

Interpretation of age-structure gaps
in hemlock (*Tsuga canadensis*) populations of Algonquin Park

by

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in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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CHAPTER 1

INTRODUCTION

Casual observation has suggested that an intermediate size gap may exist in eastern hemlock (*Tsuga canadensis* (L.) Carr.) in Algonquin Provincial Park, Ontario. Seedlings and mature canopy trees are common but sapling sized individuals (especially stems less than 20 cm diameter at breast height (1.3 m) (dbh)) are noticeably less frequent. In comparison, sapling-sized individuals of other conifers such as spruce (*Picea* spp.) and balsam fir (*Abies balsamea* (L.) Mill.) and deciduous species such as sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britt.) are commonly encountered (S. Vasiliauskas, pers. obs.).

The preliminary objective of the present study was to examine whether this apparent size gap is real and if so, whether it reflects an intermediate age gap in the hemlock population in Algonquin Park. The principal objective was to explore possible underlying causes of this intermediate size/age gap. For example, has something killed large numbers of hemlock before they reached intermediate ages? If so, and if the cause(s) of this early mortality is (are) persistent and continuing, the population of hemlock in Algonquin Park may be threatened with local extinction.

The genus Tsuga

Hemlocks are evergreen coniferous trees of the genus *Tsuga* (Endl.) Carr. (Pinaceae), a

gymnosperm family with 9 genera and 210 species worldwide. There are 10 - 18 species of Tsuga (depending on the botanical interpretation) found in North America, Japan, Taiwan, China and the Himalayas (Hosie 1979, Krussman 1985, Elias 1989). No species of hemlock are native to Europe, but hemlock pollen fossils have been found in peat bogs in Poland and France, and wood fossils elsewhere.

Four species of hemlock are native to North America. Western hemlock (Tsuga heterophylla (Rafn.) Sarg.) and mountain hemlock (T. mertensiana (Bong.) Carr.) are western cordillera species, while Carolina hemlock (T. caroliniana (Engelm.)) is restricted to the lower slopes of the Blue Ridge Mountains in North and South Carolina, Tennessee, Virginia and northern Georgia (Elias 1989). Eastern hemlock is found within the Great Lakes-St. Lawrence and Acadian forest regions of Canada (Hosie 1979) and in the northern United States from Minnesota and Wisconsin east to New England and south in the Appalachians to Tennessee and northern Alabama (Elias 1989).

Hemlocks can be readily identified by a drooping leader and an irregular branching pattern compared to other members of the Pinaceae. The needles are single and borne on a very short stalk. The bark is usually deeply furrowed and reddish brown to cinnamon red in colour (Krussman 1985, Elias 1989).

Silvics of eastern hemlock

Hemlocks are monoecious, with small cones compared to other members of the Pinaceae. Average ovulate cone length is 15-30 mm, while T. mertensiana has the longest cones at 50-80 mm (Krussman 1985). The cones are produced in the spring, mature in the same year, and shed small, winged seeds in the fall and early winter. The cones can persist on the tree into the second year (Fowells 1965, Krussman 1985, Godman and Lancaster 1990). Wind pollination of the ovules occurs within 2 weeks of bud burst and fertilization within 6 weeks of pollination. The seeds are 1.6 mm

long in eastern hemlock, larger than seeds of western hemlock, but smaller than those of mountain or Carolina hemlock. Most seeds are shed within 1 tree height of the parent tree due to the small seed wing, but seeds can also drift on crusted snow for up to 1 km (Anderson *et al.* 1990, Godman and Lancaster 1990). Seed production starts at about 40 years and can continue for the next 4 centuries. Good cone crops in eastern hemlock occurred in 61% out of 32 years in a study in Wisconsin. Successive good crops occurred for one 5-year period, while poor crops only occurred for a maximum of 2 consecutive years (Godman and Lancaster 1990).

The seeds must go through cold stratification before they can germinate. Seeds can be easily damaged by drying. A constant temperature of 15 °C is optimum for germination in eastern hemlock, which is similar to that for yellow birch (an associated species), but higher than sugar maple (Fowells 1965, Godman and Lancaster 1990). A warm, moist site is necessary for seedling establishment, rather than a cool, moist site as commonly thought (Godman and Lancaster 1990). These microsites are usually found on rotten logs, stumps and mounds that normally are warmer and more moist than the forest floor. Similar sites are necessary for western hemlock, and this is combined with the avoidance of competition from other vegetation that occurs on the forest floor (Harmon and Franklin 1989). The seedlings have 3 - 6 seed leaves and usually grow 25 - 38 mm with roots penetrating 13 mm into the soil in the first year. Growth picks up after the second year, once the roots are deeper into the soil (Hosie 1979, Elias 1989, Godman and Lancaster 1990). No hemlock species are known to form root or stump sprouts, and only rarely is layering encountered (rooting of a lateral branch into the substrate, followed by upward growth of the branch end to form a new trunk) (Fowells 1965, Godman and Lancaster 1990).

Growth is slow in the young seedling stages, usually due to suppression from an existing canopy, which is also considered necessary for initial seedling establishment. Usually hemlock stands have a large component of even-aged trees with older age classes present that provide shelter for the next generation. In Pennsylvania, hemlock were found to rarely germinate and establish in open

areas, and also few seedlings germinated under an open canopy because of moisture stress.

Germination was good on prepared sites under a young canopy, especially on north slopes (Godman and Lancaster 1990).

Eastern hemlock is considered among the most shade tolerant of all tree species (Rowe 1972, Elias 1989) and can withstand suppression for up to 400 years (Godman and Lancaster 1990). Kavanagh and Kellman (1986) found that hemlock stands were more frequent on cooler and drier, moderate to steep north and west facing slopes in Algonquin, while less frequent on warmer east aspect and knoll sites. Hemlock were displaced from mesic areas by hardwood competition and so restricted more to slopes and cooler aspects.

Forest succession and eastern hemlock

Eastern hemlock has most of the features characteristic of a late successional, or k-selected, species (Finegan 1984, Anderson *et al.* 1990). It is long-lived, grows slowly to a large size, and is reproductively mature after 40 years, later than most conifers (Godman and Lancaster 1990). The seedlings and saplings are very shade tolerant and can photosynthesize at low light levels. However, it also has several features characteristic of early successional, or pioneer, species. The seeds are light and can be wind-dispersed for up to 1 km. It is also a prolific seeder, with up to 29,000,000 seeds/ha in a good seed year, but usually about 25% of these are viable (Anderson *et al.* 1990). All of these features would help to maintain hemlock in a dominant position in late successional forests.

A Clementsian view of forest succession was given by Martin (1959) with hemlock dominated forests as the climatic climax for Algonquin Park. Forests dominated by pioneer species after a disturbance would be succeeded by white pine (*Pinus strobus* L.) forests with a gradual change to hardwood forests dominated by sugar maple and yellow birch, and ultimately, hemlock dominated forests. The successional sequence would require 1000 years from the initial disturbance,

provided a disturbance did not set back the successional pathway to an earlier stage. Martin (1959) considered that the abundance of a species in the understory was not indicative of the future forest composition. Instead, the ability of a species to grow into the canopy while under suppression and shading was more important, and so hemlock with its greater shade tolerance would eventually dominate the hardwood forests. Martin arrived at this conclusion despite a lack of hemlock seedlings and saplings in the study areas that would suggest that this process was taking place. Curtis (1958) considered hemlock less shade tolerant than sugar maple, and would eventually be replaced by sugar maple as the climax species for northern mesic forests. Curtis based this on the lack of hemlock regeneration compared to the abundance of sugar maple in the understory of Wisconsin forests.

Connell and Slatyer (1977) presented three models to explain the successional pathways that can occur on a site following a disturbance. The problem with the models, as has been outlined by Finegan (1984) and others, is that the same field situation can be interpreted differently. For example, hemlock can fit into any of these models, depending on the point of view of the observer and the current forest structure. The facilitation model could be used to explain how hemlock is invading a stand dominated by pioneer species such as poplar and white birch, provided hemlock are younger than the pioneer canopy. This is because the canopy would provide some shading to prevent seedling dessication and facilitate seedling establishment. However, if the hemlock are the same age as the pioneer overstory, such as a post-fire stand, then the tolerance model would be applied (also described as initial floristic composition). The hemlock are tolerating the presence of the overstory, but would probably grow faster without it. If the stand was surveyed while it was in the stem exclusion phase of forest stand development (Oliver and Larson 1990), this could be viewed as inhibition because of the lack of regeneration or undergrowth. As can be seen, hemlock does not neatly fit into a particular model, hence the inadequacy of these models. Other models must be used to adequately describe the successional pathways within hemlock stands.

It is more important to understand forest dynamics rather than concentrate on fixed

successional pathways. How can species coexist with other species with different life histories within the same stand? Forcier (1975) presented a model to explain coexistence of sugar maple, beech and yellow birch within the same stand. Any model must incorporate disturbance as a normal feature of the forest, and that the scale of the disturbance can affect species composition (Pickett and McDonnell 1989). Small disturbances such as single tree falls would favour late successional species, while larger disturbances such as windthrow or fire would favour early successional species.

Size and age distributions in tree populations

In a forest dominated primarily by shade tolerant species, the forest structure is characterized by the presence of all age and size classes. These different classes are the result of past disturbances creating many small, even-aged patches from gaps caused by tree mortality or windthrow. The frequency of these different classes is best described by an inverse J-shaped curve (Leak 1965, Lorimer 1980, Anderson and Rice 1993). The greatest stem frequency is in the younger and smaller stem classes, and stem frequency decreases rapidly into the mature stem classes, with a low frequency of stems in each class, but a wide range of classes. Even-aged forests can also be characterized by this same distribution when considering a number of stands of different ages (Lorimer 1980). Age structures have been investigated in many studies for a variety of species, and most have described an inverse-J age or diameter distribution (eg. Morey 1936, Hett and Loucks 1976, Lorimer 1980, Shotola *et al.* 1992, Mikan *et al.* 1994, Tardif *et al.* 1994).

Age gaps have been described for a number of woody species (Wardle 1963, Beveridge 1965, Mellanby 1968, Veblen and Stewart 1982, Watson 1983, Mikan *et al.* 1994). An age gap at the stand level would be considered normal due to the stem exclusion stage in forest dynamics (Oliver and Larson 1990). However, when considering stands on a landscape level, with a variety of stand ages and disturbance histories, an age gap for one or more species could be indicative of one or more factors affecting regeneration of a species.

A number of factors have been implicated for creating age gaps in tree populations, and usually involves the prevention of successful seedling establishment or sapling recruitment. This includes biotic factors such as ungulate browsing (Mellanby 1968, Watson 1983, Anderson and Katz 1993), and allogenic factors such as climate change (Wardle 1963) or changes in disturbance regimes (Mikan *et al.* 1994), or a lack of disturbance (Veblen and Stewart 1982, Stewart and Rose 1989, Lusk and Ogden 1992).

In the Pennsylvania Piedmont, an age gap has developed in chestnut oak (*Quercus prinus* L.) stands due to a change in the disturbance regimes. Fires and logging of coppice stands promoted oak regeneration and sapling growth and prevented establishment of other hardwoods. Once the logging stopped and fires were suppressed, other hardwoods such as red maple (*Acer rubrum* L.) could get established and excluded any new oak growth. At present, oak seedlings survive for only a few years (Mikan *et al.* 1994).

In Scotland, age gaps in Scots pine (*Pinus sylvestris* L.) are attributed to red deer (*Cervus elaphus*) browsing eliminating regeneration since the late 1700's (Watson 1983). Age gaps in English oaks (*Quercus robur* L.) in England are attributed to grazing and deer browsing (Mellanby 1968).

Age gaps in mountain cedar (*Libocedrus bidwillii* Hook. f.) in New Zealand are attributed to a lack of disturbances that would have created suitable seedling establishment sites (Veblen and Stewart 1982, Stewart and Rose 1989). The age gap in several New Zealand podocarp species in the South Island is attributed to drier conditions between 1300 and 1800 creating conditions unsuitable for seedling establishment (Wardle 1963, Beveridge 1965). Other species such as *Weinmannia racemosa* L.f. and *Dacrydium cupressinum* Lamb. were replacing *Dacrycarpus dacrydioides* (A. Rich. de Laub.) in South Westland, New Zealand. The former two species were favoured by the lack of major disturbances causing unsuitable conditions for seedling establishment for the latter species (Duncan 1993).

Graham (1941) suggested that the even-aged structure and lack of hemlock regeneration in

northwestern Michigan to frequent groundfires eliminating the younger hemlock. Anderson and Katz (1993) attributed the lack of hemlock regeneration and saplings to deer browsing in the northern Great Lakes states.

It is apparent that age gaps are a widespread phenomena. They may be more widespread than the literature indicates, as high ungulate populations, a frequent cause of age gaps, currently exist in eastern North America (Butt 1984). Changes in forests can be important from a wildlife perspective, as these changes can adversely affect wildlife populations. For example, a change in forest cover from conifer dominated to hardwood dominated in areas with deep snow cover would adversely affect white-tailed deer (Odocoileus virginianus Zimmerman) populations that utilize the conifer stands for shelter and food (Verme 1965, Butt 1984). Consequently, it is important to document age gaps and understand the possible causes of age gaps.

Hypotheses for a contemporary intermediate age gap in hemlock

Size and age are often poorly correlated within plant populations due to phenotypic plasticity (Silvertown and Lovett-Doust 1993). If the intermediate size gap of hemlock in Algonquin Park does not reflect an intermediate age gap, the most likely cause of the gap would be persistent suppression of understory trees by long-lived canopy trees. However if the intermediate size gap reflects an intermediate age gap (eg. between 40 and 100 yr), there are at least six hypotheses to consider based on the literature and preliminary field observations (Figure 1). More hypotheses may exist and could be considered for future work. It should be noted that more than one hypothesis may contribute to the age gap.

Seed predation hypothesis. *Between about 40 to 100 years before present (ybp), a period of intense seed predation limited seed dispersal and/or germination.* Hemlock seeds in Algonquin Park are probably consumed by crossbills (Loxia spp.), red squirrels (Tamiasciurus hudsonicus Erxleben), red-backed

voles (Clethrionomys gapperi Vigors), chipmunks (Tamias striatus L.) and other rodents. No data are available on population numbers of these species, but none of these seed predators feeds exclusively on hemlock. Moreover, periodic seed masting in hemlock would have permitted several seeds to escape predators over this time period. Hence, this hypothesis is less plausible than others, and will not be considered further.

Seedling establishment hypothesis. *Between about 40 to 100 ybp, environmental conditions (e.g. climate) were unusually poor for seed germination and/or seedling establishment compared with before and after this period.*

Under this hypothesis, hemlock should be currently recruiting into intermediate age classes. General remarks of an unusual climate during this period are unknown. Nevertheless, local data on mean monthly rainfall in the summer months were obtained for as far back as records are available to explore this possibility more carefully.

Seedling establishment could also be limited by a lack of suitable germination sites. In west coast Picea - Tsuga forests, seedling establishment was limited to logs due to competition from moss and understory vegetation (Harmon and Franklin 1989). Preliminary surveys suggested that although hemlock was abundant on old logs, it was not limited to these sites. Heavy competition from understory vegetation was found to limit white pine regeneration in a number of sites in Algonquin Park (Carleton et al. 1995). Due to the open nature of most hemlock stand understories and the current abundance of regeneration on some sites, along with a minor moss presence, these factors appear unlikely to play a part in the age gap, except to restrict regeneration in local areas.

Hare browsing hypothesis. *Between about 40 to 100 ybp, the snowshoe hare (Lepus americanus Erxleben) population in Algonquin Park was much larger than both before and after this period, thus causing heavy hemlock seedling mortality during this period.* Browsing by snowshoe hare can limit hemlock and other conifer seedling growth (Krefting 1953, Telfer 1972, Rogers 1978). Hares may assist in maintaining a

continuing age gap if tree mortality occurs as a consequence of bark removal in older saplings and cutting of seedlings. To address this hypothesis, a search was made for records of snowshoe hare numbers in Algonquin Park and browse damage of hemlock seedlings and saplings by hares was quantified in vegetation surveys.

Stem exclusion hypothesis. *In a young, recently established stand, intense competition (eg. for growing space, moisture and nutrients) among crowded saplings prevents further seedling establishment until the canopy matures and random tree mortality frees up growing space and a new cohort can establish in the understory.* The period between cohorts would create an age gap at the stand level. This has been reported in numerous studies and is considered a normal feature of forest stand dynamics (Alaback 1982, Oliver and Larson 1990). The stem exclusion stage has been estimated at about 80 to 90 years in mixed oak, maple and birch stands in New England (Oliver and Larson 1990), while for shade tolerant species such as coastal Alaskan silver fir (*Abies amabilis* (Dougl.) Forb.) and western hemlock stands it can last for 100 to 150 years (Oliver *et al.* 1985).

Cyclic recruitment has been suggested by Hett and Loucks (1976) to explain gaps in age structures of hemlock and balsam fir populations. Because stands will be in different stages of development, age gaps should involve older age groups in older stands to be consistent with the stem exclusion hypothesis. This was tested in the present study.

Ungulate browsing hypothesis. *Heavy browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) and/or moose (*Alces alces* L.) reaches a threshold level resulting in sapling mortality and leaving a bulk of young hemlock seedlings (which avoid winter browsing beneath the snowline) under an aging hemlock canopy.* Heavy browsing of hemlock by white-tailed deer has been reported in numerous studies (Hosley and Ziebarth 1935, Stoeckler *et al.* 1957, Graham 1958, Curtis 1959, p. 188, Beals *et al.* 1960, Telfer 1972, 1978, Rogers 1978, Anderson and Loucks 1979, Butt 1984, Whitney 1984, Frelich and Lorimer 1985,

Runkle 1990, Anderson and Katz 1993, Mladenoff and Stearns 1993). Browsing may be concentrated especially above the snowpack when food is scarce in the winter. Deer browsing can alter sex ratios (more male plants) and reproductive fitness (less seeds produced) in yew (Taxus canadensis Marsh.) (Allison 1990, 1992). In many cases, deer populations have increased to very high densities in the northern Great Lakes states, especially in the winter yard areas (Verme 1965, Anderson and Katz 1993).

No studies have implicated moose browsing as affecting hemlock regeneration, but studies have shown that moose have adversely affected balsam fir regeneration on Isle Royale (Snyder and Janke 1976, Risenhoover and Maass 1987, Brandner et al. 1990, McInnes et al. 1992), and moose have almost eliminated yew and mountain ash (Sorbus L. spp.) from the same area. Heavy browsing has resulted in a more open forest as canopy trees die and are not replaced. Balsam fir and white birch regeneration has also been adversely affected by high moose populations in Newfoundland (Bergerud and Manuel 1968, Thompson et al. 1989, Thompson and Curran 1993). Heavy ungulate browsing in many areas has greatly reduced regeneration of other conifer and hardwood species in eastern North America (Hough 1965, Verme 1965, Butt 1984, Heinen and Sharik 1990) following legislation and implementation of game laws. Cut areas in hardwood stands have become more open and dominated by ferns, goldenrods (Solidago L. spp.) and woody shrubs (Butt 1984).

This hypothesis was explored in the present study by comparing age structure and evidence of ungulate presence in a variety of hemlock stands that are likely to have experienced different levels of impact from ungulates. I predicted that intermediate age gaps would be most distinct in sites where deer are known to have congregated (eg. deer yards).

Canopy suppression hypothesis. *In hemlock dominated stands, hemlock canopy trees are so long lived that saplings are suppressed to their tolerance limit and then die leaving a bulk of younger seedlings under an aging canopy.*

This effect has been previously reported with a high seedling mortality rate in sugar maple stands

(Forcier 1975). Suppressed understory hemlock trees, however, have been commonly observed in excess of 100 - 200 years of age (Curtis 1959, Fowells 1965). Suppressed understory hemlock can also omit some annual rings (Turberville and Hough 1939), resulting in underestimates of ages for saplings. Hence, support for this hypothesis would require that age gaps should generally involve age groups in excess of 100 years. This was tested in the present study.

History of hemlock in Algonquin Provincial Park

Hemlock migrated onto the Algonquin Dome approximately 7900 ybp with the gradual shift from boreal to mixed forests following glacial retreat of the last ice age. White pine and hemlock were the dominant species when sugar maple and beech arrived about 5700 ybp and became codominants. White pine subsequently declined in importance and hemlock remained dominant for the next 2000 years until approximately 4800 ybp, when hemlock declined rapidly over a 60 year period and became a minor forest component (Earle 1979).

Differing views concerning the cause of this hemlock decline exist. Allison *et al.* (1986) maintain that a pathogen precipitated the decline, as it was rapid (approximately 60 years) and occurred simultaneously over the entire range of hemlock in northeastern North America (Boucherle *et al.* 1986). Other species affected by pathogens in this century include chestnut (*Castanea dentata* (Marsh.) Borkh.) from chestnut blight (*Endothia parasitica*) in the eastern United States (Sinclair *et al.* 1987), and larch killed by larch sawfly (*Pristiphora erichsonii*) in northwestern Ontario and Minnesota (Webb and Drooz 1967). These declines corresponded with rapid decreases in pollen amounts in sediment cores.

Others (Earle 1979) consider that the hemlock decline was more prolonged and started at different times in different regions, presumably due to a climatic change to warmer and drier conditions. McAndrews (1973, cited in Earle 1979) estimated that the decline took about 530 years, starting at 5800 ybp at Van Nostrand Lake, and 6000 ybp at Second Lake, Ontario. At Belmont Bog,

New York, the decline took 600 years (Spear and Miller 1976 cited in Earle 1979). As a result, the 'hemlock decline' appears to have occurred over a period of 600 years, rather than 60 years, in southern Ontario (Earle 1979).

Other species have also shown rapid declines in the pollen record, apparently due to a climatic change to warmer and drier conditions. Spruce and pine in the early Holocene declined 20 fold within 50 to 100 years around Lake Ontario (McAndrews 1972, cited in Earle 1979), and from 90% to 5% of the pollen content at Van Nostrand Lake (McAndrews 1973, cited in Earle 1979). Other rapid pollen declines include poplar (Populus sp. L.) and larch (Larix laricina (Du Roi) K.Koch.) at Basswood Road Lake, New Brunswick (Mott 1975, cited in Earle 1979) and Rogers Lake, Connecticut (Davis 1969).

The hemlock decline may be a combination of both pathogen and climatic effects, as older hemlock may have been weakened by warmer, drier conditions and this may have facilitated a pathogen attack. Declines are a complex phenomenon and usually not caused by a single factor. Sugar maple declined in Quebec during the 1980's (Houle 1990) and this was considered due to acid rain. The decline may have been from a combination of acid precipitation, winter thaws causing premature budbreak, drought, tapping for maple syrup and insect attack mediated by the promotion of maple monocultures in sugar bushes. Sugar maple decline in four Pennsylvania stands was initiated by a series of summer droughts and defoliations in the mid-1960's and early 1970's (Kolb and McCormick 1993). There was repeated pear thrip (Taeniothrips inconsequens Uzel) damage in the 1980's and a 1988 drought, along with further defoliations by fall cankerworm (Alsophila pemetaria (Harris)) and linden looper (Erannis tiliaria (Harris)) in 1984-86. Crown dieback was >30% on 21% to 78% of all trees scored across the four stands.

Another consideration regarding the pathogen hypothesis is that there are few contemporary diseases affecting hemlock. Heartrot is caused by Fomes pini (= Phellinus pini), Polyporus schweinitzii (= Phacolus schweinitzii), Polyporus balsameus, and Poria subacida. Armillaria mellea

can damage weakened trees (Fowells 1965, Sinclair *et al.* 1987). Hemlock loopers (Lambdina fiscellaria and L. athasaria) can defoliate trees and cause mortality of weakened trees (Fowells 1965, Rose and Lindquist 1985). A new serious pest of hemlock is hemlock wooly adelgid, (Adelges tsugae Annand) accidentally introduced to Virginia in around 1960 and with recent reports of spread to as far as Rhode Island and Connecticut (McClure 1990). It has killed thousands of trees in hemlock stands in Connecticut within 2-3 years of infestation, and has the potential to cause a major hemlock decline in New England if it spreads farther, and is not limited by cold winter temperatures (McClure 1990).

The hemlock minimum continued up to about 3800 ybp. During this period white pine, sugar maple and spruce increased in dominance, replacing the hemlock which had declined (Earle 1979). The climate was dry and warm compared to more recent climate. From 3800 to 450 ybp, beech was at a maximum, but hemlock increased in importance along with sugar maple, yellow birch and white spruce, while white pine declined to minor importance. This period was more moist than before. During the same time, the northern limit of hemlock in Ontario did not change (Kavanagh and Kellman 1986). Over the last 450 years and up to about 100 years ago, while the climate became cooler and still more moist, white pine and spruce increased, sugar maple and beech decreased and hemlock remained dominant. Over the last century white pine has declined due to harvesting, with hemlock, beech and white elm (Ulmus americana L.) slowly declining as well. Sugar maple abundance has increased, suggesting replacement of white pine by sugar maple (Earle 1979).

A pollen study in Algonquin Park at Greenleaf Lake in Barron Township (Cwynar 1977) does not reveal much about hemlock decline or importance, as hemlock is currently not a characteristic species on the east side of the park. Instead early and intermediate successional species such as white and red pine (Pinus resinosa Ait.), white birch (Betula papyrifera Marsh.) and aspen (Populus spp.) are dominant, primarily due to a fire cycle of 80 to 100 years, compared to a fire cycle of 900 - 1000 years on the west side of the park (Cwynar 1977, Quinby 1988).

Hemlock was cut for tanbark in the adjacent districts of Parry Sound, Muskoka and Haliburton from the 1880s until the 1930s. This resulted in the loss of most hemlock stands and their replacement by maple. The only hemlock cut in the park for this purpose was in the extreme southwest of the park adjacent to Muskoka and Haliburton (MacFie 1971, Strickland 1987). No major cutting of hemlock took place in the park until the 1950s and 1960s, when large volumes were cut for the construction of the Toronto subway system. Some authorities have blamed the demise of the deer in the park on this logging, but this may have been coincidental with the maturation of forests disturbed at the turn of the century (Strickland 1987). Currently small volumes of hemlock are cut on a selective basis in Algonquin when markets exist for the lumber, as it is usually in low demand and low in value. Trees are marked and only about 20% of the canopy cover is removed as the species is sensitive to sudden exposure to sunlight from overcutting (Anderson *et al.* 1990). Hemlock within hardwood stands are left for wildlife shelter and stand diversity. During the period 1978 - 1984, hemlock accounted for 8% of the annual volume of wood cut from the park (Strickland 1987).

History of ungulates in Algonquin Provincial Park

At the outset of this study, the most compelling hypothesis for age structure gaps in hemlock was the ungulate browsing hypothesis. Accordingly an overview of ungulate presence in Algonquin Park is provided here. White-tailed deer were not present in the Algonquin area prior to European settlement and logging in the 1800s (Smith and Borczon 1977). It is believed that deer were only present in Ontario south of the Canadian Shield and were very rare or absent from Central Ontario in 1620 (Smith and Borczon 1977) due to unsuitable habitat (mature forests with infrequent disturbances and little available browse combined with severe winters).

As logging for white and red pine moved up the Ottawa Valley in the 1820's, the disturbances from cutting and subsequent fires fuelled by the slash resulted in major changes to the

forests of the area. Ideal deer habitat was created in the burned and cut areas from the abundant regrowth of trees, shrubs and herbaceous vegetation, including many areas in Algonquin.

Creation of the park in 1893 protected the deer population from hunting and they rapidly increased in numbers. No organized surveys were conducted at this time, but estimates from park rangers in the 1920's gave figures of tens of thousands of deer (Robinson 1933) and other anecdotal evidence cites figures of 60,000 or more deer (Bice 1980, R. Tozer, pers. comm.). Even in the 1920's, rangers noted the lack of available browse in the deeryards and along lakeshores (Robinson 1933) and deer dying from winter starvation (Strickland 1990).

The high deer population of the 1920's crashed to an estimated 3,000 animals by 1932 (Robinson 1933) and subsequently recovered to an estimated 30,000 - 36,000 animals by 1958 (Runge and Theberge 1974). A study was conducted by Stephenson (1958) in Biggar and Wilkes townships in the north-west part of the park to determine deer densities and browsing in a 205 km² area. Light and moderate winter concentration areas were mapped and densities were determined in winter and summer for the two density types. Winter densities were much higher than summer densities for both types, with winter densities of 16 deer/km² in the light areas and 24.5 deer/km² in the moderate areas. During the summer the deer disperse more widely, and densities in the light concentration areas dropped to 7.5 deer/km² and 5.9 deer/km² in the moderate winter concentration areas. Extrapolating the summer densities to the present park area would give a population estimate of 45,500 to 58,000 deer. Populations crashed again during the severe winters of 1958-59 and 1959-60 and only moderately recovered to 14,000 by 1974, subsequently declining to the present estimate of 1,000 deer, most of which are in the east part of the park (Strickland and Rutter 1993).

It is considered that moose have always been in the park area, with an estimated population of 1200 before human intrusion (Wilton 1987). Moose numbers remained low due to the high incidence of brainworm (*Parelaphostrongylus tenuis*) carried by the deer and fatal to the moose (Strickland and Rutter 1993). Moose numbers increased in the 1930's with low deer numbers

(Robinson 1933), but have since remained low up until the late 1970's. Moose numbers have since expanded and based on winter aerial surveys are estimated at 4,000 (0.5/km²). This has been considered the highest moose density in Ontario (Addison et al. 1985, Morgan and Quinn 1991).

The negative impact of deer on forest regeneration in Algonquin Park was first noted in the 1940's with the lack of yellow birch regeneration in recently cut areas (Strickland and Rutter 1993). No reports have cited damage to hemlock regeneration at this time. Stephenson (1958) found that hemlock constituted 0.2% to 0.3% of the stems in the study area, and 27% of the hemlock twigs available from these stems were browsed in the light concentration area, and increased to 70% in the moderate concentration area.

A central question in the present study was: is the current level of browsing intense enough to maintain age gaps in hemlock populations, or are age gaps a consequence of past intense browsing with populations currently expanding into intermediate age classes? Data collection in the present study included evidence of current ungulate browsing and ungulate droppings, as well as any evidence of recent mortality of browsed seedlings and saplings in vegetation surveys. In addition, current browsing effects and other potential causes of mortality were recorded in a seedling and sapling monitoring study spanning a period of two years, and in a sapling transplant experiment.

CHAPTER 2

METHODS

Study area

The study was conducted within an approximate area of 3500km² in the western half of Algonquin Provincial Park in southern Ontario, from 78°02'00" to 79°02'00" W longitude and 45°11'30" to 46°10'00" N latitude (Appendix I). Geologically the area is referred to as the Algonquin Dome, as it is 200 - 300 metres higher than the surrounding area and with a cooler, more humid climate. The soils on the upland areas are primarily sandy loams originating from glacial tills and till veneers and are usually less than 1 metre deep. Low areas usually have organic soils while former glacial spillways have deeper sands, gravels and sandy loams (Anderson *et al.* 1990). The area is primarily northern hardwood forest, dominated by sugar maple, yellow birch, eastern hemlock, and beech. Lakeshores are dominated by coniferous species, especially hemlock, but including balsam fir, white pine, *Thuja occidentalis* L. (white cedar), and yellow birch.

Selection of stands

A total of 18 stand types were initially selected based on a factorial design of 3 working groups by 3 aspects by 2 cutting categories, with 20 replicate stands per type (Fig. 2a). The three distinct working groups were based on the Forest Resource Inventory (FRI) mapping (OMNR 1977).

A working group is defined as a group of forest stands (group of trees that are similar in age, height, density and species composition) of the same species or group of species and are managed silviculturally in the same manner. The first working group, 'hemlock dominant' stands, had greater than 50% basal area (defined as the cross-sectional area of all standing trees on a unit area, usually expressed as m²/ha) coverage by hemlock. The second working group consisted of hemlock groves or patches ('hemlock patch' stands) within hardwood-dominated stands with the basal area of

hemlock less than 50% and sugar maple as one of the hardwood species. Within the patches, the hemlock had their crowns touching (i.e. not separated by other species). The patch must have a minimal area of 0.04 ha. The third working group consisted of hard maple stands with hemlock present as scattered individuals (referred to as 'scattered hemlock' stands). Based on the FRI, hard maple has the greatest basal area while the hemlock component is less than 30%.

Aspect (direction that a slope faces expressed in degrees from true north) is important with respect to understory vegetation variation in white pine stands (B. Chambers, pers. comm.). The same could be true in hemlock stands; sites were classified into northern and southern aspects with knolls as a third category. South facing slopes will have an aspect between 91 degrees and 270 degrees, while north facing slopes will be between 271 degrees and 90 degrees. North facing slopes may be cooler and more humid than south slopes; thus hemlock growth may differ on them. Knolls are defined as small hills or ridges elevated at least 10 m above the immediately surrounding terrain with a top not exceeding 1 ha (M. Wilton, pers. comm.). The top would not have any definite aspect and would usually be flat or very gently sloping. Knolls are important for ungulates such as moose and deer as a place for bedding (Hosley and Ziebarth 1935) and calving, as they have a clear view of predators that may be approaching from below and so can escape down the other side of the hill (Wilton and Garner 1991). Hemlock are also important for these same species for cover and food, and so they may affect hemlock regeneration.

Cutting was another factor that I was interested in examining due to its possible effects on hemlock regeneration. I used this as another selection factor and classified potential sites as either cut or uncut. I chose the year 1945 as a separation between cut and uncut sites, as some sites may have been cut for white pine during the 1800's and not since, or they may have been cut for yellow birch during the Second World War. I was primarily interested in sites cut within the last 40 years.

There are 25 townships in the study area and I randomly placed the plots within the study area in proportion to the number of stands of each working group within a township. That is, if a

township had 10% of all of the hemlock working group stands in the study area, then 10% of the hemlock dominated plots would be placed within that township. This was accomplished by counting all of the hemlock working group stands and all of the sugar maple-hemlock working group stands within the study area. From these findings, I determined what percentage of stands from these two working groups were within each township compared to the whole study area and assigned that percentage of the preselected plots for each working group to that township. Stands were then selected at random from the FRI using random number tables as each FRI stand is numbered consecutively starting at 1 for each township. Each stand was subsequently classified by aspect, stand type and cut history using aerial photographs and FRI cutting maps and records.

As the study progressed, it appeared that hemlock regeneration and age structure may relate to past and current browsing by deer and moose, proximity to a lakeshore and the history of early (pre-1945) disturbance (i.e. pine harvest or fire). Accordingly, stands were classified a posteriori based on these factors (Fig. 2b). In the second field season, I increased the sample size of lakeshore plots and concentrated on plots that were within deeryards (areas where white-tail deer congregate every winter for food and shelter, exerting high browsing pressure on hemlock) and areas outside of yards which appear to have low browsing pressure. Lakeshore plots were defined as plots located within 60 m of a permanent water body.

Field survey methods

Field work was conducted from April - November 1991, May - November 1992, April - October 1993, and October - November 1994. During the first field season 181 plots were established. Thirty-five additional plots were established in the second field season, bringing the total to 216 plots. Additional data including tree mortality was recorded from all plots in the second and third field seasons. A seedling monitoring study and a transplant experiment were set up in the second field season and followed up during the third and fourth field season (see below).

Once a stand had been located in the field, the plot centre was placed randomly using a random number table for distance and direction. Once the centre was identified, a visual inspection was made to determine if the site satisfied the three criteria that it was preselected for (stand type, aspect, cut/uncut). If these criteria were not met, either the stand was reclassified (eg, if it was an uncut site and had been previously classed as cut), or another direction and distance was selected from the random number table in order to select a plot that met the required criteria. Plots on knolls were determined differently. Once a knoll or ridge was located, a compass direction that approximated the direction to the knoll was chosen, rather than the next direction on the random number table.

To locate the plot centre in stands with scattered hemlocks, a hemlock was first located based on a random compass bearing (as above). To randomly place the selected hemlock stem within the plot, the centre was located at a random distance and direction from the centre of the hemlock (using a random number table) up to a maximum distance of 11.28 m.

Main plots

The main plots were circular with an area of 400 m² (radius 11.28m). Within each plot, data were recorded for all trees starting from true north relative to the plot centre and proceeding in a clockwise direction. Tree distance was measured from the plot centre to the centre of the tree, and recorded with the azimuth (direction) from the plot centre for relocation. All trees greater than or equal to 9.5 cm dbh were identified by a number painted on the trunk and recorded by species, height and diameter at breast height (dbh, or 1.3 m). All trees between 5.0 cm and 9.4 cm dbh were classified as saplings and data recorded included species, height and diameter but not direction and azimuth. Diameters were taken to the nearest 0.1 cm and heights were taken to the nearest 0.1 m. Increment cores were used to age all trees (>5.0 cm dbh) and hollow trees were recorded with their minimum age. The cores were stored in plastic straws, taped at the ends, and labelled with stand and

tree number for aging in the lab.

Cut stumps were recorded by species, year of cut, and diameter. Year of cut was known from cut history maps obtained from the Ministry of Natural Resources. In the case of pre-1945 stumps (for which records do not exist), year of cut was estimated from the date of release (abrupt increase in radial growth of stems upon removal of competition from adjacent stems) of neighbouring stems. All dead trees were identified by species, diameter and decay class (Thomas 1979).

Hemlock seedling and small sapling data

Data on all hemlock seedlings defined as <5 cm dbh were recorded in 1991 within 10 m X 10 m subplots centred within the main plots and the sides oriented in a N-S direction. To enlarge the data set, these data were recorded within the remainder of the circular plots in 1992. Seedlings were aged by counting terminal bud scale scars or by cutting the seedlings and collecting a stem section from the base for ageing in the lab. Larger seedlings up to 5.0 cm dbh were aged by increment coring at the stem base. Age, height, and browse damage were recorded for each seedling. Browse damage was expressed as the length of the seedling damaged by browsing divided by seedling height and recorded as a percentage. Browsing was classified as hare or ungulate (moose or deer) browsing based on twig ends. Ungulates break twigs off leaving a rough twig end whereas hares bite through the twig leaving a smooth twig end. If it was not possible to identify the browsing species, it was recorded as unknown. Seedlings which germinated in 1990 were counted and recorded separately. For all dead seedlings, height and evidence of browsing were recorded. Pellet groups encountered within the plot were identified by species, (deer, moose or hare) and number of groups.

The Microflex PC-1000 datalogger was used in the field for data collection. This reduced time spent on data entry and provided preliminary data compilation. The basis for the program was provided by Scott Christilaw of the North Bay Technology and Development Unit of the Ministry of

Natural Resources based on the Integrated Timber and Wildlife Cruising (ITAWCRUZ) program currently in use for timber cruising. Data collection methodology described above was adapted from the Central Ontario Forest Ecosystem Classification field manual (Chambers and Lee 1993), so that some of the data could be used in other research studies.

Seedling monitoring

Two thousand hemlock seedlings were tagged with aluminum tags from September to November 1992 to examine the relationships between seedling height, browsing and mortality. An additional 819 seedlings that germinated in 1990 and 74 that germinated in 1992 were also monitored within 26 randomly selected patches that were outlined with tree marking paint for ease of relocation. Study sites were located in the townships of Clyde, Lawrence, Peck, Finlayson, Canisbay, Nightingale and Sproule (Appendix I). Accessibility in the winter by road, snowmobile or skis was important for obtaining snow depth measurements. Fifty-six sites were selected with a desired goal of 40 tagged seedlings per site. However, some sites had as few as 10 tagged seedlings due to a scarcity of seedlings. Most sites were from the main hemlock survey for ease of seedling relocation. A few sites were randomly selected outside of the main hemlock survey. The majority of sites were in hemlock dominated stands due to low numbers of seedlings on hardwood dominated sites. In order to include a range of seedling sizes, approximately half of the selected seedlings were more than 50 cm tall (above approximate snowline), and the other half were less than 50 cm tall (below the snowline). Seedlings were otherwise selected randomly.

Initial data recorded for each seedling included height to tip of the leader, estimated age, overhead canopy type (conifer, hardwood or mixed), estimated percent canopy cover, previous browse damage (recorded by the methods described above), and location of the seedling for future relocation. Maximum snow depths were taken over three weekends in March 1993 at five randomly selected points within each site. The snow was considered to be at the maximum depth at this time

based on personal observations throughout the winter.

In 1993 and 1994 I recorded new seedling height to the tip of the leader, browse damage since the last inspection, and cause of mortality if it could be determined. All marked patches of 1990 and 1992 germinants were also recounted to determine mortality rates.

Hemlock transplants

To further study the relationship between height and browsing 730 hemlock saplings were collected at random along roadsides and within forest stands during November 1992 (Appendix I). Only saplings between approximately 50 cm and 200 cm tall and with little or no previous browse damage were selected. The saplings were otherwise selected haphazardly. The saplings were transplanted in groups of 40 - 45 to 17 separate plots which lacked hemlock saplings of similar size. Transplant plots were selected haphazardly and had to be easily accessible. The plots were classified as cut (10) and uncut (5) hardwood stands, and cut (1) and uncut (1) hemlock-hardwood stands. Saplings were transplanted into randomly selected locations within the plot. Each sapling was staked using dead branches to prevent premature uprooting or burial by snow, and marked with a numbered piece of flagging tape attached near the base for relocation.

Initial data recorded on each sapling included height, estimated age, and percentage of crown previously damaged. The saplings were reexamined in April 1993 after snowmelt. New browsing was identified by source (ungulate or hare) and the length of crown damaged and new sapling height were recorded.

Data analyses

Statistical analyses were performed using Statgraphics Plus 7.0 (Manugistics Inc. 1994). Parametric statistics were used wherever assumptions of normality and variance homogeneity were met. If heterogenous variances remained after data transformation, non-parametric statistics (eg. Kruskal-Wallis, Mann Whitney-U tests) were used.

CHAPTER 3

RESULTS

General stand structures

Twenty-five tree species with dbh ≥ 9.5 cm were encountered in the study (Table 1). The five most frequently encountered species were hemlock (N=1999), sugar maple (N=1079), balsam fir (N=223), red maple (N=216), and yellow birch (N=212). Eleven species were uncommon, with only 1 to 5 stems found. The diameter distributions of all stems ≥ 5 cm dbh (Figure 3a, N = 5159) displayed an inverse-J decrease in stem frequency with increasing diameter and with a low relative frequency of stems greater than 70 cm dbh. Sugar maple stems also showed an inverse-J diameter distribution, with most stems < 20 cm dbh (Fig. 3b, N=1312). However, the diameter distribution of hemlock stems ≥ 5 cm dbh compared to sugar maple stems was more skewed toward the larger diameter classes (Fig. 3c, N=2213) (Mann-Whitney U-test, Z=17.48, P<0.001). The two largest trees were white pine: 101 cm and 103 cm dbh. The largest hemlock was 98.6 cm dbh.

A total of 982 stems (23.3%) ≥ 9.5 cm dbh (for all species) could not be aged due to rot, but are included in the diameter distribution histograms (Fig. 3). It should be noted however that all of the age histograms reported below do not include hemlock stems with rot (N=423) as only a minimum age could be obtained for them (range of 18 - 276 years).

When examining age distributions of all stems from all species within the study sites, a negative exponential curve is evident (Figure 4a, N=4139). The oldest tree was a 430-year-old hemlock followed by a 387-year-old yellow birch (Table 1). Addition of stems < 5 cm dbh would greatly increase the frequency of the younger age classes. (The slight increase in relative frequency of stems in the 90 to 120 year age classes may be due to the increased

disturbances in the park in the late 1800s from logging and fires. This may have caused an increase in recruitment at this time.) Sugar maple ages were strongly skewed toward the younger age classes, (<100 years) with a small peak at 120 years and tapering rapidly beyond 120 years to a maximum age of 284 years (Fig. 4b, N=1107). Hemlock stems ≥ 5 cm dbh had more of a unimodal, or normal distribution, with most stems in the 100 - 200 year age classes (Fig. 4c, N=1787). This suggests that an age gap is not present when considering the forest as a whole and sugar maple separately, but for hemlock there is a noticeable scarcity of trees between 40 - 100 years of age. Correcting for the difference in hemlock age between ground and breast height (1.3m) where increment cores were taken, this would put the age gap at about 64 - 124 years. (The mean age of 1.3 m tall hemlock seedlings was 24 years).

Hemlock seedlings and saplings less than 5 cm dbh (N=19794) were generally < 40 years old (Fig. 5a). Of this number, only 6.4% (N=1264) were ≥ 1.3 m tall and only 435 seedlings were 2 m or more tall, but still less than 5 cm dbh (Fig. 5b). This does not include the 1990 (2-year-old) cohort (N=5400).

Total basal areas were significantly different between cut and uncut plots (One-way ANOVA, F-ratio=69.9, P<0.001), between the three working groups (Kruskal-Wallis Test statistic =49.1, P<0.001) and between lakeshore and nonlakeshore plots (One-way ANOVA, F-ratio=9.7, P=0.002). Uncut plots had more basal area (41.75 m²/ha) than cut plots (29.5 m²/ha). Hemlock dominant plots (42.00 m²/ha) had more basal area than hemlock patch plots (37.00 m²/ha) and these had more basal area than scattered hemlock plots (28.25 m²/ha). Nonlakeshore plots had less basal area (35.25 m²/ha) than lakeshore plots (41.75 m²/ha). Basal area was not related to aspect (ANOVA, F-ratio=0.20, P=0.8).

The number of seedlings (< 5 cm dbh and > 2 years old) per plot differed

significantly between stand types (Kruskal-Wallis Test statistic =93.67, N=216, $P<0.001$), between lakeshore and nonlakeshore plots (Kruskal-Wallis Test statistic =34.16, $P<0.001$) and between cut and uncut plots (Kruskal-Wallis Test statistic =6.6, $P=0.01$). More seedlings were within lakeshore plots (4984/ha) and hemlock dominated plots (4562/ha), and the least number of seedlings were within scattered hemlock plots (319/ha) and nonlakeshore plots (1650/ha). Cut plots had less seedlings than uncut plots. There was no significant difference in seedling number based on aspect type ($P=0.9$) or deeryard versus non-deeryard plots ($P=0.7$).

Basal area of hemlock on all plots was positively related to the number of hemlock seedlings per plot (linear regression, F-ratio=57, $r^2=0.211$, $P<0.001$, d.f.=215). Conversely, basal area of all other species was negatively related to the number of hemlock seedlings (linear regression, F-ratio=16.5, $r^2 = 0.071$, $P<0.001$, d.f.=215). There was a stronger negative relationship for sugar maple basal area alone (F-ratio=30.9, $r^2 = 0.126$, $P<0.001$).

On cut plots (N=95), the number of hemlock seedlings had a significant positive relationship with total basal area (linear regression, $T= 3.37$, $r^2=0.109$, $P=0.001$) and hemlock basal area (linear regression, $T= 5.1$, $r^2=0.22$, $P<0.001$), but had a negative relationship with sugar maple basal area (linear regression, T-value=-4.23, $r^2=0.162$, $P<0.001$). Removed basal area was not related to the number of hemlock seedlings (linear regression, T-value=-1.58, $r^2=0.01$, $P=0.11$). The only site factor that was significantly related to mean canopy age (all species) was stand type (One-way ANOVA, F-ratio=40.0, $P<0.001$). Hemlock dominated plots were significantly older than hemlock patch plots which were significantly older than hardwood-hemlock plots. Aspect type, whether the plot was cut or uncut, within or outside of a deeryard, or near a lakeshore was not significantly

related to mean canopy age (ANOVA, F-ratio<2.3, P>0.13).

1990 was an apparent mast year based on the number of seedlings from this cohort (N=5400). The only site factor that was significantly related to mast seedling number was stand type (Kruskal-Wallis test statistic = 32.6, N=216, P<0.001). Within cut plots, significantly more mast seedlings were found (multiple regression, T-value=-2.41, P=0.018, d.f.=119) as sugar maple basal area decreased, while removed basal area had no significant effect (T-value=1.38, P=0.17). Interestingly, mast seedlings on cut plots decreased slightly with increasing hemlock basal area (T-value=-1.7, P=0.09), suggesting that other factors may affect mast seedling establishment. Total basal area of cut plots had a slight positive relationship with the number of mast seedlings (T-value=1.93, P=0.06). The number of mast seedlings increased significantly as seedling numbers increased (linear regression, F-ratio=6.35, $r^2=0.03$, P=0.012).

Climate factors affecting seedling establishment

Climate records were analyzed to examine whether the hemlock age gap might be related to factors that may have defined an earlier period of poor seedling establishment. Huntsville, Ontario (79°15' W., 45°20'N.) was selected as the nearest weather station for climatic data (approximately 75 km west of the study area) because it has records available to 1879. Dwight (79°01'W, 45°20'N) is closer to Algonquin Park but has records to only 1973 (S. Radecki, Ontario Climate Centre, pers. comm.). There are gaps in the record for which one or more months are unavailable.

From 1894 to 1985 the total annual rainfall (\bar{x} =697 mm) did not change significantly (linear regression, $r^2 = 0.021$, P=0.33, d.f.=47). Records were incomplete or unavailable for

1904, 1905, 1908-1924, 1926-1928, 1941, 1942, 1945, 1949, 1951-1964, 1967, 1979, 1984 and 1985, and partial values are not included in the analysis. However, the total annual snowfall (\bar{x} = 269 cm) increased significantly over the same period (linear regression, F-ratio = 7.99, r^2 = 0.14, $P=0.007$, d.f.=47) as did the total annual precipitation (\bar{x} = 967 mm) (Fig. 6a, linear regression, F-ratio = 5.9, r^2 = 0.114, $P=0.019$, d.f.=47). Summer rainfall (May - August) since 1879 did not change significantly (linear regression, d.f. = 67, $p=0.84$). Summer records were not complete for 1880, 1884-1890, 1909-1922, 1967, 1979 or 1985.

Mean annual temperature (\bar{x} =5.15° C, range =2.9° C - 7.1° C)has not changed significantly since 1911 (Fig. 6b, linear regression, F-ratio = 2.18, r^2 = 0.04, $P=0.15$, d.f.=47). Consequently, global warming does not appear to be increasing local annual temperatures. Temperature records were incomplete or unavailable for 1879-1910, 1923, 1924, 1927, 1929, 1948-1951, 1953, 1954, 1957, 1958, 1960, 1961, 1963, 1965, 1967, 1978-1980, 1982 and 1985.

Hare browsing

There have been very few studies on snowshoe hares (Lepus americanus Erxleben) in Algonquin Provincial Park. MacLulich (1937) provided data from Biggar Lake in Biggar Township, from 1932 to 1935. The density of hares in an area of about 5 acres (2 ha) ranged from a high of 7 in 1933 to 1 in 1934 and 1935. The forest in this area was typical of the west side of the park, with a predominance of sugar maple in the upland areas, hemlock, white pine and spruce on the slopes, and balsam fir and black spruce in the lower areas. There have been no recent studies on snowshoe hares in Algonquin Park (R. Tozer, pers. comm.). Similar hare numbers may exist in the park today.

Hare droppings were checked in all plots during the main surveys. Only one pellet group was found in 1991, 6 pellet groups in 1992 and 2 in 1993. Pellets could have easily been missed by falling in amongst the ground litter after snowmelt and/or being obscured by ground vegetation.

Hares had a minor browsing effect on seedlings compared to moose. Hares browsed 1/10 as many seedlings as moose did in the main hemlock survey but with about the same percentage removed from each seedling (Table 2). Hares appear to browse significantly more per seedling (T-test, $T=2.07$, $P=0.04$) in lakeshore (31.5%, $N=132$) compared to nonlakeshore plots (27.7%, $N=253$). This may be due to lower snow depths near lakeshores as they are usually conifer dominated compared to upland sites. Hares also browsed significantly more (T-test, $T=-2.00$, $P=0.046$) in plots outside of deeryards (30.5%, $N=165$) compared to plots in deeryards (27.0%, $N=220$). The percentages given in Table 2 may be less than what was actually lost, as it was not possible to determine the original heights of the browsed seedlings. During the field work, I estimated an absolute loss of 10 cm from the leader of each browsed seedling, and the monitoring experiment demonstrated that it was greater than this amount (See Fig. 23). Hare browsing was a minor factor in the seedling monitoring experiment, as only 39 seedlings (1.95% of all seedlings) were browsed by hares in 1992-1993 and 56 (2.8%) in 1993-1994.

Effect of stand structure on seedling growth

Hemlock grew faster in hemlock patch and scattered hemlock plots compared to hemlock dominated plots. Hemlock may have benefitted from the adjacent hardwoods, by receiving more light in the lower part of the crown and with more fertile and less acidic soils.

Percent height increases over two years in the tagged seedlings were significantly different between conifer and mixed or hardwood cover types for unbrowsed seedlings (One-way ANOVA, F-ratio=9.13, P=0.0001, d.f.=1160). Unbrowsed seedlings with conifer cover had the least percent height increase (\bar{x} =22.0%, N=776) and seedlings under hardwood cover had the greatest increase (\bar{x} =33.1%, N=78), while seedlings with mixed cover had an intermediate increase (\bar{x} =26.9%, N=307). Seedlings did not differ significantly in percent height increase between hardwood and mixed cover. There were no significant differences among the three cover types in percent height increase over two years for initially browsed seedlings (One-way ANOVA, F-ratio=1.99, P=0.14, d.f.=347).

Stem exclusion

Mean canopy ages had an approximately normal distribution (Fig. 7), with a slight skew to the left. The range was from 17.9 years to 281.4 years. Mean ages are based on stems ≥ 9.5 cm dbh. As mean canopy age increased, the number of hemlock seedlings increased significantly across plots in the main survey (exponential linear regression, F-ratio=28.8, $r^2 = 0.119$, P<0.001) (Fig. 8). Sites with younger canopies were more likely in the stem exclusion stage of forest stand development (Oliver and Larson 1990) and so would have fewer seedlings, as conditions had not improved to the point where greater seedling recruitment was likely. This trend was also significant within cut sites (exponential linear regression, F-ratio=15.8, $r^2 = 0.145$, P<0.001), uncut sites (linear regression, F-ratio=15.3, $r^2 = 0.114$, P<0.001) and nonlakeshore sites (linear regression, F-ratio=42.7, $r^2 = 0.198$, P<0.001), but not significant for lakeshore sites (F-ratio=1.67, $r^2 = 0.04$, P=0.2). As lakeshore sites are usually more humid and cooler, they may support more regeneration

and be at an earlier stage of stand development. However, no such trend was apparent within each stand type (i.e. hemlock dominant, hemlock patch or scattered hemlock) (linear regression, $P > 0.18$).

Age distributions of hemlock stems ≥ 5 cm dbh differed significantly between the youngest and oldest stands (Fig. 9). Deeryard sites were not considered in order to minimize potential browsing effects. From the 29 youngest stands (mean age range of 17 to 86 years, Fig. 9a, $N=253$), the age distribution was strongly skewed to the left with a few individuals > 200 years old. These older stems would be survivors from earlier cohorts that were largely eliminated by some unknown catastrophic event. The age histogram for the 24 oldest stands (mean age range of 156 to 281 years, Fig. 9b, $N=280$) had a bimodal distribution with most of the stems between 100 - 300 years and some stems between 35 - 60 years. These data suggest a period of stem exclusion that the stands went through, based on the 50 - 100 year age gap.

There were 48 upland (non-lakeshore) plots (Figure 10a-c) in which there was no evidence of major disturbance (cutting, fire or wind) within the past century, but some were within former deeryards. They tended to have few stems less than 100 years old, with the majority of trees between 100 and 220 years old. Hemlock were significantly older ($\bar{x}=166$, $N=312$) than hemlock on sites logged for pine or yellow birch, or burned ($\bar{x}=135.6$, $N=580$, Mann-Whitney U-test, $Z=-6.81$, $P<0.001$). This suggests that disturbance released suppressed or understory hemlock stems and promoted hemlock growth. However, it also promoted sugar maple growth (see below).

Ungulate browsing and the age gap

Deeryard sites had greater browsing pressure in the past from winter deer usage compared to nondeeryard sites, which would have had most of the browsing pressure during the snow free months. Currently, lakeshore sites appear to have less browsing pressure from moose compared to sites away from lakeshores (M. Wilton and S. Vasiliauskas, pers. obs., see also below). High browsing pressure with low hemlock recruitment and a greater percentage of browsed seedlings would be expected in upland areas, as moose appear to use these areas more during the fall and winter, and move into lakeshore conifer stands late in the winter and early spring (M. Wilton, pers. comm.). Lakeshore areas would be expected to have more hemlock recruitment and a lower percentage of damaged seedlings. Consequently, a wider age gap is predicted in deeryard-nonlakeshore sites (where browsing is continuing) than in lakeshore-nondeeryard sites under the ungulate browsing hypothesis.

When examining all hemlock greater than 3 years old at both ends of this browsing continuum, a scarcity of saplings and trees between 40 and 120 years of age is evident in the deeryard-nonlakeshore plots but not in the lakeshore-nondeeryard plots (Fig. 11). In Fig. 11, ages of hemlock stems ≥ 5 cm dbh were increased by 24 years to allow for the age difference between the ground and breast height where increment cores were taken. The correction factor is based on a subsample of 1.3 m tall seedlings (N=300) from the 1991 seedling dataset that had a mean age of 24 years. Seedlings were vastly more abundant than canopy trees and saplings which made it difficult to examine frequency distributions of stems greater than 5cm dbh. For this reason, seedlings and small saplings (<5cm dbh) are not included in the age histograms considered below.

Hemlocks were significantly older in the deeryard-nonlakeshore plots (\bar{x} =161.4 yr, N=529) compared to the lakeshore-nondeeryard plots (\bar{x} =104.3 yr, N=434, Fig. 12a, b,

Mann-Whitney U-test, $Z=-10.47$, $P<0.001$).

Hemlocks within the 41 lakeshore plots were significantly younger ($\bar{x}=115.8$ yr., $N=582$) compared to hemlocks within the 175 nonlakeshore plots ($\bar{x}=156.6$ yr., $N=1205$) (Fig. 13a, b, Mann-Whitney U-test, $Z=13.15$, $P<0.001$). Age distributions differed, with relatively few stems less than 100 years old in the nonlakeshore plots (Fig. 13b), while the lakeshore plots had significantly more stems in the younger age classes.

The 96 plots within deeryards (Fig. 14a) had a distinct age gap with few hemlock less than 100 years old compared to the 120 plots outside of deeryards (Figure 14b). The mean ages of hemlock were significantly greater in deeryard plots ($\bar{x}=166.5$ yr., $N=669$) compared to non-deeryard plots ($\bar{x}=129.3$ yr., $N=1117$, Mann-Whitney U-test, $Z=-12.52$, $P=0.001$).

Effects of current ungulate browsing

The percentage of the seedlings that were browsed on a plot generally decreased with increasing hemlock basal area and was significantly related to the working group (One-way ANOVA, $F\text{-ratio}=28.7$, $P<0.001$), and lakeshore effect (One-way ANOVA, $F\text{-ratio}=8.1$, $P=0.005$), but not to aspect or cutting history (ANOVA, $F\text{-ratio}=0.8$, $P>0.4$). Hemlock dominant plots had a significantly lower percentage ($\bar{x}=24.9\%$, $N=88$) of browsed seedlings than hemlock patch plots ($\bar{x}=38.1\%$, $N=63$) which were significantly lower than scattered hemlock plots ($\bar{x}=59.5\%$, $N=65$) (Fig. 15).

Most plots had less than 50% of the seedlings damaged by browsing (Fig. 16a). There was no significant difference between deeryard and nondeeryard plots (Mann-Whitney U-test, $Z=0.8$, $P=0.4$). This is most likely because current browsing is primarily by moose

and they would not frequent the deeryard areas more than nondeeryard areas. Lakeshore sites had a significantly lower percentage of browsed seedlings (\bar{c} =26.8%, N=41) than nonlakeshore sites (\bar{c} =42%, N=175, Mann-Whitney U-test, Z=2.63, P=0.008), suggesting that current browsing by moose is concentrated away from lakeshore areas. Ungulates use knolls for bedding sites (Hosley and Ziebarth 1935, M. Wilton, pers. comm.) and moose prefer to use them for calving sites (Wilton and Garner 1991), so more browsed seedlings might be expected on knoll sites, but this was not the case. Knolls did not have a greater percentage of browsed seedlings per plot compared to north or south aspect plots (Fig. 16d, e, Mann-Whitney U-test, Z=1.11, P=0.27 and Z=1.05, P=0.29 respectively).

Browsing was concentrated on the larger seedlings and small saplings (Fig. 17), with browsing recorded in stems up to 4.5 m tall (only 3 stems > 4 m tall were browsed, and are not shown in the figure). The percent browsed per height class is based on the number of browsed stems divided by the total number of stems in that height class. Although the larger size stems accounted for a small proportion of the total number of stems, in these height classes more than one-quarter of the stems were browsed. Hence, the likelihood of being browsed increases dramatically with height up to 1 m and then falls off gradually to zero once foliage is generally above the reach of ungulates.

As hemlock seedling density decreased on a plot, a significantly greater percentage of seedlings were browsed (Fig. 18, linear regression, F-ratio=30.68, r^2 =12.5, P<0.001). An exponential regression model had a much poorer fit than the linear model and so was not used. As hemlock basal area decreased, the percentage browsed significantly increased (linear regression, F-ratio=48.5, r^2 =0.185, P<0.001).

Aspect type was a significant factor with respect to moose usage based on pellet

group frequency in 1992 (N=196) (ANOVA, F-ratio=5.27, P=0.0058, d.f.=215), but not in 1993 (N=234) (Kruskal Wallis test statistic=4.04, P=0.13, N=216). Knoll plots in 1992 had significantly more pellet groups (\bar{x} =1.38) than north (\bar{x} =0.67) or south (\bar{x} =0.75) aspect plots, which did not differ (Fig. 19a, b). The difference between 1992 and 1993 may have been due to moose preferentially browsing hemlock tops from windthrown trees resulting from a storm in November 1992, and concentrating winter activity around these trees. Pellet group numbers did not differ between working groups, cut and uncut plots, lakeshore or nonlakeshore plots in either survey year (Kruskal-Wallis Test statistic $Z < 0.57$, $P > 0.6$). Deeryard plots had more pellets than nondeeryard in 1993 (Kruskal-Wallis Test statistic $Z = 4.34$, $P = 0.037$), but not in 1992.

The percentage of a seedling browsed by moose (Table 2) did not differ significantly between deeryard-nonlakeshore plots (\bar{x} =32.0, N=3789) and lakeshore-nondeeryard plots (\bar{x} =32.3%, N=3946, T-test, $T = -1.55$, $P > 0.1$, N=3789). It also did not differ between lakeshore (\bar{x} =32.1%, N=1247) and nonlakeshore plots (\bar{x} =32.4, N=2542, T-test, $T = -0.55$, $P = 0.6$) or deeryard (\bar{x} =31.8%, N=1533) and nondeeryard plots (\bar{x} =32.7, N=2254, T-test, $T = -1.46$, $P = 0.14$). This would suggest that the amount removed from a seedling does not relate to where the seedling is located, and moose tend to be consistent in the amount removed from a seedling. The percentages given in Table 2 may be lower than the actual loss, as it was not possible to determine the original heights of the browsed seedlings. I estimated an absolute loss of 10 cm from the leader of each browsed seedling which is lower than the actual loss as determined from the tagging experiment (Fig. 23).

The age-height distribution of seedlings did differ between lakeshore-nondeeryard

and deeryard-nonlakeshore sites (Fig. 20a, b). Unbrowsed seedlings were much larger and older in the lakeshore-nondeeryard sites compared to the deeryard-nonlakeshore sites. Seedlings with less than 50% of the crown damaged by browsing were similar in age and height to seedlings with greater than 50% of the crown damaged within the above site types, but browsed seedlings were taller and older in the lakeshore-nondeeryard sites compared to the deeryard-nonlakeshore sites. Saplings greater than 3 m tall were more frequent in the former site type compared to the latter, which only had 2 saplings over 3 m tall. Saplings above this height had little or no evidence of browsing, as they are out of the reach of ungulates.

Snow depths measured in March 1993 varied from 30 - 70 cm, depending on the amount of hemlock canopy cover. The percentage, per site, of the tagged stems browsed over the winter was not significantly affected by maximum snow depths (linear regression, F-ratio=2.98, $r^2 = 0.052$, $P=0.09$, d.f.=55). Deep snow apparently does not provide adequate protection for seedlings as browsing starts in the fall before there is much snow accumulation.

Three hundred and thirty-six (46%) of the saplings transplanted into hardwood sites were significantly shorter in April 1993 compared to their original heights in November 1992 (Fig. 21). Heights of browsed individuals decreased from a mean of 1.16 m to 0.86 m (mean height loss of 27%) (Mann-Whitney U-test, $Z=13.38$, $P<0.001$, $N=336$). The percentage of the sapling lost was significantly greater with shorter saplings (Fig. 22, linear regression, F-ratio=360, $r^2=0.519$, $P<0.001$), suggesting that browsing may involve an approximately constant twig diameter (not recorded in this study). An additional 29 saplings lost side branches but not the leader and are not included in these calculations. Browse damage was

observed on some saplings within two weeks of transplanting.

Moose damaged 328 seedlings (16.4%) in the tagging experiment. The probability of being browsed (by either moose or hare) was greater if the seedling had been previously browsed. If a seedling had not been previously browsed, it had a 18.3% chance of being browsed. If it had been previously browsed, it had a 36.6% chance of being rebrowsed. If it had been browsed twice, the chance of being browsed a third time was 34.8% (Table 3).

Initial mean heights (in 1992) of browsed and unbrowsed seedlings differed significantly (Table 3, Mann-Whitney U-test, $Z=7.66$, $P<0.001$). Unbrowsed seedlings were 0.58 m high ($N=1421$), while browsed seedlings were 0.70 m ($N=579$). Initial heights of seedlings browsed in 1993 or 1994 (but not before) ($N=254$), and seedlings browsed before tagging ($N=330$) and not after, did not differ significantly in height (Mann-Whitney U-test, $Z=0.19$, $P=0.8$, $\bar{x} = 0.64\text{m}$ and $\bar{x} = 0.68$ respectively). Hares browsed significantly smaller seedlings ($\bar{x} = 0.39$ m, $N=88$) than moose ($\bar{x} = 0.74$ m, $N=411$) (Mann-Whitney U-test, $Z=5.17$, $P<0.001$) in 1993 and 1994, but hares removed a significantly greater percentage of the plant ($\bar{x} = 48\%$) compared to moose ($\bar{x} = 34\%$) (Mann-Whitney U-test, $Z=4.26$, $P<0.001$) which is probably coincidental with the smaller seedling size browsed by hares. However, the percent change in height for 1994 did differ significantly between moose ($\bar{x} = 16.4\%$) and hare ($\bar{x} = 21.9\%$) (Mann-Whitney U-test, $Z=3.45$, $P=0.005$).

The percent browsed (which also included damage to side branches) ($\bar{x} = 37.2\%$, $N=538$) significantly decreased as initial seedling height of the tagged seedlings increased (Fig. 23, exponential linear regression, $F\text{-ratio}=87.7$, $r^2 = 0.141$, $P<0.001$, $d.f.=537$), also suggesting that browsing may usually involve a preferred twig size (c.f. Fig. 22). The percent

loss in height significantly decreased with greater initial seedling height (Fig. 24, exponential linear regression, F-ratio= 36.2, $r^2 = 0.063$, $P < 0.001$, d.f.=538).

Heights of hemlock stems ≥ 5.0 cm dbh had a normal distribution but differed significantly between nondeeryard (\bar{x} = 15.6 m, Fig. 25a) and deeryard (\bar{x} = 17.9 m, Fig. 25b) sites (T-test, $T=9.73$, $N=2213$, $P < 0.001$). Lakeshore sites also had significantly shorter stems (\bar{x} = 15.3m, $N=688$, Fig. 26a) than upland sites (\bar{x} = 17.1 m, $N=1525$, Fig. 26b, T-test, $T=-6.9$, $P < 0.001$). This would also suggest that past browsing limited sapling recruitment in deeryard areas compared to nondeeryard areas, while current browsing may be limiting sapling recruitment in upland areas compared to lakeshore areas.

Age and mortality risk

Mortality rates of all canopy trees greater than 9.5 cm dbh varied between 1991-92 and 1992-93 (Table 4), with 49 and 79 trees lost respectively. Cut trees were a minor part of the loss (7 and 9 respectively) and are included in the mortality figures. The great increase in 1993 (at least 21 of the 79 dead trees) was partly due to a windstorm on November 13, 1992 which downed thousands of trees across Ontario including Algonquin Park.

Hemlock mortality was only 0.33% in 1991-92 and 1.1% in 1992-93 (Table 4). This suggests a canopy generation time between 100 and 300 years. Mortality, however, was primarily in suppressed understory trees and wind breakage of canopy stems. Few canopy stems appeared to die from decline due to logging or other factors (pers. obs.). Sugar maple mortality was 1.2% in 1991-92 and 2.3% in 1992-93. Longer term surveys are required to more accurately assess mortality rates.

Seven hundred sixty two snags and fallen trees ≥ 9.5 cm dbh were recorded in the main survey (Table 5). Hemlock, sugar maple and beech had low percentages of dead stems, possibly because they are long-lived and shade tolerant (7.1%, 7.4% and 10.5% respectively). Of the 153 dead hemlock, 45 had died within the last few years (Class 1). Species with relatively short lifespans (Fowells 1965), such as white birch (46.8%), striped maple (35.4%), and balsam fir (41.5%) are reflected in the high percentage of snags and fallen stems relative to the number of live stems. In the case of balsam fir, the high number of stems in classes 3 to 6 reflects the mortality caused by spruce budworm (*Choristoneura fumiferana* (Clemens)) in the 1970s (Strickland and Rutter 1993). The large number of dead white cedar (53.9%) suggests greater earlier dominance of white cedar in Algonquin, either as a pioneer species or as a canopy codominant with a variety of species, including hemlock. Most of these stems have been dead for several decades, as the snags were weathered, with no bark, few limbs left, and were either fallen over or leaning into live trees. The high percentage of yellow birch snags (34.0%) reflects birch dieback from the 1950s (Anderson *et al.* 1990).

Mortality of tagged seedlings (>3 years old) was very low (2.45%) over the two years of the survey. Several seedlings could not be relocated and were presumed dead and removed by moose. Nineteen seedlings were killed directly by browsing or by subsequent decline from heavy browsing. Twelve dead seedlings had no browse damage and died from unknown causes. Seventeen seedlings were lost when one site was cut, and are not included in subsequent calculations. Mortality appeared to differ between seedlings <50 cm tall and those >50 cm tall (approximate snowline), as 26 dead seedlings were in the former group and 5 in the latter group. Dead browsed seedlings were significantly older (Kruskal-Wallis Test statistic $Z=2.45$, $P=0.014$) and taller (Kruskal-Wallis Test statistic $Z=-2.09$, $P=0.037$)

than dead unbrowsed seedlings from the tagging experiment (Fig. 27).

This low mortality rate parallels the low percentage of dead seedlings (> 3 years old and < 5 cm dbh) found in the main survey up to 1992. Only 487 dead seedlings were found, or 2.4% of all seedlings more than 3 years old ($N=19794$). Of these dead stems, 75% had no evidence of browsing and the other 25% had browse damage. I would assume that the dead seedlings/saplings would be visible for at least one year after death, and probably more than two years, before falling over and blending in with the woody debris on the ground. It is not known how much browse damage seedlings can tolerate before dying from lack of foliage. Moose may not have exerted the extensive browse pressure that deer probably had in the past, and mortality rates may increase with time in the larger size classes with repeated browsing.

Mortality rates were highest in the youngest age classes. Forty-nine percent of the mast seedlings that had germinated (and were marked) in 1992 ($N=74$) were missing (dead) by 1994, while 18.7% of the mast seedlings that germinated in 1990 (and were marked in 1992) ($N=819$) were missing (dead) by 1994. Mortality of these seedlings was due to several factors including trampling by moose, desiccation, browsing by hares or voles, or being on a poor microsite such as bark that had not adequately decayed.

Population structure of sugar maple versus hemlock

Diameters of hemlock stems ≥ 5 cm dbh differed significantly between lakeshore ($\bar{x}=25.8$ cm, $N=688$) and nonlakeshore plots ($\bar{x}=32.0$ cm, $N=1525$) (Mann-Whitney U-test, $Z=9.41$, $P<0.001$)(Fig. 28). Lakeshore plots had an inverse-J distribution with most stems in the smaller diameter classes (less than 20 cm diameter), while nonlakeshore plots had a more

unimodal or normal distribution with more large diameter stems.

The diameter frequency distribution of sugar maple in nonlakeshore sites (Fig. 29a, $\bar{x}=19.4$ cm, N=1271) was strongly skewed towards the smaller size classes (less than 20 cm dbh). Age frequency distributions were also skewed toward the younger age classes (Fig. 29b, $\bar{x}=67.9$ yrs, N=1075).

Sugar maple appears to have expanded into the hemlock age gap in the upland, nonlakeshore plots, as sugar maple is significantly younger ($\bar{x}=67.9$, N=1075, Fig. 29b) than hemlock ($\bar{x}=156.6$, N=1205) (Fig. 13b) in these plots (Mann-Whitney U-test, $Z=32.3$, $P<0.001$). Sugar maple was significantly younger (Fig. 30a, $\bar{x}=60$, N=572) than hemlock (Fig. 14a, $\bar{x}=166.5$, N=669) in the deeryards (Mann-Whitney U-test, $Z=28.0$, $P<0.001$). Sugar maple also appears to be replacing hemlock in deeryards, with significantly younger sugar maple in deeryard plots than non-deeryard plots ($\bar{x}=76.6$, N=535, Fig. 30b, Mann-Whitney U-test, $Z=9.22$, $P<0.001$). This may suggest that maple has been promoted by deer browsing suppressing hemlock regeneration, giving maple a competitive advantage in filling canopy gaps after disturbances. Outside of deeryards, hemlock may not have been as heavily browsed, giving less of an advantage to sugar maple.

Sugar maple appears to be replacing hemlock in deeryard-nonlakeshore plots, as the maple were significantly younger (Fig. 31b, \bar{x} =66.4 yr, N=570) than hemlock (Fig. 31a, \bar{x} =161.4 yr, N=529, Mann-Whitney U-test, $Z=23.3$, $P<0.001$). Sugar maple in nondeeryards were older (Fig. 30b, \bar{x} =76.6 yr, N=535) than sugar maple in the deeryard-nonlakeshore plots (Mann-Whitney U-test, $Z=-7.7$, $P<0.001$). It would appear that areas which are likely to have had greater browsing pressure in the past century (i.e. deeryard/nonlakeshore plots) had less hemlock and more sugar maple recruitment compared to areas with less browsing pressure (eg. nondeeryard areas).

In comparing sugar maple age distribution in sites with no evidence of disturbance by fire or logging in the last century with sites that had been disturbed before 1945, the undisturbed sites had significantly older maples (Fig. 32a, \bar{x} =79.1, N=317) than the disturbed sites (Fig. 32b, \bar{x} =63.9, N=267, Mann-Whitney U-test, $Z=-5.35$, $P<0.001$). Hemlock on sites disturbed before 1945 by fire or logging were younger (Fig. 33a, \bar{x} =135.6, N=580) than hemlock on sites undisturbed by fire or logging in the last century (Fig. 33b, \bar{x} =165.7, N=312)(Mann-Whitney U-test, $Z=6.8$, $P<0.001$). Disturbances have apparently promoted sugar maple regeneration as well as hemlock regeneration, as there was some hemlock recruitment on the disturbed sites, but not as much as there was sugar maple recruitment.

CHAPTER 4

DISCUSSION

Intermediate age gaps are present in hemlock populations of Algonquin Provincial Park, particularly on the west side of the park. A number of hypotheses were considered in the Introduction to account for the age gap, involving mortality risks concentrated at different points in the life cycle (Fig. 1). Evidence presented in this study from field surveys and monitoring studies suggests that some hypotheses, such as climatic change affecting seedling regeneration and hare browsing limiting seedling establishment, are not likely to have caused the current age gap. Other hypotheses, involving ungulate browsing and stem exclusion, have stronger support. Below, I examine each hypothesis in more detail, and the part that it may play in age gap formation.

***Seedling establishment hypothesis.** Between about 40 to 100 ybp, environmental conditions (e.g. climate) were unusually poor for hemlock germination and/or seedling establishment compared with before and after this period.*

Climate changes in the past have caused forest changes in the Algonquin area (Earle 1979), particularly with the last glacial recession and the northward migration of species. Current interest in global warming has created concerns for rapid forest changes, and Algonquin may be affected by these changes, but it is difficult to predict the nature of the changes. The data from the Huntsville weather station strongly suggests that climatic conditions between 40 to 100 ybp were different from current conditions with respect to total precipitation and total snowfall. However, summer precipitation (May - August) has not changed significantly (Fig. 6). It appears that conditions may have been suitable for

seedling establishment in the past and that this hypothesis is not adequate to explain the age gap in hemlock in Algonquin Park. In addition, many of the hemlock stands in Algonquin were established during the Little Ice Age, which ended in the mid 1800s (Frelich and Lorimer 1991). Local conditions at this time are unknown, but it was cooler in many parts of the world. The ideal way to test this hypothesis would be with local climatic data prior to the age gap, but unfortunately these data do not exist.

Seedling establishment clearly does not appear to be a current problem and seedling density varies according to site. Lower seedling densities would be expected (and were found) in sites with few hemlock canopy trees (hardwood dominated sites) due to a smaller seed source and a lack of suitable germination sites from the presence of hardwood litter (Mladenoff and Stearns 1993). A new seedling cohort would probably start every few years based on the observed seedling age range and the abundance of recent germinants. Despite the high mortality in the youngest seedlings, enough would survive for the establishment of a new cohort and continual regeneration in the area. Seedlings appear to tolerate poor conditions for several years before dying, based on casual observations of seedlings on inadequately decayed downed logs.

A number of studies have commented on the need for adequate moisture for seedling establishment due to the small radicle after the first year's growth and the seedlings sensitivity to desiccation (Coffman 1978, Anderson *et al.* 1990). Hemlock canopy decline was related to drought in the Menominee Indian Reservation, Wisconsin (Secret *et al.* 1941), but no mention was made of the effect of drought on seedlings. Moist years are considered to aid hemlock reproduction and establishment (Graham 1941). In New Zealand, the podocarp regeneration gap in several podocarp species on the South Island is attributed to

drier conditions between 1300 and 1800 A.D. limiting seedling establishment (Wardle 1963).

Hare browsing hypothesis. *Between about 40 to 100 ybp, the snowshoe hare (Lepus americanus) population in Algonquin Park was much larger than both before and after this period, thus causing heavy hemlock seedling mortality during this period.*

Unfortunately, little data were available on hare numbers in the past, apart from the work by MacLulich (1937). In the current study, hares appear to exert a minor influence on hemlock seedlings, as only about 10% of the browsed seedlings were hare browsed, and the rest were ungulate browsed (Table 2). Hare browsing was also concentrated on the smaller seedlings, ($\bar{x}=0.45$ m) compared to ungulates ($\bar{x}=0.70$ m). In the seedling monitoring study, only 3% of the seedlings were browsed by hares over 2 years. No evidence was found of girdling of hemlock saplings by hares in the main survey. Only a few studies have considered damage by hares to hemlock seedlings (Krefting 1953, Telfer 1972, Rogers 1978).

I conclude that snowshoe hares play only a minor role in limiting hemlock regeneration and recruitment and are probably not responsible for the age gap in the hemlock population in Algonquin Park.

Beavers (Castor canadensis) have been observed cutting hemlock saplings and using them for food and dam construction at Shirreff Pond, Algonquin Park (pers. observ.), but this would only affect hemlock regeneration on a local scale.

Canopy suppression hypothesis. *In hemlock dominated stands, hemlock canopy trees are so long*

lived that saplings are suppressed to their tolerance limit and then die leaving a bulk of younger seedlings under an aging canopy.

There was little support for this hypothesis, as the hemlock gap involves relatively young ages (40 - 100 yr), which should be able to tolerate shading. More seedlings were found in older stands compared to younger stands, and past browsing effects may mask canopy suppression. Seedling mortality was quite low in the seedling monitoring study (37 from natural causes over 2 years) and none of these appeared to be older seedlings that died from canopy suppression. Mortality and turnover was highest in suppressed and understory hardwood stems, based on a 60 year study (Ward and Stephen 1994). Canopy suppression can occur in sugar maple stands (Forcier 1975), but the greater shade tolerance of hemlock commonly permits survival in the understory to well over 100 years (Curtis 1959). However, this hypothesis cannot be discounted as a contributing factor, perhaps coupled with other factors causing the age gap.

Ungulate Browsing Hypothesis. *Heavy browsing by white-tailed deer (Odocoileus virginianus) and/or moose (Alces alces) concentrated especially above the snow line, reaches a threshold level resulting in sapling mortality and leaving a bulk of younger hemlock seedlings (which avoid winter browsing beneath the snowline) under an aging hemlock canopy.*

The results of this study strongly support the ungulate browsing hypothesis as the primary cause of the hemlock age gap in Algonquin Provincial Park. Areas which would have had the greatest browsing pressure in the past, such as deeryards and upland areas, have the most pronounced age gap, while the age gap is less marked in nondeeryard areas and lakeshore areas (Fig. 11). As deer populations increased rapidly in the late 1800s, seedlings

and saplings up to a height of 1.5 - 2 m would have been browsed (the approximate reach of a deer). Saplings beyond this height would probably have escaped browsing and grown into the canopy, while those within reach of deer would have been heavily browsed and eventually would have died. Browsed seedlings would have little potential for regrowth (Curtis 1959). Snow offers little protection to seedlings, as browsing starts in the fall before there is much snow on the ground. Browsed seedlings also have a higher chance of being rebrowsed, based on the seedling monitoring study. Consequently, the start of the age gap is best determined by ages at breast height, rather than ages at ground level. Nevertheless, the age gap is about 60-70 years wide, having started in the 1890s and terminating around 1960 with the decline of the deer population. Seedling losses from browsing probably decreased rapidly in the late 1950s, allowing the establishment of the present seedling bank. Stands which have abundant hemlock seedling growth today were devoid of hemlock regeneration in the 1950's (N.D. Martin, pers. comm.). As demonstrated by the seedling monitoring study, current seedling mortality tends to be low, with browsing as the primary cause of death in older seedlings.

With the decline of deer populations and the recent increase in moose populations (Runge and Theberge 1974, Wilton 1973, Wilton 1987), current browsing pressure has shifted away from deeryard areas to upland areas. This is evident from the lack of a significant difference in the percentage of browsed seedlings per site between deeryard and nondeeryard areas, but a significantly higher percentage of browsed seedlings in upland areas compared to lakeshore areas. Browsing is also concentrated on larger seedlings which are more visible (Fig. 17). This was dramatically demonstrated in the sapling transplant study, with 50% of the saplings browsed after one winter and with a mean height loss of 30 cm.

The age and diameter distribution histograms from deeryard and upland sites in this study are similar to those of Whitney (1984) and Anderson and Katz (1993), who report a unimodal or bell-shaped age distribution for hemlock in areas with heavy deer browsing. The classic inverse-J curve characteristic of shade-tolerant species in all-aged forests (Leak 1965, Davis and Johnson 1987, Anderson and Rice 1993) was most evident in lakeshore sites which also had the least amount of recent browsing. Similar negative-exponential curves were reported from North Carolina for hemlock and for the forest as a whole (Lorimer 1980).

Numerous studies have reported white-tailed deer limiting hemlock sapling recruitment through browsing (Graham 1958, Beals *et al.* 1960, Hough 1965, Hett and Loucks 1976, Eckstein 1980, Butt 1984, Whitney 1984, Frelich and Lorimer 1985, Anderson and Katz 1993). Red deer have limited oak (*Quercus robur*) regeneration in England (Mellanby 1968), Scots pine (*Pinus sylvestris*) regeneration and recruitment in Scotland (Watson 1983), and hazel coppice growth in England (Tabor 1993).

Little research has been done on moose browsing of hemlock as the ranges of both species have little overlap (Fowells 1965, Banfield 1974). Algonquin Park may be unique in having a high moose population over the last decade (Wilton 1987), but moose numbers also increased during the deer decline in the 1930s (Robinson 1933). Moose appear to select hemlock stands disproportionately on a local scale (<100km²) compared to other stands in Algonquin based on winter aerial surveys (Forbes and Theberge 1994). All evidence currently points to moose browsing exerting a major impact on hemlock in Algonquin.

Several factors may affect ungulate usage of lakeshore hemlock stands. Wolf predation in the winter may be an important factor, as wolves utilize lakes and rivers as travel

corridors (Banfield 1974). Ungulates walk on the ice and browse accessible foliage, but appear not to venture into the stand and browse heavily on understory conifers. As visibility may be limited from these areas, they may avoid them for fear of predation. Upland areas are more open and have better visibility, providing more safety for ungulates who can see predators coming from a distance and escape more easily.

Foliage palatability may be another factor affecting lakeshore usage by ungulates. In Newfoundland, balsam fir was more heavily browsed by moose in stands that had been thinned compared to unthinned stands (Thompson *et al.* 1989). The foliage from thinned stands had significantly more protein compared to the foliage of dense, unthinned stands. This was primarily because the balsam fir in thinned stands obtained more light and were able to produce more photosynthates and other products (Thompson *et al.* 1989). Twig and foliage composition also varies among woody species. Mautz *et al.* (1976) found low percentages of digestible crude proteins in hemlock, balsam fir and red maple (5% to 11%) compared to striped maple, mountain maple, hobblebush (*Viburnum alnifolium* Marsh) and beaked hazel (*Corylus cornuta* Marsh.) (44% to 51%). There was higher fat digestibility in softwoods compared to hardwoods. The percent crude fibre digested was 3 to 4 times higher in hemlock and hobblebush (36% to 43%) compared to beaked hazel (12%) and red maple (18%).

Hemlock may react similarly to light levels and photosynthesis. Hemlock growing in dense shade would produce less protein and less palatable foliage compared to hemlock seedlings growing in hardwood stands, which get higher light levels, especially in the spring and autumn. Hemlock seedlings were most abundant under a hemlock dominated canopy and least abundant under a hardwood canopy, but the highest percentage of browse damage

was in the hardwood dominated sites. Casual observations during the summer of 1993 indicated that windthrown hemlocks from the previous winter were stripped of all accessible foliage by moose. This foliage would be the most palatable as it gets full sunlight and can photosynthesize more than seedlings on the forest floor. Future work could investigate foliage palatability between different sites and may help explain differences in browsing intensity.

Stem exclusion hypothesis. *Based on stand dynamics, once the canopy has closed in a young stand, further seedling recruitment is limited due to high stem density and occupation of all available growing space.*

Forest stand dynamics may partially explain the lack of hemlock seedlings and saplings in some stands. Stands that are in the stem exclusion stage of forest stand development (Alaback 1982, Oliver and Larson 1990) have sparse woody and herbaceous vegetation on the forest floor due to the dense shade from the canopy. Competition, including root competition, is intense as all available growing space, including soil growing space, is occupied (Hett and Loucks 1976, Oliver and Larson 1990). Shallow rooting of saplings causes moisture stress (Hett and Loucks 1976). Most germinants would survive briefly in the understory before dying from inadequate light and moisture (Alaback 1982). Some of the stands in this study were clearly in the stem exclusion stage of development, as they had a dense canopy with a sparse understory and few young seedlings of any species.

As the canopy matures, tree mortality from competition and suppression frees growing space and roots penetrate deeper into the soil. Coarse woody debris such as trunks and large limbs from previous disturbances, would also have decayed sufficiently to provide more suitable germination sites for hemlock seedlings. Once site conditions have

ameliorated and more light and moisture are available, the stand enters the understory reinitiation stage (Sprugel 1976, Oliver *et al.* 1985). Species diversity in the stand increases during this stage and tree seedlings regenerate and form a seedling and sapling bank in the understory (Oliver and Larson 1990). The timing of this stage is variable, and can range from 60 years in southern pine stands to 150 years in stands of shade-tolerant conifers (Oliver and Larson 1990). Hough and Forbes (1943) identified two waves of establishment of 165 years and 155 years for hemlock. Hett and Loucks (1976) suggest cyclic recruitment in balsam fir and eastern hemlock, with a periodicity of 31 to 39 years from 3 balsam fir stands and 126 - 398 years from 4 different hemlock stands. However, Tyrrell and Crow (1994) found few hemlock saplings and seedlings in old hemlock-hardwood stands compared to younger stands. A variation on stem exclusion can occur when a change in disturbance regimes limits or stops seedling establishment. In the Pennsylvania Piedmont, changes in the fire regime caused by fire suppression have limited chestnut oak (*Quercus prinus*) sapling establishment since the 1920s (Mikan *et al.* 1994). In other cases an age gap can be caused by the silvics of the species. Species that require adequate light for seedling establishment can suppress their regeneration for long periods due to self shading and canopy longevity (Wardle 1963, Stewart and Rose 1989).

The stem exclusion stage may explain an apparent age gap on certain sites, especially younger stands, but it is not sufficient to explain an age gap on all sites, as mean canopy ages varied from 49.9 to 281.4 years. However, when we combine browsing effects by ungulates with stand dynamics, the stem exclusion stage may be prolonged due to heavy browsing of hemlock seedlings and saplings, preventing their establishment. Any regeneration would be limited to species that are not heavily browsed, or can tolerate browsing, such as spruce and

sugar maple (Graham 1958). Hett and Loucks (1976) considered deer populations low in their study areas (Haliburton Highlands, south of Algonquin Park; and Wisconsin), and so did not consider ungulate browsing as a factor influencing the length of the recruitment cycle. Examination of their age distributions suggests an age gap ranging from 100 to 200 years. Once browsing pressure was lifted, hemlock seedlings could regenerate and enter the understory reinitiation stage (Oliver and Larson 1990, Anderson and Katz 1993). This could explain the large seedling population in this study, which would have originated in the late 1950s after the major collapse of the deer population in the park. It would also support the reason for the hemlock age distribution of sites from former deeryards and upland areas which had an age gap in the population structure. Both factors may be responsible in Algonquin, but I would consider ungulate browsing as maintaining any gap that would have been initiated after the stem exclusion stage. Browsing would also limit sapling recruitment on heavily browsed sites with an established seedling population.

Can hemlock recover from browsing?

Hemlock lost a mean of 16.4% from their height due to moose browsing, while mean height increases of undamaged seedlings varied from 22% - 33%, depending on the stand type. Recovery from height loss due to browsing would not just be a matter of regrowth, as browsing causes leader loss and a new leader would have to form. Additionally, apical dominance would be released, resulting in multiple leaders. Growth may also be reduced due to foliage losses. The additional problem is that the probability of being browsed doubles once a seedling has been browsed once (from 17% to 39% over two years).

Consequently, recovery from browsing would be difficult at present, due to the heavy

browsing pressure from moose and the time required to compensate for lost height and foliage, and the increased risk of being rebrowsed.

Hemlock populations can recover once browsing pressure is removed, as demonstrated by exclosure experiments from several studies (Stoeckler *et al.* 1957, Graham 1958, Anderson and Katz 1993). Stoeckler *et al.* (1957) estimated that hemlock seedlings required 6 - 8 years to grow out of the reach of deer.

A model of hemlock/sugar maple dynamics

The mechanisms of the stem exclusion and browsing hypotheses can be interpreted using a model of the dynamics of hemlock and sugar maple which are commonly co-dominant in late successional stands in Algonquin Park. The model (Fig. 34) incorporates two main variables:

1) Degree of canopy removal. Logging, fire, windstorms and disease are the main extrinsic factors affecting the degree of canopy removal. Within the study area, fire is of minor importance; forests on the Algonquin dome have been described as the "asbestos forest" (H. Anderson, pers. comm. 1992). Large scale natural fires are rare and small fires do little damage to the canopy trees. They usually burn some of the litter layer and kill seedlings and small saplings (Curtis 1959). The natural fire cycle was estimated at 1000 years for the Algonquin Dome prior to human intervention (Quinby 1988). Catastrophic windstorms occur in Algonquin (Strickland and Rutter 1993), and an individual storm can level several hundred hectares of forest, usually without damage to the regeneration layer. In Wisconsin the frequency of these disturbances was approximately once every 1000 years on a site (Canham and Loucks 1984). Logging has occurred in the study area since the 1840s

(Saunders 1946, OMNR 1983) and has usually been selective, initially for white and red pine and subsequently for hardwoods. Some of the early logging activity started large fires, as fire suppression was not started until the 1920s (Addison 1974). Diseases and insects are not a major factor affecting large numbers of hemlock and sugar maple, but usually affecting one tree at a time.

2) Browsing intensity. Population sizes of ungulates (and hence browsing intensity) will vary depending on a number of factors. Protected ungulate populations are commonly larger than hunted populations, but their size is limited by the availability of browse, especially in wintering areas. Predators would not normally cause large variations in population size, but severe winters and disease can greatly decrease ungulate numbers (King 1976). The presence of exclosures and deer yards also introduces variation in browsing intensity (Verme 1965).

The model is also based on six main assumptions:

1) **Both maple and hemlock seeds can disperse readily into a given site with equal probability.** In a review of the literature with respect to seed dispersal, hemlock has a greater dispersal distance due to its lighter seed compared to maple. Maple can disperse up to 300 m in a strong wind, while hemlock seeds can be blown up to one kilometre on snow crust (Anderson et al. 1990). Differences do exist in number of seeds per hectare that may be produced. In Wisconsin, hemlock can produce up to 29,700,000 seeds/ha but only 25% are viable (Eckstein 1980). Anderson et al. (1990) cites a germination rate of 30%. Coffman (1978) cites a viability rate of 60% for dissected hemlock seeds. Experimental results by Coffman (1978) gave hemlock germination rates as high as 45% using moist decomposed yellow birch wood under moderate light levels and down to 12.8% using moist loamy soil in

uncovered petri dishes (watered twice daily). Sugar maple can produce up to 18,800,000 seeds/ha in Michigan (Fowells 1965), but has a greater germination rate of 39% (Anderson *et al.* 1990). In Wisconsin, sugar maple can produce up to 13,000,000 seeds/ha and more than 10,000,000 seeds/ha 3 years out of 12 (Curtis 1959). Considering the high number of seeds that may be produced under most conditions it appears reasonable to assume that both species have equal probability of arriving at a given site. High seed numbers are episodic for both species.

2) **Maple has a faster growth rate.** Under moderate light levels, maple saplings can average 30 cm/year in height growth, while hemlock averages 20 - 30 cm/year (Logan 1973). Hemlock seedlings under full light can grow up to 45 cm/year, while sugar maple saplings can grow up to 90 cm/year when released. Logan (1973) found optimal hemlock height growth under 45% shade intensity, with decreasing growth as shade intensity increased or decreased. Sugar maple seedlings at 5 years of age were already much higher than hemlock seedlings 7 years old. For example, maple seedlings were 90 cm tall and hemlock seedlings were 45 cm tall at full light levels. Sugar maple height growth was greatest at 60% shade intensity (Logan 1973). Saplings under heavy shade can grow as slow as 2.5 cm in diameter in 50 years for maple and 100 years for hemlock. First year growth for hemlock is low (2 - 5 cm) and they can be easily smothered by hardwood leaf litter (OMNR 1983, Anderson *et al.* 1990). In the sapling stage, sugar maple can grow at least twice as fast as the hemlock saplings, and an even-aged stand can stratify within 30 years of establishment (Kelty 1986). Hemlock was the slowest growing species in a mixed hemlock-hardwood forest and usually required several release and suppression cycles to reach the canopy (Hibbs 1982).

3) **Maple produces more litter.** The leaf litter produced by maple is quite different from that produced by hemlock. Maple litter forms a thick mat on the forest floor that can smother all seedlings except those with a strong leader, and so can exclude hemlock seedlings (Korhonen 1980). In this study this was reflected in the low number of hemlock seedlings in hardwood-dominated stands with scattered hemlock compared with sites dominated by hemlock. Germination and survival of seeds is limited to large-seeded individuals that have a strong radicle which can penetrate this mat, such as sugar maple and beech (Anderson *et al.* 1990). Sugar maple has the highest percentage germination on maple leaf mould, while the lowest percentage germination was on hemlock needle litter (Darlington 1930, cited in Hett and Loucks 1971). Maple litter has a higher nitrogen content which favours hardwood growth and gives it a competitive advantage (Curtis 1959, Mladenoff and Stearns 1993). The overall decline of hemlock in hemlock-hardwood stands was attributed to failure to reproduce effectively in secondary hardwood forest in the Catskill Mountains, New York (McIntosh 1972). Hemlock litter is quite fine and does not smother seedlings, or bury ideal seedbeds such as moist, well-decomposed litter, rotted logs, or moss mats on logs or rock.

4) **Hemlock is the preferred browse of deer.** This is supported by several studies reporting heavy hemlock browsing in mixed maple/hemlock stands (Hosley and Ziebarth 1935, Stoeckler *et al.* 1957, Graham 1958, Curtis 1959, p. 188, Beals *et al.* 1960, Rogers 1978, Anderson and Loucks 1979, Korhonen 1980, Whitney 1984, Runkle 1990). Telfer (1972) did not consider hemlock as a preferred browse species, but hemlock was not abundant in his study area. Sugar maple is not a preferred browse item by deer (Beals *et al.* 1960, Korhonen 1980), even though it is considered good quality (Verme 1965). Graham (1958)

found heavy browsing of sugar maple, but considered it as only delaying the eventual success of maple.

The replacement of hemlock by sugar maple may reflect preferential browsing of hemlock by ungulates, permitting sugar maple establishment (Beals *et al.* 1960, Anderson and Katz 1993). A review by Rogers *et al.* (1981) on food preferences of white-tailed deer in the Great Lakes region based on stomach contents and bite counts indicates that sugar maple constitutes <5% of the diet at any season, while hemlock is important in the fall based on one study (Aldous and Smith 1938, cited in Rogers *et al.* 1981).

5) **Hemlock is more shade tolerant.** Although both species are very shade tolerant, I would consider hemlock to be more tolerant than sugar maple. Light levels are lower in hemlock stands compared to hardwood stands, and hemlock crowns are deeper compared to maples. Turnover rates in dense maple seedling populations are high in dense shade (Curtis 1959, Rogers 1978, OMNR 1983). On a scale of 1 to 10 hemlock was rated as 8 in tolerance by Curtis (1959) and he gave maple a value of 10. However, Curtis's work was in Wisconsin, which is at the western limit of hemlock, and drier conditions may affect hemlock tolerance to shade more than sugar maple. Moisture is more critical than light for hemlock seedling survival except in the densest shade (Coffman 1978, OMNR 1983). Hemlock can be suppressed for up to 200 years and still grow when released (Marshall 1927, Fowells 1965, Fajvan and Seymour 1993). These features can give hemlock a comparative advantage under a dense hemlock canopy that precludes other species (Korhonen 1980). No indication is given of how long sugar maple can be suppressed.

6) **Hemlock is longer lived.** The oldest known hemlock is 988 years (Fowells 1965) and has a growth potential of 600 years (Eckstein 1980). Anderson *et al.* (1990)

indicates that mature hemlock are frequently 250 years or more in age with individuals known in excess of 500 years. Sugar maple can grow to ages in excess of 300 years. Frelich *et al.* (1993) found that the average age at death of a sugar maple was 145 years, while it was 195 years for hemlock. Tyrrell and Crow (1994) had a mortality rate of 0.5% trees/year for hemlock and 0.9% trees/year from several stands with survey periods of 1.8 years to 16.3 years. In this study mortality rates of sugar maple canopy trees were higher in both survey years compared to hemlock mortality rates (ignoring cut trees). Sugar maple is also more prone to butt and trunk rots that would structurally weaken it compared to hemlock (Anderson *et al.* 1990), so maple could have a shorter average age compared to hemlock. The oldest hemlock recorded in the current study was 430 years, while the oldest sugar maple was 291+ years (had centre rot) of age.

Taking into account the two main variables and the six assumptions described above, I arrived at a model (Fig. 34) to explain the possible dynamics of hemlock and sugar maple that may be associated with the 'stem exclusion' and 'browsing' hypotheses for the intermediate age gaps in hemlock populations.

The model will start with canopy removal, which can vary in intensity from one tree to all trees on a site, and I will assume that the site has hemlock and sugar maple in a subcanopy and/or understorey. (If the gap is <5 m in width, then neighbouring trees will enlarge their crowns and close the gap before any understorey stems will reach the gap (Kelty 1986). If the disturbance was a severe fire which removed all of the stems and regeneration, I will assume that both hemlock and sugar maple seed into the site.

As sugar maple will grow faster than hemlock (Logan 1973), hemlock will tend to remain in the new subcanopy unless it is in a position to reach the canopy. New hemlock

regeneration may be restricted to rotting logs and tip-up mounds if there is a large maple component. As the canopy closes, sugar maple will tend to die out faster than hemlock due to maple's slightly lower shade tolerance and higher turnover rate (Rogers 1978), resulting in a maple-hemlock canopy with mainly hemlock in the subcanopy (Oliver and Larson 1990). Once the canopy closes, no new regeneration will be established and an age gap will start in the population, and this is part of normal stand dynamics (Oliver and Larson 1990) (the 'stem exclusion hypothesis').

As the canopy matures, growing space is freed up in the understory by random tree mortality, crown abrasion and other factors. Soil growing space will be increased as surface roots penetrate farther into the soil, and decay of coarse woody debris will provide favourable microsites for seedling germination (Oliver and Larson 1990). The stand will now enter the understory reinitiation stage and a new hemlock-maple cohort is established. At this point the age gap stops and passes through the population. Hemlock would be favoured due to its greater shade tolerance and canopy maple would gradually be replaced by hemlock as it is longer lived. Eventually, hemlock would dominate the stand. This outcome has been postulated for hemlock-maple-beech stands at Lake George, New York, with hemlock-beech as an intermediate stand between a maple dominated stand and a hemlock dominated stand (Nicholson *et al.* 1979).

If browsing was a major factor on the site at any time, any understorey hemlock could be lost through overbrowsing and no new hemlock regeneration would get established. At this point an age gap would start in the hemlock population and maple would be favoured even more with the removal of hemlock as a competitor. Canopy hemlock would gradually be lost through windthrow and other factors and would not be

replaced due to a lack of hemlock saplings. Deer numbers may consequently decline from the decrease in available shelter (Verme 1965). The end result would be a maple dominated stand.

If browsing is a factor during the understory reinitiation stage, then the age gap from stem exclusion will widen due to browsing (browsing hypothesis) suppressing hemlock seedlings. If browsing decreases during the understory reinitiation stage, then hemlock can re-establish (Anderson and Katz 1993) and at this point the age gap will stop and pass through the population, with hemlock gradually assuming greater dominance. At any point, a disturbance can create a new gap, hence returning to the start of the model.

Mladenoff and Stearns (1993) presented a model to explain the dynamics behind the hemlock decline in the western Great Lakes area. In their model, region-wide logging eliminated hemlock from large areas. Subsequent slash fires removed the conifer forest floor and large woody debris, removing hemlock regeneration and altering seedbed conditions to favour hardwood growth over hemlock and creating the present deciduous forests. This has resulted in a positive feedback loop whereby hardwood litter and higher nitrogen cycling favours hardwoods and further reduces hemlock numbers and causes regeneration failure. Factors driving this loop include fire suppression, a sparse hemlock seed source with local seed dispersal, moderate seed crops and low seed viability. This, combined with a less favourable climate (drier) and selective logging have further reduced hemlock numbers. The remaining hemlock pockets, usually in low, wet areas, are favoured by deer for shelter and any hemlock regeneration is browsed (Eckstein 1980, Mladenoff and Stearns 1993).

Their model does not explain the reason for a hemlock age gap in Algonquin as

historical factors differ. Hemlock stands were not heavily logged and burned compared to hemlock stands in Wisconsin and Michigan, so there was no regional elimination of hemlock and conifer seedbeds. Major fires did occur in Algonquin at the turn of the century, and while some of these fires affected hemlock stands, scattered hemlock and patches of hemlock were left behind. These fires appear to have promoted hemlock regeneration on the east side of the park, and hardwood regeneration on the west side (S. Vasiliauskas, pers. obs.). I believe that hemlock may have seeded in at the same time as the hardwoods onto the burned sites, but differential browsing by deer eliminated the hemlock and promoted hardwood, especially sugar maple, growth. Fire suppression since the 1920s has limited the number of large scale fires, but with a natural fire cycle of approximately 1000 years on the west side of Algonquin (Quinby 1988), fires are infrequent and a minor factor in forest dynamics. The absence of fire would help to create unfavourable seedbed conditions for hemlock regeneration in hardwood areas, but not necessarily within conifer stands.

Current conditions are slightly different in Algonquin compared to the upper Great Lakes area. In hardwood stands with some hemlock, substrate conditions would be similar, with higher nitrogen cycling and a deciduous leaf mat more suitable for hardwoods. However, there appears to be no current problem with hemlock seed dispersal, viability and availability based on recent masting events (1989 and 1991). It is not known if any problems existed with seeding during the period of the age gap, and no records exist. Current climatic conditions appear to be favourable for seedling establishment, based on the regeneration present. Mladenoff and Stearns (1993) maintain that most of their stands were established during the Little Ice Age, which ended about 1850, and conditions have been unsuitable since then for hemlock establishment, especially in upland areas. Many hemlock stands on

the west side of the park did establish during the Little Ice Age, but weather records are not available for this time period and cannot be compared with present conditions.

Mladenoff and Stearns considered browsing as a minor factor in the hemlock decline after the other factors have acted on the hemlock. I consider this factor as the main difference between their model and the situation in Algonquin. Past intense browsing limited hemlock sapling recruitment and this is reflected in the gap in the age structure of hemlock. The other factors given by Mladenoff and Stearns (1993) (such as hardwood leaf litter, sparse seed source, etc.) no doubt play a contributing factor by reducing the availability of seed sites within hardwood dominated stands and resulting in sporadic hemlock regeneration. However, their model does not explain the age gap within hemlock dominated stands that currently appear to have abundant hemlock regeneration, but few hemlock saplings. There is no doubt that hemlock stands in Algonquin are diminished compared to 100 years ago, based on reduced recruitment, logging and normal mortality rates, but there does not appear to be the hemlock regeneration failure as described by Mladenoff and Stearns (1993).

Conclusions

What is the future of hemlock in Algonquin? Based on the research from this thesis, hemlock can be expected to decrease in importance on the west side of the park and be increasingly restricted to lakeshore areas and areas with low browsing intensity. Hemlock will senesce and may eventually be replaced by hardwoods such as sugar maple and yellow birch. On the east side of the park, with lower ungulate populations, hemlock could maintain local dominance and perhaps spread into adjacent stands where conditions are

suitable for establishment. An unknown factor is whether hemlock wooly adelgid (see Chapter 1) will spread to Algonquin from its current range in Connecticut and adjacent New England States. It could cause the demise of hemlock similar to Dutch elm disease and chestnut blight.

The main factor affecting this outcome is ungulate browsing, primarily by moose. If current ungulate numbers are maintained, hemlock will decline in numbers as the canopy trees die, and be restricted to lakeshore areas. However, if moose numbers decline, either from hunting, disease, predation or other factors (and are not replaced by deer), hemlock may recover and slowly replace itself in upland areas. Ungulate numbers would have to remain low for several decades for saplings to get out of the reach of ungulates and be in a position to replace canopy trees as they senesce. If logging were to stop, the forests would over the next century or two return to the old-growth stage, with less available browse, and moose populations may return to pre-European levels. It is not clear whether hemlock would be able to regain habitat lost to sugar maple over the last century. Frelich *et al.* (1993) found that old-growth hemlock and hardwood stands tend to maintain separate identities without reciprocal replacement for the past 3000 years since the arrival of hemlock in the upper Great Lakes. Consequently, hardwoods that now dominate on former hemlock sites, will probably remain as such, and hemlock will probably exist as scattered individuals with these stands. If conditions became more suitable for hemlock compared to hardwoods on these sites, (through a ground fire, for example) hemlock could increase its dominance. Otherwise, hardwoods would continue to dominate, and hemlock would be restricted to sites where it can regenerate. The pattern of events over the next century will dictate whether hemlock can maintain its current dominance in Algonquin Park, or diminish.

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Captions only

Figure 1. Hypotheses for intermediate age gaps in hemlock populations in Algonquin Provincial Park. See text for description.

Figure 2. A priori and a posteriori classification of 216 stands in Algonquin Provincial Park showing number of stands in each group (see text for description) Aspect classes are N (north), S (south) and K (knoll). The number below each Y(yes) and N(no) indicates the number of stands that fall into that group.

Figure 3. Relative diameter frequency distribution of stems ≥ 5 cm diameter at breast height (dbh) (1.3 m) from 216 - 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 1 cm diameter classes. a) all species (N=5159); b) sugar maple (N=1312); c) all hemlock stems (N=2213). Note: total number of hemlock stems < 5 cm dbh and ≥ 1.3 m tall was 1264 (not shown).

Figure 4. Relative frequency distribution of ages (at 1.3 m) of stems ≥ 5 cm dbh from 216 - 0.04 ha plots in Algonquin Provincial Park surveyed in 1991 - 1992. Histogram bars are in 10 year age classes. a) all species (N=4139); b) sugar maple (N=1107); c) hemlock (N=1787).

Figure 5. Frequency distribution of all hemlock seedlings >2 years old and <5 cm dbh (N=19794) from 216 - 0.04 ha plots in Algonquin Provincial Park surveyed in 1991 - 1992. 2-year-old seedlings (N=5400) are not included. a) Age frequency distribution. Histogram

bars are in 5-year age classes. b) Height frequency distribution. Histogram bars are in 0.25 cm classes.

Figure 6. a) Total annual precipitation, annual snowfall and annual rainfall for Huntsville, Ontario for which complete records are available. Y-axis is scaled in mm for precipitation and rainfall, and in cm for snowfall. b) Mean annual temperature for Huntsville, Ontario for which complete records are available.

Figure 7. Frequency distribution of mean canopy ages from 216 - 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 10-year age classes. The range was from 17.9 years to 281.4 years. Means are based on stems ≥ 9.5 cm dbh.

Figure 8. Linear regression of number of hemlock seedlings versus mean canopy age from 216 - 0.04 ha plots in Algonquin Provincial Park. (F-ratio=31.7, $r^2=0.129$, $P<0.001$). Mean canopy ages are based on stems ≥ 9.5 cm dbh.

Figure 9. Relative frequency distribution of ages of hemlock stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 10-year-age classes. Mean canopy ages are based on stems ≥ 9.5 cm dbh. a) 29 youngest sites outside of deeryards (N=253) with a mean canopy age < 86 years. b) 24 oldest sites (mean canopy age >155 years) outside of deeryards (N=280).

Figure 10. Relative frequency distribution of ages (at 1.3 m) of all hemlock stems ≥ 5 cm

dbh from 48 - 0.04 ha nonlakeshore plots undisturbed for the last century in Algonquin Provincial Park. Histogram bars are in 10-year age classes. a) 12 hemlock dominant plots ($\bar{x} = 172.3$, $N=160$); b) 17 hemlock patch plots (mean = 161.4, $N=128$); c) 19 hemlock scattered plots (mean = 144.9, $N=24$).

Figure 11. Log frequency distribution of ages of all hemlock ≥ 3 years old from 0.04 ha plots in Algonquin Provincial Park. Frequencies are based on 10-year age classes. a) 84 deeryard-nonlakeshore plots ($N=6714$); b) 29 lakeshore-nondeeryard plots ($N=4378$).

Figure 12. Relative frequency distribution of ages (at 1.3 m) of hemlock stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 10-year age classes. a) 84 deeryard-nonlakeshore plots (mean = 161.4 yr., $N=529$); b) 29 lakeshore-nondeeryard plots (mean = 104.3 yr., $N=434$).

Figure 13. Relative frequency distribution of ages (at 1.3 m) of all hemlock stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 10-year age classes. a) 41 lakeshore plots (mean = 115.8, $N=582$); b) 175 nonlakeshore plots (mean = 156.6, $N=1205$).

Figure 14. Relative frequency distribution of ages (at 1.3 m) of all hemlock stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 10 year age classes. a) 96 deeryard plots (mean = 166.5, $N=669$); b) 120 nondeeryard plots (mean = 129.3, $N=1117$).

Figure 15. Percentage of hemlock seedlings (<5.0 cm dbh) browsed per plot versus total plot basal area (m²) separated by stand type (hemlock dominant, hemlock patch, scattered hemlock) for 216 - 0.04 ha plots in Algonquin Provincial Park. The percentage of browsed seedlings was determined by dividing the number of browsed seedlings per plot by the total number of seedlings in the plot.

Figure 16. Relative frequency distribution of percentage of hemlock seedlings (<5.0 cm dbh) browsed from 0.04 ha plots in Algonquin Provincial Park. The percentage of browsed seedlings was determined by dividing the number of browsed seedlings per plot by the total number of seedlings in the plot. The histogram bar to the left of 0 on the x-axis indicates the relative frequency of plots with no browsing (this would include plots with no seedlings).
a) all 216 plots; b) 84 deeryard and nonlakeshore plots; c) 29 lakeshore and nondeeryard plots; d) 63 knoll plots; e) 153 north aspect and south aspect plots.

Figure 17. Bar chart of percentage of all seedlings >2 years old and < 5 cm dbh (N=19794) and percentage of browsed seedlings (N=4214) by 20 cm height classes for 216 - 0.04 ha plots in Algonquin Provincial Park. Percent browsed per height class was determined by dividing the number of browsed seedlings in each height class by the total number of seedlings in that height class. Only 3 stems > 4 m tall were browsed and are not included in the figure. No stems > 5 m tall had browse damage.

Figure 18. Linear regression of percentage of browsed seedlings per plot versus number of seedlings per plot from 216 - 0.04 ha plots in Algonquin Provincial Park. The percentage of

browsed seedlings was determined by dividing the number of browsed seedlings per plot by the total number of seedlings in the plot.

(F-ratio=30.68, $r^2=0.185$, $P<0.001$).

Figure 19. Relative moose pellet group frequency distribution per plot from 0.04 ha plots in Algonquin Provincial Park. The number of pellet groups per plot was based on 1992 data.

a) 63 knoll plots; b) 153 north aspect and south aspect plots.

Figure 20. Mean heights (\pm S.E.) versus mean ages (\pm S.E.) (at ground level) for seedlings (< 5 cm dbh) that were non-browsed, <50% browsed and \geq 50% browsed by ungulates and hares in a) 29 lakeshore-nondeeryard plots (N=3946) and b) 84 deeryard-nonlakeshore plots (N=3789).

Figure 21. Scatterplot of height in April 1993 versus height in November 1992 of 730 transplanted hemlock saplings in Algonquin Provincial Park. 336 (46%) of the saplings had a mean height loss of 27% from browsing.

Figure 22. Scatterplot of percentage sapling height lost versus initial height in November 1992 of 336 browsed transplanted hemlock saplings in Algonquin Provincial Park.

Figure 23. Scatterplot of percentage browsed per seedling versus initial seedling height from 539 tagged seedlings in Algonquin Provincial Park.

Figure 24. Scatterplot of percent height lost per seedling versus initial seedling height from 539 tagged seedlings in Algonquin Provincial Park. The loss is significantly correlated with initial seedling height ($r^2 = -0.27$, $p=0.0002$)

Figure 25. Relative frequency distribution of heights of hemlock stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 1 metre height classes. a) 120 nondeeryard plots (mean = 15.6 m, $N=1359$); b) 96 deeryard plots (mean = 17.9 m, $N=854$).

Figure 26. Relative frequency distribution of heights of hemlock stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 1 metre height classes. a) 29 lakeshore plots (mean = 15.3 m, $N=688$); b) 175 nonlakeshore plots (mean = 17.1 m, $N=1525$).

Figure 27. Mean heights (\pm S.E.) and mean ages (\pm S.E.) (at ground level) for tagged seedlings (< 5 cm dbh) that died between 1992 and 1994 and were browsed before dying ($N=19$) or showed no evidence of browsing ($N=12$). Ages are estimated based on branching and terminal bud scars of seedlings.

Figure 28. Relative frequency distribution of diameters of all hemlock stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 1 cm diameter classes. a) 41 lakeshore plots (mean = 25.8, $N=688$); b) 175 nonlakeshore plots (mean = 32.0, $N=1525$).

Figure 29. Relative frequency distribution of all sugar maple stems ≥ 5 cm dbh from 175 - 0.04 ha nonlakeshore plots in Algonquin Provincial Park. a) diameter distribution (mean = 19.4 cm, N=1271). Histogram bars are in 1 cm classes. b) Age distribution (mean = 67.9 yrs, N=1075). Histogram bars are in 10-year age classes.

Figure 30. Relative frequency distribution of ages (at 1.3 m) of all sugar maple stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 10-year age classes. a) 96 deeryard plots (mean = 60 yr., N=572); b) 120 nondeeryard plots (mean = 76.6 yr., N=535).

Figure 31. Relative frequency distribution of ages (at 1.3 m) of stems ≥ 5 cm dbh from 84 - 0.04 ha deeryard and nonlakeshore plots in Algonquin Provincial Park. Histogram bars are in 10-year age classes. a) Hemlock stems (mean = 161.4 yr., N=529); b) Sugar maple stems (mean = 66.4 yr., N=570).

Figure 32. Relative frequency distribution of ages (at 1.3 m) of sugar maple stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 10-year age classes. a) 48 plots undisturbed for the last century (mean = 79.1, N=317); b) 56 plots disturbed by cutting or fire before 1945, (mean = 63.9, N=267). This includes lakeshore plots.

Figure 33. Relative frequency distribution of ages (at 1.3 m) of hemlock stems ≥ 5 cm dbh from 0.04 ha plots in Algonquin Provincial Park. Histogram bars are in 10-year age classes.

a) 56 plots disturbed by cutting or fire before 1945, (mean = 135.6, N=580); b) 48 plots undisturbed for the last century (mean = 165.7, N=312). This includes lakeshore plots.

Figure 34. A model of hemlock/sugar maple dynamics.