variables.

Analysis of the soil data focused on six dependent and four independent variables. The dependent variables were soil solution calcium, soil solution aluminum, and soil pH in both the organic and mineral layers. Their significance has already been discussed. The independent variables were stand age (time since cutting), geology, acid deposition and elevation. The importance of stand age, geology and acid deposition have also been discussed. Elevation is generally correlated with several variables thought to be important in determining soil calcium and aluminum concentrations – temperature, decomposition rates, soil depth, weathering rates, vertical variation in acid deposition (McLaughlin 1996; Likens *et al.* 1998; McLaughlin and Wimmer 1999) – as well as often being correlated with calcium itself (Johnson and Todd 1998; Likens *et al.* 1998; Arthur *et al.* 1999; Lawrence *et al.* 1999; Johnson *et al.* 2000). Elevation also offers the advantage of being determined easily and inexpensively from standard topographic maps or GPS. In the context of forest management, therefore, it is an ideal surrogate measure to replace more labor-intensive and expensive field measurements.

Other measured variables included latitude, longitude, soil organic content (loss on ignition), soil depth, and organic layer thickness. None of these variables were significant in models predicting soil solution calcium, soil solution aluminum, Ca/Al molar ratios or pH.

Soil sampling

Soil samples were collected in late summer and early autumn. Most sampling occurred in 1996, with supplemental sampling in 1997 and 1999.

16 soil samples were taken at each site, following a stratified, non-random sampling pattern (Figure 3.01). Because of the size of the overall sample plots (0.64 ha), and the highly variable terrain, samples were taken from four different locations in each site. Four samples were collected at each location in order to obtain sufficient material for analysis (4 locations x 4 samples = 16 samples/site). When bare rock was encountered, the sampling point was displaced to the nearest point of soil cover.

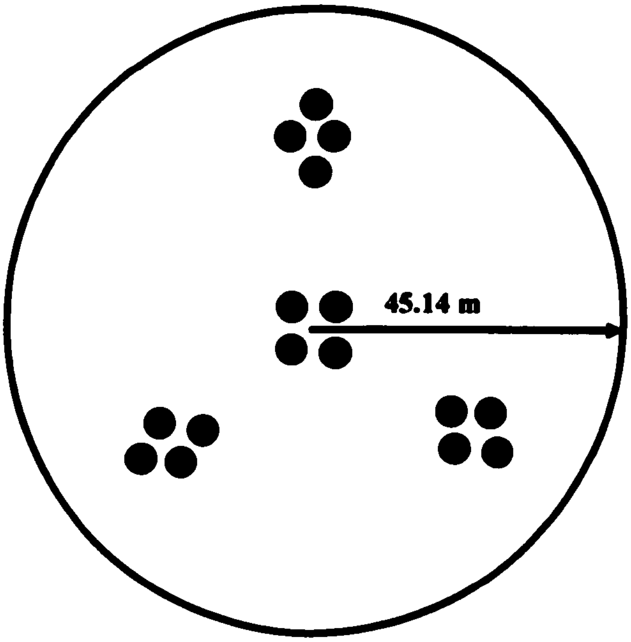


Figure 3.01. Soil sampling layout

Soil samples were collected to a depth of 30 cm with a standard 2 cm diameter soil corer, after hand removal of loose litter. Organic material matted by fine tree roots and fungal hyphae was left in place and included in the organic soil sample. Soil cores were separated into organic and mineral layers on the basis of color and texture, approximately along the boundary between the A and B horizons. Where present, the E horizon was included in the mineral layer. All soil samples were collected and separated by the same investigator, thereby reducing the potential effects of investigator bias in determining soil boundaries (Federer 1982). In some places, only a thin organic layer was present over bedrock. All organic layer and all mineral layer samples were combined and manually mixed to provide two composite samples, organic and mineral, for each site.

The field-moist soil samples were double-bagged in plastic, placed in a chilled cooler for 6 to 48 hours, then frozen on return to the laboratory. They remained frozen in a field-moist state until analysis 4 to 16 months later. Prior to analysis, samples were thawed at 4° C for 48 hrs. They were then separated into 3 portions for analysis of organic content, pH, and mineral content of soil solution.

Physical and chemical analyses

pH

pH was measured in water using the slurry method (Hendershot *et al.* 1993; Thomas 1996): 25 g of soil were mixed with 25 ml of deionized water and allowed to equilibrate for 1 hour. A standard desktop pH meter was used, with 2-point pH calibration (pH 7 & pH 4) and temperature calibration. Organic matter content was measured by loss on ignition at 540° C for 8 hours, in line with the recommendations of Nelson and Sommers (1996).

Calcium and aluminum in soil solution

Measurement of calcium and aluminum in soil solution began with saturation of all samples with deionized water, in order to provide sufficient soil solution for analysis (Soon and Warren 1993). Ideally, the samples would have been saturated to field capacity, but field capacity was not measured during sampling. Additionally, the structures of the soil samples were disrupted during sampling, and their densities greatly reduced. As this was certain to affect their water capacity, I compacted the soils under a standard pressure. In this way, the structure of soil – whether organic or mineral – would determine the final density and water-holding capacity.

The soils were compacted in a glass cylinder, using a flat-bottomed plunger, under a pressure of 160 kg/m^2. The bottom of the cylinder was covered with a perforated stainless steel plate. This pressure was maintained for 5 minutes, and was sufficient to compress both organic and mineral samples. After 5 minutes, the plunger was removed from the cylinder, leaving the soil sample compressed in the cylinder, and the sample was saturated with deionized water. Saturation was judged to have been reached when the first evidence of free water was present to sight or touch through the perforations of the bottom plate.

Once saturated, soil samples were emptied into flasks, sealed, and allowed to equilibrate for 8 hours at room temperature. The soil solution was extracted using the table top centrifuge method described by Soon and Warren (1993). Cation concentrations in soil solution extracted by the centrifuge method most accurately represent real chemical equilibria with exchangeable cations (Nissinen *et al.* 2000). The soil solution was decanted, acidified and stored at 4° C until chemical analysis.

The soil solution samples were analysed for total Ca and Al using an Inductively Coupled Argon Plasma Atomic Emission Spectrophotometer (ICaP-AES) (instrument: *Thermo Atomscan 25*). Elements were background corrected, and both internal and external calibration standards were used. The samples were run twice, at full strength and at a dilution factor of 21.83, in order to obtain concentrations of both Ca and Al within their respective calibration curves. The concentration measurements were then converted into molar concentrations (mol/ml), using the following formula (illustrated for Ca):

$$C_m = C(mg/L) \times L/1000ml \times g/1000mg \times mol/40.08g$$

where: C_m = molar concentration, and C = concentration (ppm or mg/L).

Statistical analyses

All statistical analyses were done using Systat 8.0 (SPSS Inc. 1998). General linear modeling was used to examine the factors controlling the dependent soil variables. Model fits were evaluated on the basis of residual mean square values, r^2 values, p-values and residual plots. Preliminary analyses showed that it was necessary to log-transform elevation, time since cutting, calcium (both soil layers), aluminum (both soil layers) and Ca/Al ratios (both soil layers) in order to meet the assumptions of normal, homoscedastic residuals for standard parametric statistical analyses. Residuals were normal and homoscedastic unless otherwise noted. Sample sizes varied between models, due to outliers and analytical errors with some soil samples. One site appeared as an outlier in both the organic calcium and organic aluminum analyses. Levels of calcium and aluminum at this site were approximately 3 times higher than at any other site, suggesting a dilution error in the chemical analysis. This site was excluded from the analysis of organic calcium and organic aluminum, but was retained for analysis of Ca/Al ratios.

Results

Soils were mostly semi-podzols or alfisols; true spodosols were only observed in the Adirondack sites, where hemlock was the dominant canopy tree. Mean pH levels were 5.3 (5.0 – 5.5, 95% CI) in the organic layer and 5.2 (5.0 – 5.4) in the mineral layer.

Organic content was 36.2% (32.3% – 40.2%) in the organic layer and 6.5% (5.9% – 7.3%) in the mineral layer. The pH levels are higher, and organic contents lower than one would expect for podsols. In comparison, the spodosols at Hubbard Brook have average pH values of 3.9 and 4.3 in the organic and mineral layers respectively, and organic contents of 60% and 10% (Hubbard Brook Experimental Forest 2002) There were no significant differences in pH levels or organic contents between selection-cut and old-growth sites (t-tests for separate variances, with Bonferroni adjusted p-values: organic layer pH, $t = -1.91$, $df = 8$, p = 0.37; mineral layer pH, $t = -1.86$, $df = 11.5$, $p = 0.35$; organic layer OG, $t = 0.42$, $df = 8.5$, $p = 1.0$; mineral layer OG, $t = 1.65$, $df = 6.6$, $p = 0.58$). Soil A horizons consisted of well-decayed mull, averaging 5.4 cm thick (95% C.I. 4.9 – 6.0, n = 20), and the soil depth averaged 32.1 cm (95% C.I. 28.2 – 36.1, n = 20). There was no relationship between soil depth and elevation (Pearson correlation: n = 20, r = 0.10; p = 0.68). E horizons were infrequent and thin. B horizons usually consisted of grey-brown earth, with little differentiation and abundant parent material. On sites with deeper, glacio-fluvial deposits, distinct layers of sand and gravel were observed.

In siliceous sites (n = 28), soil solution calcium concentrations averaged 11.4 ppm (range: 3.0 – 29.7) in the organic layer and 8.3 ppm (range: 1.2 – 42.2) in the mineral layer, while aluminum concentrations averaged 4.6 ppm (range: 0.1 – 4.8) in the organic layer and 9.8 ppm (range: 1.4 – 31.9) in the mineral layer. In calcareous sites (n = 13), soil solution calcium concentrations averaged 16.6 ppm (range: 4.1 – 33.1) in the organic layer and 10.4 ppm (range: 2.7 – 27.0) in the mineral layer, while aluminum concentrations averaged 0.6 ppm (range: 0.2 – 2.1) in the organic layer and 2.8 ppm (range: 0.3 – 6.8) in the mineral layer. Comparisons to other forest studies are very difficult due to differences in bedrock, vegetation, and methods of sampling and analysis. Soil solution calcium levels at Hubbard Brook, for example, range from 1 – 2 ppm (Likens *et al.* 1998). At Hubbard Brook, however, soil solution was collected using lysimeters, which produce cation concentrations up to 10 times more dilute than extraction by centrifuge (Nissinen *et al.* 2000). Data from the Ontario Maple Decline study found available aluminum concentrations in mineral layers to average 18 ppm (range: 6.6 – 37 ppm) in acid sensitive sites (McLaughlin 1996).

Table 3.1 shows the correlation matrix for the dependent variables. Notable results include the strong relationships between pH and aluminum in both soil layers, the lack of a relationship between pH and calcium in the mineral layer, and the apparent independence of calcium and aluminum in both soil layers.

General linear modeling was used to examine the factors controlling the dependent soil variables. The fits of models were evaluated on the basis of residual mean square values, r^2 values, p-values for the independent variables and residual plots.

Table 3.1. **Correlation matrix for dependent soil variables**
(*Uncorrected p-values: * < 0.05, ** < 0.01, *** < 0.001*)

	PH organic	PH mineral	Ca organic	Ca mineral	Al organic
PH mineral	0.520**				
Ca organic	0.473**	0.235			
Ca mineral	0.414*	0.047	0.649***		
Al organic	-0.561***	-0.415*	-0.150	-0.312	
Al mineral	-0.626***	-0.584**	-0.293	0.043	0.580***

Sample sizes varied between models, due to outliers and analytical errors with some soil samples. One site appeared as an outlier in both the organic calcium and organic aluminum analyses. Levels of calcium and aluminum at this site were approximately 3 times higher than at any other site, suggesting a dilution error in the chemical analysis. This site was excluded from the analysis of organic calcium and organic aluminum, but was retained for analysis of Ca/Al ratios.

Since the same independent variables appeared in the models for all dependent variables, the results are summarized in Table 3.2, and the models are given in Table 3.3.

Underlying geology, elevation, acid deposition and time since cutting all explained significant amounts of variation in soil solution calcium levels in both the organic and mineral layers (Table 3.2). Geology was the single most important predictor, appearing both as an independent factor and in interactions with other factors, especially elevation (Table 3.2). Soil solution calcium levels in both soil layers were significantly higher in calcareous sites than in siliceous sites (Table 3.2; Figure 3.02). In siliceous sites, calcium levels in both soil layers declined as elevation increased, whereas there was no effect in calcareous sites (Figure 3.03). It should be noted, however, that the range of elevation was much more restricted in the calcareous sites (Fig. 3.03). In both soil layers, calcium levels were lower on high acid deposition sites (Figure 3.04).

Once variation in soil solution calcium levels arising from variation in geology, elevation and acid deposition was removed, a statistically significant proportion of the remaining variation was attributable to differences among sites in time since cutting (Table 3.2). For both soil layers, calcium levels declined logarithmically with time since cutting (Fig. 3.05). In the organic and mineral layers, soil solution calcium declined

Table 3.2. A summary of the general linear models predicting forest soil properties, showing the partial r^2 value and statistical significance for each term when added to the model, as well as the partial r^2 values for pH when added to the original models.

*(Uncorrected p-values: * < 0.05; ** < 0.01; *** p 0.001)*

		Soil Property					
		Log organic calcium	**Log mineral calcium**	**Log organic aluminum**	**Log mineral aluminum**	**Log organic Ca/Al ratio**	**Log mineral Ca/Al ratio**
Model term	**N**	39	41	39	41	40	41
	Model r^2 (without pH)	0.54	.51	0.52	0.49	0.70	0.65
	Geology	0.0.20***	0.19***	n.s.	0.16**	0.26***	0.17***
	Log elevation	n.s.	n.s.	0.43***	0.123**	n.s.	n.s.
	Acid deposition	0.072*	0.11**	n.s.	n.s.	n.s.	n.s.
	Geology x Log elevation	0.21***	0.20***	n.s.	n.s.	0.30***	0.19***
	Geology x Acid deposition	n.s.	n.s.	0.08*	n.s.	0.11**	0.04*
	Log age	0.11**	0.13**	n.s.	n.s.	0.09**	0.04*
	Geology x Log age	n.s.	n.s.	n.s.	n.s.	0.06*	n.s.
	pH	*0.004*	*0.05*	*0.02*	*0.035*	*0.016*	*0.008*

Table 3.3. General linear models predicting soil properties.
(for geology: calcareous = 1, siliceous = -1; acid deposition: high = 1, low = -1)

Log organic calcium = -3.8 ± 1.0(geology) $- 0.14 \pm 0.05$(log age) $-$ 0.09 ± 0.04(acid deposition) $+ 1.5 \pm 0.39$(geology x log elevation) $+ 1.377$
Log mineral calcium = -4.53 ± 1.22(geology) $- 0.19 \pm 0.06$(log age) $-$ 0.13 ± 0.05(acid deposition) $+ 1.84 \pm 0.49$(geology x log elevation) $+ 1.26$
Log organic aluminum = 2.33 ± 0.41(log elevation) $- 0.10 \pm 0.04$(acid deposition x geology) $- 6.00$
Log mineral aluminum = -0.22 ± 0.06(geology) $+ 1.83 \pm 0.60$(log elevation) $- 4.03$
Organic layer Ca/Al ratio = -7.98 ± 1.47(geology) $- 0.33 \pm 0.10$(log age) $- 0.29 \pm 0.11$ (geology x log age) $+ 0.20 \pm 0.06$(geology x acid deposition) $+$ 3.42 ± 0.59(geology x log elevation) $+ 1.66$
Mineral layer Ca/Al ratio = -7.39 ± 1.78(geology) $- 0.17 \pm 0.08$(log age) $+$ 0.14 ± 0.07(geology x acid deposition) $+ 3.07 \pm 0.70$(geology x log elevation) $+ .46$

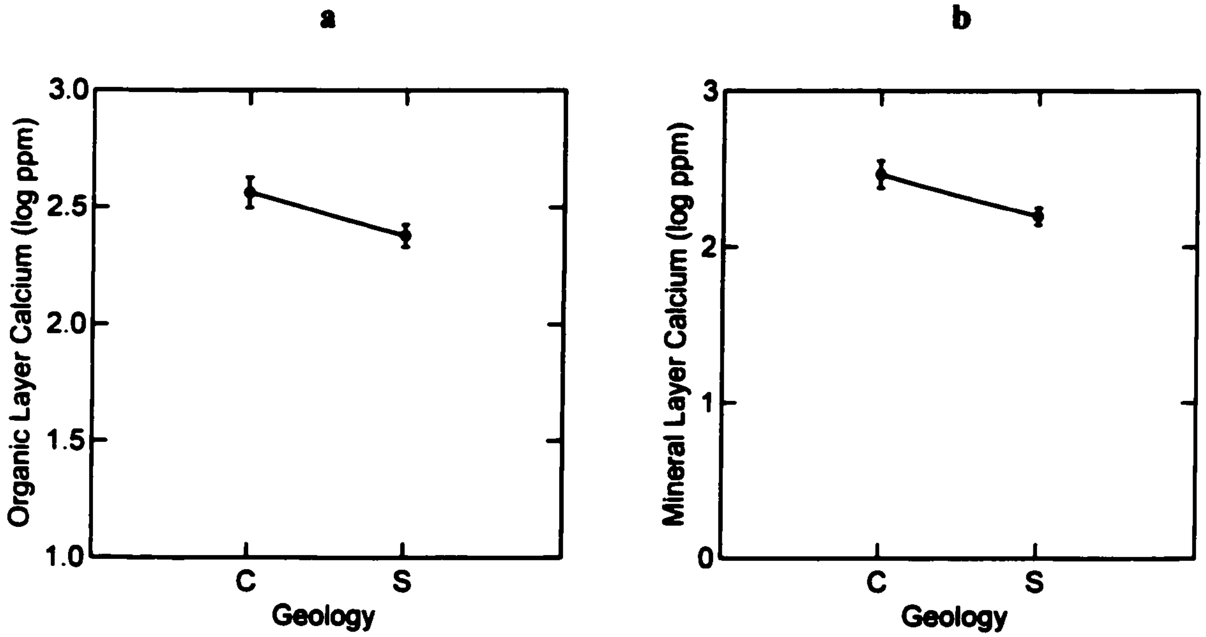


Figure 3.02. The relationships between bedrock geology and soil solution calcium in (a) the organic soil layer, and (b) the mineral soil layer (with S.E.M.).

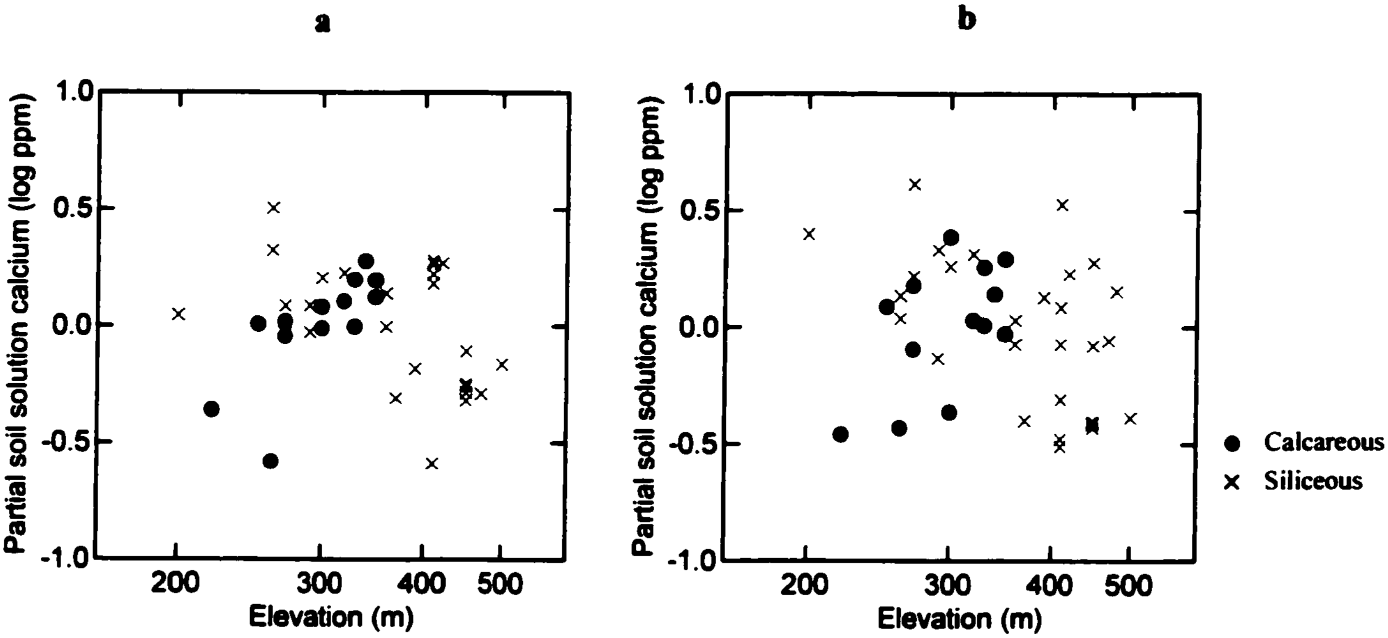


Figure 3.03. Half partial plots showing the relationships between elevation, geology and soil solution calcium in the (a) organic soil layer, and (b) mineral soil layer.

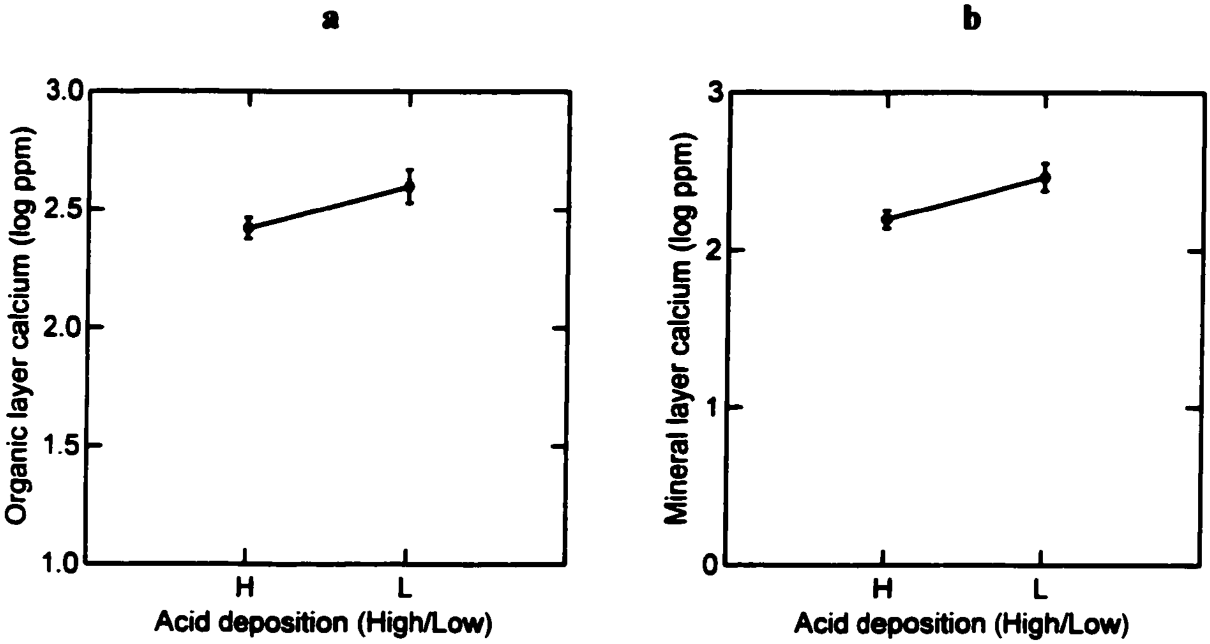


Figure 3.04. The relationships between acid deposition and soil solution calcium in (a) the organic soil layer, and (b) the mineral soil layer (with S.E.M.).

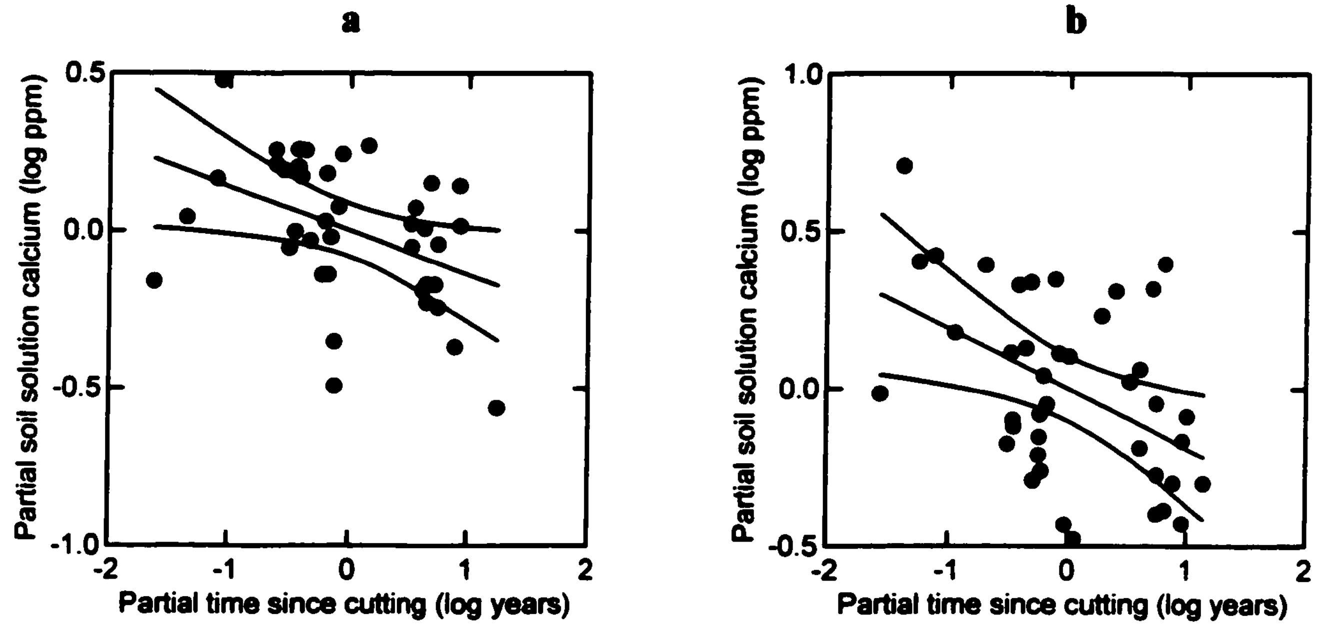


Figure 3.05. Partial plots of the relationships between time since cutting and calcium in the soil solution of the (a) organic layer, and (b) mineral soil layer, showing 95% confidence intervals for the slopes of the regression lines.

38% and 47% respectively over the first 25 years after cutting, and 42% and 54% respectively over the first 50 years.

For aluminum, elevation was the most important model predictor in the organic layer, and showed a statistically significant, but smaller, effect in the mineral layer (Table 3.2), with aluminum increasing with elevation in both the calcareous and siliceous sites (Figure 3.06). Geology was also an important predictor of aluminum concentrations in both soil layers, in interaction with acid deposition in the organic layer, and as an independent factor in the mineral layer (Table 3.2; Figures 3.07, 3.08). The interaction between geology and acid deposition in the model for the organic layer did not improve the statistical fit over a model without acid deposition (difference in rmse = 0.002), but the residuals were much better. Soil solution aluminum levels were higher on siliceous sites than on calcareous sites (Figures 3.07, 3.08).

Geology, elevation, acid deposition and time since cutting all had statistically significant effects on Ca/Al molar ratios in the soil solutions of both soil layers (Table 3.2). The effects of geology, elevation and acid deposition were consistent between soil layers – geology appearing both as an independent effect, and in interactions with elevation and acid deposition (Table 3.2). In most cases the results were predictable from the models for calcium and aluminum. Ca/Al molar ratios were lower in siliceous sites than in calcareous sites (Figure 3.09, 3.10). They also decreased with elevation in siliceous sites, whereas they were not related to elevation in calcareous sites (Figure 3.11). Unlike the independent results for calcium and aluminum, however, the models for Ca/Al ratios were improved by interactions between geology and acid deposition.

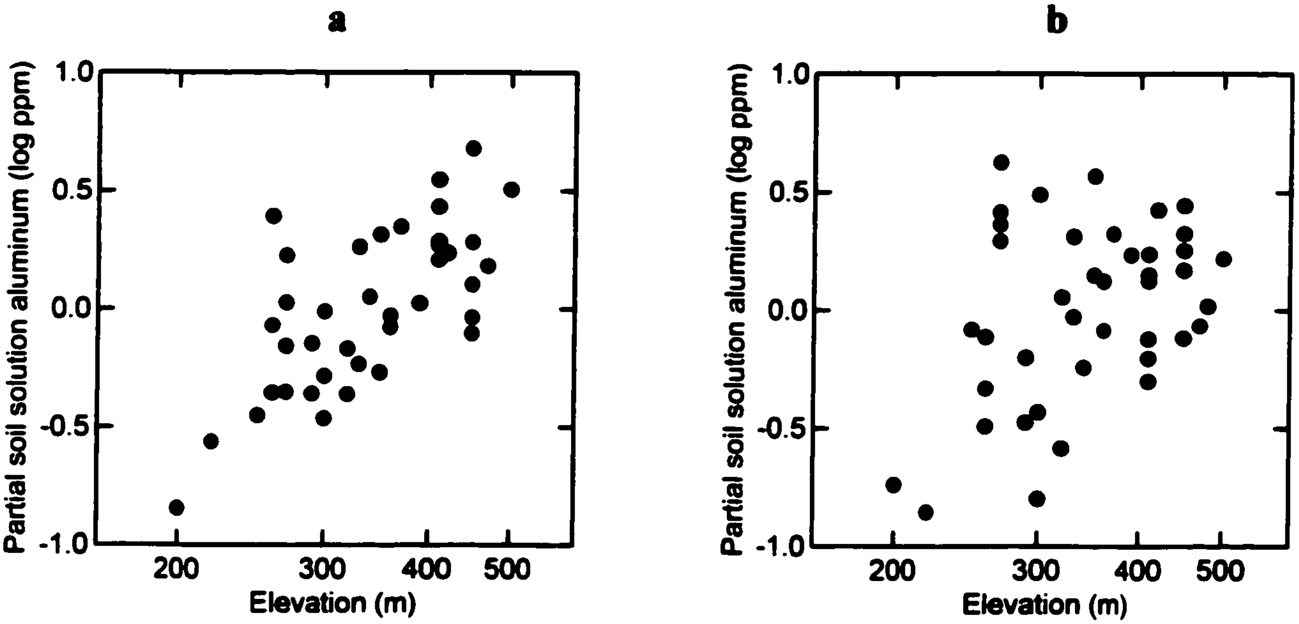


Figure 3.06. Half partial plots of the relationships between elevation and soil solution aluminum in the (a) organic layer, and (b) mineral soil layer.

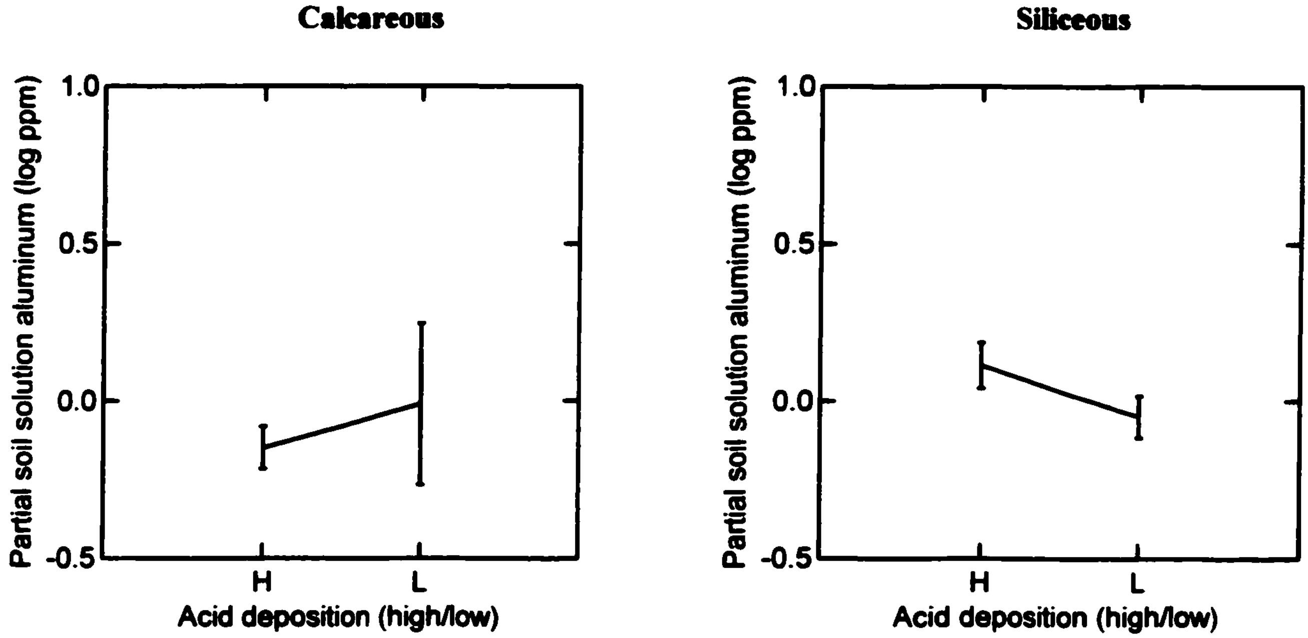


Figure 3.07. Half partial plot showing the relationship between acid deposition and soil solution aluminum in the organic layer of calcareous and siliceous sites (with S.E.M.).

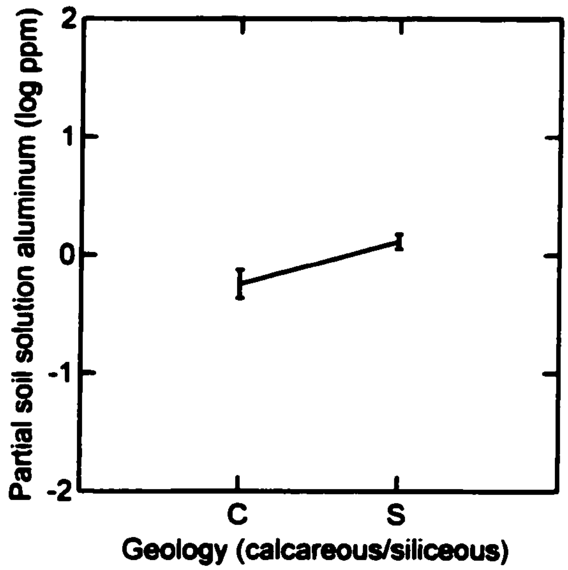


Figure 3.08. Half partial plot showing the relationship between geology and soil solution aluminum in the mineral layer (with S.E.M.).

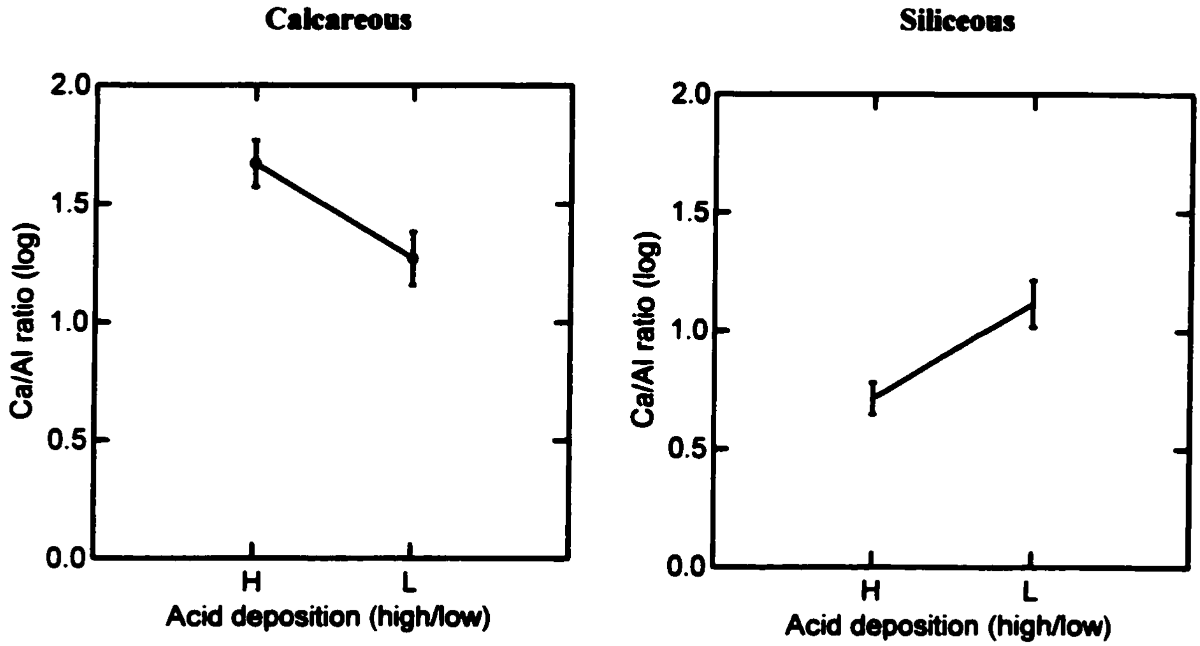


Figure 3.09. The relationships between geology, acid deposition and Ca/Al molar ratios in the soil solution of the organic layer (with S.E.M.).

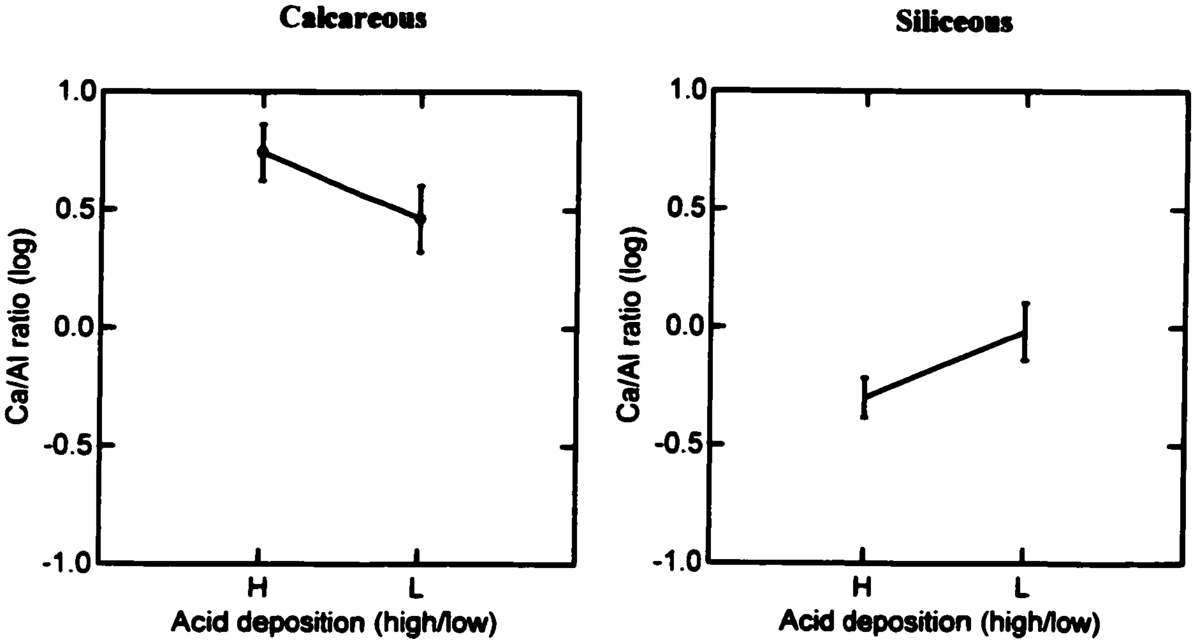


Figure 3.10. The relationships between geology, acid deposition and Ca/Al molar ratios in the soil solution of the mineral layer (with S.E.M.).

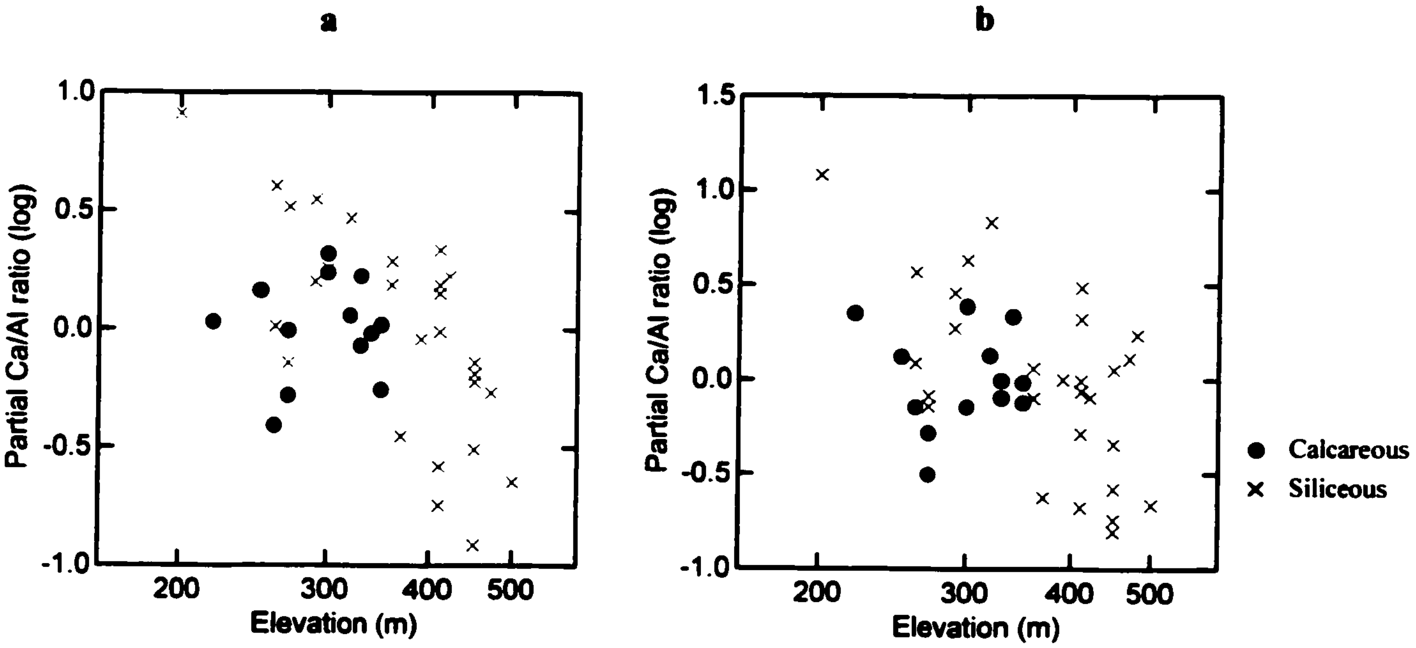


Figure 3.11. Half partial plots of the relationships between elevation and Ca/Al ratios in the (a) organic layer, and (b) mineral soil layer.

In siliceous sites, Ca/Al ratios were lower under high levels of acid deposition (Figures 3.09, 3.10). In calcareous sites, they tended to be higher under high acid deposition (Figures 3.09, 3.10). In the case of the calcareous sites, however, the small number of low deposition sites (n = 3) makes any inference problematic.

As with calcium, significant relationships were found between time since cutting and Ca/Al molar ratios in the soil solution of both soil layers (Table 3.2; Figure 3.12). The relationship in the organic layer was complicated by time since cutting appearing both as a main factor and in interaction with geology. Removal of either variable resulted in the other becoming statistically non-significant, although the interaction with geology was less important. Once again, the relatively small amounts of overall variance explained by time since cutting belied its strong effects on Ca/Al ratios. In the organic soil layer, Ca/Al molar ratios declined by 39% over the first 25 years since cutting, and 41% over the first 50 years. In the mineral soil layer, they declined by 50% over 25 years and 55% over 50 years.

The inclusion of pH as an independent variable had no significant effect on any of the models for calcium, aluminum or Ca/Al molar ratios. Table 3.2 shows the partial r^2-value of pH (for the appropriate soil layer) when added to each model. In no case was pH statistically significant, and declines in the statistical significances of other factors were minor when pH was included. Attempts were made to find alternate models which included pH as a significant factor. Though it was possible to find alternate models, these had either similar or lower r^2 values, were usually more complicated, and sometimes had problematic residuals. In none of them was pH the most important factor.

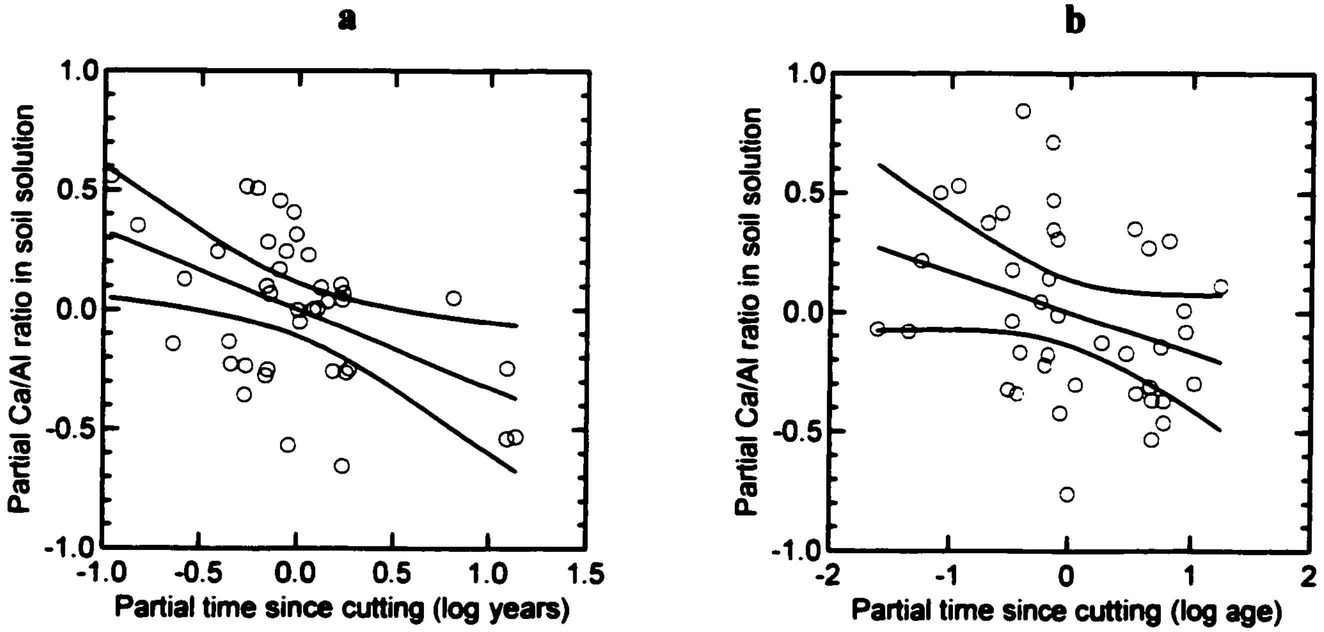


Figure 3.12. Partial plots of the relationships between time since cutting and Ca/Al ratios in the soil solution of the (a) organic layer, and (b) mineral soil layer, showing 95% confidence intervals for the slopes of the regression lines.

General linear modeling showed that pH in the organic soil layer declined significantly with elevation and high acid deposition (Table 3.4). PH in the mineral soil layer was related to geology and elevation, declining on siliceous sites and at higher elevations (Table 3.4). The model for mineral pH excluded one Adirondack old-growth site, Ampersand Mountain, with high leverage and a high Cook value. This site was very moist, with occasional sphagnum appearing in wetter areas. Models which included this site had additional significant independent variables and higher r^2 values, but the differences were due entirely to the one site. There was no effect of time since cutting on pH levels in either soil layer (Table 3.4).

Figure 3.13 compares aluminum concentrations in soil solution to critical values of 3 ppm and 15 ppm (Cronan *et al.* 1989, see introduction). Bedrock geology and elevation are shown in the figures because of their importance in the models for soil solution aluminum. Both figures show that a large proportion of the stands have aluminum concentrations with the potential to reduce tree health and stand productivity. This is particularly true for the mineral soil layer, where more than 2/3 of the sites exceed 80 ppm aluminum. The risks increase with elevation, and are higher on siliceous stands.

When Ca/Al ratios are compared to critical values of 1.0 and 0.7 (Lazerte 1988; Cronan 1994; Cronan and Grigal 1995, see introduction), the differences between soil layers and bedrock types become more apparent (Figures 3.14). In the organic layer, only two sites – both siliceous, old-growth stands – fall below the critical Ca/Al ratio of 1.0, and only one of those falls below 0.7, whereas all calcareous sites exceed the critical threshold. In the mineral layer, 19 sites –all siliceous – fall below the critical ratio of 1.0

Table 3.4. General linear models predicting pH in the organic and mineral soil layers.
(Uncorrected p-values: * < 0.05; ** < 0.01; *** p 0.001)

		Soil Property	
		Organic pH	**Mineral pH**
Factor	**N**	39	39
	R^2	0.528	0.304
	Geology		0.121*
	Elevation	0.527***	0.069 (n.s.: p = 0.068)
	Acid deposition	0.115**	
	Geology x Elevation		
	Geology x Acid deposition		
	Age (time since cutting)		
	Geology x Age		

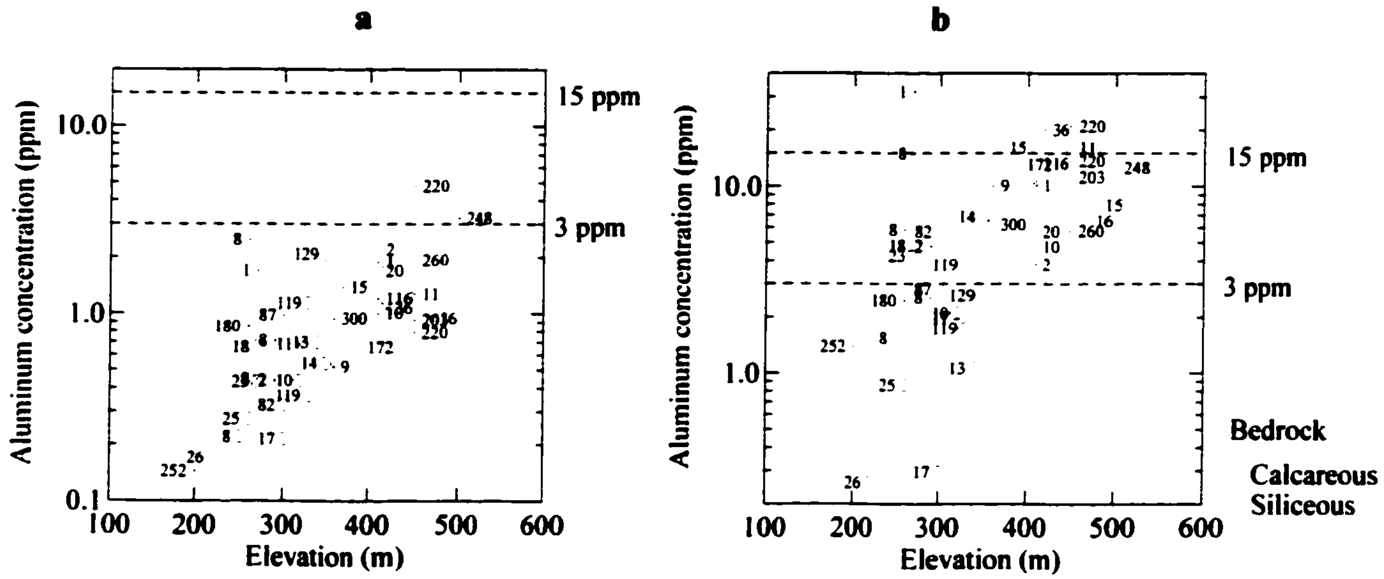


Figure 3.13. The relationships between elevation and aluminum in the soil solutions of the (a) organic and (b) mineral soil layers, showing critical concentrations, the effects of bedrock type, and time since cutting.

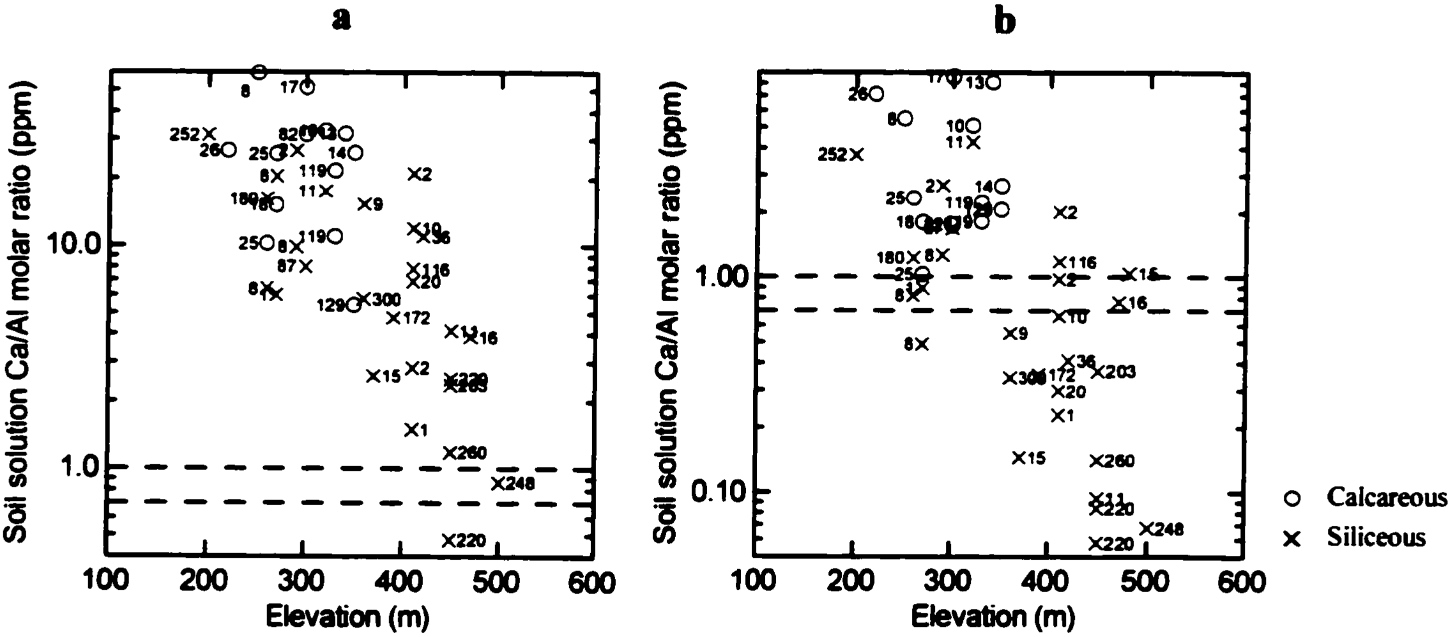


Figure 3.14. The relationships between elevation and Ca/Al ratios in the soil solutions of the (a) organic and (b) mineral soil layers, showing critical concentrations, the effects of bedrock type, and time since cutting.

and 15 fall below 0.7, whereas all calcareous sites exceed the threshold. In both soil layers, risk increases with elevation.

Discussion

Contrary to expectations, it was clear from their appearance, structural properties and chemical properties that the majority of the soils sampled in this study had not undergone significant podsolization, or were undergoing conversion to less acidic soil types, such as alfisols. However, when comparing soil pH values in this study to other studies, it should be noted that pH in this study was measured in water, which tends to produce higher pH readings than measurements in potassium solutions (Thomas 1996). Although Perera *et al.* (2000) describe the soils of the main research area (the Frontenac Axis) as primarily consisting of spodolsols, they note that these are interspersed with alfisols. It is possible, however, that the general lack of spodosols may reflect an on-going process of change, perhaps because of the elimination of conifers from the forest canopy (Perera *et al.* 2000), or because of some larger ecological process, such as global warming. Unfortunately, this study was not designed to address this question.

Our results suggest that selection cutting and stand regeneration in northern hardwood forests depletes soil solution calcium. Loss of soil solution calcium, in turn, reduces soil solution Ca/Al molar ratios. These effects occur on sites that are already at risk due to geology and elevation, and which have already suffered damage from acid deposition. Reductions in calcium levels and Ca/Al ratios on these sites increase the future risks to forest health and productivity.

Not all of the observed declines, however, represent long-term losses in soil calcium *capital*. Although it is not apparent from the data, some portion of the declines are probably due to the Assart effect: an initial pulse of nutrients after logging caused by the decay of logging slash (Kimmins 1997a). By looking at previous work on calcium budgets in northern hardwood and eastern deciduous forests, it is possible to estimate the magnitude of the Assart effect following selection cutting and to calculate the real decline in soil calcium capital.

We begin with the assumption that a single selection cut removes 1/3 of the basal area of a stand, and that this timber will regenerate over a 25 year cutting cycle. Under the basic assumptions of selection-cutting, regeneration will require the same uptake of calcium (U) as contained in the original cut trees. Part of the required calcium can come from the decay of logging slash, part from new inputs from bedrock weathering and atmospheric deposition, and the remainder from the initial soil calcium capital (solution calcium + exchangeable calcium). Recent work by Blum *et al.* (2002), suggest that conifers (specifically balsam fir and red spruce) may also obtain calcium directly from apatite *via* ectomycorrhizae, making it available in litter to deciduous trees. However, their work is not applicable to the following calculations, due to the low incidence of conifers in the selection-cut sites of the present study (basal area for sites < 25 years: mean = 1.8%±0.7 SEM, maximum = 7.9%).

The amount of calcium available from logging slash depends upon which parts of the harvested trees are removed from the site. In their 1990 guidelines for Ontario, Anderson *et al.* (1990) recommended that bole-only or sawlog harvesting be used in selection-cutting, in order to minimize skidding damage to residual trees. They noted, however, an increasing trend toward "tree-length" harvesting, in which much of the tree-tops are used to produce secondary, non-lumber products. My observations of newly cut sites and discussions with local foresters suggest that this method is closer to whole-tree harvesting than sawlog harvesting. This may be because the expensive, labor-intensive nature of selection cutting exerts pressure on foresters to make full use of secondary products, or because one of the silvicultural benefits of selection cutting is the production of tall, straight trees with a reduced amount of branching (Anderson *et al.* 1990).

Data on northern hardwood and eastern deciduous forests from Federer *et al.* (1986) show that whole-tree harvesting removes approximately 72% of the calcium in cut trees from the site, leaving 28% of the calcium remaining in slash. Therefore, the decay of logging slash can contribute a maximum of 28% of the calcium uptake required for stand regeneration (*i.e.* $0.28U$). Data on the calcium biogeochemistry of Hubbard Brook (Likens *et al.* 1998) show that, on siliceous sites, the net input (after normal leaching) of calcium from weathering and atmospheric deposition over 25 years could supply a maximum of 22% of the calcium required for stand regeneration (*i.e.* $0.22U$). Hubbard Brook has nearly identical surficial and bedrock geology to my siliceous sites, and supports similar stands of mature, second-growth northern hardwood forest. On siliceous sites, therefore, about 50% of the calcium required for stand regeneration can be provided by slash, bedrock weathering and atmospheric deposition, with the remainder (*i.e.* $0.50U$) coming from the soil capital.

Figure 3.15 shows the relationships between calcium uptake and supply from slash, weathering/deposition and soil capital, using the example of the organic layer. Ca_i is the initial, observed level of soil solution calcium, including any calcium from logging slash.

Ca_b is the original, baseline level of soil solution calcium, prior to cutting. Ca_f is the final, observed level of soil solution calcium. The observed decline in soil solution calcium over 25 years was 39%, and represents at least 78% of the total calcium uptake during regeneration (0.78*U*). Expressed in terms of *U*, calcium from logging slash could contribute a maximum of 0.28*U* to the observed decline, with the remainder of the calcium, 0.50*U*, coming from the original soil solution capital. When the ratio of 0.28 to 0.50 is applied to the percentage decline in soil solution calcium, we find that the decline in the soil solution capital is equal to 25% of the initial observed calcium level (Ca_i), or 29% of the original baseline calcium level (Ca_b).

The same ratio can be applied to the mineral layer calcium. And since the declines in Ca/Al molar ratios with time since cutting are due to the declines in calcium concentrations (aluminum concentrations showing no response to time since cutting), we can use the same ratio to estimate their net response to time since cutting. Thus, the net decline in soil solution calcium capital in the mineral layer over 25 years is estimated at 35%, and the net declines in baseline Ca/Al molar ratios in the organic and mineral layers are estimated at 28% and 37% respectively.

The use of bole-only harvesting, rather than whole-tree harvesting, significantly reduces the estimated declines in soil Ca capital and Ca/Al ratios. Data from Hubbard Brook (Likens *et al.* 1998) on the calcium content of sugar maple, American beech and yellow birch trees, shows that removal of bole-only harvesting (*i.e.* "sapwood".

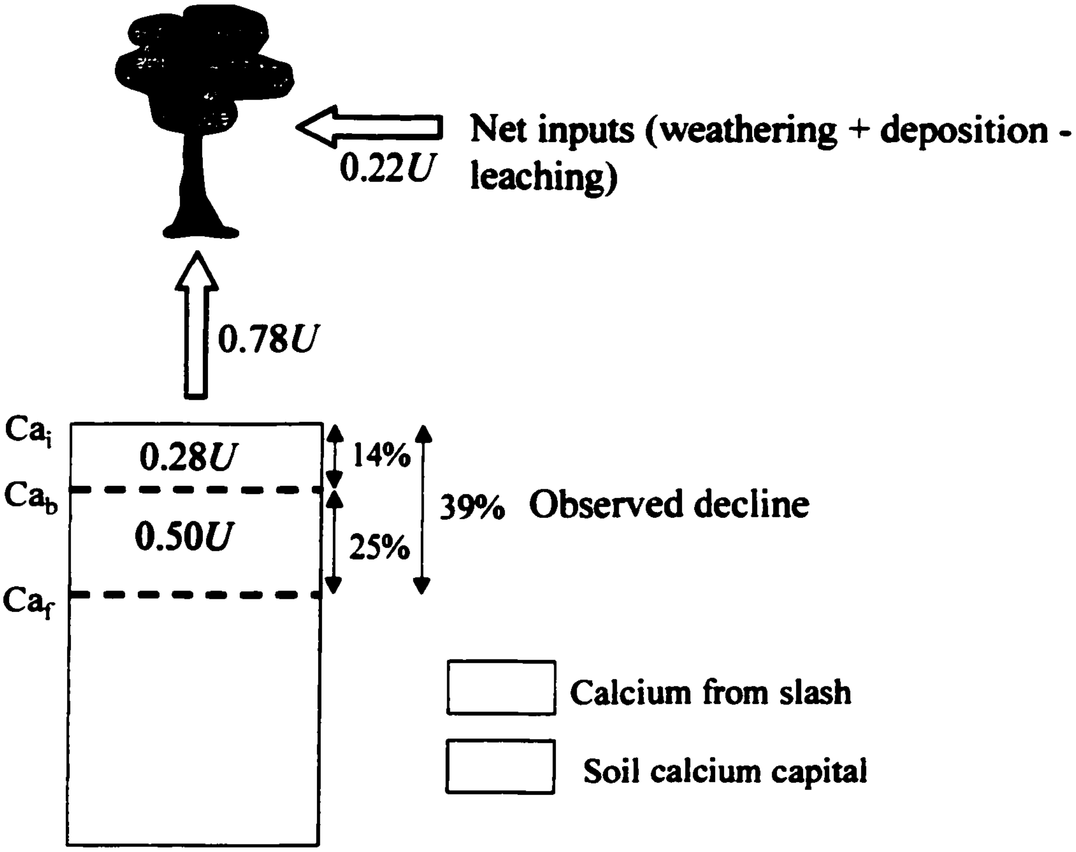


Figure 3.15. The effect of regeneration of a 1/3 selection-cut on soil solution calcium capital in the organic layer of the siliceous sites.

"heartwood" and "bark" of Table 8, p. 110) should export 40% of the calcium in effected trees from the site, leaving 60% remaining in logging slash (excluding foliage). Under these conditions, the estimated reductions in original soil calcium capital would be 12% and 13% in the organic and mineral layers respectively, and the estimated reductions in original Ca/Al ratios would be 11% and 16%.

These estimates are based on calcium inputs from siliceous bedrock (at Hubbard Brook) and, as such, do not apply to calcareous sites. Weathering of dolomite (which underlies several of the calcareous sites in this study) can provide 4 times as much calcium as weathering of gneiss (Clayton 1979). If all of this additional calcium was available for tree growth, then, according to the aforementioned calculations, forest regeneration following cutting could in principle have a negligible effect on the soil calcium. Although a calcium budget for northern hardwood forest on calcareous bedrock has not yet been produced, the net effect of selection cutting on soil calcium capital is almost certainly much less than on siliceous stands. One cannot say, in fact, that the observed declines on calcareous sites are not due entirely to the Assart effect.

The aforementioned estimates of calcium depletion in siliceous sites are also very rough. Other factors will also influence the true declines: (a) both total and available soil calcium are divided unevenly between the organic and mineral layers, as are calcium inputs from weathering and atmospheric deposition; (2) most nutrient uptake occurs in the organic layer; (3) calcium in solution can move freely between layers. Therefore, while the estimates above reflect the overall effects of selection cutting on calcium and Ca/Al molar ratios in the soil solution, the proportionate effects on the organic and mineral soil layers may be skewed: the actual calcium depletion may be higher than estimated in one layer, and proportionately lower in the other. The estimates are also conservative, assuming 100% conservation of calcium from logging slash.

While it is clear from this study that selection cutting depletes soil solution calcium over a normal cutting cycle, the analysis does not span a sufficiently long chronosequence to permit an assessment of the effects of multiple cycles. Thus, empirically, the question of whether multiple cycles results in cumulative depletion over longer time-scales is still unresolved. *A priori*, however, there is no reason to believe that it will not continue. The loss of soil calcium capital continues for at least the length of a normal cutting cycle. And with additional calcium being exported from the system at each cutting, the only way that soil calcium levels could stabilize would be for calcium inputs to increase dramatically or calcium leaching to fall dramatically. There are no theoretical reasons to expect such changes in calcium biogeochemistry in selection-cut stands, nor have they been reported.

This study supports previous studies on calcium budgets which identified whole-tree clear-cutting as a significant risk factor for calcium depletion in some forest soils (Voigt 1979; Wells and Jorgensen 1979; Hornbeck and Kropelin 1982; Johnson *et al.* 1982; Johnson *et al.* 1988; Federer *et al.* 1989; Johnson and Todd 1990; Lawrence and Huntington 1998). In fact, it goes beyond these studies to show that significant risks exist even when selection-cutting is employed – a harvest method generally regarded as significantly more benign than clear-cutting. By contrast, Yanai *et al.* (1999) found no effect of forest age on calcium levels in the forest floors of a chronosequence of 13 clear-cut northern hardwood forest stands. Similarly, Johnson *et al.* (1997) found no significant differences in total available calcium in a northern hardwood forest stand at

Hubbard Brook before and 8 years after clear-cutting. Although calcium declined in upper soil layers (Oa and E), the loss was offset by calcium gains in the Bh and Bs1 soil layers (Johnson *et al.* 1997). The gains in the Bh and Bs1 layers were accompanied by increases in C.E.C., which Johnson *et al.* (1997) attribute to changes in the quality of soil organic matter. These results suggest that the severe disturbance of clear-cutting may may induce mechanisms of calcium mobilization or conservation that are not found in selection-cut stands.

The present study also disagrees with the conclusions of Johnson and Todd (1998), who reported that whole-tree harvesting had no long-term effects on soil calcium levels in a southern oak forest stand. In their analysis, however, they did not take into account soil calcium changes in their reference (*i.e.* control) stand, saying that they lacked sufficient replication to analyze that data. Their figure 4, however, clearly shows more than a doubling of exchangeable calcium in the A horizon of their reference stand over the study period, along with error bars for standard deviation. Given this large, unexplained input of calcium into the soil system, their conclusion that cutting does not deplete calcium is unwarranted. In fact, for the A horizon, the constant soil calcium concentration in the whole-tree logging treatment, in comparison to the calcium increase in the reference stand, suggests a strong negative effect of whole tree logging.

This study is consistent with previous studies showing that geology and elevation may predispose certain sites to calcium depletion and aluminum toxicity (Tomlinson 1983; Ulrich 1988; Johnson and Friedland *et al.* 1992; Johnson and Ragsdale *et al.* 1992; Richter *et al.* 1992; Cronan 1994; Miller-Weeks *et al.* 1994; U.S. EPA 1994; McLaughlin 1996; Lawrence and Huntington 1998). As expected, calcium concentrations were lower and aluminum concentrations higher on siliceous bedrock. These patterns were also reflected in lower Ca/Al ratios on siliceous sites. This undoubtedly reflects the lower calcium content and higher aluminum content of the parent material

Determining the causes of the elevation effects is not the purpose of this study, but it should be noted that the different responses of calcium and aluminum suggest that several mechanisms are at work. They could be related to the influence of temperature on decomposition rates or to vertical variation in acid deposition rates. The pertinent point is that high elevation sites on siliceous bedrock are most prone to damage from acid deposition and logging.

Acid deposition was a significant factor in every model except the one for mineral layer aluminum – usually in interaction with geology. This agrees with previous work in North America and Europe (Ulrich 1988; Johnson and Friedland *et al.* 1992; Johnson and Ragsdale *et al.* 1992; Richter *et al.* 1992; McLaughlin 1996). However, the weakness of the acid deposition effects is surprising – until one looks at the actual range of variation in the acid deposition data. While the means for cumulative H^+ deposition over 25 years are statistically different between the "high deposition" and "low deposition" categories ($p < 0.001$ in a two-tailed t-test), they are actually very similar in magnitude: 7.037 kg/ha in high deposition sites ($N = 27$), and 6.619 kg/ha in the low deposition sites ($N = 12$). There are, in fact, no real "low deposition" sites; all sites are located within a region where acid deposition rates exceed critical soil and water levels (United States – Canada Air Quality Committee 1998). Given the very small difference in H^+ deposition between the high and low sites – a cumulative total of 0.418 kg/ha over 16 years – it is actually surprising that the effects of acid deposition could be detected, and illustrates the sensitivity of siliceous sites to acid deposition.

The greater susceptibility of siliceous sites to damage from acid deposition and logging becomes particularly evident when we compare observed aluminum concentrations and Ca/Al ratios to critical levels (Figures 3.13 – 3.14). Organic layer aluminum concentrations and Ca/Al molar ratios are generally acceptable in both siliceous and calcareous sites, but there are serious problems in the mineral layers of the siliceous sites. 22 of 27 siliceous sites exceed critical aluminum concentrations, and 19 exceed critical Ca/Al concentrations. Of the latter, 12 have been selection cut in the past. These are sites for which the risk of reduced forest health and growth is greater than 50% (Cronan and Grigal 1995). In contrast, the current risk to forest health or growth in calcareous sites is low.

Repeated selection-cutting has the potential to increase the risks to forests on siliceous sites. If repeated selection cutting depletes soil calcium – as it appears to have the potential to do – then logging could put at greater risk some sites currently above critical Ca/Al ratios. It would also aggravate problems on sites where Ca/Al ratios are already below critical levels. This is particularly true for the siliceous sites, where the effect of selection-cutting on soil calcium capital over a single cutting cycle is unequivocal.

I expected that the changes in soil calcium and aluminum levels would be accompanied by changes in soil pH. Calcium and aluminum are both involved in pH buffering in northern hardwood forest soils (Tomlinson 1983); low pH tends to mobilize aluminum (Cronan 1994); and calcium and aluminum are both more susceptible to leaching at low pH (Johnson and Ragsdale *et al.* 1992). Not surprisingly, therefore, pH was correlated with aluminum concentrations in both soil layers and with calcium in the organic layer (Table 3.2). Despite this, however, pH was not a useful indicator or surrogate measure for calcium, aluminum and Ca/Al molar ratios in soil solution. First, it was not significantly correlated with calcium in the mineral layer (Table 3.2). Second, predictive models with pH generally explained less variation in calcium and aluminum concentrations than models containing only geology, elevation, acid deposition and time since cutting – and none of the latter require field sampling. Third, pH did not reflect the effects of selection cutting on calcium and Ca/Al ratios, which could be critical to future forest health and productivity. These conclusions regarding the usefulness of pH as a measure of soil acidification and an indicator of forest stress are similar to those reached by Cronan and Grigal (1995).

The results of this study undermine an essential premise underlying the use of selection-cutting in northern hardwood forests: that soil nutrient levels are adequate for the natural regeneration of healthy trees (Kimmins 1997b; Perry 1998). They show that there is a strong possibility of reduced tree health and forest productivity in much of the current production northern hardwood forest. Such effects, in fact, are likely already occurring (McLaughlin 1996; United States – Canada Air Quality Committee 1998). McLaughlin *et al.* (1992), for example, have reported statistically significant declines in productivity and tree health in acid-sensitive stands in Ontario northern hardwood forests. Economically, the long-term effect of these impacts may be a smaller supply of high-quality hardwood than presently anticipated from selection-cut forests.

Ecologically, the effects of calcium depletion and aluminum increases (along with soil acidification) are difficult to predict. Forest stands may be more susceptible to stresses such as drought, disease and insect damage (McLaughlin 1996). Weakened trees could be more susceptible to damage from broad disturbances, like blowdowns or ice storms. Changes in the composition of herbaceous vegetation are likely to occur (Falkengren-Grerup and Tyler 1993; Falkengren-Grerup *et al.* 1995; Brunet *et al.* 1996), along with changes in soil microbial communities (Pennanen *et al.* 1998). Populations of certain sensitive groups of animals, such as annelids and gastropods may decline (Wäreborn 1992; Rungren and Nilsson 1997).

The first step to avoiding or reducing these impacts is to begin monitoring calcium, aluminum and Ca/Al ratios in all production northern hardwood forests. As this study has shown, it need not be unduly difficult or expensive. The use of calcium, aluminum and Ca/Al ratios in routine monitoring would help forest managers to determine which stands under their care could be safely managed using short-rotation selection-cutting. It would identify sites where soils are too sensitive to support cutting. And it would provide the necessary on-going information for managers to make the best management choices for the remainder.

Chapter Four

The responses of canopy and herbaceous layer vegetation to selection-cutting in northern hardwood forests.

Introduction

One advantage that selection-cutting in northern hardwood forests is presumed to offer over other silvicultural methods is greater protection of native plant biodiversity (Matthews 1989; Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999). Selection-cutting, it is argued, preserves the natural microclimate of the forest floor through retention of an intact canopy, as well as associated hydrological and decomposition cycles (Matthews 1989; Waring and Running 1998). It is also believed to mimic the natural processes of "gap-phase replacement" (*sensu* Watt 1947), creating openings and opportunities in the forest canopy for the regeneration of species which cannot tolerate full shade (Shugart 1984; Brokaw and Lent 1999; Frelich and Puettmann 1999; Spies and Turner 1999). Nonetheless, foresters and ecologists have recognized that even selection-cutting poses some risks to forest plant biodiversity (Jenkins and Parker 1998; Brokaw and Lent 1999; Palik and Engstrom 1999; Seymour and Hunter, Jr. 1999; Spies and Turner 1999), including the deliberate weeding of economically undesirable tree species such as *Tsuga canadensis* (Eastern Hemlock) (Walker 1999), physical damage to plants by the "skidding" of trees from the forest, and damage to roots and underground meristems by the physical disruption or compaction of the forest soil (Gjedtjernet 1995; Frelich and Puettmann 1999; Aber *et al.* 2000).

Less obvious is the potential for selection-cutting to reduce the number of "regeneration niches" (*sensu* Grubb 1977) in a forest. This includes reduced gap sizes (and variability therein), decreased abundance and size of coarse woody debris, and the elimination of "tip-ups" or "pits and mounds" created by the toppling of large, old trees (Thompson 1980; Harmon *et al.* 1986; Frelich and Puettmann 1999; Kimmins 1997; McComb and Lindenmayer 1999; Spies and Turner 1999). Selection-cutting also has the potential to introduce weedy plant species where they might out-compete slower-growing, shade-adapted forest species (Perry 1988; Aber *et al.* 1979; Reader and Bricker 1994; Perry 1998; Aber *et al.* 2000).

Recognizing the potential risks to plant diversity, foresters have exploited the flexibility of the selection-cut system to develop methods for risk mitigation. These include the use of "group" selection-cutting, in which trees are removed in groups rather than singly, leaving gaps of varying sizes and facilitating the growth of both shade-tolerant and semi-tolerant tree species (Matthews 1989; Anderson *et al.* 1990); and "variable retention" systems, designed to retain features such as large, old trees, snags, and large, decomposing logs (Bull 1978; Thomas *et al.* 1979; Harmon *et al.* 1986; Lindenmayer and Franklin 1997; Goodburn and Lorimer 1998; Brokaw and Lent 1999; McComb and Lindenmayer 1999; Aber *et al.* 2000). These methods are often explicitly incorporated into stand marking and management guidelines (*e.g.* Tubbs *et al.* 1987; Anderson *et al.* 1990; Anderson and Rice 1993; GFERG 1997).

Despite these efforts to make selection-cutting more ecologically sustainable, its effects on the diversity of northern hardwood forest vegetation have not been greatly studied. Notable exceptions include the experimental studies of Bricker and Reader (1992a, 1992b) and Metzger and Schultz (1981, 1984), and the surveys of Fredericksen *et al.* (1999). The experimental studies focused on short-term and long-term responses respectively and showed no significant effects of selection-cutting on extirpation rates. diversity or community composition. As one would expect of experimental studies.

however, the treatment plots in each case were situated close together and were relatively homogenous. Furthermore, only the responses of herbaceous layer vegetation were reported. The survey work of Fredericksen *et al.* (1999) looked at short-term herbaceous layer responses to harvesting intensity in both hickory – oak and northern hardwood forests, finding short-term effects on community composition, but no effects on richness or diversity.

Here I evaluate the effects of selection cutting on both the canopy and herbaceous layer vegetation of northern hardwood forests across a wide range of stand types and ages. The species compositions of the overstory, subcanopy, sapling and herbaceous layers were enumerated in a set of selection-cut and old-growth stands. For all vegetation layers, I compared species richness and community composition in old-growth and selection-cut stands and looked for changes in richness and community composition in relation to time since cutting. For the canopy, comparisons were also made between the compositions of the overstory, the subcanopy and the sapling layers, in order to assess regeneration. For the herbaceous layer, attempts were made to detect species or groups of species which might be particularly sensitive to selection-cutting. The effect of selection-cutting on the overall floristic quality of the herbaceous layer was also examined using a Floristic Quality Assessment system developed specifically for the region (Oldham *et al.* 1995). In all analyses, attempts were made to control statistically for the effects of other variables which might otherwise be expected to influence vegetation community structure, such as bedrock geology, elevation and soil pH.

Methods

Sampling

Site selection and locations are described in Chapter 2, as are the general sampling methods.

Canopy layer sampling was done using the Growth and Yield system of the Ontario Ministry of Natural Resources (Hayden *et al.* 1995). Three circular 11.28 m radius growth plots were located at 120° intervals at random distances from the center of a circular 45.14 m. radius mortality plot (see ch. 2). Within each growth plot, all trees with a dbh ≥ 2.5 cm were identified to species and measured. The total number of stems and the total basal area was calculated for each species in each growth plot. Total number of stems *per* hectare was calculated from the mean number of stems of the three growth plots (*i.e.* dbh/ha = mean dbh/0.04). Species basal areas were calculated from the sum for each species in all three growth plots (*i.e.* basal area/ha = basal area/0.12 ha).

Trees were classified as "overstory", "subcanopy" and "sapling" on the basis of dbh: trees with a dbh ≥ 20 cm were included in the overstory layer; trees with a dbh ≥ 10 cm and < 20 cm were classified in the subcanopy layer; trees with a dbh ≥ 2.5 cm and $<$ 10 cm were classified in the sapling layer. In the Ontario Ministry of Natural Resources (OMNR) classification system, all trees $\geq$ 10 cm are considered "merchantable", with those between 10 cm and 24.9 cm being classified as "poles" and those ≥ 25 cm being classified as "sawlogs". During my sampling, however, I observed that trees as small as 20 cm dbh sometimes occupied space in the overstory of selection-cut stands, and I felt that my classification system better represented the actual canopy structure.

Herbaceous layer sampling was done in 25 x 1 m^2 circular sub-plots randomly placed within the 45.14 m radius mortality plot. Initially, only 20 plots were sampled, but examination of the resulting species-area curves suggested that an additional 5 plots were necessary for adequate sampling (Figure 4.01). In each sub-plot, all vascular herbaceous plant species were recorded, as well as all woody plant species less than 1 m tall.

Plants were usually identified to species in the field. Unknown plants were either collected for identification in the laboratory, or recorded as "unknown", depending upon the condition of the plant. Plants were identified in the field using common field guides (Newcomb 1977; Cody 1978; Neiring and Olmstead 1979; Petrides 1986; Chambers *et al.* 1996). Plants were identified in the laboratory using Gleason and Cronquist (1991). If no identification was possible in the laboratory, then the plants were recorded as "unknown." Unknown plants were not included in any calculations of diversity or community composition.

In some cases, plants were only identified to the genus level, particularly those without inflorescences. This applied to all of the *Trillium*, many of the *Viola* and many of the *Carex*. When these plants could be distinguished from other species present in a stand, then they were included in calculations of diversity and community composition; otherwise they were excluded.

Vegetation sampling occurred between the months of June and September. Earlier sampling of the ephemeral Spring flora was not possible because spring flooding and muddy conditions made many of the study sites inaccessible.

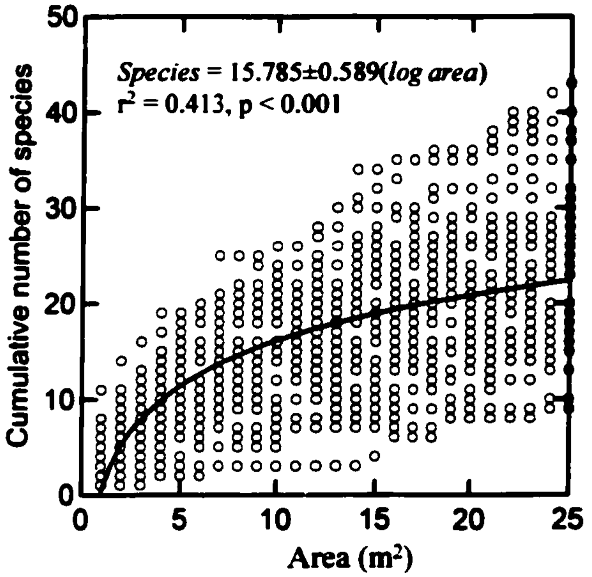


Figure 4.01. Overall herbaceous species - area curve for 1025 1 m subplots in 41 northern hardwood forest sites. The data points show the cumulative number of species at each increase in sampling area.

Selection and measurement of variables

The principal attributes of interest for both the canopy and herbaceous analyses were plant community composition and plant diversity. In addition, in the canopy layers, Bray-Curtis dissimilarity coefficients were calculated for overstory – subcanopy and overstory – sapling comparisons (Legendre and Legendre 1998). In the herbaceous layer, floristic quality was also evaluated using a system developed for the region (Oldham *et al.* 1995), and attempts were made to detect species or groups of species particularly sensitive to cutting.

The independent variables of interest initially included cutting treatment (selection-cut/old-growth), time since cutting, latitude and longitude, elevation, sampling date, bedrock geology, certain soil characteristics, acid deposition, basal area, and volume and variance of coarse woody debris (see Chapter 2). Latitude and longitude were later dropped as independent variables after preliminary analyses showed that their effects in all models were due solely to the influence of the outlying Adirondack Park and Algonquin Park sites (southeast and northwest respectively). Soil variables for both the organic and mineral soil layers were also measured, including organic content, soil pH, soil solution Ca, soil solution Al, soil solution K, and Ca/Al molar ratios in soil solution. During the course of the analyses other measures were calculated and used as independent variables, including stand type (using site scores from a correspondence analysis of the canopy; see below and results), and an index of site wetness (see below).

Canonical correspondence analysis (CCA) was used to assess the relationships between time since cutting (as well as environmental variables) and community composition in both the canopy and herbaceous layers. CCA is designed for the ordination of site-species-environment data, and is appropriate for use on the kind of unimodal relationships which generally characterize plant responses to edaphic factors (McCune 1997; Legendre and Legendre 1998). Species basal areas were used for ordination of the canopy layers, and relative abundance was used for ordination of the herbaceous layer. Relative abundance was calculated as the frequency of occurrence of a species in the 25 herbaceous sample sub-plots.

Canopy composition was also assessed independently of time since cutting and environmental factors. Because CCA is not appropriate for the simple description of community structure (McCune 1997), this ordination was done using correspondence analysis (CA) and cluster analysis, both of which measure the co-occurrence of species across sites (Legendre and Legendre 1998). CA site scores and cluster memberships were subsequently used as independent variables in other canopy and herbaceous layer analyses.

The Bray-Curtis measure of dissimilarity was used to compare the compositions of the different canopy layers. This measure is ideal for use on species – site data matrices, because it is not affected by "double-zeros" – *i.e.* species which are absent from both matrices – and can be used on raw species abundance data (Legendre and Legendre 1998). In this case, species basal areas were converted to species importance values, in order to factor out differences in total basal area between canopy layers. The importance of a species was taken to be its contribution (as a percentage) to the total basal area. Species not normally found in the overstory (*e.g. Ostrya virginiana* and *Acer pensylvanicum*) were excluded from the analyses.

Species richness (α-diversity) was used to assess plant diversity, because it is the measure most sensitive to uncommon or rare species (Legendre and Legendre 1998). Because uncommon species are often those which have specific regeneration requirements or microhabitats (*e.g.* large decaying logs, large gaps, exposed mineral soil), it was felt that they would likely be most sensitive to any homogenizing effects of selection-cutting on stand structure. Although sample species richness may systematically underestimate species richness of the community as a whole (Hellman and Fowler 1999), the magnitude of the bias is constant for fixed sample size (Hellmann and Fowler 1999). Hence, because the number of sub-plots was the same in each stand (*i.e.* 25), among-stand comparisons should be unaffected.

The Floristic Quality Assessment (FQA.) system used in this study was developed for the Southern Ontario Region by the Natural Heritage Information Center of the Ontario Ministry of Natural Resources (Oldham *et al.* 1995). Under this system, each native plant species is assigned a score, a "coefficient of conservation" (C.C.), based upon its fidelity to specific environmental conditions, ranging from 0 (occurs anywhere) to 10 (narrow habitat requirements). The quality of a site's herbaceous community is then calculated as the mean of the C.C. ratings for all species found therein. The FQA also includes a "coefficient of wetness" (C.W.) for each species, ranging from –5 (obligate wetland species) to +5 (obligate upland species). The standard deviation of the CW ratings for all species (CW-SD) was used as an index of the diversity of moisture regimes in each site. Species were not weighted by abundance in order to maintain sensitivity to uncommon species with more extreme microhabitats (*i.e.* C.W. scores near –5 or +5). The standard deviation was used as an index of moisture diversity because it is less sensitive to sample size over the range of species richness encountered in this study (9 to 38 species *per* site) than the variance.

Three methods were used to look for herbaceous species or groups of herbaceous species which might be particularly sensitive to cutting. First, species – environment plots and site – environment plots from the CCA of the herbaceous layer were examined to look for species associations with either time since cutting or old growth sites. Second, a sub-group of "forest species" was derived from the overall species list by selecting only species with a coefficient of conversion ≥ 7, i.e. "…those taxa associated with a plant community in an advanced successional stage that has undergone minor disturbance …" (CC 7 – 8), and "plants with high degrees of fidelity to a narrow range of synecological parameters" (CC 9 – 10) (Oldham *et al.* 1995, p. 7). General linear modeling was then used to look for relationships between the richness of forest species and time since cutting or cutting treatment. Third, a tentative list of "old-growth" species was compiled by examining the species lists for 14 old-growth, northern hardwood forest stands , nine from my study and five from other published studies (Hough 1936; Brewer 1980; Metzger and Schultz 1984; Mladenoff 1990; Host and Pregitzer 1991). Those species appearing in at least 7/14 old-growth sites were tentatively defined as "old-growth" species. The validity of this list was then evaluated using general linear modeling to look for relationships with time-since-cutting or cutting treatment.

Because of its potential relationship with richness and floristic quality, the diversity of weedy species was also measured. "Weeds" were defined as any species with a CC ≤ 3, corresponding to "plants found in a wide variety of plant communities, including disturbed sites…" (Oldham *et al.* 1995, p. 7).

Soil variables were primarily those collected during the analysis of the effects of selection-cutting on Ca/Al ratios in soil solution (ch. 3). Details on soil sampling and analysis can be found in Chapters 2 and 3. Briefly, sixteen soil samples were collected in each stand using a 2.5 cm soil corer, each separated into organic and mineral layers on the basis of color and texture, and then mixed by hand to provide a one composite organic sample and one composite mineral sample for each site. Percent organic content was measured by the incineration method (Nelson and Sommers 1996). Soil pH was measured using the slurry method, with a 1:1 ratio of soil to deionized water (Hendershot *et al.* 1993; Thomas 1996). Soil solution was collected from each sample using the centrifuge method (Soon and Warren 1993), following saturation with deionized water to approximately field capacity. Mineral concentrations were measured using an Inductively Coupled Argon Plasma Atomic Emission Spectrophotometer (ICaP-AES) (instrument: *Thermo Atomscan 25*).

In addition to the soil variables already described, phosphorus levels in soil solution were also measured. These were below detection limits for the IcaP-AES in many sites, and consequently P was not included in the analyses. Nitrogen was not measured, but previous studies have shown total nitrogen to be well-correlated ($r^2 = 0.81$) with organic content in northern hardwood forests (Pregitzer 1981, cited in Pregitzer and Barnes 1982).

Statistical analyses

Statistical analyses were done using Systat 8 (SPSS 1998), Canoco 4.0 (ter Braak 1998) and RT 1.02C (Manly 1994). All p-values for statistical significance were defined as 0.05. Most quantitative variables were log-transformed prior to analysis in order the meet the requirements of normality and homoscedasticity for parametric statistics. CA and CCA models were tested for significance using Canoco's randomization routines, with the data being randomized 999 times under the full models.

For both the canopy and herbaceous layers, general linear modeling was used to determine the best models for predicting species richness. Model fits were evaluated on the basis of residual mean squares (rms), coefficients of variation (r^2), correlations among independent variables (tolerances), p-values for the independent variables and residual plots. The CA and CCA models were evaluated similarly, using Canoco's manual selection option for the selection of independent variables.

Results

Over all sites, 25 species were recorded for the canopy layer (Table 4.01), and 168 species for the herbaceous layer (Table 4.02). The mean richness of the canopy was 7.5 ± 0.43 (1 standard error) species *per* site (Figure 4.02), while the mean richness of the herbaceous layer was 24.8 ± 1.3 species *per* site (Figures 4.03). There was a logarithmic relationship between the cumulative number of herbaceous species recorded and the number of herbaceous subplots (Figure 4.01).

Table 4.1 Canopy Layer Species List

	Abbreviation	Latin name	Common Name	Sites (of 39)
1	fB	*Abies balsamea*	Balsam Fir	15
2	stM	*Acer pensylvanicum*	Striped Maple	22
3	Mh	*Acer saccharum*	Sugar Maple	39
4	yB	*Betula allegheniensis*	Yellow Birch	11
5	wB	*Betula papyrifera*	White Birch	14
6	gB	*Betula populifolia*	Grey Birch	1
7	Cc	*Carpinus caroliniana*	Ironwood	2
8	Hs	*Carya ovata*	Shagbark Hickory	1
9	Be	*Fagus grandifolia*	American Beech	32
10	aF	*Fraxinus americana*	White Ash	24
11	Jc	*Juglans cinerea*	Butternut	1
12	Iw	*Ostrya virginiana*	Hop Hornbeam	37
13	Sw	*Picea glauca*	White Spruce	6
14	Sr	*Picea rubens*	Red Spruce	2
15	Pw	*Pinus strobus*	White Pine	6
16	dP	*Populus deltoides*	Eastern Cottonwood	2
17	Pg	*Populus grandidenta*	Largetooth Aspen	5
18	tP	*Populus tremuloides*	Trembling Aspen	2
19	Ps	*Prunus serotina*	Black Cherry	6
20	Ow	*Quercus alba*	White Oak	1
21	Or	*Quercus rubra*	Red Oak	16
22	Ce	*Thuja occidentalis*	Eastern White-Cedar	3
23	Ta	*Tilia americana*	Basswood	29
24	He	*Tsuga canadensis*	Eastern Hemlock	7
25	U	*Ulmus sp.*	Elm	3

Table 4.02 Herbaceous Layer Species List

	Species	Sites (of 42)		Species	Sites (of 42)
1	*Abies balsamea*	17	42	*Carpinus caroliniana*	1
2	*Acer pensylvanicum*	27	43	*Caulophyllum thalictroides*	5
3	*Acer rubrum*	2	44	*Chimaphila umbellata*	2
4	*Acer saccharum*	42	45	*Cinna latifolia*	7
5	*Acer spicatum*	6	46	*Circea alpina*	2
6	*Acorus calumus*	1	47	*Circea lutetiana*	2
7	*Actea rubra*	1	48	*Cirsium arvense*	1
8	*Adiantum pedatum*	1	49	*Clinopodium vulgare*	1
9	*Allium tricoccum*	1	50	*Clintonia borealis*	2
10	*Alnus incana*	1	51	*Coptis trifolia*	1
11	*Alnus sp.*	2	52	*Corallorhiza maculata*	1
12	*Amelanchier arborea*	1	53	*Corylus cornuta*	4
13	*Amelanchier sanguinea*	1	54	*Cypripedium calceolus*	1
14	*Amelanchier sp.*	1	55	*Cystoperis bulbifera*	1
15	*Anaphalis margaritacea*	1	56	*Danthonia spicata*	2
16	*Aquilegia canadensis*	1	57	*Deschampsia flexuosa*	2
17	*Aralia nudicaulis*	30	58	*Diervilla lonicera*	2
18	*Aralia racemosa*	2	59	*Dirca palustris*	12
19	*Arisaema triphyllum*	9	60	*Dryopteris carthusiana*	26
20	*Asclepias sp.*	1	61	*Dryopteris marginalis*	15
21	*Aster cordifolius*	7	62	*Epifagus virginiana*	1
22	*Aster lanceolatus*	1	63	*Epipactus heleborine*	24
23	*Aster macrophyllus*	15	64	*Equisetum scirpoides*	3
24	*Aster sp.*	2	65	*Erythronium americanum*	1
25	*Athyrium felix-femina*	6	66	*Eupatorium perfoliatum*	1
26	*Athyrium theliptroides*	1	67	*Fagus grandifolia*	22
27	*Betula alleghaniensis*	3	68	*Fragraria vesca*	4
28	*Betula papyrifera*	1	69	*Fragraria virginiana*	2
29	*Botrychium virginianum*	6	70	*Fraxinus americana*	26
30	*Brachyelytrum erectum*	12	71	*Galium palustre*	1
31	*Bromus ciliatus*	1	72	*Galium triflorum*	18
32	*Calamagrostis canadensis*	1	73	*Geranium robertianum*	3
33	*Carex arctata*	18	74	*Glyceria striata*	1
34	*Carex communis*	11	75	*Gymnocarpium dryopteris*	6
35	*Carex deflexa*	4	76	*Hepatica americana*	2
36	*Carex deweyana*	6	77	*Hieracium aurantiacum*	1
37	*Carex gracillima*	2	78	*Impatiens capensis*	1
38	*Carex houghtoniana*	1	79	*Laportea canadensis*	2
39	*Carex intumescens*	3	80	*Lonicera canadensis*	20
40	*Carex lucorum*	20	81	*Lonicera hirsuta*	1
41	*Carex sp.*	4	82	*Lonicera sp.*	1

	Species	Sites (of 42)		Species	Sites (of 42)
83	*Lycopodium dendroideum*	9	126	*Medeola virginiana*	3
84	*Lycopodium digitatum*	1	127	*Milium effusum*	4
85	*Lycopodium lucidulum*	7	128	*Mitchella repens*	7
86	*Lycopus americanus*	1	129	*Mitella diphylla*	6
87	*Maianthemum canadense*	32	130	*Mitella nuda*	5
88	*Maianthemum racemosum*	7	131	*Monotropa uniflora*	4
89	*Matteuccia struthiopteris*	1	132	*Oryzopsis asperifolia*	19
90	*Osmorhiza claytonii*	11	133	*Sambucus racemosa*	8
91	*Ostrya virginiana*	33	134	*Schizacne purpurascens*	3
92	*Oxalis acetosella*	4	135	*Scutelaria lateriflora*	2
93	*Oxalis stricta*	1	136	*Solidago canadensis*	8
94	*Panax cinquefolia*	1	137	*Solidago hispida*	1
95	*Parthenocissus inserta*	3	138	*Solidago rugosa*	2
96	*Phegopteris connectilis*	1	139	*Solidago sp.*	4
97	*Picea glauca*	1	140	*Sonchus asperifolia*	1
98	*Picea rubens*	2	141	*Streptopus amplexifolius*	1
99	*Pinus strobus*	3	142	*Streptopus roseus*	20
100	*Plantago major*	1	143	*Taraxacum officinale*	2
101	*Plantago rugellii*	1	144	*Taxus canadensis*	2
102	*Poa saltuensis*	4	145	*Thalactrim dioicum*	1
103	*Polygonatum pubescens*	24	146	*Thalactrim pubescens*	2
104	*Polygonum cilinode*	7	147	*Thelypteris noveboracensis*	2
105	*Polypodium virginianum*	3	148	*Thuja occidentalis*	2
106	*Populus deltoides*	1	149	*Tiarella cordifolia*	2
107	*Populus grandidentata*	4	150	*Tilia americana*	17
108	*Prenanthes sp.*	1	151	*Trientalis borealis*	15
109	*Prunus pensylvanica*	1	152	*Trifolium hybridum*	1
110	*Prunus serotina*	8	153	*Trifolium sp.*	1
111	*Prunus virginiana*	4	154	*Trillium sp.*	34
112	*Pteridium aquilinium*	1	155	*Tsuga canadense*	3
113	*Pyrola americana*	10	156	*Uvularia grandiflora*	22
114	*Quercus rubra*	20	157	*Verbascum thapsus*	1
115	*Rhamnus alnifolia*	1	158	*Viburnum acerifolium*	7
116	*Rhus radicans ssp. negundo*	1	159	*Viburnum cassinoides*	1
117	*Ribes cynosbati*	14	160	*Viburnum lantanoides*	6
118	*Ribes glandulosum*	2	161	*Viola adunca*	2
119	*Ribes triste*	1	162	*Viola canadensis*	2
120	*Rubus allegheniensis*	4	163	*Viola mackloskeyii*	1
121	*Rubus canadensis*	1	164	*Viola pubescens*	3
122	*Rubus idaeus*	18	165	*Viola septentrionalis*	1
123	*Rubus odoratus*	4	166	*Viola sororia*	2
124	*Rubus pubescens*	3	167	*Viola sp.*	24
125	*Sambucus canadensis*	2	168	*Waldsteinia fragarioides*	1

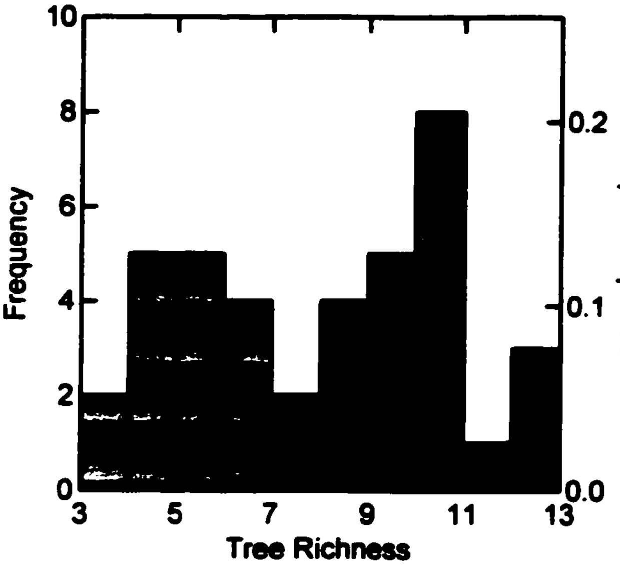


Figure 4.02. Histogram of canopy richness

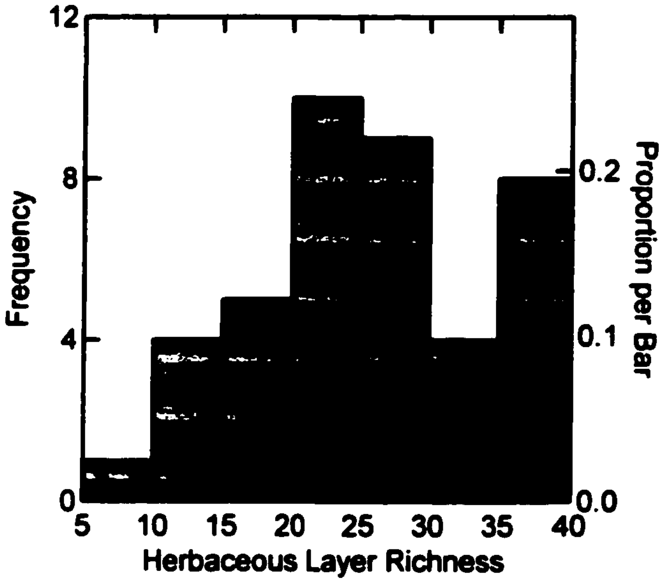


Figure 4.03. Histogram of herbaceous layer richness

CANOPY LAYERS

Composition

The first three CCA axes explained 29.5% of the variation in species data (Table 4.03). The CCA model was statistically significant ($p = 0.001$) and included three statistically significant variables: cutting treatment (old growth/selection-cut, $p = 0.002$), basal area ($p = 0.008$) and soil organic layer pH ($p = 0.003$).

The effect of cutting treatment on canopy composition was due primarily to the effect of hemlock-dominated sites, which made up four of the eight old growth sites and dominated axis 1 (Figure 4.04a). When the hemlock-dominated old-growth sites were excluded from the analysis, the species-environment correlations and the proportion of variance explained by axes 1 and 2 dropped substantially (Table 4.04), as did the significance of the model ($p = 0.010$) and the effects of all three independent variables: cutting treatment ($p = 0.044$), basal area ($p = 0.027$) and soil organic layer pH (n.s., excluded from model). With the hemlock-dominated old-growth sites excluded, the effect of cutting treatment was mostly due to the effects of a small number of outlying selection cut sites, with the remaining old growth sites being clustered with a number of similar selection-cut sites around the "old growth" centroid (Figure 4.04b). Both analyses suggest a gradient of sites from maple-dominated to oak-dominated canopies (Figures 4.04a,b). *Populus deltoides* and *P. grandidentata* appeared as outliers in both plots.

Correspondence analysis (CA) confirmed the patterns suggested by the CCA . showing orthogonal gradients from maple-dominated sites to oak-dominated and

Table 4.3 Eigenvalues and explained variance for the three axes of a canonical correspondence analysis of the canopy composition data.

	1	2	3
Eigenvalues	.341	.172	.080
Species – environment correlations	.741	.656	.655
Cumulative percentage variance of species data	17.0	25.5	29.5
Cumulative percentage variance of species-environment relation	57.6	86.5	100

Table 4.4 Eigenvalues and explained variance for the two axes of a canonical correspondence analysis of the canopy composition data, excluding hemlock sites.

	1	2
Eigenvalues	.186	.074
Species – environment correlations	.691	.519
Cumulative percentage variance of species data	13.3	18.6
Cumulative percentage variance of species-environment relation	71.7	100

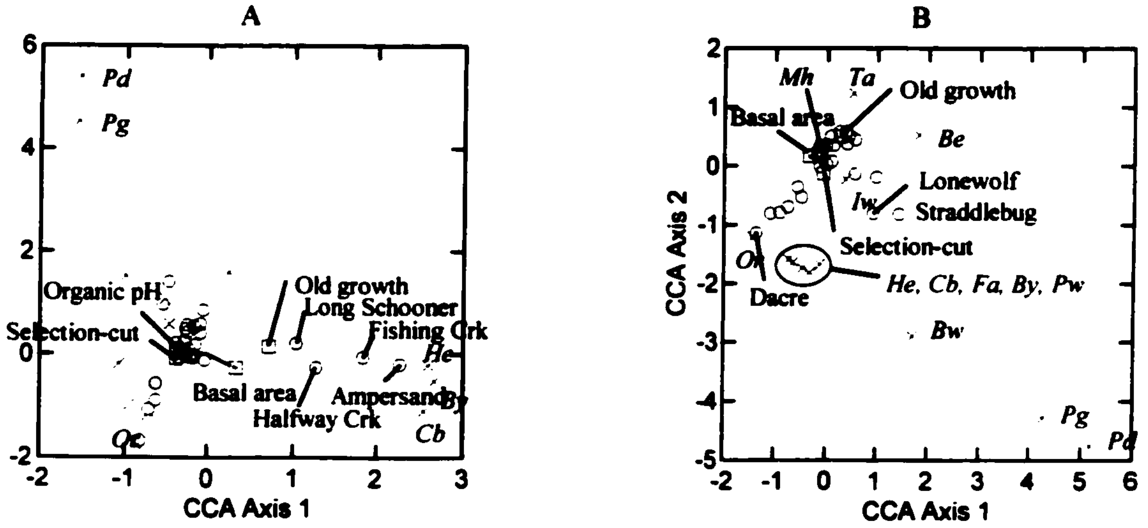


Figure 4.04. Ordination of the first two axes of two canonical correspondence analyses of environmental factors (☐) sample sites (o) and canopy species (x), scaled for sites, with a confidence kernels for site densities of 0.683 (1 standard deviation). (A) With hemlock stands. (B) Without hemlock stands.

hemlock dominated sites (Figure 4.05; Tables 4.05, 4.06). Complete linkage clustering generated four recognizable groups: (1) sugar maple-dominant; (2) hemlock-dominant; (3) oak-dominant; (3) maple co-dominant (Figure 4.06). In the CA the maple-dominant group occupies a central position at the intersection of the two species-site gradients. The hemlock-dominant group is positioned in the upper right corner of the plot, while the oak-dominant group occupies the center left (Figure 4.05). The maple co-dominant group is not distinguishable in the plot of CA axes 1 and 2, but corresponds well with axis 3.

Regeneration

Overall canopy regeneration is strongly correlated with patterns of canopy composition. CA axes 1 and 2 predict 69% of the variation in canopy – subcanopy distance, while CA axes 1, 2 and 3 predict 85% of the variation in canopy – sapling distance.

The best model for predicting the Bray-Curtis dissimilarity between the canopy and subcanopy layers was:

Eq. 4.1

$$Distance = -0.08 \pm 0.029(CA\ Axis\ 1) + 0.27 \pm 0.032(CA\ Axis\ 2) + 0.408 \pm 0.002$$

Both *CA Axis 1* and *CA Axis 2* were statistically significant (partial $r^2 = 0.05$, $p = 0.01$; partial $r^2 = .59$, $p < 0.001$ respectively) with the model explaining almost 69% of

Table 4.5 Eigenvalues and explained variance for the first four axes of a correspondence analysis of the canopy composition data.

Axis	**1**	**2**	**3**	**4**	**Total**
Eigenvalue	.656	.525	.246	.144	1.977
Cumulative percent variance of species data	33.2	59.8	72.2	79.5	

Table 4.6 Fit *per* species as a fraction of species variance for the first three axes of a correspondence analysis of the canopy composition data (*bold italics indicate large fit*).

	Axis 1	**Axis 2**	**Axis 3**
Beech (Be)	0.0353	0.0699	***0.5679***
Yellow Birch (By)	***0.3895***	***0.2306***	0.0134
White Birch (Bw)	0.0046	0.0063	***0.6176***
Black Cherry (Cb)	0.0786	0.0093	0.0511
White Ash (Fa)	0.04	0.0178	0.0022
Hemlock (He)	***0.5955***	***0.3907***	0.0002
Hop-Hornbeam (Iw)	0.0142	0.0082	0.0075
Sugar Maple (Mh)	0.0768	***0.691***	0.1751
Red Oak (Or)	***0.6085***	***0.3736***	0.0057
Balsam Poplar (Pd)	0.0004	0.0174	***0.467***
Bigtoothed Aspen (Pg)	0.0575	0.0083	***0.3117***
White Pine (Pw)	0.0065	0.0007	0.1394

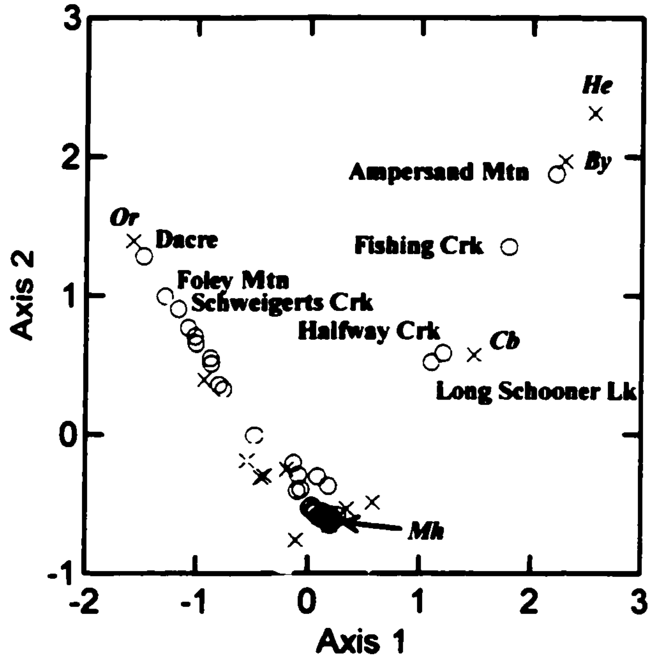


Figure 4.05. Ordination of the first two axes of a correspondence analysis of sample sites (o) and canopy species (x), scaled for sites, with a confidence kernel for site density of 0.683 (1 standard deviation).

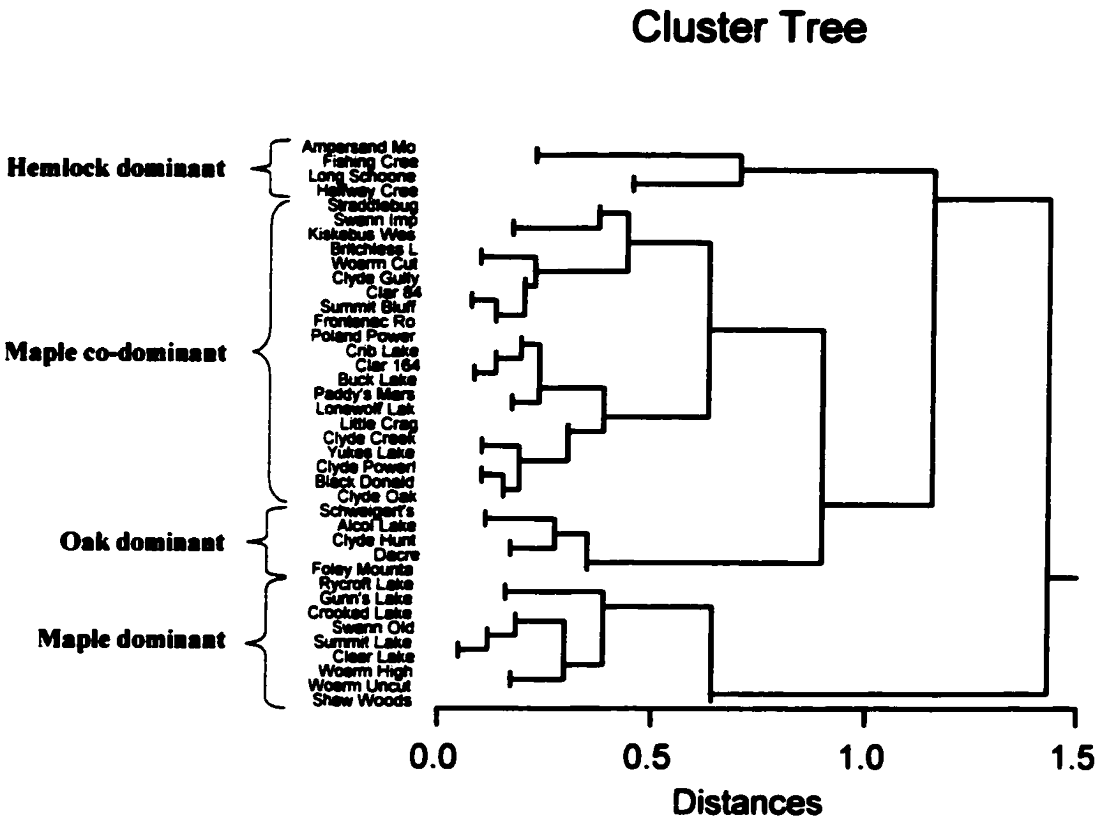


Figure 4.06. Complete linkage hierarchical clustering of sample sites on the basis of canopy composition, showing major clusters.

the variation in canopy-sapling distance ($F_{model} = 42.80$, df = 2, $p < 0.001$). Neither cutting treatment ($p = 0.83$), time-since-cutting ($p = 0.97$) nor canopy tree richness ($p = 0.99$) had an effect on canopy – subcanopy distance.

The best model for predicting the Bray-Curtis dissimilarity between the canopy and sapling layers was:

Eq. 4.2

$$\begin{aligned} \mathit{Distance} = & -0.055 \pm 0.023(\mathit{CA\ axis\ 1}) + 0.330 \pm 0.025(\mathit{CA\ axis\ 2}) + \\ & 0.143 \pm 0.034(\mathit{CA\ axis\ 3}) + 0.432 \pm 0.017 \end{aligned}$$

CA Axis 1, *CA Axis 2* and *CA Axis 3* were all statistically significant (partial $r^2 = 0.02$, $p = 0.020$; partial $r^2 = 0.75$, $p < 0.001$; partial $r^2 = 0.07$, $p < 0.001$ respectively) with the model explaining 84% of the variation in canopy-sapling distance ($F_{model} = 71.63$, df = 3, $p < 0.001$). One hemlock-dominated site had high leverage and another old-growth site appeared as an outlier, but did not significantly effect the model. Neither time-since-cutting ($p = 0.50$) nor canopy tree richness ($p = 0.44$) had an effect on canopy – subcanopy distance. The effect of cutting treatment approached statistical significance ($p = 0.077$), but only because of the outlier.

Figures 4.07 to 4.12 show the differences in composition between overstory, subcanopy and sapling layers for each of the four stand types (maple dominant, maple co-dominant, oak dominant, hemlock dominant) identified in the cluster analysis. In maple-dominant stands, there was little difference in composition between canopy layers (Figure 4.07; two-way non-parametric ANOVA: $H_{species} = 78.23$, df = 2, $p = < 0.0001$; $H_{layer*species} = 0.76$, df = 4, $p < 0.66$). In maple co-dominant stands, Sugar Maple increased in the subcanopy and sapling layers, but the increases were statistically non-significant (Figure 4.08; two-way non-parametric ANOVA: $H_{species} = 82.53$, df = 3, p = < 0.0001; $H_{layer \bullet species} = 1.85$, df = 6, p < 0.09). Oak dominated stands showed the most dramatic effects (Figure 4.09), with the importance of red oak dropping from more than 70% in the overstory to less than 10% in the subcanopy and less than 5% in the sapling layer. Sugar maple showed a corresponding increase importance, rising from about 15% in the overstory, to nearly 70% in the subcanopy and sapling layers (Figure 4.09; two-way non-parametric ANOVA: $H_{species} = 12.06$, df = 2, p = < 0.001; $H_{layer \bullet species} = 19.82$, df = 4, p < 0.001).

Hemlock stands differed in that regeneration in 3 of the 4 stands was predominantly Beech. When all four stands are considered, there are no statistically significant changes in composition between canopy layers (Figure 4.10; two-way non-parametric ANOVA: $H_{species} = 3.35$, df = 3, p = < 0.030; $H_{layer \bullet species} = 2.11$, df = 6, p < 0.076) due to the influence of the only non-Adirondack Hemlock stand (Long Schooner Lake) which had a large Hemlock presence in its subcanopy (Figure 4.12). Within the three Adirondack Hemlock stands, however, there was a significant decline in the importance of Hemlock down through the canopy, and a corresponding increase in the importance of Beech (Figure 4.11; two-way non-parametric ANOVA: $H_{species} = 4.19$, df = 3, p = < 0.016; $H_{layer \bullet species} = 5.15$, df = 6, p < 0.002).

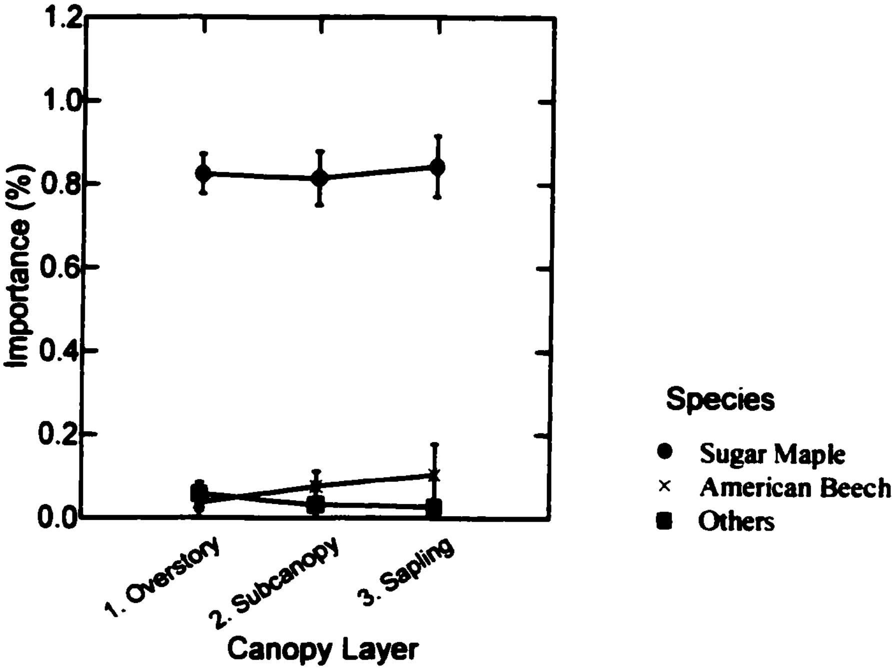


Figure 4.07. Importance values of major tree species by canopy layer in the Maple dominant sites (* indicates statistically significant difference between layers).

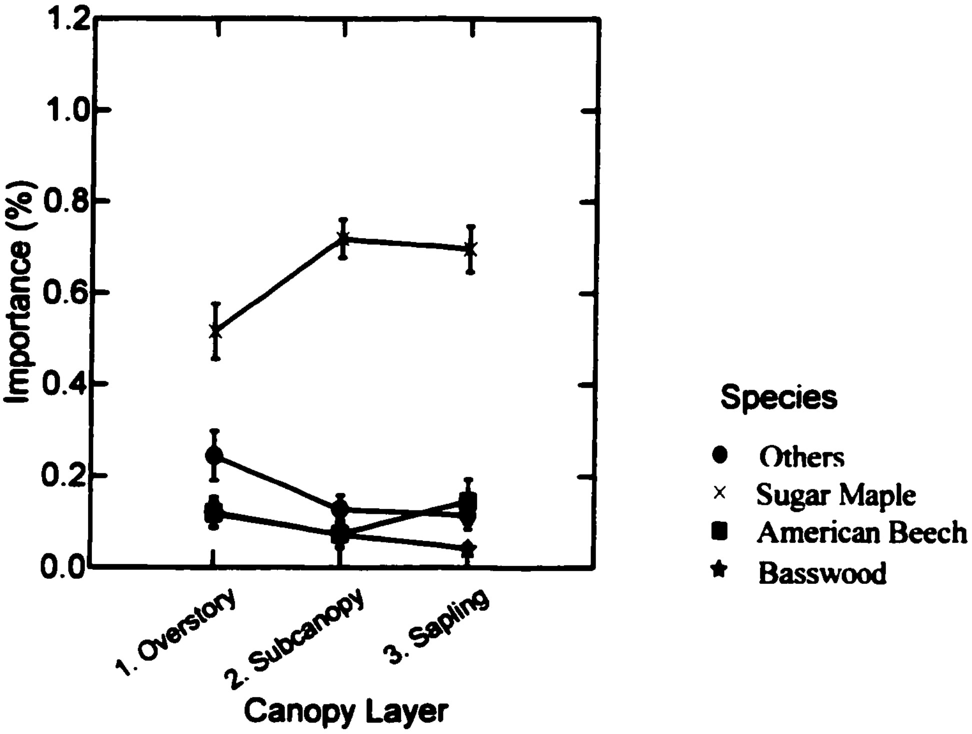


Figure 4.08. Importance values of major tree species by canopy layer in the Maple co-dominant sites (* indicates statistically significant difference between layers).

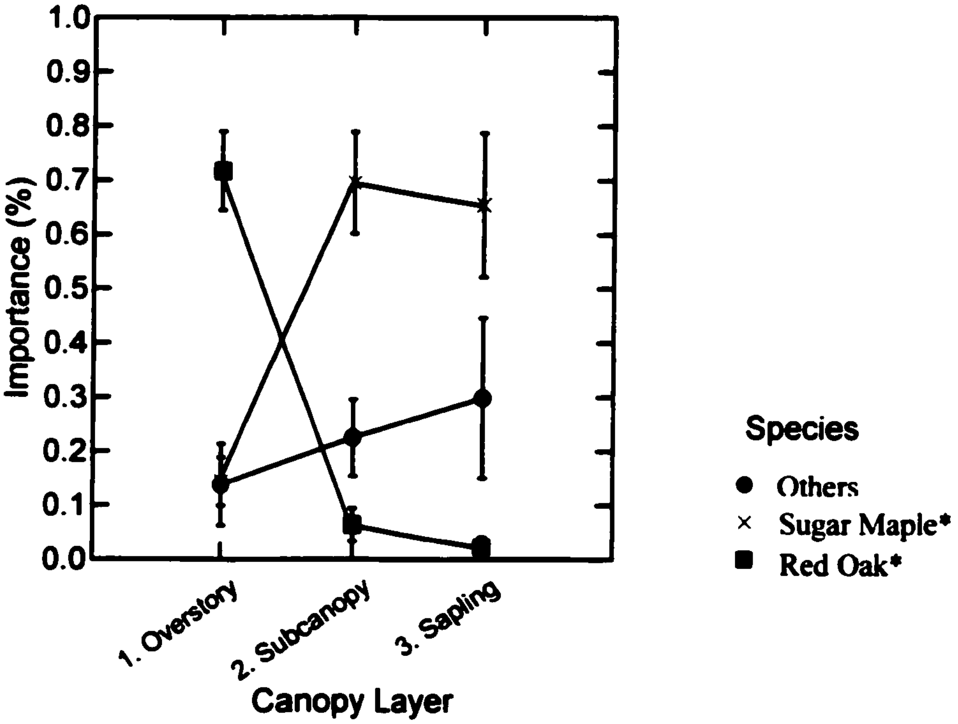


Figure 4.09. Importance values of major tree species by canopy layer in the Oak dominant sites (* indicates statistically significant difference between layers).

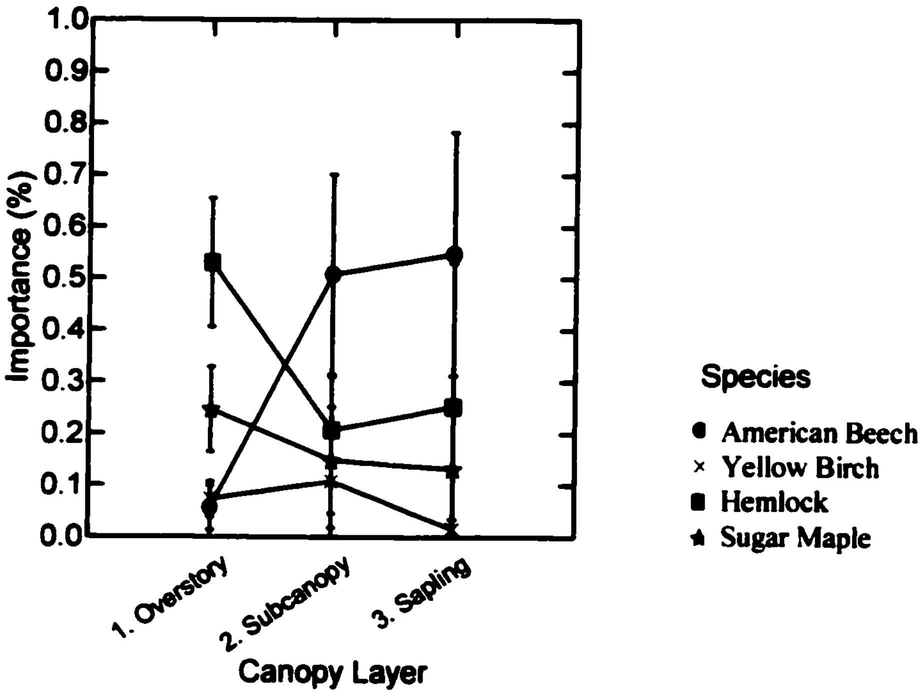


Figure 4.10. Importance values of major tree species by canopy layer in the Hemlock dominant sites (* indicates statistically significant difference between layers).

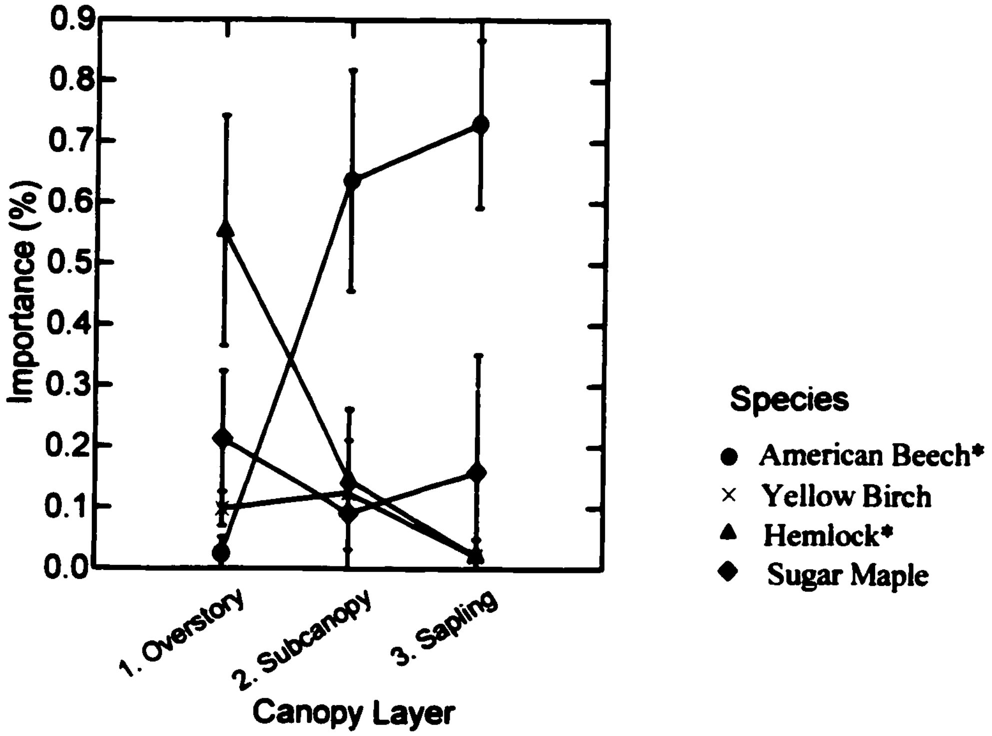


Figure 4.11. Importance values of major tree species by canopy layer in the Adirondack, hemlock dominant sites (* indicates statistically significant difference between layers).

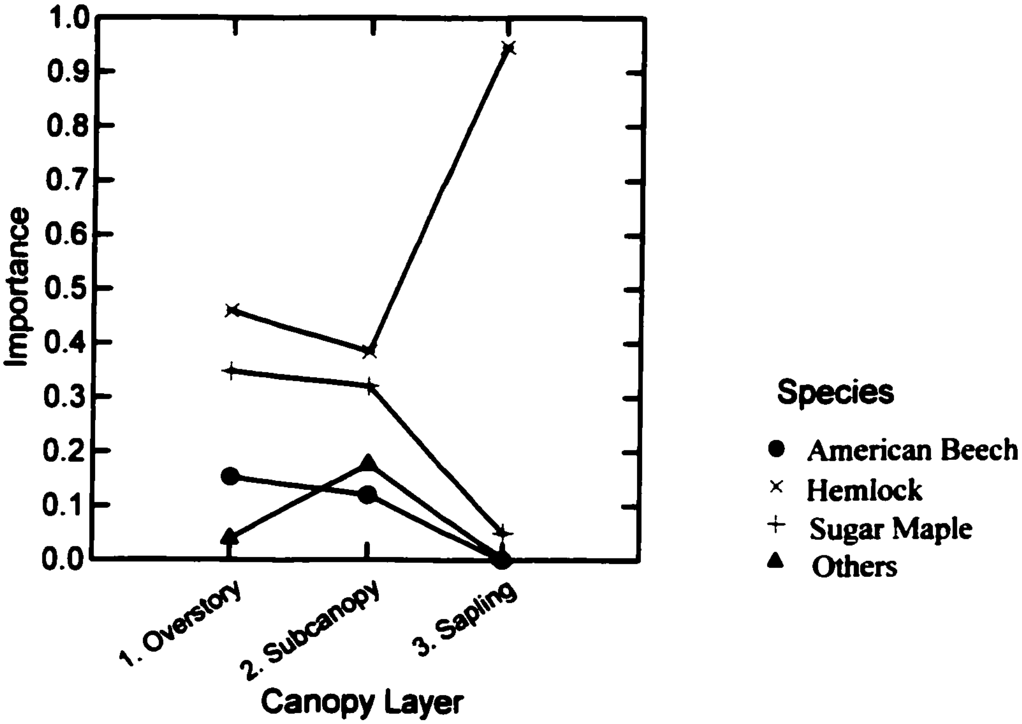


Figure 4.12. Importance values of major tree species by canopy layer in the Long Schooner, hemlock dominant site.

Richness

Canopy richness was best predicted by canopy CA axes 2 and 3, the standard deviation of the Coefficient of Wetness (CW-SD), and cutting treatment (*age_cat: old* = 0, *selection* = 1).

Eq. 4.3.

$$\begin{aligned}\textit{Tree richness} &= 1.35 \pm 0.38(\textit{Log CA axis 2}) + 1.84 \pm 0.63(\textit{CA axis 3}) + \\ &\quad 1.70 \pm 0.51(\textit{CW - SD}) + 1.77 \pm 0.797(\textit{cutting treatment}) + 3.88 \pm 0.41\end{aligned}$$

Log CA Axis 2, *CA Axis 3*, *CW-SD* and *cutting treatment* were all statistically significant (partial $r^2 = 0.21$, $p = 0.002$; partial $r^2 = 0.14$, $p = 0.008$; partial $r^2 = 0.10$, $p = 0.043$; partial $r^2 = 0.08$, $p = 0.040$ respectively) with the model explaining 57% of the variation in tree richness ($F_{model} = 8.33$, df = 4, $p < 0.001$). On average, selection-cut sites had 1.77 more tree species than old-growth sites. When the Adirondack stands were excluded, the p-value for *cutting treatment* increased slightly to 0.060, although the difference of means increased to 2.284 species.

HERBACEOUS LAYER

Composition

Analysis of the herbaceous layer vegetation began with canonical correspondence analysis. The ordination was limited to those species with at least three occurrences.

because species with single and double occurrences always appear as outliers in a CCA, and provide little information. Sugar maple seedlings were also excluded from the ordination because they are ubiquitous and abundant.

The first four axes of the CCA explained 27.3% of the variation in species data (Table 4.07). The CCA model was statistically significant ($p = 0.001$) and included four statistically significant variables: CA axis 2 ($p = 0.001$), the coefficient of wetness ($p = 0.001$), bedrock geology (calcareous/siliceous, $p = 0.035$) and age ($p = 0.052$). A scatterplot of axes 1 and 2 shows a large cluster of herbaceous species near the center of the plot, with outlying species oriented along two gradients: *Fragraria vesca* and *Carex communis* are associated with drier, oak-dominated sites; *Betula alleghenicnsis*, *Rubus pubescens*, *Picea sp.*, *Viburnum lantanoides*, *Mitella nuda* and *Oxalis acetosella* are associated with older, moister, hemlock-dominated sites (Figure 4.13a).

The association of *B. alleghenicnsis*, *R. pubescens*, *Picea*, V. *lantanoides*, *M. nuda* and *O. acetosella* with time since cutting initially suggested that this group of species might be particularly sensitive to cutting. However, the old-growth sites most closely associated with this group are the hemlock sites of Adirondack Park (Figure 4.13b). A second CCA, without the Adirondack sites, explained 24.3% of the species variance (Table 4.08). The CCA model was statistically significant ($p = 0.001$) and included four statistically significant variables: CA axis 2 ($p = 0.001$), organic content of the organic layer ($p = 0.008$), CA axis 1 ($p = 0.018$), and CA axis 3 ($p = 0.055$). Without the Adirondack sites, the frequency of several species fell below 3, but these were retained in the analysis, so that any shifts in their associations could be seen.

CCAs with and without the Adirondack hemlock-dominated sites both produced a central cluster of species, and both show *F. vesca* and *C. communis* associated with oak

Table 4.7 Eigenvalues and explained variance for the four axes of a canonical correspondence analysis of the herbaceous composition data.

	1	2	3	4
Eigenvalues	.433	.191	.097	.073
Species – environment correlations	.945	.829	.832	.708
Cumulative percentage variance of species data	14.9	21.4	24.8	27.3
Cumulative percentage variance of species-environment relation	54.6	78.7	90.8	100

Table 4.08 Eigenvalues and explained variance for the four axes of a canonical correspondence analysis of the herbaceous composition data, excluding Adirondack sites.

	1	2	3	4
Eigenvalues	.266	.183	.134	.074
Species – environment correlations	.874	.896	.846	.723
Cumulative percentage variance of species data	9.8	16.6	21.5	24.3
Cumulative percentage variance of species-environment relation	40.5	68.3	88.7	100

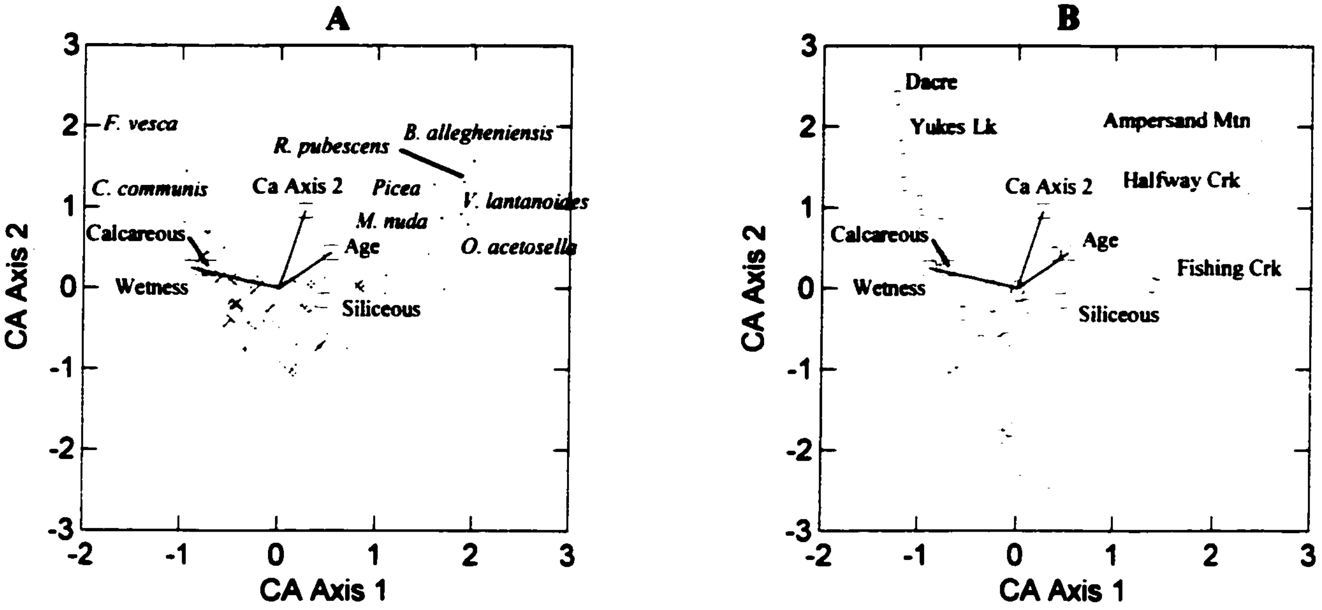


Figure 4.13. Biplots of the first two axes of a CCA ordination of herbaceous species (x), sample sites (o) and environmental factors (□), scaled for herbaceous species, with a confidence kernel of 0.68 (1 S.D.) around regions of high species density.

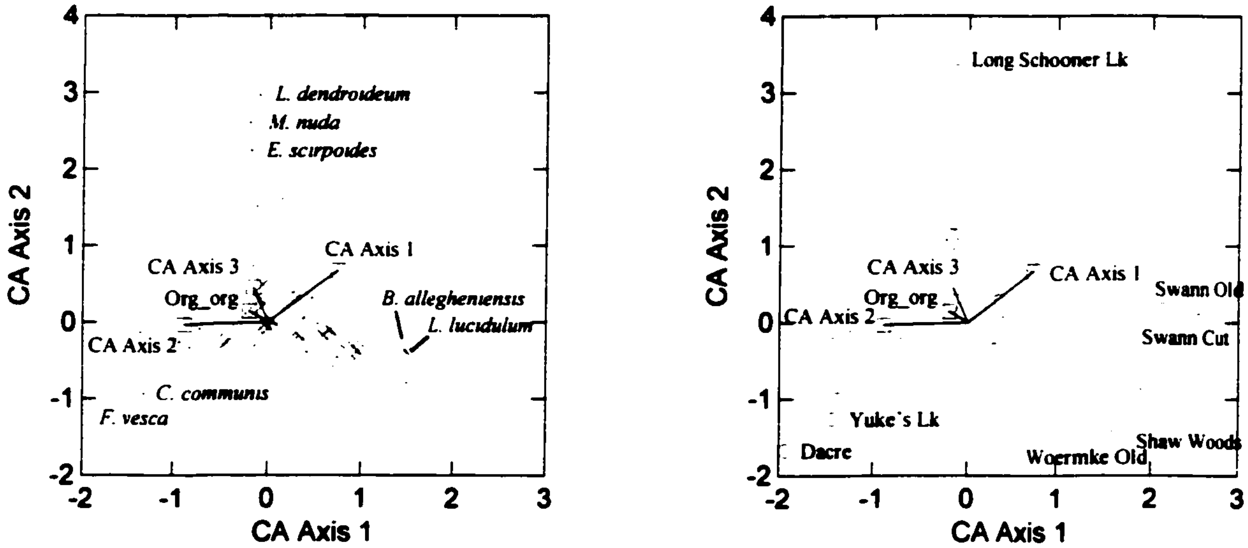


Figure 4.14. Biplots of the first two axes of a CCA ordination of herbaceous species (x), sample sites (o) and environmental factors (□), excluding Adirondack sites, scaled for herbaceous species, with a confidence kernel of 0.68 (1 S.D.) around regions of high species density.

dominated sites (Figs. 4.13, 4.14). However, of the six species associated with the time since cutting in the first ordination. only *B. allegheniensis* and *M. nuda* appear again as outliers in the second ordination, with the latter appearing strongly associated with the sole, remaining old-growth hemlock site (Long Schooner).

Richness

Herbaceous layer richness (*richness*) was best predicted by canopy CA axis 2 (*Log Ca axis 2*), calcium concentrations in the soil solution of the mineral layer (*Log Ca min*) and the standard deviation of the Coefficient of Wetness (*CW-SD*):

Eq. 4.4.

$$\begin{aligned} \textit{Log richness} &= 0.112 \pm 0.025(\textit{log axis 2}) + 0.242 \pm 0.059(\textit{log Ca min}) + \\ &\quad 0.197 \pm 0.053(\textit{CW - SD}) + 0.420 \pm 0.182 \end{aligned}$$

Log CA axis 2, log Ca min, and *CW-SD* were all statistically significant (partial $r^2 = 0.42$, $p < 0.001$; partial $r^2 = 0.25$, $p < 0.001$; partial $r^2 = 0.21$, $p = 0.001$ respectively) with the model explaining 58% of the variation in herbaceous richness ($F_{model} = 14.155$, df = 3, $p < 0.001$). While there were no overall effects of cutting treatment ($p = 0.45$) or time since cutting ($p = 0.77$), a plot of model residuals against time since cutting (Fig. 4.15) suggests a pattern of initial decline over the first approximately 23 years (Fig. 4.16), followed by a relatively rapid resurgence in richness and a second period of decline in old-growth stands . Much of the increase in richness immediately

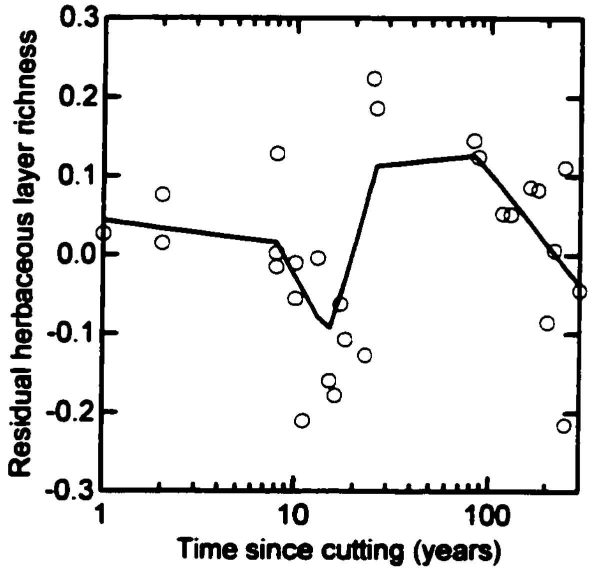


Figure 4.15. The relationship between time since cutting and the residuals of the general linear model predicting total herbaceous layer richness, with LOWESS smoothing

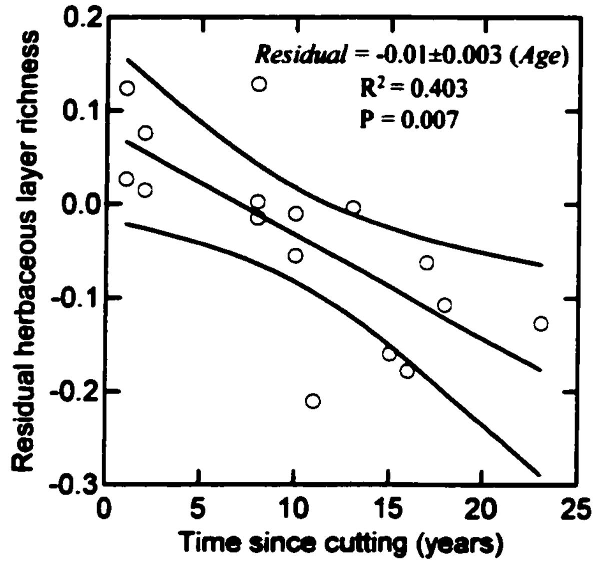


Figure 4.16. The relationship between time since cutting and the residuals of the general linear model predicting total herbaceous species richness in sites less than 23 years old, showing 95% confidence intervals for the slope of the regression line..

after 23 years is due to two sites situated close together on calcareous bedrock, although bedrock type was not statistically significant in the overall model. Removal of the hemlock sites had no effect on the appearance of the LOWESS plot, apart from the reducing the number of old-growth sites.

When the herbaceous layer analysis was limited to forest species (*i.e.* $CC \geq 7$) the best model for predicting richness was a simple linear regression on overall herbaceous richness.

Eq. 4.5.

$$\textit{Forest species richness} = 0.182 \pm 0.039(\textit{richness})$$

The regression was statistically significant ($F_{model} = 21.94$, df = 1, $p < 0.001$), explaining 34% of the variation in forest species richness. There was no statistically-significant effect of time since cutting ($p = 0.484$), but there initially appeared to be a marginally significant effect of cutting treatment ($p = 0.029$). The residuals for that model were heteroscedastic, however, and closer examination suggested that the statistical effect of cutting treatment was due to greater variance in the old growth treatment. Therefore a two sample t-test was conducted to look for an effect of cutting treatment on the residuals from the model in Eq. 4.5, using the p-value for samples with separate variances. The difference was non-significant ($p = 0.132$).

Examination of species lists for 14 old-growth, northern hardwood sites (nine from this study, and five from the literature) revealed 7 putative "old-growth species" – defined here as a species or a genus occurring in at least 7 of the sites (Table 4.09). The best model for predicting the richness of old-growth species included herbaceous richness and cutting treatment (Eq. 4.6).

Table 4.9. "Old-growth species" appearing in at least 7/14 old-growth, northern hardwood forest sites.

"Old-growth species"
Aralia nudicaulis
Dryopteris carthusiana
Lycopodium lucidulum
Maianthemum canadense
Polygonatum pubescens
Trillium sp.
Viola sp.

Eq. 4.6.

$$\textit{Old-growth herb richness} = 0.075 \pm 0.02(\textit{richness}) - 1.154 \pm 0.20(\textit{cutting treatment}) + 2.73$$

Richness and *cutting treatment* were both statistically significant (partial $r^2 = 0.28$, $p = 0.001$; partial $r^2 = 0.16$, $p = 0.007$ respectively) with the model explaining 36%% of the variation in old-growth herb richness ($F_{model} = 9.1$, $df = 2$, $p = 0.001$). On average, old-growth stands had approximately 1 more old-growth species than the selection-cut stands (Figure 4.17). Examination of the original site – species data matrix, as well as the earlier CCA, showed that the difference in richness could not be attributed to any one of the seven species.

When the herbaceous layer analysis was limited to weedy species (*i.e.* CC ≤ 3) the best model for predicting richness was a multiple linear regression on overall herbaceous richness (*richness*) and time since cutting (*Log_age*) (Figure 4.18).

Eq. 4.7.

$$\textit{Weed richness} = 0.066 \pm 0.022(\textit{richness}) - 0.821 \pm 0.252(\textit{time since cutting})$$

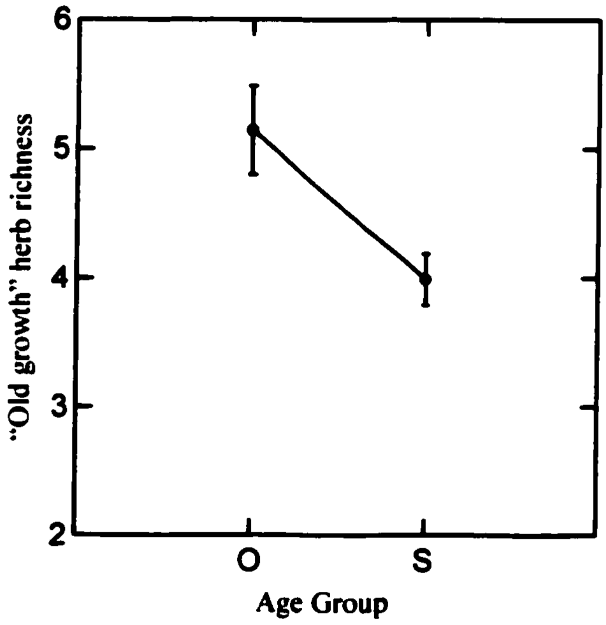


Figure 4.17 "Old growth" herb richness is significantly lower in the selection cut sites (S) than in the old growth sites (O).

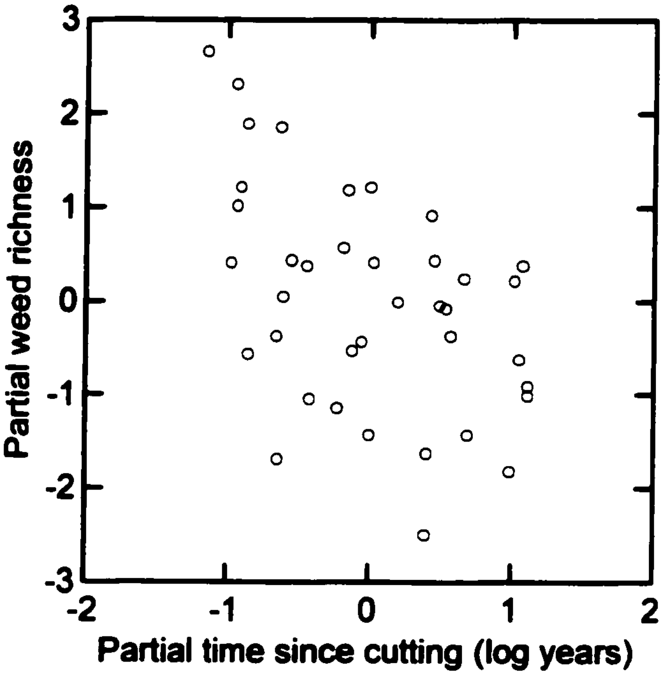


Figure 4.18. Full partial plot showing the decline in weedy species richness with time since cutting.

For this model, residuals were normal, but heteroscedastic. As no suitable transformation was found to reduce heteroscedasticity, randomization was used to test the model for statistical significance, using the RT 1.02c program for randomization (Manly 1994). The *y*-variables (*Weed richness*) were randomized 999 times. Both *richness* and *time since cutting* were statistically significant (partial $R^2 = 0.12$, $p = 0.001$; partial $R^2 = 0.18$, $p = 0.011$ respectively), as was the overall regression ($N = 38$; $p = 0.001$; adjusted $r^2 =$ 0..456). One outlier, Straddlebug Lake, was excluded from analysis. It had the highest number of weedy species of any site, was sampled immediately after cutting, and included part of a tree landing.

The best model for predicting the quality of a site's herbaceous community (*CC_mean*) included *CA axes 1* and *2*, residual stand basal area (*log_basal*) and an interaction between acid deposition and bedrock geology (*deposition*bedrock: low* = 0, *high* = 1; *siliceous* = 0, *calcareous* = 1).

Eq. 4.8

$$\begin{aligned} \textit{Herbaceous quality} = {} & 0.183 \pm 0.067(\textit{CA axis 1}) + 0.186 \pm 0.048(\textit{log axis 2}) + \\ & 1.23 \pm 0.451(\textit{log basal}) + 0.135 \pm 0.049(\textit{deposition x bedrock}) \end{aligned}$$

CA Axis 1, *log_axis 2*, *log_basal* and *dep_hi_low*geo_typeb* were all statistically significant (partial $r^2 = 0.12$, $p = 0.012$; partial $r^2 = 0.23$, $p = 0.001$; partial $r^2 = 0.17$, $p = 0.012$; partial $r^2 = 0.12$, $p = 0.011$ respectively) with the model explaining 64% of the variation in herbaceous community quality ($F_{model} = 6.7$, df = 4, $p = 0.001$). The model does not include one outlier, Fishing Creek, which had lower herbaceous quality than predicted. This hemlock site was adjacent to a deer-hunting hide, and there has been some evidence that deer browsing can reduce the diversity and abundance of forest herbs (Anderson 1994). When the outlier is included, CA Axis 1 becomes statistically insignificant. Otherwise the model residuals were normal and homoscedastic.

Time since cutting and basal area are correlated (Pearson correlation co-efficient 0.730) (Figure 4.19), and when time since cutting (*log age*) is substituted for basal area (*log basal*) in the model for herbaceous community quality, it is statistically significant ($p = 0.004$; $r^2 = 0.63$). However, the residuals for this model are non-normal. Furthermore, when *log age* and *log basal* appear in the same model, *log basal* explains more variance.

Discussion

Canopy Composition and Richness

The results of this study suggest that current selection-cutting practices are contributing to the replacement of red oak by sugar maple, and that such a trend will result in a reduction in the canopy diversity of northern hardwood forests.

Despite the statistical significance of cutting treatment in the canopy CCAs, it was not possible to determine from those analyses if cutting history is responsible for current canopy composition. Because the sample plots did not include any selection-cut hemlock stands nor old-growth oak stands, the statistical effects of cutting treatment could not be distinguished from the effect of the sampling bias.

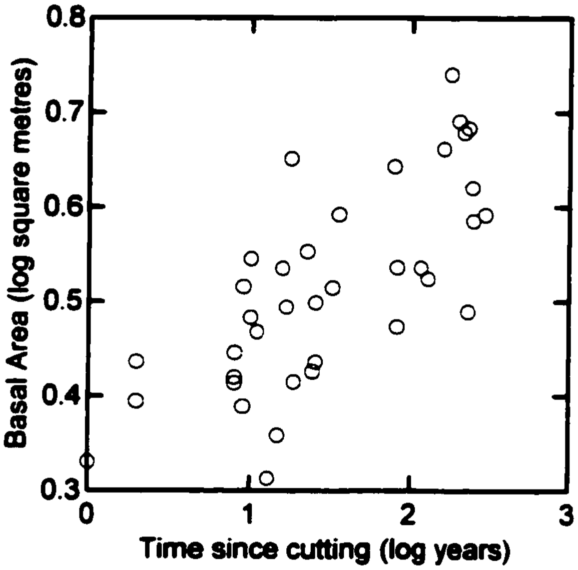


Figure 4.19. Correlation between time since cutting and stand basal area.

Regeneration patterns suggest, however, that current cutting practices are not responsible for the observed patterns of canopy composition. If selection-cutting created the conditions responsible for the establishment red oak, then selection-cutting should perpetuate them. Similarly, if old-growth conditions were responsible for the dominance of hemlock, then the maintenance of old-growth conditions should continue to favor hemlock. However, the regeneration data show that selection-cut oak stands are regenerating as sugar maple, while three of the four old-growth hemlock stands are regenerating as beech.

There are two likely explanations for the lack of old-growth, oak-dominated stands. First, many stands of red oak became established or spread in the aftermath of the large fires which often followed the unrestrained and unregulated logging of white pine during the square timber era of the 19th century, and which have become rare in the last century (Keddy 1993; Dey and Buchanan 1995; Epp 2000; Thompson 2000). Second, red oak is the most economically valuable northern hardwood tree (Anderson *et al.* 1990), making oak stands particularly attractive to loggers.

Although the regeneration data suggest that selection-cutting has played no role in the establishment of oak-dominated stands, it does suggest that selection-cutting is threatening their survival by favoring the regeneration of sugar maple. Difficulties in regenerating red oak after harvest have been reported throughout the northern hardwood forest, as well as in other eastern deciduous forests (Anderson *et al.* 1990; Anderson and Rice 1993; Dey and Buchanan 1995). The on-going replacement of red oak by sugar maple is the replacement of a moderately shade-tolerant species by a highly shade-tolerant species (Anderson *et al.* 1990; Pacala *et al.* 1996). Selection-cutting, it appears, does not open the canopy sufficiently for oak seedlings to compete effectively against maple seedlings (Anderson *et al.* 1990). The problem may be exacerbated by increased acorn predation by burgeoning squirrel and deer populations (Anderson *et al.* 1990; Dey and Buchanan 1995).

This study does not provide the data necessary to explain the absence of selection-cut hemlock sites, nor to explain the lack of hemlock regeneration in the old-growth Adirondack sites. These may result from related or entirely different causes. Historical studies have shown that hemlock was a common – albeit patchily distributed – species throughout the northern hardwood forest (Keddy 1993; Frelich 1995; Davis *et al.* 1996; Cogbill 2000). It is possible, therefore, that at least some selection-cut sites originally contained hemlock. If so, then logging of hemlock for tannin during the 19th century may have been responsible for much of the loss (Frelich 1995; Frelich and Reich 1996). More recently, because of its low commercial value, hemlock may have been deliberately "weeded out" in order to release to release other, more commercially-valuable species (Walker 1999).

Neither of these possibilities explains, however, why hemlock has not regenerated in the selection-cut stands, nor why it is declining in the old-growth, Adirondack stands. Hemlock decline is a problem that has been observed throughout the northern hardwood forest (Keddy 1993, 1994; Frelich and Reich 1996; Larson *et al.* 1999; Burgi *et al.* 2000; Zhang *et al.* 2000). Much research has examined the effects of browsing by white-tailed deer, and overgrazing would explain why hemlock has not regenerated in the selection-cut stands and is declining in the Adirondack old-growth sites (Anderson and Loucks 1979; Frelich and Lorimer 1985). Mladenoff and Stearns (1994) disagree with this explanation, however, suggesting that recent warming trends favor the growth of deciduous tree species over hemlock, particularly near the limits of its range. In contrast, the SORTIE forest dynamics model of Pacala *et al.* (1996) suggests that hemlock, along with beech, should dominate northern hardwood forests in the absence of major disturbances. Similarly, Davis *et al.* (1996) argue that the most recent period of hemlock expansion occurred at a time, approximately 3200 years ago, when the climate was warmer and drier than now. They attribute the decline in regeneration primarily to logging, which reduces the abundance of the coarse woody debris needed by Hemlock seeds as germination sites, reduces Hemlock seed production, and opens stands to invasion by Sugar Maple (Davis *et al.* 1996). This explanation received some support by Rooney and Waller (1998), who showed that the distribution of Hemlock seedlings is highly clumped in response to substrate type and the basal area of Sugar Maple, and by Woods (2000), who found Hemlock maintaining or increasing in dominance in old-growth stands. Almost all of this work, however, was confined to Michigan, and it does not explain the lack of Hemlock regeneration in the Adirondack old-growth sites of this study.

As already noted, the current failure of hemlock regeneration in the Adirondack sites disagrees with the predictions of the SORTIE model. In these stands, the high incidence of Beech Bark disease (caused by the fungus *Nectria coccinea*) may be having an effect on community dynamics, perhaps by inducing infected trees to mast or resprout and overwhelm young hemlocks with abnormally high numbers of beech seedlings. Significantly, the SORTIE model does not incorporate inter-specific or temporal differences in fecundity.

While these results raise questionss about the future of Adirondack old-growth hemlock stands. there is no need for immediate alarm. Given the long canopy residence time of hemlock (Woods 2000) and the likelihood of the current cohorts of beech seedling and saplings being struck by beech-bark disease once they reach maturity, it is unlikely that major changes in canopy composition are imminent. There is, however, sufficient uncertainty regarding the relationship between selection-cutting and hemlock regeneration to warrant caution, particularly give the scarcity of hemlock stands.

Although cutting practices do not appear responsible for current patterns of canopy composition, selection-cutting is associated with higher canopy richness, with selection-cut stands having, on average, about 2 more tree species than old-growth stands. The effect was larger when the hemlock old-growth stands were excluded, leaving only the maple old-growth stands. This is consistent with an overall increase in canopy diversity as maple dominance decreases, whether the changes in composition are towards oak, hemlock, or more disturbance-adapted species such as big-toothed aspen. The changes are not simply due to the addition of oak or hemlock, but represent the addition of other species, such as black cherry, yellow birch, white pine and white spruce. Along with the difference in richness between the selection-cut and old-growth stands, they demonstrate the ability of sugar maple to suppress the growth of less shade-tolerant species, and the importance to biodiversity of maintaining a mosaic of stand types across the northern hardwood forest landscape (Spies and Turner 1999).

Herbaceous composition and richness.

The results of this study suggest that there are minimal, long-term, direct effects of selection-cutting on herbaceous layer composition, but that there could be effects of selection-cutting on herbaceous layer richness if repeated cutting cycles are allowed to deplete soil calcium, and if cutting cycles are shorter than 25 years.

The CCA of the herbaceous layer vegetation suggested that the composition of the herbaceous layer is not associated with cutting treatment or time since cutting, but is strongly related to canopy composition. Herbaceous layer composition changed significantly as the canopy changed from maple-dominant stands to either oak-dominant, hemlock-dominant or maple co-dominant stands. These changes are not necessarily causal. Many herbaceous layer species of the northern hardwood forests are sensitive to local edaphic factors (Host and Pregitzer 1991). It is probable that the associations between stand types and herbaceous communities represent shared preferences for soil conditions, light levels or disturbance regimes.

Similarly, canopy composition was the most important factor predicting herbaceous layer richness, followed by mineral layer calcium and intra-stand variation in moisture regimes. In turn, total richness predicted much of the variance in the richness of forest herbs, old-growth species and weedy species. Again, there is no way to know if the relationship between canopy composition is causal or not – both variables could just as likely be responding to the same edaphic factors – but it is clear that high herbaceous richness is associated with low sugar maple dominance.

The associations of herbaceous layer richness with mineral layer calcium and variation in soil moisture are more likely to be causal. Other studies have shown significant correlations between measures of soil acidification (*e.g.* pH, Ca/Al ratios) and the distribution and richness of herbaceous forest plants (Falkengren-Grerup and Tyler 1993; Falkengren-Grerup *et al.* 1995; Brunet *et al.* 1996). Furthermore, as discussed in chapter 3, Ca/Al molar ratios at many sites are approaching or below the levels at which adverse effects on plant health and growth can be expected, mainly due to declines in soil calcium levels. As for the positive effects of variation in soil moisture on herbaceous layer richness, the relationship is obviously due to changes in the range of microhabitats available to species with specific moisture requirements. Since CW-SD and CW-mean are negatively correlated (Figure 4.20; $r = -0.819$), species enrichment generally occurs in sites where the normal upland habitat is supplemented by moist or wet microhabitats.

Independent of the association between canopy composition and herbaceous layer composition, there were temporary effects of selection-cutting on herbaceous layer diversity. During the first 23 years following selection-cutting, there was a sharp decline in the total richness of the herbaceous layer (Figure 4.15), reflecting an overall logarithmic decline in the richness of weedy species (Figure 4.16). This suggests that selection-cutting causes a temporary increase in overall herbaceous layer richness by opening the stand to invasion by weedy species. However, recovery of the herbaceous layer is swift. Forest species are unaffected by cutting, and the logarithmic form of the decline in weedy species means that they are largely eliminated over the course of one cutting cycle (approximately 25 years). This result is consistent with other work on selection-cutting in northern hardwood forests (Metzger and Schultz 1981, 1984; Reader and Bricker 1992, 1994; Brunet *et al.* 1996; Fredericksen *et al.* 1999).

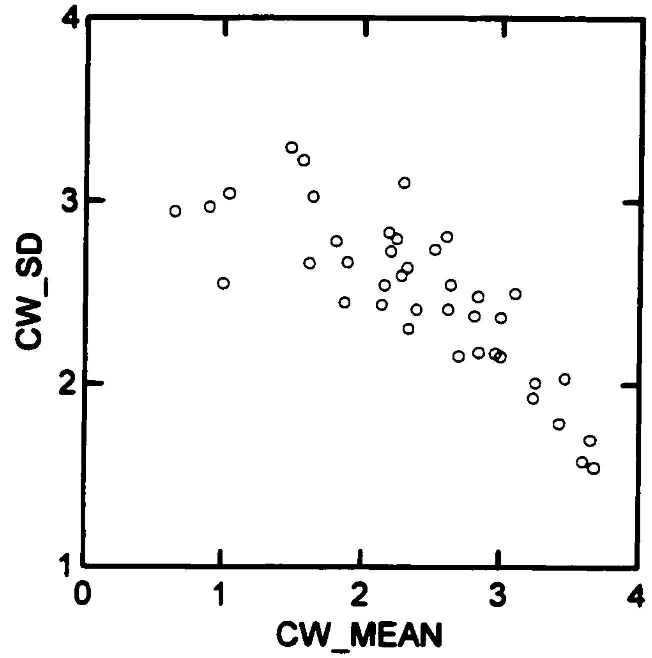


Figure 4.20. The correlation between the mean and standard deviation for the coefficient of wetness in each site.

Not surprisingly, given the effect of age on the richness of weedy species, there appeared to be an indirect effect of time since cutting on site floristic quality – an effect mediated by stand basal area. Canopy composition was, again, the most important factor predicting floristic quality, with the coefficient of conservation increasing as sugar maple dominance decreased. Independent of canopy composition, however, floristic quality also increased with age and basal area as a result of the decline in weedy species with time. This decline is probably in response to declining light levels with increasing canopy closure (Reader and Bricker 1994).

There was a small effect of cutting treatment on the richness of 7 "old-growth" herbs – defined here as species found in at least half of the old-growth stands. The difference between treatments was small, however, with old-growth sites averaging 5 species, and selection-cut sites averaging 4 species. All of the old-growth species were common, and the difference in richness could not be attributed to any species in particular. These results again suggest that there are no plant species specifically associated with old-growth sites.

It is possible, of course, that there are some ephemeral spring species associated with time-since-cutting or cutting treatment. Many of the study sites were inaccessible until late Spring, when the trees were already in leaf and most of the ephemeral species had already lost their inflorescences or begun to senesce. To the best of my knowledge, however, there is no evidence of selection-cutting affecting the diversity of spring ephemerals. In fact, Metzger and Schultz (1981) found that selection-cutting had no effect on the diversity of spring ephemerals. This is not surprising, since the presumed mechanism by which selection-cutting would reduce diversity – the opening up of the canopy – should have little effect on species adapted to flowering before leaf-out.

In over 1000 1 m^2 subplots in more than 40 sites, only one listed rare, endangered or threatened species was recorded: *Panax cinquefolia*. While a census of all of the plants present at each site may have revealed additional rare species (Hellmann and Fowler 1999), the flatness of the species-area curve past 25 m^2 suggests that the amount of additional data collected would not have justified the additional time commitment nor the attendant risk of investigator bias. Nonetheless, species observed outside of the subplots were noted on an *ad hoc* basis, without encountering any additional rare species. It is possible, of course, that rare members of the ephemeral spring flora may have been overlooked, since only the summer flora was surveyed.

While rare plants may have been overlooked, it seems more likely that they were absent because the study focused on the most common, mesic habitat type in northern hardwood forests. Plants are generally rare because their habitat is rare, or because they are limited to peripheral habitats by more competitive species (Keddy 1990; Keddy and MacLellan 1990; Keddy 2001). The exception, in this case, proves the rule: *P. cinquefolia* is endangered because it has been heavily collected throughout the northern hardwood forest for nearly 300 years. Historically, it appears to have been quite common (Conrad *et al.* 1993).

Implications for Management

My results suggest that the effect of selection-cutting on canopy and herbaceous layer biodiversity in northern hardwood forests should be small provided that precautions are taken to prevent: (a) the conversion of red oak and hemlock stands to sugar maple and beech, (b) depletion of soil calcium, and; (c) to insure that cutting cycles are sufficiently long to permit recovery of the herbaceous layer.

The primary threat posed by selection-cutting is the conversion of red oak stands to sugar maple. Management of northern hardwood forests must take into account the strong associations between stand type and the biodiversity of both the canopy and herbaceous layers. Not only do stands dominated by oak or hemlock have greater species richness (α-diversity) than stands dominated by sugar maple, but their distinct floras contribute to greater biodiversity at a landscape scale (β-diversity). Whether these associations with stand type are causal or not, one of the keys to the maintenance of floral biodiversity will be the maintenance of a mosaic of stand types across the landscape.

Management aimed at regenerating the current canopy cover will not only protect tree diversity, but is likely to maintain the appropriate conditions of light, soil moisture and disturbance for the current herbaceous communities. It will also protect specific tree-herb associations, such as *Fagus greandifolia – Epifagus virginiana*.

In my study region, oak stands are regenerating as sugar maple, and maintenance of oak will require active intervention. Methods for promoting oak regeneration are well known to foresters, and are generally aimed at opening the canopy to greater light penetration, suppressing competition (especially from maple seedlings), and reducing acorn predation. They include such practices as group selection-cutting, controlled burning, application of herbicides and hand seeding (Anderson *et al.* 1990; Dey and Buchanan 1995). Use of these measures should be accompanied by monitoring, not only to assess their effectiveness at regenerating red oak, but to assess their effects on the biodiversity of herbaceous vegetation and other taxa.

Hemlock stands should not be cut. Although this study could not assess the effects of selection-cutting on hemlock stands, it failed precisely because selection-cut hemlock stands were not found. In fact, in eastern Ontario, where much of this study took place, hemlock stands of any age were difficult to find, suggesting that logging (at least as historically practiced) is not compatible with the protection of hemlock. The Greater Fundy Ecosystem Research Group (1997) has made a similar recommendation for hemlock stands in its northern hardwood forests. Existing stands of hemlock should be mapped, as should sites with the potential to support hemlock. Hemlock regeneration should be monitored, and experiments conducted with fenced exclosures to assess the effects of browsing by white-tailed deer.

Selection-cutting poses a secondary threat to herbaceous layer biodiversity, through its effects on soil calcium. 25% of the variation in total herbaceous richness was due to variation in mineral layer calcium. As discussed in chapter 3, selection-cutting on siliceous bedrock depletes calcium levels in both the organic and mineral soil layers at unsustainable rates. In many sites, mineral layer Ca/Al ratios are near or below the levels at which damage to plant health and growth can be expected. Based on results from Europe, continued declines in calcium availability will probably result in the loss of acid-sensitive species, producing measurable changes in herbaceous layer composition and diversity (Falkengren-Grerup and Tyler 1993; Falkengren-Grerup *et al.* 1995; Brunet *et al.* 1996). Soil monitoring should be conducted regularly to identify the most sensitive sites. and in these areas logging should be restricted or prohibited. More research should be done on the effects of liming on herbaceous layer diversity and composition. Finally, cutting cycles should not be less than 25 years. This appears to be the minimum period necessary for the herbaceous layer community to recover from selection-cutting. Cutting cycles of less than 25 years are likely to result in the persistence of weedy species and lower floristic quality. Although not evidenced by this study, increases in weedy species could lead in time to the competitive exclusion of forest species.

This study suggests that selection-cutting, carefully applied, is compatible with maintaining both canopy and herbaceous layer diversity. In fact, careful selection-cutting could enhance biodiversity by providing an opportunity to re-introduce a once-common species to the forest. White pine was once a significant component of northern hardwood forests. both in pure stands and as individuals within deciduous stands (Braun 1964; Keddy 1993; Frelich and Reich 1996; Larson *et al.* 1999; Epp 2000). but was almost eliminated by intense logging in the late 19th and early 20th centuries (Keddy 1993; Epp

2000; Thompson 2000). Although there are a few protected areas where mature specimens can still be seen thrusting above the deciduous forest canopy, fire suppression policies and the lack of seed trees have prevented a general recovery (Frelich and Reich 1996). Even now, remaining stands of white pine are eagerly sought by logging companies. During this study, in fact, a large, apparently mature stand of white pine was cut adjacent to two of the old-growth study sites in Lanark County, Ontario.

As a requirement of their harvesting licenses for public land, logging companies could be required to transplant white pine into larger gaps following harvesting. Group selection-cutting would be particularly useful in this respect. Transplanted seedlings could be grouped to facilitate re-entry into stands during subsequent harvest, and to facilitate other measures designed to increase successful establishment, such as the erection of temporary deer exclosures, or hand application of herbicides to suppress hardwood advance growth.

In general, the protection and regeneration of conifer species should be encouraged. In addition to their direct and indirect contributions to biodiversity, recent research has demonstrated the potential importance of conifers to the forest calcium biogeochemical cycle (Blum *et al.* 2002). Conifers, *via* ectomycorrhizal fungi, appear capable of accessing an additional store of calcium in the mineral apatite (Blum *et al.* 2002). This calcium is then available to the forest ecosystem as a whole through conifer litter and throughfall (Blum *et al.* 2002)

All of these proposed measures for the protection of oak and hemlock stands, and for the reintroduction of white pine, presume that we *can* and *want* to maintain the current patterns of canopy and herbaceous layer composition and diversity in northern. hardwood forests. Such patterns may not be "natural" under past or future environmental conditions. Paleoecological studies, such as those by Delcourt and Delcourt (1987, 1991) have shown that the northern hardwood forest is still in a non-equilibrium state following the disturbance of the last ice age, and that it is sensitive to long-term, continental weather patterns. Its major tree species only finished recolonizing the post-glacial landscape in the last 3000 years, they arrived from different southern refugia, and their distributions reflect the Individualistic model of plant community assembly more than the Community-Unit or Climax model (Gleason 1926; Clements 1936; Delcourt and Delcourt 1987, 1991; Jackson and Whitehead 1991). The current composition of the northern hardwood forest may only be the temporary co-occurrence of species responding to synchronous environmental factors. As synchronicity is lost – as the climate changes, as disturbance cycles vary, as diseases strike and communities respond – new associations may develop. Forest management, therefore, must not be based upon a static model of what the forest *should be*, but reflect a vision and understanding of what is possible and desirable. Nonetheless, protecting forest biodiversity will allow us and the forest to retain the greatest potential for adaptation (Christensen *et al.* 1996; Aber *et al.* 2000).

Chapter 5

Structural Properties of Selection-cut Forests: Cavity trees, snags and coarse woody debris.

Introduction

In addition to the effects discussed in chapters 3 and 4, selection-cutting alters the age and size structure of the canopy, as well as the abundance and properties of both standing dead trees (snags) and coarse woody debris (CWD) (Brokaw and Lent 1999; Frelich and Puettmann 1999; Aber *et al.* 2000). In general, selection cutting results in fewer large, overmature trees (Goodburn and Lorimer 1998), reducing the number of canopy layers and thereby reducing the vertical structural diversity of the forest (Brokaw and Lent 1999). Large old trees are also those most prone to disease, accumulated damage and blowdowns (Tyrrell and Crow 1994).

Several studies have shown correlations between biodiversity and forest structural diversity (Seymour and Hunter Jr. 1999; Brokaw and Lent 1999; Aber et al. 2000). These correlations are reflected in the general homogenization of forest biota, usually more evident at the landscape scale (Kimmins 1997b; Spies and Turner 1999; Seymour and Hunter Jr. 1999). At a stand scale, reductions in structural diversity are often accompanied by changes in the composition of animal and plant communities. Particularly at risk are species which require special habitat features, particularly large, old trees (Kimmins 1997b; Aber et al. 2000). Loss of these trees reduces: (1) the availability of substrates for epiphytic plants such as lichens and mosses; (2) the abundance of seeds and nuts for mast-dependent species, such as black bear (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*) and wild turkey (*Meleagris gallopavo*); (3) the abundance and size of dying and dead trees available for animals dependent on tree cavities or snags; and (4) the abundance and size of CWD available on the forest floor for shelter and habitat (Thomas et al. 1979; Harmon *et al.* 1986; Bucher 1992; Kimmins 1997a; Brokaw and Lent 1999; Frelich and Puettmann 1999; Aber *et al.* 2000). These attributes have been shown to contribute to the abundance of plant, animal and microbial species (Bull 1978; Thomas et al. 1979; Davis *et al.* 1983; Harmon *et al.* 1986; Perry 1998; Brokaw and Lent 1999; McComb and Lindenmayer 1999; *Aber et al.* 2000).

Attempts have been made to retain or recreate some of these old-growth features in selection-cut forests (Kimmins 1997b; Perry 1998). In some cases, managers have used artificial means such as building artificial snags, erecting nest boxes, or dynamiting the tops of healthy trees (Davis *et al.* 1983). The more usual method, "variable harvest retention", allows for a certain number of older trees in each stand to be retained (Thomas et al. 1979; Perry 1998; McComb and Lindenmayer 1999; Seymour and Hunter 1999; Spies and Turner 1999; Aber et al. 2000). Trees may be left singly, in groups, or around sensitive areas such as watercourses or nest sites, where logging may already be restricted (Thomas et al. 1979; Hicks 1983; Perry 1998; McComb and Lindenmayer 1999; Spies and Turner 1999).

In order to make variable harvest retention systems operational, various researchers have established guidelines and management targets for the retention of cavity trees, snags and coarse woody debris (*e.g.* Keddy and Drummond 1996; Greater Fundy

Ecosystem Research Group 1997; McGee et al. 1999; McGee 2000). Few studies (*e.g.* Carey 1983; Goodburn and Lorimer 1998), however, have examined whether these targets are actually being met. In this chapter, I measure or estimate the levels of these features in 29 selection-cut stands of northern hardwood forest, comparing them to existing targets and natural levels in 7 old-growth stands. I also judge the feasibility of the current management targets by comparison to old-growth stands, and I recommend revised targets where I deem necessary. Finally, I discuss the implications of these results and those of chapters 3 – 5 for the use of selection-cutting in the management of northern hardwood forests.

Methods

Selection of guidelines and sampling

Several different guidelines for cavity trees, snags and coarse woody debris in variable-retention harvest systems have been proposed for northern hardwood forests (*e.g.* Keddy and Drummond 1996; Greater Fundy Ecosystem Research Group 1997; McGee *et al.* 1999). In selecting guidelines, I used three criteria: (1) an explicit ecological foundation; (2) specific management targets; (3) operational feasibility. Some guidelines were based on an estimation of wildlife needs, while others were based on levels found in old-growth stands. In several instances, it was necessary to adapt recommendations to the survey methods used in this study.

Guidelines were taken from ten sources: Evans and Conner 1979, Conner *et al.* 1983, DeGraaf 1984, Runde and Capen 1987, Tubbs et al. 1987, Anderson and Rice 1993, Keddy and Drummond 1996, Greater Fundy Ecosystem Research Group 1997, McGee et al. 1999, McGee 2000. These sources are not independent. For example, Anderson and Rice (1993) partly base their recommendations on Tubbs et al. (1987), which in turn draws upon the work of DeGraaf (1984) and Evans and Conner (1979) on the needs of cavity-nesting animals. Conner (1983) and Runde and Capen (1987) also base their recommendations on the needs of cavity-nesting animals, particularly birds. The Greater Fundy Ecosystem Research Group (1997) base their recommendations both on estimated wildlife needs and natural old-growth levels, drawing heavily on previously published work – particularly studies from the Fundy Model Forest and Fundy National Park. McGee et al. (1999) and McGee (2000) base their recommendations on their own measurements of old-growth stands in the Adirondack Mountains. Keddy and Drummond (1996) base their recommendations on a survey of previous published studies on old-growth, eastern deciduous forests.

In this study, the general survey methods (see Ch. 3) were adapted from the Growth and Yield (GY) Program of the Ontario Ministry of Natural Resources (OMNR) (Hayden *et al.* 1995). The GY protocol uses nested plots, with all standing dead trees (snags) with a diameter at breast height (dbh) greater than or equal to 2.5 cm being surveyed in a circular "mortality plot" of radius 45.14 m (0.64 ha), with dbh, species and decay class being recorded. The decay of snags was assessed using 5 classes taken from the GY system (Hayden *et al.* 1995): (1) recently dead, top intact; (2) top intact, no fine branches, more than 50% coarse branches; (3) top intact, fewer than 50% coarse branches; (4) top broken, no coarse branches, height > 6 m.; (5) top repeatedly broken, no coarse branches, height < 6 m. Live trees greater than or equal to 2.5 cm dbh are measured and identified to species in three "growth plots" of radius 11.29 m situated at

180 arcs around the mortality plot. Coarse woody debris (CWD) with diameter greater than or equal to 7.5 cm is measured along 3 transects of 45.14 m running from the center of the mortality plot through the growth plots, with diameter, species and decay class being recorded. The decay of CWD was assessed using 5 classes taken from the GY system (Hayden *et al.* 1995): (1) recently fallen, intact twigs and bark, round, firm texture, elevated on support points; (2) intact bark, no twigs, round, firm to partly soft, slight sagging; (3) some bark, round, soft to partly firm with some fragmentation, extensive sagging; (4) no bark, round to oval, soft with extensive fragmentation, entirely on ground; (5) oval, soft and powdery, entirely on ground.

In the present study, four modifications were made to the above protocols. First, tree cavities were not recorded for the majority of sites: these were too difficult to see through summer foliage, and analysis of preliminary results indicated a strong observer effect. For this reason, Rowe (1994) recommends surveying cavities when trees are leafless. In most cases the densities of cavity trees were estimated from the total densities of live trees in specific size classes, using data from Goodburn and Lorimer (1998) on the percentages of live northern hardwood forest trees containing cavities in a sample of 10 selection-cut and 6 old-growth hardwood stands, and 5 selection-cut and 4 old-growth hemlock-hardwood stands in northern Michigan and Wisconsin (Table 5.1). These stands are very similar in both canopy and herbaceous layer composition to northern hardwood stands in southeastern Ontario and northern New York (Host and Pregitzer 1991; Goodburn and Lorimer 1998; ch. 4), and the estimated incidences of cavities fall within the range of values provided by Anderson and Rice (1983) for northern hardwood forests in eastern Ontario. Goodburn and Lorimers's (1998) data for trees ≥ 30 cm dbh was used

Table 5.1. Mean values for the occurrence of cavity trees in 15 selection-cut and 10 old-growth northern hardwood forest sites in Wisconsin and Michigan (from Goodburn and Lorimer 1998)

	Northern hardwood		Hemlock-hardwood	
	Selection	**Old-growth**	**Selection**	**Old-growth**
Cavity tree density ≥ 10 cm dbh, including snags (no./ha)	12.5	18.1	7.0	13.8
Cavity tree density ≥ 45 cm dbh, including snags (no.ha)	5.2	11.4	5.0	8.8
Percent of live trees ≥ 10 cm dbh with cavities	2.1	4.5	1.3	3.0
Percent of live trees ≥ 30 cm dbh with cavities	5.5	9.0	4.8	6.7
Percent of live trees ≥ 45 cm dbh with cavities	13.0	12.3	14.7	11.5

to estimate the incidence of cavities in the 25 cm and 30 cm dbh size classes, and their data for trees ≥ 45 cm dbh was used to estimate the incidence of cavities in the 46 and 50 cm size classes. Data from Kingsley on the development of cull trees in New Hampshire forests was used to estimate the incidence of cavities for trees ≥ 61 cm dbh. In production forests, Kingsley found that approximately 55% of the deciduous trees and 15% of the softwood trees with a dbh of 61 cm could be classified as "rough" or "rotten" cull. Cull trees of this size almost always contain cavities (*pers. obs.*).

The second modification was the use of percent cover data (calculated from the transect data) to estimate the density of pieces of CWD. These estimates were based on work by Rowe (1994) who found a strong linear relationship ($r^2 = 0.96$; $p = 0.02$) between percent cover and CWD density in a study of 5 plots. While Rowe cautions that the confidence intervals for parameter estimates in this model are too large for it to be used in actual forest management (owing to the small sample size), the model can provide rough estimates of log densities.

The third modification was used in very dense growth plots (usually those with significant amounts of Balsam Fir). These plots were divided into six wedge-shaped segments, with measurements being done on alternate segments.

The fourth modification adjusted the measured volumes of CWD in the Adirondack Park sites to account for the additional contribution of Beech Bark Disease to tree mortality. Volumes were adjusted downwards by 22%, based on the recommendations of McGee (2000).

Statistics

The Kolmogorov – Smirnov test was used to test for significant differences in the size distributions of live trees, and both the Kolmogorov – Smirnov test and log-linear modeling were used to test for differences in the size and decay class distributions of snags and CWD. For the purposes of log-linear modeling, snags were divided into three size classes: small, < 25 cm; medium, 25 – 49.9 cm; large, ≥ 50 cm. CWD was also divided into three size classes: small, < 20 cm; medium, 20 – 39.9 cm; large, ≥ 40 cm. Regression analysis and general linear modeling was used to examine the relationships between time since cutting and cavity trees, snags and coarse woody debris. The p-value for significance was 0.05 in all tests, and all residuals were normal and homoscedastic unless otherwise noted. For log-linear analysis, p-values above 0.05 indicate an acceptable fit between a model and the observed data frequencies (*i.e.* no statistically significant difference between the two) (Wilkinson *et al.* 1996). In cases where the assumptions of parametric statistics were not met, and where no suitable transformation could be found, randomization was used to test for statistical significance using the RT-Manly 1.02c program (Manly 1994).

Results

Distributions of diameter and decay classes

There was a statistically significant difference in the diameter distribution of live trees between the selection-cut and old-growth plots, with the old-growth plots having a greater proportion of large trees than the selection-cut sites (Kolmogorov – Smirnov Test, $p < .001$) (Figure 5.01). Selection-cut and old-growth sites were also significantly different in terms of the diameter and decay class distributions of both snags (G^2_{model} = 14.69, df = 12, $p = 0.26$) and coarse woody debris (G^2_{model} = 9.27, df = 9, $p = 0.42$) (Figures 5.02 & 5.03). Old-growth sites had proportionally more large snags than selection-cut sites (9.5% versus 0.75% with dbh ≥ 50 cm respectively; chi^2 = 171.2, df = 2, $p < 0.0001$ for change in model fit), and a greater proportion of large snags than small snags were in the late stages of decay (82% versus 41% in classes 4 and 5; chi^2 = 143.2, df = 8, $p < 0.0001$) (Figure 5.02). Old-growth sites had proportionally more large pieces of CWD (> 40 cm) and proportionally fewer small pieces of CWD (≤ 20 cm) than selection-cut sites (% large/small = 9/63 versus 2/84 respectively; chi^2 = 174.5, df = 2, $p < 0.0001$) and though a slightly greater proportion of large CWD than small CWD was in advanced stages of decay (39% versus 34%; chi^2 = 24.1, df = 8, $p = 0.002$), the selection-cut sites had a slightly higher proportion of CWD in advanced stages of decay than the old-growth sites (39% versus 33%; chi^2 = 25.7, df = 4, $p < 0.0001$)(Figure 5.03).

Cavity trees, live trees and basal area

The Greater Fundy Ecosystem Research Group (1997) and Anderson and Rice (1993) both provide guidelines for the retention of live cavity trees with a dbh ≥ 25 cm. Figure 5.04 plots the estimated density of cavity trees with dbh ≥ 25 cm against time since cutting, showing the management targets recommended by Anderson and Rice

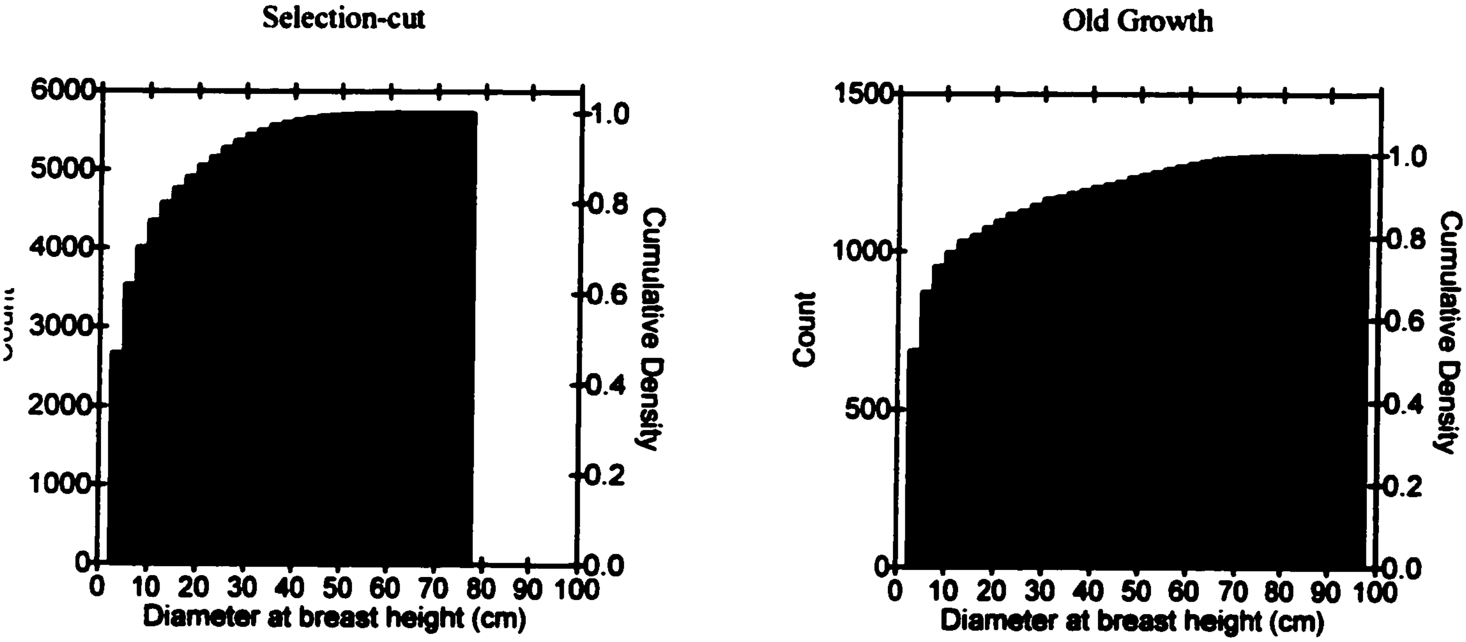
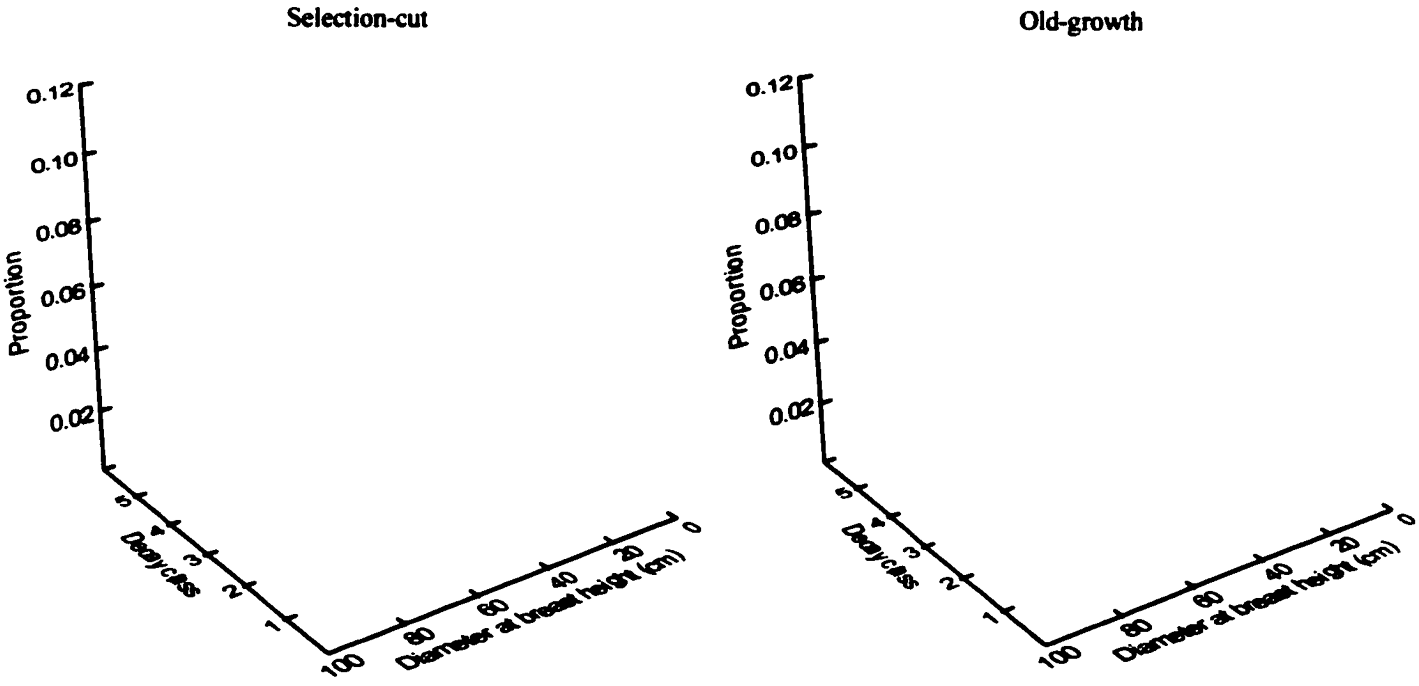
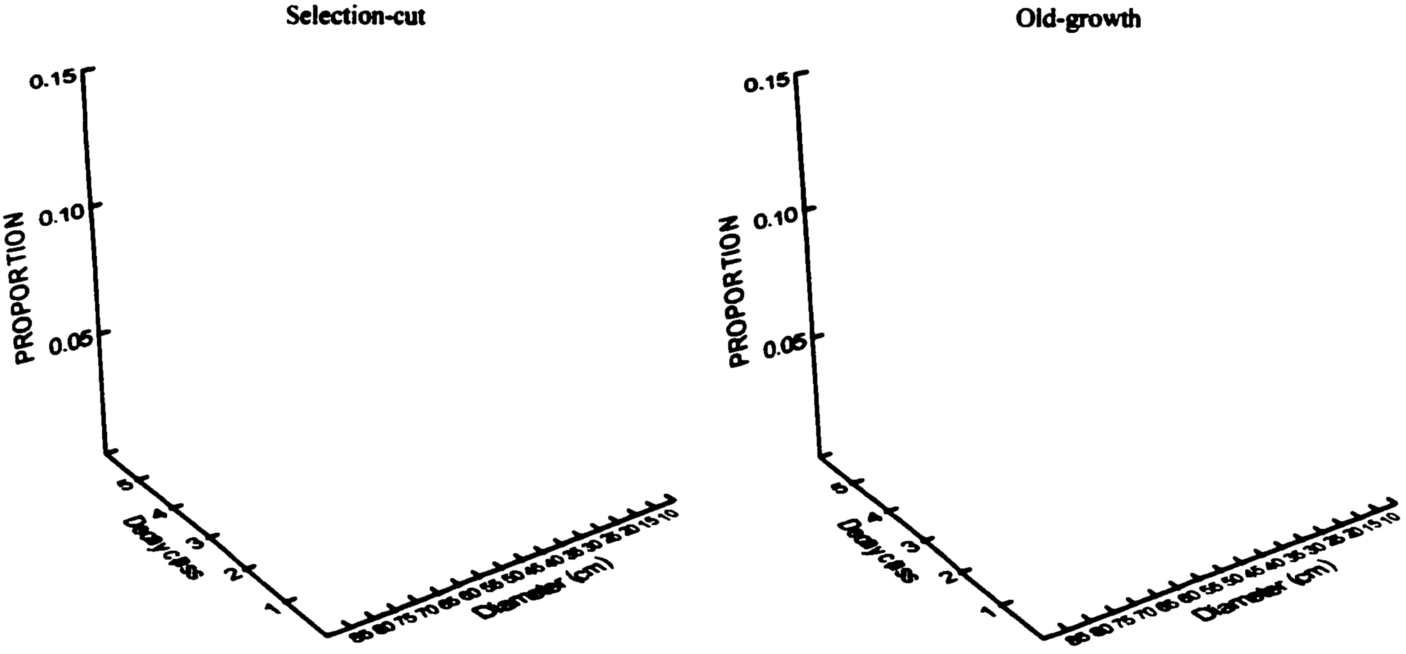


Figure 5.01. Cumulative histograms of the size distributions of living trees greater than or equal to 2.5 cm dbh in 29 selection-cut and 7 old-growth forests.


Selection-cut

Old-growth

Figure 5.02. Histograms of the size and decay class distributions of standing dead trees greater than or equal to 2.5 cm dbh in 29 selection-cut and 7 old-growth stands.


Selection-cut

Old-growth

Figure 5.03. Histograms of the size and decay class distributions of coarse woody debris greater than or equal to 7.5 cm dbh in 30 selection-cut and 7 old-growth stands.

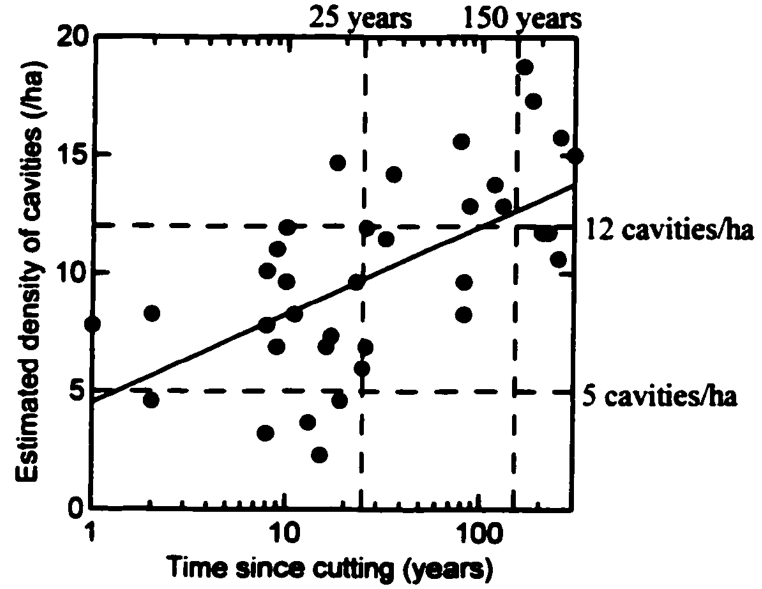


Figure 5.04. The relationship between time since cutting and the estimated number of cavity trees greater than or equal to 25 cm dbh showing management targets recommended by Anderson and Rice (1993) (5 trees/ha) and the GFERG (1997) (12 trees/ha).

(5 cavity trees/ha) and the Greater Fundy Ecosystem Research Group (12 cavity trees/ha). The estimated density of cavity trees increased with time since cutting (*estimated density* = 3.73±0.80(log age) + 4.52±1.31; $r^2 = 0.36$; $p < 0.0001$).

Conner *et al.* (1983) and Runde & Capen (1987) both suggest that the minimum cavity tree size for some common cavity-nesting birds (*e.g.* hairy woodpecker, *Picoides villosus*, and pileated woodpecker, *Dryocopus pileatus*) is about 30 cm dbh. Their suggestions were integrated with those of the Greater Fundy Ecosystem Research Group (1997) and Anderson and Rice (1993) to generate new management targets of 5 and 12 cavity trees/ha with dbh ≥ 30 cm. Figure 5.05 plots the estimated density of cavity trees with dbh ≥ 30 cm against time since cutting, showing these recommendations. Regression analysis showed significant changes in the estimated density of cavity trees over time (*estimated density* = 3.52±0.69(log age) + 1.85±1.12; $r^2 = 0.41$; $p < 0.0001$). One maple-dominant old-growth stand, Shaw Woods, appeared as an outlier.

Several authors make specific recommendations for live cavity trees in larger size classes. Both DeGraaf (1984) and Evans and Conner (1979) recommend retaining 0.5 – 0.6 cavity trees/ha with dbh ≥ 46 cm. Figure 5.06 plots the estimated density of cavity trees with dbh ≥ 46 cm against time since cutting, showing this recommendation. Regression analysis showed significant changes in the estimated density of cavity trees over time (*estimated density* = 0.035±0.006(*age*) + 1.05±0.63; $r^2 = 0.498$; $p = 0.0009$, using randomization). The regression includes an apparent outlier at year 2. This stand also appears as an outlier in models for 46 cm and 50 cm cavity trees, and in the model for 50 cm live trees (see below and discussion). Unusual care appears to have been taken

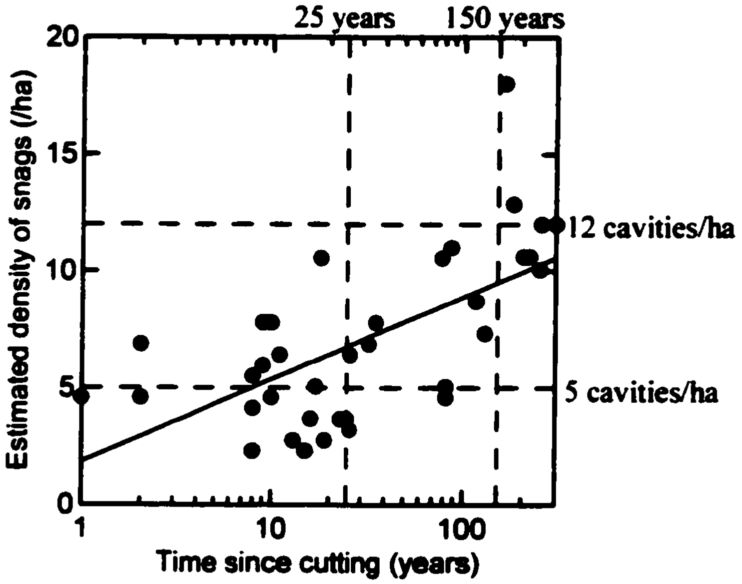


Figure 5.05. The relationship between time since cutting and the estimated number of cavity trees greater than or equal to 30 cm dbh showing management targets recommended by Anderson and Rice (1993) (5 trees/ha) and the GFERG (1997) (12 trees/ha).

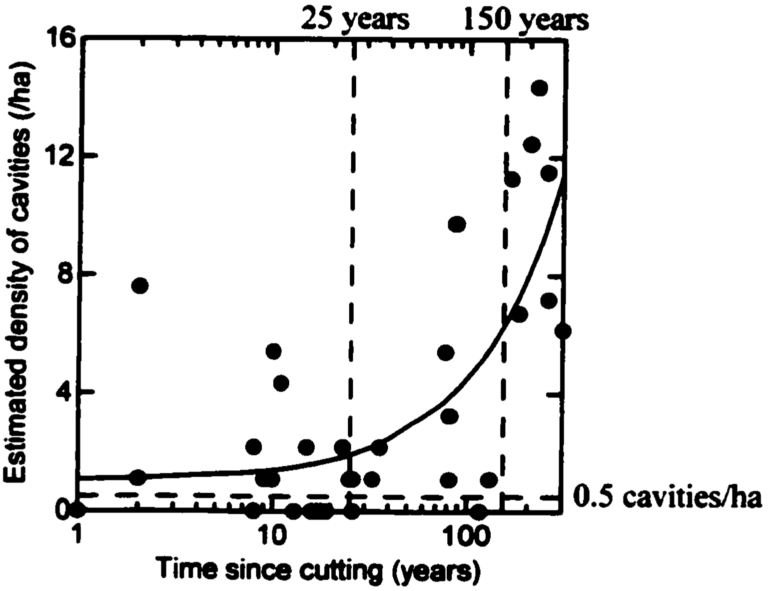


Figure 5.06. The relationship between time since cutting and the estimated number of cavity trees greater than or equal to 46 cm dbh showing the management target recommended by DeGraaf (1984) and Evans and Conner (1979).

to retain large trees in this stand, which the responsible forester specifically identified as a "very good cut" (Martin Strite, *pers. comm.*).

Anderson and Rice (1993) recommend retention of 1 cavity tree/ha in the "large sawlog" (*i.e.* ≥ 50 cm dbh) class. Figure 5.07 plots the estimated density of cavity trees with dbh ≥ 50 cm against time since cutting, showing this recommendation. Regression analysis showed significant changes in the estimated density of cavity trees over time (*estimated density* = $0.027\pm0.005(age) + 0.44\pm0.51$; $r^2 = 0.481$; $p = 0.0001$, using randomization). The regression includes the apparent outlier at year 1.

DeGraaf (1984) suggests retention of 0.05 cavity trees/ha with dbh ≥ 61 cm. Figure 5.08 plots the estimated density of cavity trees with dbh ≥ 61 cm against time since cutting, showing this recommendation.

McGee *et al.* (1999) focus on the density of all live trees, as opposed to just cavity trees. They suggest management targets of 16 live trees/ha with dbh ≥ 50 cm, including 5 trees/ha with dbh ≥ 70 cm. Figure 5.09 plots the density of live trees with dbh ≥ 50 cm against time since cutting, as compared to a management target of 16 trees/ha.. Regression analysis showed significant changes in the density of live trees over time (*estimated density* = $0.23\pm0.04(age) + 2.89\pm4.23$; $r^2 = 0.500$; $p = 0.0001$, using randomization). The regression includes the apparent outlier at year 1. Figure 5.10 plots the estimated density of live trees with dbh ≥ 70 cm against time since cutting, as compared to a management target of 5 trees/ha.

Keddy and Drummond (1996) take a different approach to managing tree size by focussing on total basal area rather than diameter. They recommend quantitative

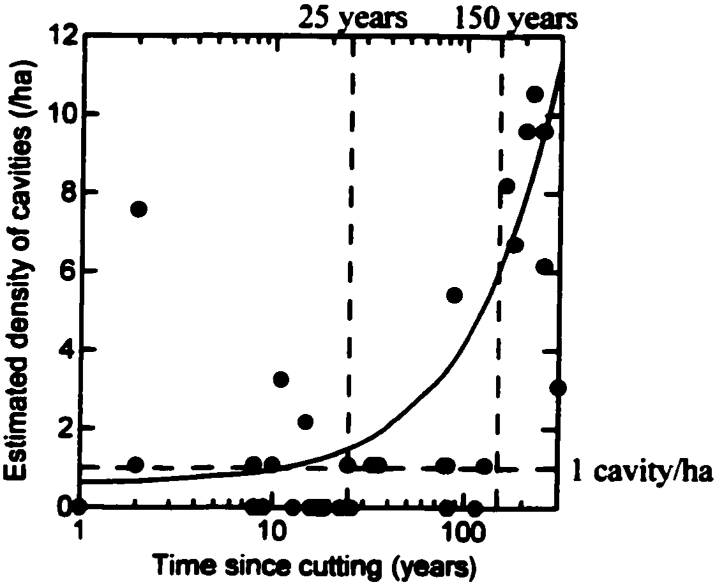


Figure 5.07. The relationship between time since cutting and the estimated number of cavity trees greater than or equal to 50 cm dbh showing management targets recommended by Anderson and Rice (1993).

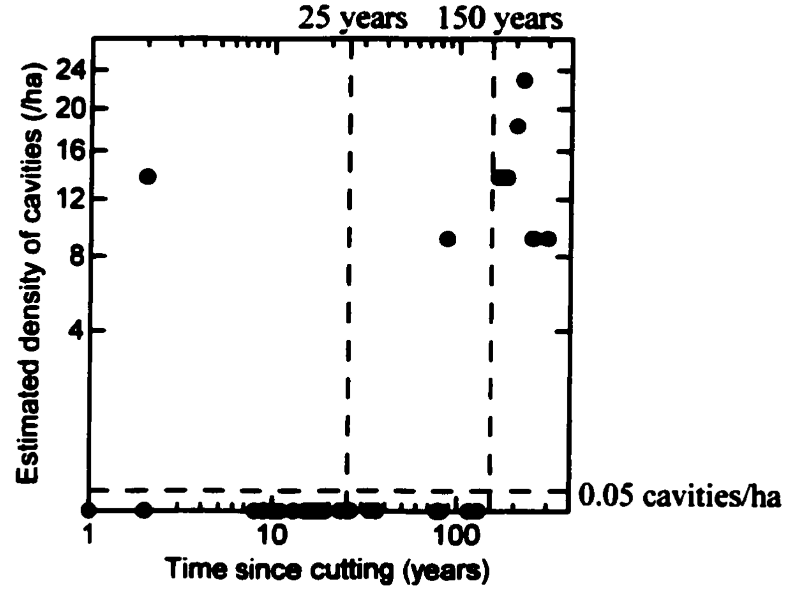


Figure 5.08. **The relationship between time since cutting and the estimated number of cavity trees greater than or equal to 61 cm dbh showing management targets recommended by DeGraaf (1984).**

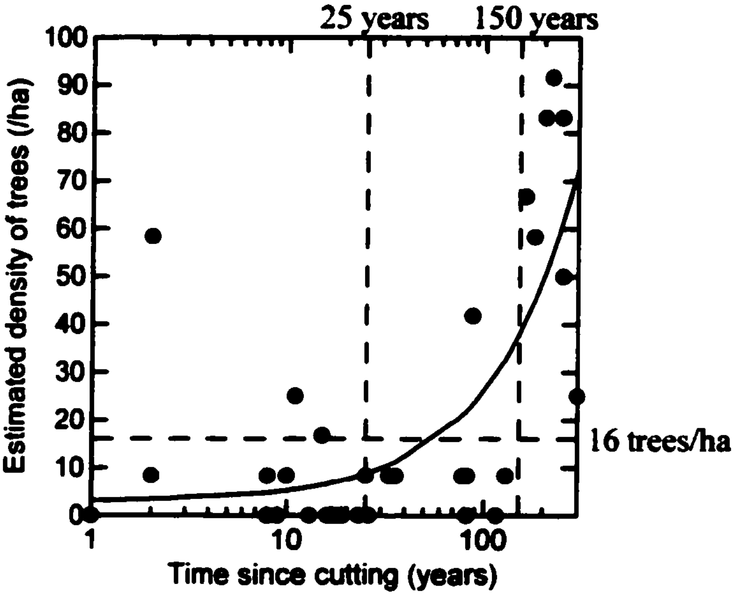


Figure 5.09. The relationship between time since cutting and the estimated number of trees greater than or equal to 50 cm dbh, compared to the management target recommended by McGee *et al.* (1999).

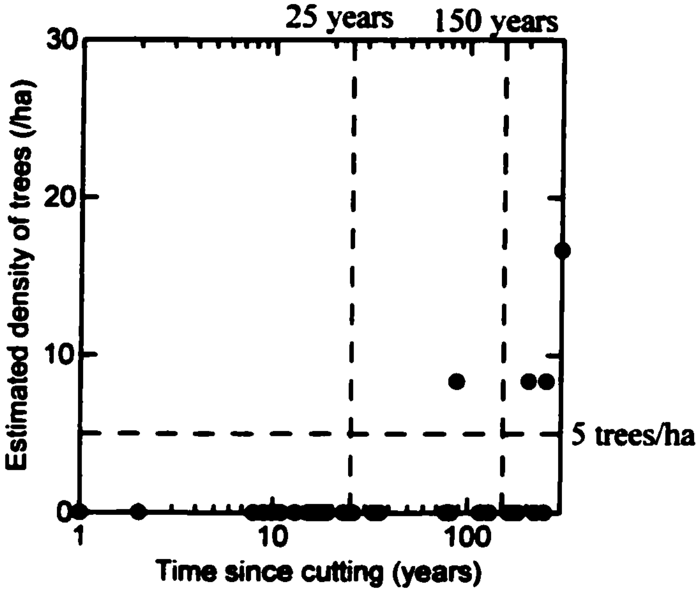


Figure 5.10. The relationship between time since cutting and the estimated number of trees greater than or equal to 70 cm dbh, compared to the management target recommended by McGee *et al.* (1999).

standards for assessing the provision of large trees in eastern deciduous forests: "*control*", > 29 m^2/ha; "*intermediate*", 20 – 29 m^2/ha; "*low*", < 20 m^2/ha. Figure 5.11 plots stand basal area against time since cutting, showing these recommendations. Regression analysis shows that basal area increases linearly with log_{10} stand age (*basal area* = 0.123±0.019(log *age*) + 0.334±0.030; $r^2 = 0.539$; $p \leq 0.009$).

Snags

Few specific recommendations exist for the retention of standing dead trees in northern hardwood forests. The Greater Fundy Ecosystem Research Group (1997) recommends a target of 12 – 15 snags/ha with dbh ≥ 20 cm. Figure 5.12 plots the density of snags with dbh ≥ 20 cm in each site against time since cutting, showing this recommendation. Regression analysis showed significant changes in the density of snags over time (*density of snags* = 9.88±4.04(log *age*) + 1.19±4.57; $r^2 = 0.24$; $p = 0.005$, using randomization). The regression includes the apparent outlier, an Adirondack hemlock stand, at year 248. This stand was particularly hard hit by beech bark disease (see discussion).

The recommendations of Conner *et al.* (1983) and Runde and Capen (1987) regarding minimum diameters were applied to the recommendations of the GFERG (1997) to generate a new management target of 12 snags/ha with dbh ≥ 30 cm. Figure 5.13 plots the density of snags with dbh ≥ 30 cm in each site against time since cutting, showing this recommendation. Regression analysis showed significant changes in the

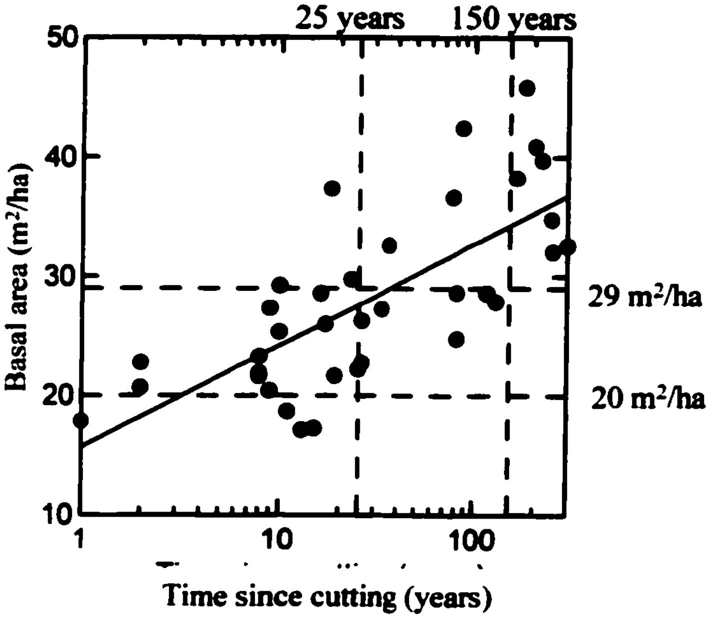


Figure 5.11. The relationship between time since cutting and basal area, showing the management targets recommended by Keddy and Drummond (1996)

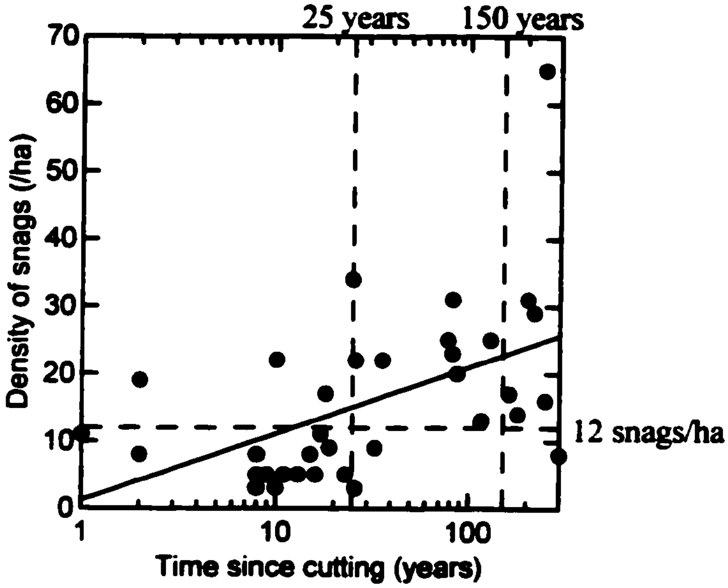


Figure 5.12. The relationship between time since cutting (or age) and the number of standing dead trees (snags) with dbh greater than or equal to 20 cm, showing a management target recommended by the GFERG (1997).

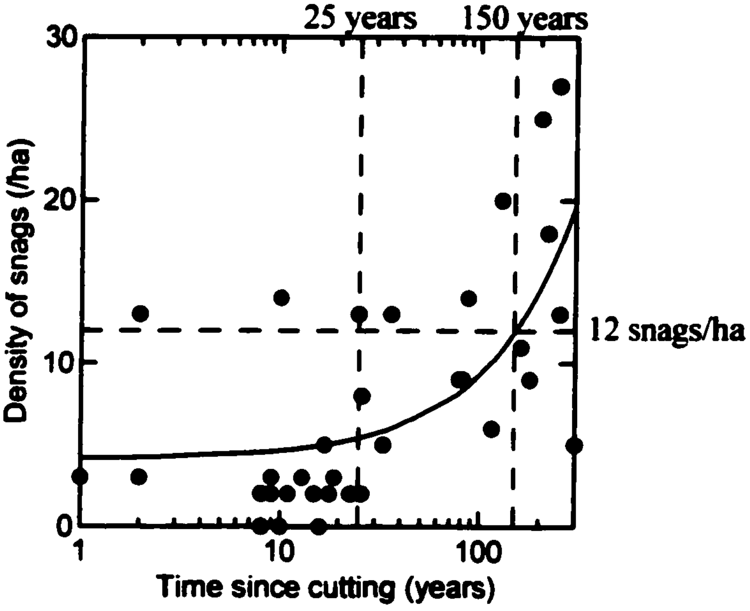


Figure 5.13. The relationship between time since cutting (or age) and the number of standing dead trees (snags) with dbh greater than or equal to 30 cm, showing a management target recommended by the GFERG (1997).

density of snags over time (*density of snags* = 0.052 ± 0.011(*age*) + 4.13 ± 1.18; $r^2 = 0.38$; p = 0.0003, using randomization).

Keddy and Drummond (1996) focus on the larger size class snags, those with a dbh ≥ 50.8 cm. They recommend three quantitative standards for assessing the provision of snags in eastern deciduous forests: "*control*", ≥ 4 snags/10 ha; "*intermediate*", 1 – 3 snags/10 ha; "*low*", < 1 snag/10 ha. Figure 5.14 plots the density of snags with dbh ≥ 50.8 cm in each site against time since cutting, showing these recommendations. Regression analysis showed significant changes in the density of snags over time (*density of snags* =0.177 ± 0.029(*age*) + 3.260 ± 3.21; $r^2 = 0.500$; p = 0.0001, using randomization).

Coarse Woody Debris

As with snags, there are few specific recommendations regarding the retention of CWD in northern hardwood forests. The Greater Fundy Ecosystem Research Group (1997) recommends retention of 10 m^3/ha of CWD ≥ 10 cm in diameter. McGee *et al.* (1999) recommend retention of 108 m^3/ha of CWD, but this includes pieces between 1 cm and 9 cm in diameter. If their recommendation is restricted to CWD ≥ 10 cm in diameter, then the volume drops to 97 m^3/ha. Figure 5.15 plots the volume of CWD in each site against time since cutting, showing these recommendations.

The Greater Fundy Ecosystem Research Group (1997) also recommend that forest stands contain at least 200 pieces of CWD/ha (presumably ≥ 10 cm in diameter, although this is not explicitly stated). Figure 5.16 plots the estimated number of pieces of CWD in each site against time since cutting, showing these recommendations.

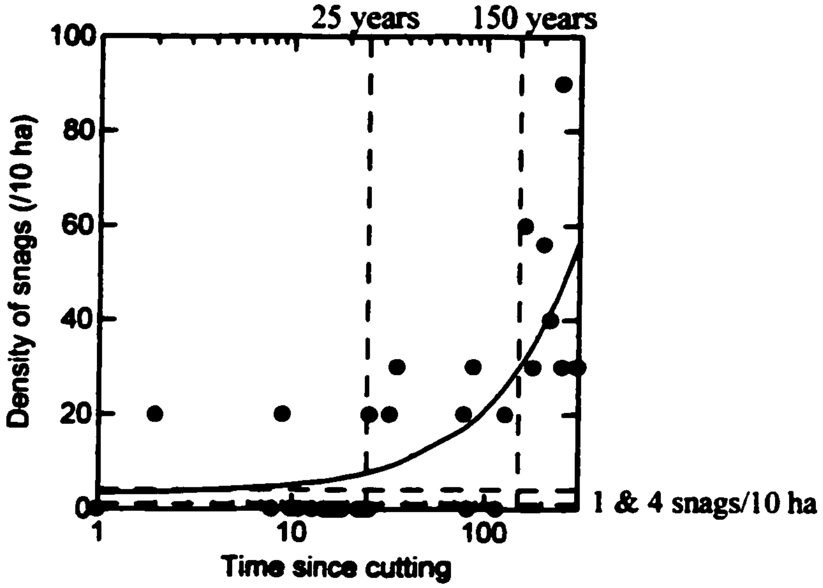


Figure 5.14. The relationship between time since cutting (or age) and the number of standing dead trees (snags) with dbh greater than or equal to 50.8 cm, showing the management targets recommended by Keddy and Drummond (1996).

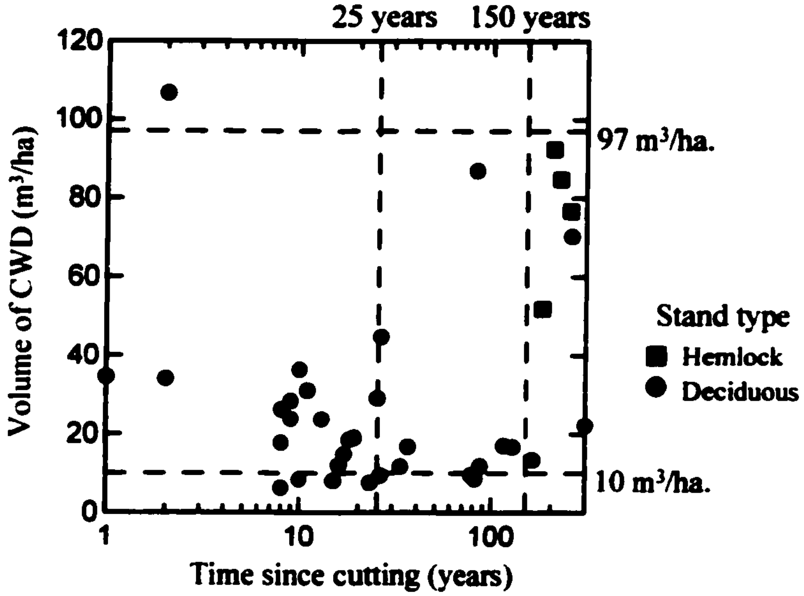


Figure 5.15. The relationship between time since cutting and the volume of CWD with diameter 10 cm or greater, showing management targets recommended by the GFERG (1997) (10 m³/ha) and McGee *et al.* (1999) (97 m³/ha).

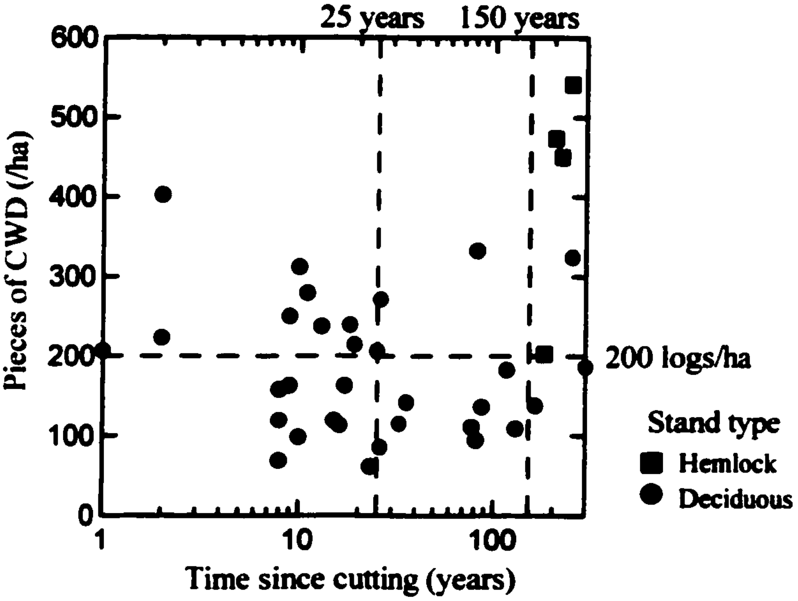


Figure 5.16. The relationship between time since cutting and the number of logs with diameter 10 cm or greater, showing management targets recommended by the GFERG (1997).

Discussion

As has been shown in other northern hardwood forests (Goodburn and Lorimer 1998; McGee *et al.* 1999), selection cut forests have fewer large diameter trees, fewer large snags, and fewer large logs than old-growth stands. This is a direct consequence of the selection-cutting method, which systematically reduces tree disease and mortality by weeding out poor quality trees and establishing a balanced age structure (Matthews 1989; Anderson *et al.* 1990; Seymour and Hunter 1999). Selection-cut sites also had proportionately fewer large snags in advanced stages of decay than old-growth sites, which reflects the greater size of snags in the latter: large snags and logs retain structural integrity longer than small snags and logs, taking longer to disintegrate once decay has become well-established (Harmon *et al.* 1986). Surprisingly, selection-cut sites had a slightly greater proportion of CWD in advanced stages of decay than old-growth sites, despite the fact that a greater proportion of large CWD was in advanced stages of decay than small CWD, and the fact that large CWD was proportionately more abundant in old-growth sites than in selection-cut sites. The apparent contradiction is due to the greater absolute abundance of small, well-decayed pieces of CWD in the selection-cut sites as a result of logging activities – *i.e.* logging slash.

One young, selection-cut site (age 2 years) differed significantly from these general patterns, having structural features more similar to old-growth sites. It appeared as an outlier in analyses of 46 cm, 50 cm and 61 cm cavity trees, 50 cm live trees, 30 cm and 50.8 cm snags, and CWD. During the initial phase of the study, when stands were being selected, this site was specifically identified by a consulting OMNR forester as being "a very good cut" (Martin Strite *pers. comm.*). In general appearance, it was similar to other selection-cut sites. However, particular care appears to have been taken to retain large trees, snags and CWD in this site, perhaps because of its proximity to a then proposed Area of Natural and Scientific Interest (the Summit Lake ANSI) (Ontario Ministry of Natural Resources 1996).

The structural differences between selection-cut and old-growth forests are reflected in the abundance of specialized habitat features. Apart from the exception noted above, old-growth sites had consistently higher estimated densities of cavity trees, and higher measured abundances of large live trees, snags, and coarse woody debris than did sites cut within the past 0 to 25 years. The greater abundance of large structural features, such as big trees, snags and logs, is complemented by the fact that large snags and logs tend to be in more advanced stages of decay. Thus, old-growth stands provide potential habitat for a greater number of species. Different cavity-dependent animals often exploit snags at different stages of decay, depending upon their particular nesting or foraging requirements, and one large snag may support a series different animals throughout its slow decay and disintegration (Harmon *et al.* 1986; Runde and Capen 1987; Martikainen *et al.* 1999; McComb and Lindenmeyer 1999; Weikel and Hayes 1999). Similarly, a large log may be occupied by a series of organisms as it decays, with old, crumbling logs supporting entirely different assemblages of species than younger logs (Harmon *et al.* 1986; Bader *et al.* 1995; Crites and Dale 1998; McComb and Lindenmeyer 1999).

Cavity trees

In general, selection-cut stands seem likely to provide sufficient cavity trees to meet the standard of 5 cavity trees/ha of Anderson and Rice (1993) when 25 cm is used as the minimum diameter, but much less likely to meet the standard when 30 cm is used as the minimum. Estimated densities of cavity trees exceeded 5 trees/ha in 74% (14/19) of the selection-cut stands in the former case, but only 37% (8/19) in the latter. The GFERG (1997) target of 12 cavity trees/ha is almost certain to be missed, particularly if it is applied to cavity trees with a minimum dbh of 30 cm. Only 5% of the selection-cut stands had an estimated density of cavity trees of least 12 trees/ha when 25 cm is used as the minimum, and none met the standard when 30 cm was considered the minimum diameter. As these cavity tree estimates are based on data from stands where wildlife tree retention has been practiced since 1980, they should already reflect the cumulative effect of cavity tree retention over several cutting cycles (8 – 15 years) (Lorimer and Goodburn 1998).

These results suggest that the target of 5 cavity trees/ha recommended by Anderson and Rice (1993) is achievable, but that the target of 12 cavity trees/ha recommended by the GFERG (1997) is unrealistic in this region of northern hardwood forest. Not only did selection-cut sites fail to meet the GFERG target, so too did half of the old-growth sites, irrespective of whether one used a minimum of 25 or 30 cm dbh. In contrast, Anderson and Rice's (1993) target density of 5 cavity trees/ha with dbh ≥ 25 is is much lower than the minimum value among old-growth sites. A more precautionary target would be 7.5 cavity trees/ha with dbh ≥ 30 cm . This is closer to the minimum for old-growth sites in the current study, and the larger diameter better accommodates the requirements of cavity-dependent wildlife species. It is probably achievable in the selection-cut sites by more aggressive retention of cavity trees through multiple cutting cycles. Longer cutting cycles could also help to provide more cavity trees, as the abundance of 25 cm dbh and 30 cm dbh trees continues to increase with time, peaking at about 150 years – when stands are passing from the "aggradation" to the "transition" phase of development (Bormann and Likens 1979).

At diameters above 30 cm, the provision and monitoring of cavity trees becomes complicated by the scale of management. The problem is small at a dbh of 46 cm, but increases rapidly at larger diameters (*e.g.* 50 cm, 61 cm). Figures 5.05 – 5.08 suggest that selection-cutting provides sufficient cavity trees in the 46 cm dbh class, but falls short in the 50 cm and 61 cm dbh classes. However, given the low density of cavity trees in the 50 cm and 61 cm classes, the size of the growth plots (3 x 400 m^2) is too small to provide an adequate sample. This is reflected in figures 5.07 and 5.08, which suggest that the incidence of cavity trees in the growth plots might better be represented by a Poisson distribution. With recommended densities of 0.5 cavity trees/ha (46 cm class), 1 cavity tree/ha (50 cm class) and 0.05 cavity trees/ha (61 cm class), a sample plot of 100 ha would be more appropriate. Logistically, however, it is not feasible to sample cavity trees at this scale.

The alternative is to manage for large cavity trees (as well as other low-density habitat features) at a landscape scale, which is the approach taken by Anderson and Rice (1993) and the GFERG (1997). This approach relies upon protected areas to provide large structural features, with targets being based – in theory – on the total area needed to provide adequate levels of those features. The GFERG (1997), for example, recommends that at least 12% of each community type be maintained in an mature or overmature state, with at least 4% in the overmature age class and a minimum patch size of 375 to 500 ha in each ecodistrict. In conjunction with other good forestry practices, such as maintaining a minimum canopy cover and forest connectivity, these stands are intended to provide the large structure necessary for wildlife.

McGee *et al.* (1999) also appear to favor a landscape approach to providing large forest structure, advocating the use of increased diameter limits in selection-cut stands, extended even-age rotations and reserved shelterwood stands to provide large, live trees as sources of cavities, snags and coarse woody debris. Their targets, however, are set at the stand scale: 16 trees/ha with a dbh ≥ 50 cm, 5 of which should be ≥ 70 cm. Under current cutting practices, selection-cut sites fall well short of these targets. In fact, even in the old-growth sites, only about half the stands sampled met the target for 70 cm trees. Nor does it seem likely that selection-cutting practices can be modified sufficiently to meet these targets in the future. Eleven 50 cm trees and five 70 cm trees *per* hectare have a total basal area of 4 m^2. Since selection-cut stands are typically cut when their basal area reaches about 25 m^2/ha, these targets represent 16% of the total basal area, and about 40% of the allowable cut (assuming a cut of 10 m^2/ha). Furthermore, as with cavity trees, *per* hectare targets for large live trees are not very useful given their low density, particularly in the 70 cm size class. Landscape indicators and targets would be more practical.

Keddy and Drummond (1996) use basal area as a surrogate measure for tree size and, implicitly, for large, live cavity trees. Although this is a stand-scale measure, it is more practical than direct counts of cavity trees, because it is already included in normal stand cruising and marking activities. 15 of 19 selection-cut stands exceeded the target for "intermediate" quality forest (20 m^2/ha), with 3 of those exceeding the target for "control" forest (29 m^2/ha). All of the old-growth stands exceeded the target for "control" forest. Overall, these results suggest that the targets set by Keddy and Drummond are realistic, and that the majority of selection-cut stands should provide a moderate amount of structural features.

The weakness of this measure, however, is that the link between stand basal area and desired wildlife habitat features may be weak. A dense stand of young balsam fir, for example, can have a very large basal area, but little structure. Keddy and Drummond (1996) partially solve this problem by adding shade-tolerance as an additional criterion (Figure 5.17), but this still does not account for other even-aged stands, such as shelterwood cuts, which could have a high basal area and a high proportion of shade-tolerant trees, yet provide little structure (Brokaw and Lent 1999; Frelich and Puettmann 1999). A more direct and stronger relationship must be established between basal area and structural features, such as tree cavities, if it is to be used to assess habitat quality.

In general, these results suggest that selection-cutting can provide sufficient cavity trees in the smaller size classes (*e.g.* 25 cm, 30 cm, 46 cm), if more effort is made to identify them and retain them through multiple cutting cycles. In the larger size classes (*e.g.* 50 cm, 61 cm, 70 cm), selection-cutting does not appear to provide sufficient cavity trees, while their low density makes management for *per* hectare or stand-scale targets impractical. Surrogate, landscape-scale targets would be more appropriate for the management of these features, provided that the correlations between these targets and

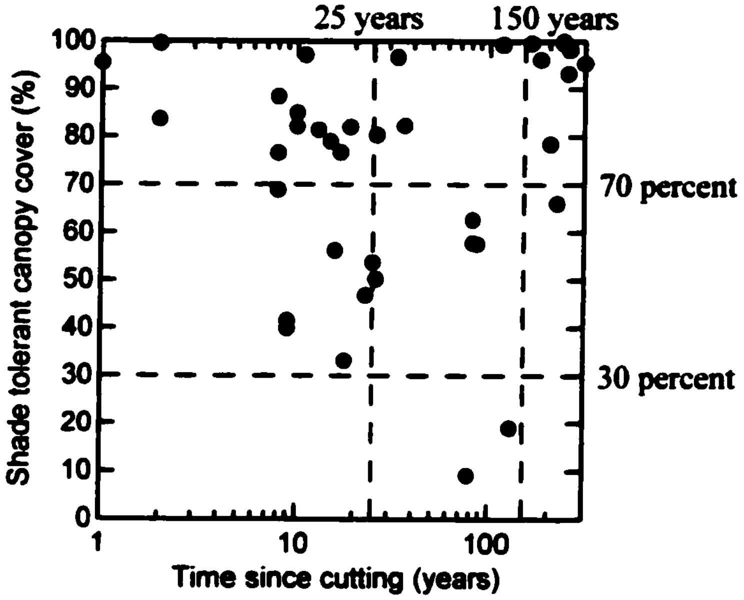


Figure 5.17. The relationship between time since cutting and the proportion of the canopy composed of shade tolerant trees, showing management guidelines of 30 (low) and 70 percent (high) (Keddy and Drummond 1996).

the desired habitat features are well-established.

Snags

The number of snags increases significantly with age whether one is using 20 cm or 30 cm as the minimum diameter. In both cases, the majority of selection-cut sites fail to meet the GFERG (1997) target of 12 snags/ha. Mature second-growth stands meet the target for 20 cm snags, but about half fall short of the target for 30 cm snags. All but 1 of the old-growth stands meet the target for 20 cm, but 4 of 7 fail to meet the target for 30 cm. One Adirondack old-growth stand, Fishing Creek, had a much larger number and basal area of snags than any other stand. The incidence of beech bark disease was very high in this stand, with 42 dead beech trees still standing in the sample plot (66 tree/ha). The other two Adirondack sites contained 5 and 14 dead beech trees.

In comparison to this study, McGee *et al.* (1999) report an average of 6.7 (+/- 5.2) snags/ha with dbh ≥ 25 cm in six selection-cut Adirondack sites, and a mean of 37.5 snags/ha with dbh ≥ 25 cm in their old-growth sites (before correction for beech bark disease). In Wisconsin and Michigan, Goodburn and Lorimer (1998) report that their selection-cut stands averaged 12 snags/ha with a dbh ≥ 30 in northern hardwood sites and 9 snags/ha in hemlock-hardwood sites. Old-growth stands averaged over 20 snags/ha in deciduous sites and over 40 snags/ha in hemlock-hardwood sites. The higher numbers in Wisconsin and Michigan may be due to a twenty-year history of wildlife tree protection (Goodburn and Lorimer 1998).

Considering the results of all three studies, a target of 12 snags/ha with dbh of either 20 cm or 30 cm seems to be realistic. Although it is generally higher than the densities currently found in this study and by McGee *et al* (1999), it is achieved in the stands studied by Goodburn and Lorimer (1999). However, most snags, we assume, will develop from live cavity trees. Consequently, the target density of snags cannot exceed the target density of live cavity trees, unless the average snag has a canopy residence time much longer than the average cavity tree – which is not the case (Tyrrell and Crow 1994). Because this target – 7.5 snags/ha with a dbh ≥ 30 cm (as discussed above) – is still within the lower range of old-growth values in this study, it should be adequate for normal wildlife needs, particularly when supplemented by landscape level provisions for larger snags.

Large snags, like large, live cavity trees, are too scarce in selection-cut sites to manage at a stand scale. Although there was a significant increase in the density of 50.8 cm dbh snags with age, comparison to the targets of Keddy and Drummond (1996) was almost meaningless. The sample plots were simply too small to extrapolate to targets for 10 ha.: half the sample plots lacked any snags, and those which contained even one snag automatically exceeded both targets. Again, this is where landscape-scale management, similar to that of the GFERG (1997), would work best.

Coarse Woody Debris

Regardless of stand age, volumes of CWD tended to be higher than the target recommended by the GFERG (1997) and lower than the target recommended by McGee *et al.* (1999). In addition, about half of the recently cut sites (0 – 25 years) exceeded the target recommended by the GFERG (1997) for pieces of coarse woody debris, with the majority of the mature, second-growth sites (25 – 150 years) falling below the target, and the majority of the old-growth sites (> 150 years) exceeding the target. These patterns appear to reflect an initial input of logging slash, its consequent decay, and the buildup of natural CWD within the stands over time (McComb and Lindenmayer 1999). It was possible to fit general linear models to these patterns, but the models were plagued with large outliers and stands with high statistical leverage. In particular, the hemlock old-growth sites appeared to have significantly greater volumes and numbers of coarse woody debris than deciduous old-growth sites, probably because conifer logs decompose more slowly than hardwood logs (Harmon *et al.* 1986).

Volumes of coarse woody debris ≥ 10 cm in diameter were lower in this study than in McGee *et al.* (1999) and Goodburn and Lorimer (1998). Volumes of CWD in selection cut stands averaged 25.5 m^3/ha (+/- 5.0 m^3/ha), whereas they averaged 49.9 m^3/ha in McGee *et al.* (1999) and 61.3 m^3/ha and 56.0 m^3/ha (for deciduous and hemlock-hardwood respectively) in Goodburn and Lorimer (1998). In old-growth sites, the volume of CWD averaged 58.8 m^3/ha (+/- 11.7 m^3/ha), versus 97 m^3/ha in McGee *et al.* (1999) (≥ 10 cm, after correction for Beech Bark Disease) and 102.2 m^3/ha and 93.9 m^3/ha (for northern hardwood and hemlock-hardwood respectively) in Goodburn and Lorimer (1998). The differences in volume could be attributable to the different plot sizes, the different methods of measurement, or the effects of regional variation in climate on rates of disturbance or decay.

In comparison to these figures, the target of 10 m^3/ha set by the GFERG (1997) for volumes of CWD is too low. In fact, it is even lower than the minimum volume found in the GFERG's (1997) own surveys (13 m^3/ha, p. 26). In contrast, the target set by McGee et al. (1999) seems too high, considering that less than half of the old-growth sites in the three studies achieve it.

The target for pieces of CWD appears realistic, judging from both the old-growth stands and the selection-cut stands. Nonetheless, about half of the selection-cut stands fall short of the target, perhaps as a result of the trend towards greater harvesting and processing of non-merchantable wood for secondary products (Anderson and Rice 1993). More stands may meet the target if logging is limited to "bole-only" harvesting, leaving tops and non-merchantable bole segments in place. In terms of volume, if we assume that the lower limit for old-growth stands reflects an adequate level of CWD, then a target of 50 m^3/ha would be appropriate for selection-cut stands. As with cavity trees and snags, this target could be supplemented by larger volumes in reserved overmature or old-growth stands.

At present, selection-cut stands fall short of this target. Eventually, however, retention of live cavity trees and snags may improve the situation. If 7.5 snags/ha with a dbh $\geq$ 30 cm are allowed to decay and topple, they can be expected to contribute between 21 and 32 m^3/ha of CWD to the forest floor (assuming a bole length of 10 to 15 m). In the short term, it may be necessary to augment current volumes of CWD by retaining and hastening the demise of some cull trees, through girdling or spot treatments with herbicides. Again, the trend away from "bole only" to more complete harvest methods such as "tree length" harvesting (Anderson and Rice 1993) should be resisted. Both MeGee *et al.* (1999) and Goodburn and Lorimer (1998) report that tree tops form a significant proportion of the CWD in selection-cut sites, and Goodburn and Lorimer

(1998) also note the important contribution of "unmerchantable" portions of boles.

The apparent difference in the abundance of CWD between the four hemlock old-growth sites and the three deciduous old-growth sites, as well as the lack of selection-cut hemlock sites, raises the issue of whether the hemlock sites should be included in any of the cavity tree, snag or CWD analyses. In the cavity tree and snag analyses, the fitted models were actually robust to the removal of the hemlock stands. Nonetheless, if the purpose of these analyses had been predictive, then it would have been prudent to limit their application to the deciduous stands. However, as the purpose of the analyses were actually descriptive and comparative, there was no compelling reason to exclude the hemlock stands.

General implications for forest management.

Chapter 3 recommended restricting selection-cutting on acid-sensitive and calcium-depleted sites, while chapter 4 recommended maintaining and restoring a diversity of forest cover types across the landscape. This chapter has discussed the usefulness of a landscape approach to providing large structural features, such as large cavity trees, snags and coarse woody debris. These observations are complementary, suggesting a unified approach to addressing the different problems of selection-cutting in northern hardwood forests.

The approach is essentially the same multi-scale approach proposed by the GFERG (1997), which combines stand-level targets for logging operations with landscape-level targets for community cover types and age classes. The stand level targets are those discussed above: (1) 7.5 cavity trees/ha with dbh $\geq$ 30 cm; (2) 7.5 snags/ha with dbh $\geq$ 30 cm; (3) 50 m^3/ha CWD with diameter $\geq$ 10 cm. The only major modifications to current selection-cutting practices required to meet these targets are a greater emphasis on the identification and retention of existing cavity trees during logging operations, and the strict use of bole-only harvesting. The use of bole-only harvesting is not only important for achieving CWD targets, but for reducing pressure on soil calcium capital (ch. 3). When there is a choice of species to retain, American beech (*Fagus grandifolia*) should be favored. This tree is preferred by cavity-dependent wildlife, it is intermediate in terms of both decay rates and persistence, and it is the least valuable economically of the hardwood species (Anderson and Rice 1993; GFERG 1997).

Identification of appropriate landscape level indicators and targets is generally beyond the scope of this research. Nonetheless, the data and analyses suggest several guidelines for selecting appropriate reserved areas. At least part of the mature and overmature forest should be provided by extending cutting cycles in calcium-deficient stands, or excluding them from cutting altogether (ch. 3). In stands where site conditions would normally favor conifers, conversion of stands from a hardwood to a conifer-dominated canopy should be considered prior to protection (see below). Mature and overmature areas should also include all significant stands of hemlock (*Tsuga canadensis*) and mature white pine (*Pinus strobus*) (ch. 4). Doing so will not only conserve these significant tree species, but will improve the wildlife habitat quality of the reserved areas. Hemlock and white pine are disproportionately over-utilized by woodpeckers for both nesting and foraging, and they persist as both cavity-trees and snags much longer than hardwood trees (Anderson and Rice 1993). In the heterogenous landscapes of the Frontenac Axis and Adirondack Park, significant proportions of the remaining mature and overmature forest can be provided by increasing the size of buffer areas around natural features, such as watercourses, or otherwise restricted areas (such as steep slopes), thereby reducing the economic impacts of conservation (Anderson and Rice 1993).

Even on the rugged Canadian Shield, however, there may be large stands of relatively homogenous forest where it is not obvious which areas should be reserved in a mature or overmature condition. Based on DeGraaf's (1984) target of 1 cavity tree/ha with a dbh ≥ 61 cm, a good guideline would be to reserve or establish 10 groups of overmature trees *per* 10 ha. If each group was 30 m in diameter, they would occupy approximately 7% of the total area. Based on a crown area of 80 to 100 m for a 50 cm dbh sugar maple (*Acer saccharum*) or American beech (Anderson and Rice 1993), each group could contain 7 to 9 overmature hardwood trees, and would go a long way to meeting stand-level targets for large cavity trees and snags. The groups would also be large enough to mark on a Forest Resource Inventory map, and to avoid during harvesting.

Steps must be taken to protect canopy diversity at both the stand and landscape scales. In addition to protecting Hemlock and White Pine, immediate action is needed to ensure the regeneration of red oak. In existing red oak stands, or stands where site conditions may favor red oak, managers should consider alternatives to single-tree selection cutting, such as group selection-cutting (Anderson *et al.* 1990; Dey and Buchanan 1995). Hand-seeding and post-cutting treatments to reduce competition from shade-tolerant tree species are essential to improve oak regeneration (ch. 4). Retention and regeneration of conifers is also important, particularly in areas of calcium depletion. Conifers, with their associated ectomycorrhizae, appear to exploit a significant pool of mineral calcium (apatite) that is unavailable to deciduous trees – particularly sugar maple, which is the only major endomycorrhizal canopy tree in the northern hardwood forest (Blum *et al.* 2002). In appropriate high elevation stands, where monitoring shows the risk of calcium depletion and aluminum toxicity to be greatest (ch. 3), managers should consider limited, bole-only clearcutting as a preliminary step to planting and re-establishing conifer-dominated stands. These would not be plantations, but would include a mix of early successional hardwood species. Once established, they would be removed indefinitely from the production forest.

Recommendations for future research

Establishing the relationships of calcium, aluminum and Ca/Al ratios with geology, elevation, acid deposition and time since cutting (ch. 3) is not sufficient for the former to be used as indicators of forest health or potential risk. Although previous research provides good evidence of their usefulness (Cronan 1994; Cronan and Grigal 1995; McLaughlin 1996) more work is needed to validate and quantify their relationships to standard forestry measures such as productivity, crown die-back and canopy transparency. In particular, local calibration of predictive models should be done for each management unit, so that managers can better estimate risks in their own jurisdictions. More work must also be done on the effects of aluminum, where there is still much to learn about the relationships between total soil solution aluminum, inorganic aluminum, toxicity, and effects on forest health. Further refinement and testing of acid deposition models would also be very helpful, particularly in order to incorporate elevation effects and to increase resolution. None of this additional research, however, should preclude earlier use of more general ecological models, or general critical values for aluminum concentrations and Ca/Al ratios.

Research is also needed on the effects of multiple cutting cycles on the nutritional status of forest soils. Due to the difficulty of obtaining long-term cutting records (in Ontario, at least), an experimental approach, using long-term monitoring of permanent sample plots would be best (*e.g.* Government of Canada 2002; Yanai 2002). However, many of the selection-cut stands in the present study are approaching the age when they are likely to be re-harvested. Assuming that the management recommendations in this thesis are not immediately implemented, these stands should be re-sampled following harvesting, using the same procedures as in the present study. This work should be accompanied by re-sampling of herbaceous vegetation, to investigate the relationships between repeated harvests, Ca levels and herbaceous layer diversity.

More long-term research is also needed on the relationship between large forest structure (*i.e.* cavity trees, snags, CWD) and plant and animal diversity. Along with soil monitoring, this should be an on-going part of a good ecosystem management program. Due to the uncertainties involved in correlational studies, research on the effects of habitat features should use repeated sampling methods, in order to control for site differences. Ironically, this research (as well as the soil research above) would benefit from the use of *poor* logging practices in a limited number of stands. These would be stands in which management was based strictly on growth and yield models, without consideration (positive or negative) for habitat features.

These recommendations imply that future management of northern hardwood forests must be considered a natural experiment, in which management plans are treated as hypotheses to be tested by long-term monitoring of their effects (Christensen *et al.* 1996). This requires a shift in paradigm for all the involved parties: for forestry companies and government management agencies, who must make the institutional changes necessary for adaptive management; and for scientific researchers, who must consider management needs when selecting and testing their hypotheses (Christensen *et al.* 1996). This are the essential requirements for effective ecosystem management (Christensen *et al.* 1996).

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Appendix A List of research sites, with descriptive information and data sets.

*Species (%) Mean age - Mean Height (m, unless otherwise specified) - Stocking, Site class, Stand area (FRI year updated).

Stand Number (OBM No.)	Stand Name	FRI Information*	Year Cut	Coring Age	Time since cutting (or age) in 1996	Source for age	Elevation	UTM Coordinates
Lavant 474	Paddy's Knoll		1997		-1	OMNR cutting records	270	49873 3732
Lavant 457h	PSP 5203 Paddy's Marsh		1996		0	OMNR cutting records	280	49881 3734
S. Canonto 671	Palmerston Lake Cut	Mh5 Or2 Bd1 He1 Be1 65-19-1.0, 1, 77 (1979)	1996		0	OMNR cutting records	300	49882 3538
108 (378)	Hardwood Lake	Po4 Mh2 Or2 B1 Be1 80-22-1.0, 1, 22 (1988)	1995		1	OMNR cutting records	410	50063 3074
S. Canonto 424	Croker Creek S.E.	Mh5 Or2 Pw1 Bw1 He1 75-21-0.7, 1, 52 (1979)	1995		1	OMNR cutting records	270	49908 3536
100-1 (326)	Heiderman Lake	Mh4 Or2 Be1 Ms 1 Ce1 Bw1 80-17-1.0, 2, 184 (1988)	1994		2	OMNR cutting records	410	50223 3219
14(305)	PSP 7000 Woermke Selection Cut	Mh7 Be2 Aw1 85-22-1.0, 1, 59 (1988)	1994		2	OMNR cutting records	410	50288 3251
Lavant 286	Paddy's Creek		1994		2	OMNR cutting records	280	49880 3732
S. Canonto 429	Summit Lake Iron Mine	Mh6 Or2 Be1 80-22-1.0, 1, 22 (1979)	1994		2	OMNR cutting records	290	49903 3545
Clarendon 84		Mh5 Or3 Po1 Be1, 60-19-1.0, x, 47 (1979)	1988		8	OMNR cutting records	350	49831 3473
Lavant G60	Poland Power Lines	Mh5 Be4 Or1 77-20-0.8, x, 10 (1988)	1988		8	OMNR cutting records	260	49929 3749
S. Canonto 417	Croker Creek N.W.	Mh4 Or2 Pw1 He1 Po1 Bd1 80-22-0.9, 1, 55 (1979)	1988		8	OMNR cutting records	290	49909 3532

S. Canonto 420	Crib Lake	Mh5 Or2 Bw2 He1 75-21-0.8, x, 10 (1979)	1988		8	OMNR cutting records	270	49906 3533
61 (370)	Black Donald Lake	Or6 Mh2 Bd1 Iw1 83-21-0.7, 1, 16 (1988)	1987		9	OMNR cutting records	280	50123 3521
68(305)	PSP 7027 Schweigerts Creek	Mh5 Or3 Bd1 Iw1 75-19-1.0, 1, 48 (1988)	1987		9	OMNR cutting records	360	50290 3291
40(303)	PSP 7013 Britchless Lake	Mh9 Bd1 102-20-0.5, 2, 24 (1988)	1986	105	10	OMNR cutting records	410	50284 3184
Clarendon 162	Crooked Lake	Mh4 Po2, Bd2, Or1, Bw1 40-15-0.9, x, 40 (1979)	1986		10	OMNR cutting records	320	49832 3478
Clarendon 100		H Or5 Mh3 Po1 Ms1 60-18-1.0, 1, 40 (1979)	1985		11	OMNR cutting records	320	49828 3478
	Swann Lake Improvement		1985		11	Anderson and Rice 1990	450	50411 6785
Clarendon 164		Mh6 Or2 Bd1 Bw1 70-21-0.9, x, 45 (1979)	1983		13	OMNR cutting records	340	49834 3475
53(327)	Two Island Lake	Mh7 Po3 80-23-0.7, x, 42 (1988)	1982		14	OMNR cutting records	350	50225 3273
S. Canonto 435	Summit Lake Bluff	Mh6 Or2 Bd1 Be1 80-23-0.9, x, 122 (1979)	1982		14	OMNR cutting records	300	49899 3555
87(303)	Buck Lake	O, Or7, Mh3 75-20-0.8, 1, 58 (1988)	1981		15	OMNR cutting records	480	50270 3165
Burns 151	PSP 7010	Mh5 Be2 Po1 Bw1 H1 52-42'-0.9, 2, 212	1981	95	15	OMNR cutting records	380	50556 2888
89 (303)	Yukes Lake	Mh3 Ms2 Or2 Bw1 Po1 By1 85-18-0.7, 2, 32 (1988)	1980		16	OMNR cutting records	470	50282 3170
Lavant 630	Clyde Forks Hunt Camp	Mh3 Bd4 Ms3 88-22-0.3, 1, 8 (1988)	1978		18	OMNR cutting records	270	49983 3645
Miller 335	Frontenac Road	Mh7 Be2 Po1 65-18-0.5, 1, 86 (1979)	1977		19	OMNR cutting records	340	49942 3336

20(329)	Crutch Lake	Mh8 Bd1 Iw1 99-21-0.8, 1, 118 (1988)	1976		20	OMNR cutting records	410	50231 3362
Lavant 506	Clyde Creek	Mh6 Or2 Bd1 Bo1 93-24-0.7, x, 44 (1988)	1973		23	OMNR cutting records	210	49995 3658
Lavant 508	Clyde Forks High Oak	Mh4 Bd3 Or2 65-23-0.8, x, 34 (1988)	1973		23	OMNR cutting records	270	49989 3656
Lavant 510	Clyde Forks Gully	Mh5 Bd3 Or2 83-21-0.7, 1, 43 (1988)	1973		23	OMNR cutting records	220	49989 3661
Lavant 511h	Clyde Forks Powerline	Mh3 Bd6 Or1 83-23-0.2, x, 10 (1988)	1971		25	OMNR cutting records	260	49985 3665
Sebastopo l 85	Clear Lake (not PSP 7002)		1963		33	OMNR cutting records	340	50330 3279
72(304)	Woermke High Oak	Mh5 Or2 Be1 Ms1 Po1 85-22-0.9, 1, 42 (1988)	1960		36	OMNR cutting records	420	50271 3244
S. Canonto 636/38	Palmerston Lake Uncut	Mh5 Or2 Bw1 Bd1 He1 40-15-1.0, x, 18 (Stand 636) (1979)			57	FRI mean age	290	49877 3528
	PSP 5009 Foley Mtn.	Or7 Bd2 Aw1			78	FRI mean age	130	49486 3912
Miller B28	Little Crag Lake	Or5 Mh2 Ms1 Bw1 65-18-1.0, 1, 60 (1979)			82	FRI mean age	350	49875 3478
N. Canonto 443	Lonewolf Lake	H Or5 Mh2 Po1 Pw1 Bw1 65-18-1.0, 1, 53 (1979)	1996		82	FRI mean age	300	50035 3590
N. Canonto 450	Straddlebug Lake	Mh6 Po2 Or1 He1 70-20-1.0, 1, 4 (1979)	1996		87	FRI mean age	305	50028 3592
14(305)	PSP 7001Woermke Mature Growth	Mh7 Be2 Aw1 85-22-1.0, 1, 59 (1988)		116	116	OMNR cutting records	410	50288 3248
56/61 (388)		Mh9 Iw1 111-22-0.9, 1, 9 (1988)			119	FRI mean age	330	50053 3596
61(388)		Mh9 Iw1 111-22-0.9, 1, 9 (1988)			119	FRI mean age	330	50053 3595
14(330)	PSP 7014 Dacre High Oak	Mh3 Or3 Bd1 Pw1 Bw1 Iw1 80-17-1.0, 2, 85 PFR (1988)		129	129	PSP coring data	350	50246 3419
Wilberforce 176	PSP 7022 Shaw Woods	Mh5 Be2 He1 By1 Pw1 97-70'-0.7, 1,		162	162	PSP coring	160	50551 3387

		210				data		
	PSP 7024 Oram Lake			172	172	PSP coring data	390	50571 2846
Miller 604	Long Schooner Lake	He3 Mh2 Bd2 Po1 Bw1 Or1 110-32-1.3, x, 12 (1979)		180	180	Oldest intact core	250	49949 3428
	Ampersand Mountain			203	203	Oldest intact core	450	48990 5620
	Algonquin Mikado			220	220	Oldest intact core	450	50384 6785
	Halfway Creek			220	220	Oldest intact core	450	49010 5630
Lanark 843	PSP 5202 Rycroft Lake	Mh 90-22-0.8, 1, 14 (1988)		Cut prior to coring			210	50086 3810
	Swann Lake Old Growth			Coring prohibited			450	50399 6785
	Saranac 1			248	248	Oldest intact core	500	49030 5640
Lanark 605.1	PSP 5201 Gunn's Lake	Mh6 Be4 75-21-0.5, 1, 9 (1988)		252	252	Oldest intact core	210	50088 3796
	Bena Lake			260	260	Oldest intact core	450	50387 6785
	Kiskebus Lake West			300	300	Oldest intact core	350	49736 3292

Appendix A continued.

Stand Number (OBM No.)	Stand Name	Structure sampled?	Herbaceous Layer sampled?	Soil sampled?
Lavant 474	Paddy's Knoll	N	Y	N
Lavant 457h	PSP 5203 Paddy's Marsh	Y	Y	Y
S. Canonto 671	Palmerston Lake Cut	N	Y	N
108 (378)	Hardwood Lake	N	Y	Y
S. Canonto 424	Croker Creek S.E.	N	Y	N
100-1 (326)	Heiderman Lake	N	N	Y

14(305)	PSP 7000 Woermke Selection Cut	Y	Y	Y
Lavant 286	Paddy's Creek	N	Y	N
S. Canonto 429	Summit Lake Iron Mine	Y	Y	Y
Clarendon 84		Y	Y	Y
Lavant G60	Poland Power Lines	Y	Y	Y
S. Canonto 417	Croker Creek N.W.	N	Y	Y
S. Canonto 420	Crib Lake	Y	Y	Y
61 (370)	Black Donald Lake	Y	N	N
68(305)	PSP 7027 Schweigerts Creek	Y	N	Y
40(303)	PSP 7013 Britchless Lake	Y	Y	Y
Clarendon 162	Crooked Lake	Y	Y	Y
Clarendon 100		N	N	Y
	Swann Lake Improvement	Y	Y	Y
Clarendon 164		Y	Y	Y
53(327)	Two Island Lake	N	Y	Y
S. Canonto 435	Summit Lake Bluff	Y	Y	Y
87(303)	Buck Lake	Y	Y	Y
Burns 151	PSP 7010	N	N	Y
89 (303)	Yukes Lake	Y	Y	Y
Lavant 630	Clyde Forks Hunt Camp	Y	Y	Y
Miller 335	Frontenac Road	Y	N	N
20(329)	Crutch Lake	N	Y	Y
Lavant 506	Clyde Creek	Y	Y	N
Lavant 508	Clyde Forks High Oak	Y	Y	Y
Lavant 510	Clyde Forks Gully	Y	Y	Y
Lavant 511h	Clyde Forks Powerline	Y	Y	Y
Sebastopol 85	Clear Lake (not PSP 7002)	Y	N	N

72(304)	Woermke High Oak	Y	N	Y
S. Canonto 636/38	Palmerston Lake Uncut	N	Y	N
	PSP 5009 Foley Mtn.	Y	N	N
Miller B28	Little Crag Lake	Y	N	N
N. Canonto 443	Lonewolf Lake	Y	Y	Y
N. Canonto 450	Straddlebug Lake	Y	Y	Y
14(305)	PSP 7001Woermke Mature Growth	Y	Y	Y
56/61 (388)		N	N	Y
61(388)		N	N	Y
14(330)	PSP 7014 Dacre High Oak	Y	Y	Y
Wilberforce 176	PSP 7022 Shaw Woods	Y	Y	Y
	PSP 7024 Oram Lake	N	N	Y
Miller 604	Long Schooner Lake	Y	Y	Y
	Ampersand Mountain	Y	Y	Y
	Algonquin Mikado	N	Y	Y
	Halfway Creek	Y	Y	Y
Lanark 843	PSP 5202 Rycroft Lake	Y	Y	Y
	Swann Lake Old Growth	Y	Y	Y
	Saranac 1	Y	Y	Y
Lanark 605.1	PSP 5201 Gunn's Lake	Y	Y	Y
	Bena Lake	N	Y	Y
	Kiskebus Lake West	Y	Y	Y

Appendix A continued.

Stand Number (OBM No.)	Stand Name	Bedrock description	Surficial geology	Bedrock category	Geology map	Notes
Lavant 474	Paddy's Knoll	Fine to medium-grained gabbro or fine to medium-grained diorite (mafic to intermediate intrusive rocks)		Siliceous	Easton 1990	
Lavant 457h	PSP 5203 Paddy's Marsh	Fine to medium-grained gabbro or fine to medium-grained diorite (mafic to intermediate intrusive rocks)	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990	
S. Canonto 671	Palmerston Lake Cut	Siliceous clastic metasedimentary rocks OR Siliceous clastic metasedimentary rocks, may include felsic and intermediate metatuffs and metasedimentary rocks of mainly volcanic origin	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990; Easton *et al.* 1995a	
108 (378)	Hardwood Lake	Biotite diorite suite intrusive rocks -- diorite and related mafic rocks	Unknown	Siliceous	Lumbers 1954	
S. Canonto 424	Croker Creek S.E.	Quartzose gneiss, gneissic metasediments OR biotite-magnetite-quartz-orthoclase dikes and veins OR biotite-hornblende-quartz-plagioclase gneiss (mafic meta-arenite, mafic metawacke)	Ice contact sediment: boulder and/or cobble gravel, gravelly sand, sand, minor silt and diamicton; 5 to 30m thick	Siliceous	Easton 1990; Easton *et al.* 1995a	
100-1 (326)	Heiderman Lake	Alkalic suite intrusive rocks -- alkalic syenite OR Alkalic granite	Drift, generally less than 1 m. with abundant bedrock exposure	Siliceous	Lumbers 1954	
14(305)	PSP 7000 Woermke Selection Cut	Alkalic granite OR mafic alkalic rocks	Drift, generally less than 1 m. with abundant bedrock exposure	Siliceous	Lumbers 1954	
Lavant 286	Paddy's Creek	Fine to medium-grained gabbro or fine to medium-grained diorite (mafic to intermediate intrusive rocks)		Siliceous	Easton 1990	
S. Canonto 429	Summit Lake Iron Mine	Gabbroic Gneiss	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990; Easton *et al.* 1995a	

Clarendon 84		Grey and white laminated marble; massive grey and white marble (carbonate metasediments)		Calcareous	Pauk and Mannard 1987
Lavant G60	Poland Power Lines	Fine to medium-grained gabbro or fine to medium-grained diorite (mafic to intermediate intrusive rocks)	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990
S. Canonto 417	Croker Creek N.W.	Tonalite gneiss, generally migmatic OR biotite-magnetite-quartz-orthoclase dikes and veins (felsic intrusive rocks)	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990; Easton *et al.* 1995a
S. Canonto 420	Crib Lake	Silicaseous clastic metasedimentary rocks: may include felsic and intermediate metatuffs and metasedimentary rocks of mainly volcanic origin	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990; Easton *et al.* 1995a
61 (370)	Black Donald Lake				Easton 1990
68(305)	PSP 7027 Schweigerts Creek	Anorthosite, or alkalic syenite, or mafic alkalic rocks	Glaciofluvial outwash and deltaic deposits: gravel, gravelly sand, sand, usually >1m, with occasional bedrock outcrops	Siliceous	Lumbers 1954
40(303)	PSP 7013 Britchless Lake	Alkalic granite	Drift (<1m) OR Till (>1m), both with bedrock exposures	Siliceous	Lumbers 1954
Clarendon 162	Crooked Lake	Grey and white laminated marble; massive grey and white marble (carbonate metasediments)		Calcareous	Pauk and Mannard 1987
Clarendon 100		mafic gneiss OR felsic to mafic gneiss of mixed volcanic and sedimentary origin		Siliceous	Pauk and Mannard 1987
	Swann Lake Improvement	Granite, gneiss, syenite	Loamy to silty sand, thin till, ground moraine, <u>drumlin</u>	Siliceous	OMNR 1972a
Clarendon 164		Grey and white laminated marble; massive grey and white marble (carbonate metasediments)		Calcareous	Pauk and Mannard 1987

53(327)	Two Island Lake	Calcareous metasediments -- carbonate metasediments	Till, >1m, sandy to silty, stony, with occasional bedrock outcrop	Calcareous	Lumbers 1954	
S. Canonto 435	Summit Lake Bluff	quartzose gneiss, gneissic metasediments OR biotite-hornblende-quartz-plagioclase gneiss (mafic meta-arenite, mafic metawacke)	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990; Easton *et al.* 1995a	
87(303)	Buck Lake	Alkalic granite	Drift, <1m, with frequent bedrock exposure	Siliceous	Lumbers 1954	FRI indicates oak working group. Cutting records show selection cut.
Burns 151	PSP 7010	Granite, gneiss, syenite		Siliceous	OMNR 1972b	Height is questionable
89 (303)	Yukes Lake	Alkalic suite intrusive rocks -- alkalic syenite	Drift, <1m, with frequent bedrock exposure	Siliceous	Lumbers 1954	
Lavant 630	Clyde Forks Hunt Camp	Calcite marble, massive (carbonate metasedimentary rocks; calcite)	Till, <1m, discontinuous over bedrock	Calcareous	Easton 1990	
Miller 335	Frontenac Road					
20(329)	Crutch Lake	Anorthosite suite instrusive rocks -- monzonite and syenite rocks	Drift, <1m, with frequent bedrock exposure	Siliceous	Lumbers 1954	
Lavant 506	Clyde Creek	Dolomite marble, massive & siliceous dolomite marble, massive, with quartz tremolite segregations (carbonate metasedimentary rocks; dolomite)		Calcareous	Easton 1990	Last species illegible
Lavant 508	Clyde Forks High Oak	Calcite marble, massive (carbonate metasedimentary rocks; calcite)	Till, <1m, discontinuous over bedrock	Calcareous	Easton 1990	
Lavant 510	Clyde Forks Gully	Dolomite marble, massive & siliceous dolomite marble, massive, with quartz tremolite segregations (carbonate metasedimentary rocks; dolomite)	Till, <1m, discontinuous over bedrock	Calcareous	Easton 1990	

Lavant 511h	Clyde Forks Powerline	Dolomite marble, massive & siliceous dolomite marble, massive, with quartz tremolite segregations (carbonate metasedimentary rocks; dolomite)		Calcareous	Easton 1990	
Sebastopol 85	Clear Lake (not PSP 7002)					
72(304)	Woermke High Oak	Alkalic granite	Till, usually >1m, sandy to silty, stony, with occasional bedrock outcrop	Siliceous	Lumbers 1954	
S. Canonto 636/38	Palmerston Lake Uncut	Diortic to gabbroic rocks	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990; Easton *et al.* 1995a	
	PSP 5009 Foley Mtn.					
Miller B28	Little Crag Lake					
N. Canonto 443	Lonewolf Lake	Calcite marble, massive (carbonate metasedimentary rocks; calcite)	Till, <1m, discontinuous over bedrock	Calcareous	Easton 1990	Cut after sampling.
N. Canonto 450	Straddlebug Lake	Migmatic quartz diorite to tonalite gneiss (Tonalitic to Trondhjemitic intrusive rocks)(Bartraw Dome).	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990	Cut after structure and soil sampling.
14(305)	PSP 7001 Woermke Mature Growth	Alkalic granite OR mafic alkalic rocks	Drift, <1m, with frequent bedrock exposure	Siliceous	Lumbers 1954	
56/61 (388)		Migmatic quartz diorite to tonalite gneiss (Tonalitic to Trondhjemitic intrusive rocks)(Bartraw Dome).		Calcareous	Easton 1990	
61(388)		Migmatic quartz diorite to tonalite gneiss (Tonalitic to Trondhjemitic intrusive rocks)(Bartraw Dome).		Calcareous	Easton 1990	
14(330)	PSP 7014 Dacre High Oak	Calcareous metasediments -- carbonate metasediments	Drift, <1m, with frequent bedrock exposure	Calcareous	Lumbers 1954	
Wilberforce 176	PSP 7022 Shaw Woods			Calcareous	OMNR 1972b	
	PSP 7024 Oram Lake	Granite, gneiss, syenite		Siliceous	OMNR 1972b	

Miller 604	Long Schooner Lake	Silicaseous clastic metasedimentary rocks: may include felsic and intermediate metatuffs and metasedimentary rocks of mainly volcanic origin	Till, <1m, discontinuous over bedrock	Siliceous	Easton *et al.* 1995a	
	Ampersand Mountain	metanorthosite and anorthositic gneiss	Till, depth varies	Siliceous	Caldwell and Pair 1991; Isachsen and Fisher 1970.	
	Algonquin Mikado	Granite, gneiss, syenite	Loamy to silty sand, thin till, ground moraine, drumlin	Siliceous	OMNR 1972a	
	Halfway Creek	metanorthosite and anorthositic gneiss	Till, depth varies	Siliceous	Caldwell and Pair 1991; Isachsen and Fisher 1970.	
Lanark 843	PSP 5202 Rycroft Lake	Dioritic to gabbroic rocks: mainly flows of mafic metavolcanic rocks	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990	Only 20 herbaceous plots. Cut prior to coring. Old sugar bush. Meets criteria for old-growth.
	Swann Lake Old Growth	Granite, gneiss, syenite	Loamy to silty sand, thin till, ground moraine, drumlin	Siliceous	OMNR 1972a	Identified as old growth by Anderson and Rice (1990). Coring prohibited by OMNR
	Saranac 1	metanorthosite and anorthositic gneiss	Till, depth varies	Siliceous	Caldwell and Pair 1991; Isachsen and Fisher 1970.	
Lanark 605.1	PSP 5201 Gunn's Lake	Fine to medium-grained diorite (mafic to intermediate intrusive rocks)	Till, <1m, discontinuous over bedrock	Siliceous	Easton 1990	

	Bena Lake	Granite, gneiss, syenite	Loamy to silty sand, thin till, ground moraine, drumlin	Siliceous	OMNR 1972a	
	Kiskebus Lake West	Diortic to gabbroic rocks (mafic intrusive rocks)		Siliceous	Easton *et al.* 1995b	

Appendix B. Soil data.

Stand number	Stand name	Age	Cutting treatment	Bedrock type	Elevation	Acid deposition	pH organic	pH mineral	Ca organic (ppm)	Ca mineral (ppm)	Al organic (ppm)	Al mineral (ppm)	Ca/Al molar ratio (organic)
PSP 5203	Paddy's Marsh	1	Select	Siliceous	270	High	6.1	5.3	15.04	42.20	1.69	31.92	5.990374
	Hardwood Lake	1	Select	Siliceous	410	High	4.2	5.2	4.15	3.42	1.87	10.08	1.493516
PSP 7000	Woermke Select	2	Select	Siliceous	410	Low	4.9	5	*79.98**	19.07	*19.08**	13.13	2.821347
	Heiderman Lake	2	Select	Siliceous	410	Low	5.9	6.1	29.67	11.37	2.19	3.80	21.067604
S. Can 429	Summit Lake	2	Select	Siliceous	290	High	5.7	5.3	17.41	18.94	0.44	4.77	26.716515
S. Can 417	Croker Crk. N.W.	8	Select	Siliceous	290	High	5.3	4.7	10.47	4.79	0.72	2.54	9.850834
Lavant G60	Poland Power	8	Select	Siliceous	260	High	5.1	5.4	23.47	7.11	2.47	5.82	6.4
Clarendon 84		8	Select	Calcareous	250	High	5.9	5.2	19.39	12.44	0.22	1.53	59.37
S. Can 420	Crib Lake	8	Select	Siliceous	270	High	5.6	5.1	13.56	10.77	0.45	14.87	20.461197
PSP 7027	Schweigerts Crk.	9	Select	Siliceous	360	Low	4.8	5.2	11.83	8.17	0.52	10.04	15.340431
PSP 7013	Britchless Lake	10	Select	Siliceous	410	Low	5.3	4.5	17.75	4.65	1.00	4.75	11.917458
Clar 162	Crooked Lake	10	Select	Calcareous	320	Low	6.1	6.3	21.31	15.83	0.44	2.10	32.82
Clarendon 100		11	Select	Siliceous	320	High	5.4	4.3	17.71	12.51	0.68	1.98	17.513659
Clarendon 164		13	Select	Calcareous	340	High	6.2	4.8	33.09	12.67	0.70	1.06	31.91
53(327)	Two Island Lake	14	Select	Calcareous	350	Low	5.4	5.3	20.93	26.96	0.54	6.84	26.062498
	Scott Lake Improve	11	Select	Siliceous	450	High	4.8	4.8	7.83	2.22	1.27	15.99	4.148
PSP 7010		15	Select	Siliceous	370	Low	5.5	5.2	5.35	3.45	1.38	15.98	2.604417
87(303)	Buck lake	15	Select	Siliceous	480	Low	5.7	4.8		12.19		7.89	
S. Can 435	Summit Lake	17	Select	Calcareous	300	High	6	6.7	16.25	3.73	0.21	0.29	51.204
89(303)	Yukes Lake	16	Select	Siliceous	470	Low	5.1	4.9	5.46	7.40	0.94	6.50	3.894988
Lavant 630	Clyde Hunt	18	Select	Calcareous	270	High	4.8	5.7	14.83	12.83	0.66	4.80	15.17944
20(329)	Crutch Lake	20	Select	Siliceous	410	Low	5.3	5.3	17.23	2.51	1.68	5.72	6.897627
Lavant 511h	Clyde power	25	Select	Calcareous	260	High	6.5	6.4	4.14	2.99	0.27	0.86	10.19242
Lavant 508	Clyde hi oak	23	Select	Calcareous	270	High	5.3	5.5	16.48	6.49	0.43	4.25	25.724558
Lavant 510	Clyde gully	26	Select	Calcareous	220	High	6.2	6.8	6.73	2.73	0.17	0.26	26.6199
72(304)	Woermke hi oak	36	Select	Siliceous	420	Low	5	5.2	17.48	12.25	1.07	20.13	10.982864
N. Canonto 4	Lonewolf Lake	82	Select	Calcareous	300	High	5.3	5.3	15.15	14.87	0.32	5.70	31.55
N. Canonto 4	Straddlebug Lake	87	Select	Siliceous	300	High	5.4	5.3	11.67	7.03	0.98	2.80	8.025211
PSP 7001	Woermke Mature	116	Select	Siliceous	410	Low	4.7	5	13.99	18.78	1.20	10.69	7.829882
61(388)		119	Select	Calcareous	330	High		5.2	18.57	5.75	1.14	1.73	10.992454
56(388)		119	Select	Calcareous	330	High	5.7	5.6	11.69	10.20	0.36	3.79	21.683026
PSP 7014	Dacre High Oak	129	Select	Calcareous	350	Low	5.5	5.2	16.66	7.93	2.07	2.60	5.41
PSP 7024	Oram Lake	172	Select	Siliceous	390	Low			4.64	6.82	0.66	13.04	4.756943
	Long Schooner Lake	180	Old	Siliceous	260	High	5.2	5.8	20.42	4.48	0.85	2.44	16.139942
	Ampersand Mtn	203	Old	Siliceous	450	High	4.5	4.4	3.24	6.08	0.92	11.16	2.365567
	Halfway Creek	220	Old	Siliceous	450	High	3.3	4.3	2.96	2.63	0.79	20.97	2.529745
	Algonquin Mikado	220	Old	Siliceous	450	High	4.4	4.5	3.39	1.17	4.78	13.60	0.476639
	Saranac	248	Old	Siliceous	500	High	4.5	4.7	4.15	1.26	3.22	12.52	0.866745
PSP 5201	Gunn's Lake	252	Old	Siliceous	200	High	6.8	5.1	6.71	7.63	0.14	1.38	31.3822
	Bena Lake	260	Old	Siliceous	450	High	4.5	5.5	3.38	1.21	1.92	5.76	1.182605
	Kiskebus Lak	300	Old	Siliceous	360	High	4.8	5.1	8.04	3.15	0.94	6.22	5.754113

*probable dilution error