OLD-GROWTH FOREST SURVEY OF CAYUGA LAKE WEST, ALGONQUIN PARK

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SUMMARY

The areas surrounding Cayuga Lake are notable for significant tracts of old-growth hemlock forest. A life science nature reserve (Cayuga Lake Hemlock N31) protects 561 hectares of old growth, however 176 hectares of old growth to the west remain unprotected. We inventoried stands within the unprotected forest (Cayuga Lake West) as part of the Algonquin Park Old-growth Forest Project. Our results show that the hemlock forest in Cayuga Lake West has ages, tree basal area, and coarse woody debris volume that are all indicative of high quality old-growth forest.

The mean age obtained by tree cores is 307 years while the maximum age is 427 years old. A conservative stand age derived only from plots on a grid is 263 years. These ages are higher than most old-growth forests in eastern North America, and comparable to some exceptionally old hemlock forests in Adirondack State Park and Algonquin Park.

The average live tree basal area from all plots was 36 m^2/ha, which compares favourably with other old-growth forest in eastern North America. The mean volume of logs from all transects was 57.9 m^3/ha, which is typical of old-growth forests in eastern North America, but somewhat lower than expected given the extremely high stand age.

Hemlock accounts for 47.3% of the basal area in our plots, and 10-60% of the Forest Resource Inventory stands where the plots are located. Although Algonquin Park makes up only 1.8% of the productive forest area of Ontario, it contains 60% of the hemlock working group over the age of 140 in the province. Land use change and logging have led to a nearly 75% decline in hemlock abundance on the landscape adjacent to and west of the Park and have virtually eliminated hemlock in many parts of southern Ontario where it was once common.

Highly decayed conifer stumps were found in only a few parts of the forest. These are likely remnants from logging of white pine that occurred 90+ years ago. They were tallied at an estimated density of 5.2 stumps/ha.

Ages obtained in the field confirm that older 1987 Forest Resource Inventory (FRI) data more accurately describes old-growth forest in Algonquin Park than updated FRI data, which significantly underestimates ages in many stands. This is important for ongoing old-growth surveys in the Park.

Logging of old-growth forest in Algonquin Park clearly undermines the ecological integrity of the park. A strategy for properly identifying and protecting remaining old-growth forest and roadless areas in the park should be included in the next review of the Algonquin Park Management Plan.

INTRODUCTION

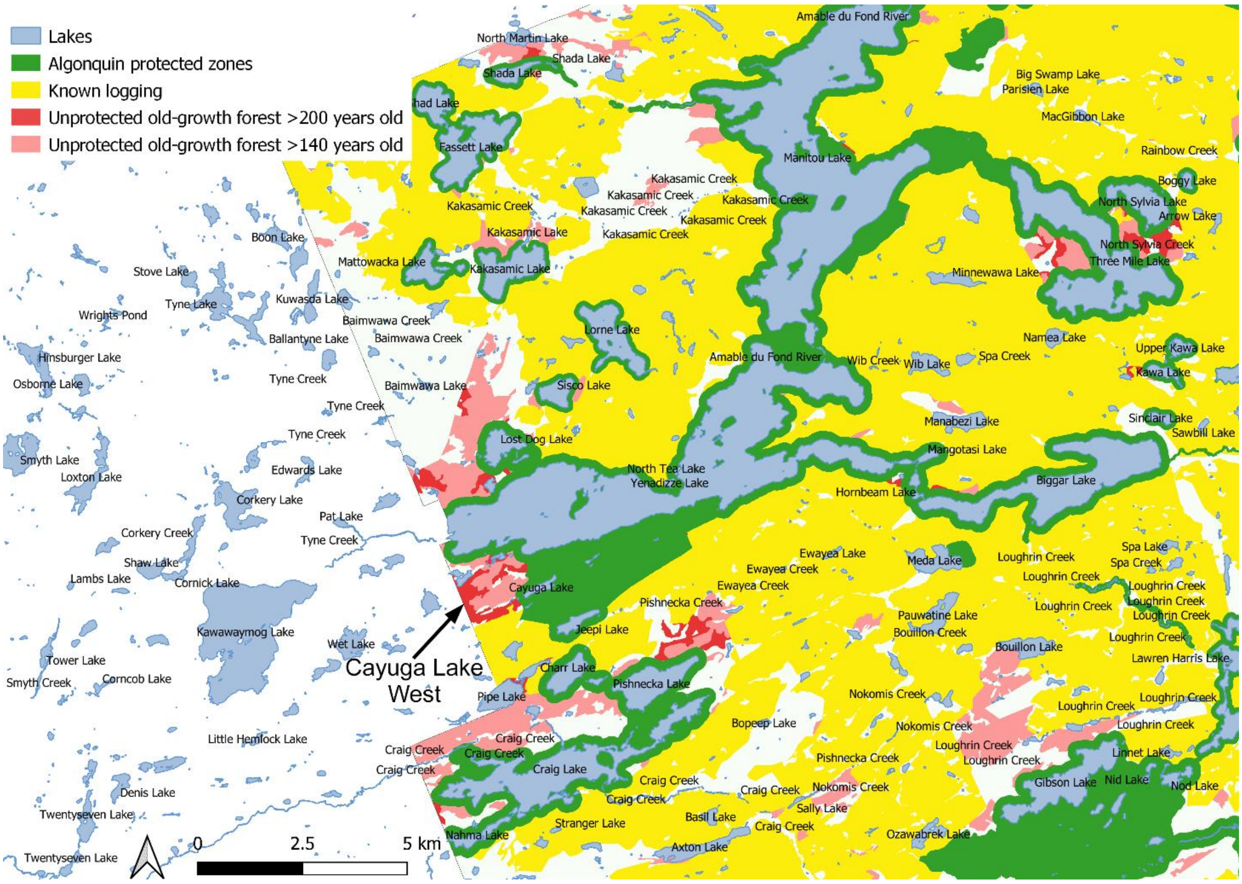
Significant tracts of old-growth forest remain unprotected in Algonquin Park, including large tracts of pristine old-growth forest with trees 300 to 400 years old that are available for logging (Henry & Quinby, 2006; Henry et al., 2018; Henry & Quinby, 2007, 2018). The Algonquin old-growth forest project was launched in 2022 to identify remaining old-growth forests in the recreation/utilization zone for protection from logging.

The Cayuga Lake area is known for its significant old-growth forest, and a life science nature reserve (Cayuga Lake Hemlock N31) protects 561 hectares of old growth. However 176 hectares of the old growth remains unprotected

("Cayuga Lake West"), and a 2018 preliminary survey confirmed that at least part of the forest was relatively pristine with trees up to 408 years old (Henry et al., 2018).

Additional stands were surveyed in 2022 using a rapid survey approach that includes collection of tree basal area, coarse woody debris volume, and standardized stump surveys.

FIGURE 1 LOCATION OF CAYUGA LAKE WEST AND KNOWN LOGGING IN NORTHWEST ALGONQUIN PARK



METHODS

We use rapid survey techniques to collect useful data as quickly and cheaply as possible. Sampling is conducted along pre-planned transects and in plots, which are located on a grid pattern oriented to fit within old-growth forest stands (in this case FRI stands with high stand ages). Hemlock forest is also prioritized in transect placement as it is a species of particular concern. Variable radius plots (prism sweeps) are located at the end points of each 150 m transect, where tree and snag basal area is recorded by species and diameter class. One or more trees are selected for coring at each point based on age characteristics.

All movement within old-growth stands is treated as an informal transect: presence of stumps is noted, and additional data collection including tree coring may take place along these routes.

A more detailed description of the methods and data sheets can be found in the first report in this series (Henry, 2023a).

TRANSECTS: GENERAL HABITAT DESCRIPTION AND STUMP SURVEY FOR HISTORICAL LOGGING

Transects are divided into 150 m sections and along each section the following data are recorded:

- stumps within line of sight of the transect are counted and grouped by decay class categories (1-3 and 4-5), decay class is used to provide an estimated time since logging. photos may be taken.
- Trees with old-age characteristics along transects may be selected for aging by tree core. Cores are collected in paper or plastic straws and counted after field work is completed.
- Qualitative observations of old-growth characteristics are recorded.
- Qualitative observations of stand age class distribution and regeneration are recorded.
- invasive species, disease resistant trees, and other conservation features are noted, locations may be saved and reported to iNaturalist projects (https://www.inaturalist.org/projects/invasive-species-in-ontario, https://www.inaturalist.org/projects/beech-bark-disease-resistance, etc.)

TREES, SNAGS, AND LOGS

Trees and snags over 10 cm were measured at the end points of each 150 m transect, using a BAF2 wedge prism and DBH of trees that were "in." Logs were measured using line intersect along 30m transects beginning at each plot center, and following the transect bearing. Log diameter was recorded at the intersect point (Van Wagner, 1982) and also at large end to allow the logs to be analyzed more accurately by size classes (Bate et al., 2009). The formula to calculate volume (from Van Wagner 1982), is:

$V= (k/L) *Sum(D^2)$

Where V is volume in m3/ha, k is a constant (1.234), L is the transect length (m), D is diameter at intersect point (cm).

When the transect crosses over highly decayed stumps they typically have very large diameter but are low to the ground. Including these significantly skewed the data, so they were omitted from the total volume calculation.

RESULTS AND DISCUSSION

TREE AGES

Twenty trees were cored at Cayuga Lake, 12 were within the prism sweeps on the predetermined grid, eight others were visible from transects or scouting routes and were selected based on age characteristics (Table 1; Figure 2). The mean age obtained from all cores is 307 years. If only cores within plots are used the mean stand age is 263 years.

While some studies use the average of tree cores to define stand age (e.g. Hale et al., 1999; Keeton et al., 2007), stand age in old growth forests is also commonly defined by the oldest trees, which represent the minimum period since a stand replacing disturbance (e.g. Tyrrell & Crow, 1994; Ziegler, 2000, 2011). Using this approach the stand age would be 427 years.

TABLE 1 AGES OF TREES FROM CORES COLLECTED AT CAYUGA LAKE

Plot	Tree species	DBH (cm)	Ring count	Adjust to pith	Adjust 1.4m	Age
	Hemlock	48.7	379	10	24	413
	Hemlock	46.6	342	15	24	381
	White Pine	63	199			
	Hemlock	55.5	396	5	24	425
	Hemlock	68	367	10	24	401
1	Hemlock	44.5	398	5	24	427
	Hemlock	47.2	308	15	24	347
	Hemlock	42.9	280	10	24	314
2	Hemlock	53	292	5	24	321
3	Hemlock	51.3	215	5	24	244
4	Yellow Birch	71.3	190	5	15	210
5	Hemlock	41	252	5	24	281
6	Hemlock	44.2	153	15	24	192
6	Sugar Maple	45.4	132	15	15	162
7	Hemlock	63.8	243	10	24	277
	Hemlock	31.2	235	15	24	274
	Hemlock	39.4	396	5	24	425
8	Yellow Birch	73.7	298		15	313
8	Hemlock	60.5	250		24	274
9	Hemlock	58.6	228		24	252
10	Sugar Maple	44.1	185		15	200

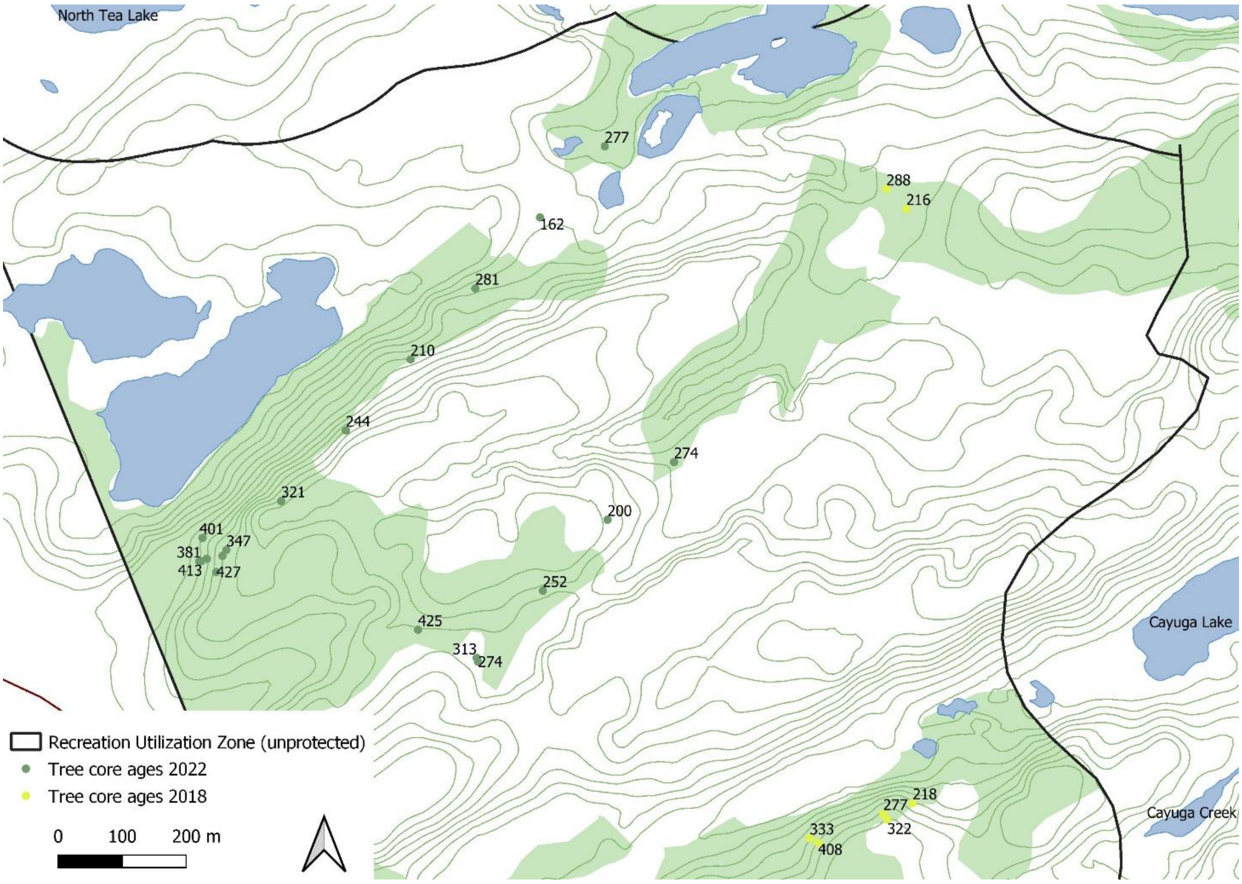
Both the mean and maximum ages place Cayuga Lake among the oldest forest stands in Eastern North America (Table 2). A literature review by Thom et al. (2019) found that "less than 0.2% of the investigated sites are currently occupied by forests older than 200 years [...] This suggests a large potential to improve joint ESB [ecosystem services and biodiversity] outcomes in temperate and boreal forests of eastern North America by enhancing the representation of late-successional and older forest stand structures."

One quarter of the trees cored in this study were over 400 years old, while another tree cored in 2018 was also over 400, for a total of six trees >400-years-old found in Cayuga Lake West to date, with a very limited sample size. Very old trees are distributed throughout the forest, with three widely separated locations for trees >400-years-old (Fig. 2).

TABLE 2 TREE AGES FROM OLD-GROWTH FORESTS IN EASTERN CANADA AND ADJACENT USA

Source	Maximum age	Mean age	Location
This study	427	263	
Henry 2023b	338	211	Longboot Lake, south Algonquin Park, ON
Henry et al. 2018	408	294	Cayuga Lake, NW Algonquin Park, ON (preliminary results)
Henry & Quinby 2006	433	287	6 old-growth sites in Algonquin Park, ON
Henry & Quinby 2018	295	232	Hurdman Creek, N Algonquin Park, ON (preliminary results)
Keeton et al. 2007		205-410	10 old-growth forests in western Adirondack Park, NY
Hale et al. 1999		124-172	11 maple-basswood forests > 120 years old in Minnesota
Hale et al. 1999		128-164	7 oak forests >120 years old in Minnesota
Vasiliauskas 1995	454	154	1,576 hemlock tree cores in Algonquin Park, ON
Ziegler 2011	253-390		12 OG hemlock forests in Adirondack Park, NY

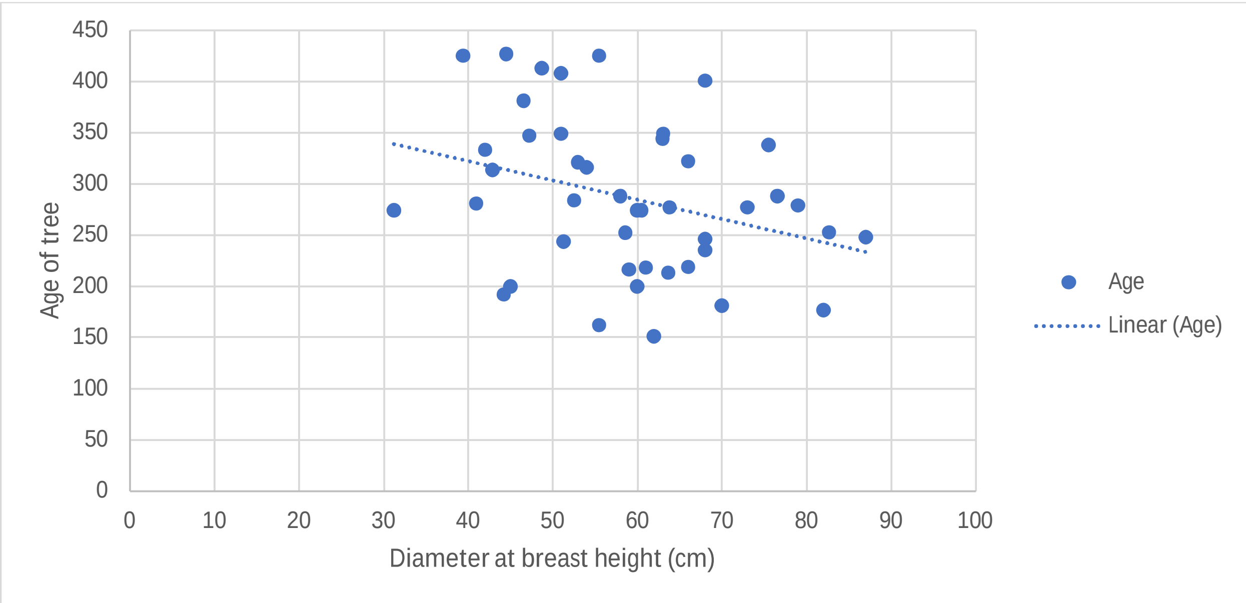
FIGURE 2 LOCATION AND AGES OF INCREMENT BORES



CHARACTERISTICS OF OLD HEMLOCK TREES

The external characteristics of old trees are becoming increasingly well understood, and guidelines for recognizing signs of old age accepted in the scientific literature (Black et al., 2008; Brown et al., 2019; Pederson, 2010; Piovesan & Biondi, 2021). Brown et al. (2019) evaluated the effectiveness of using morphological characteristics including bark and branching to categorize trees as old (>150 years) or young (<150 years) and found the method was 88% to 96% accurate depending on tree species. They also found that DBH was not very effective at identifying old trees. While many people believe that tree size is a good proxy for age this has repeatedly been shown to be untrue, particularly in older forests (Black et al., 2008; Brown et al., 2019; Guyette & Dey, 1995; Pederson, 2010; Piovesan & Biondi, 2021; Stephenson & Demetry, 1995). A scatter plot of diameter and age from 44 complete hemlock cores collected in Algonquin Park between 2006 and 2022, including this study (Fig 3), clearly illustrates why external characteristics other than diameter are essential to identifying old trees. The largest trees are rarely if ever the oldest, and very old trees are typically average size or smaller. Very few trees below 40 cm diameter were sampled in the Algonquin data, but Black et al. (2008) show that 150-year-old hemlocks average less than 40 cm diameter, and in some cases trees over 200 years old can be less than 20 cm in diameter, though this is not the norm. Site conditions play an important role, with the oldest trees often found growing on poorer sites. This in part explains the inverse relationship between age and diameter, however even on the same site smaller trees that spent centuries suppressed in the understory are often the oldest trees in the forest. In general slower growing trees tend to live longer.

FIGURE 3 DIAMETER-AGE RELATIONSHIP FOR OLD-GROWTH HEMLOCK TREES IN ALGONQUIN PARK



Henry et al. (2018) summarized external characteristics of very old hemlock trees, noting that trees over approximately 200 years in age may have low trunk taper and large upper branches. Hemlock trees over approximately 300 years in age often have pronounced bark ridging in the upper 25% of the trunk and sometimes have pronounced curves and twists in upper branches, and/or high trunk sinuosity. The current study confirms these findings and adds more information about characteristics of extremely old trees. Trunk taper consistently decreases with age, and upper branch size tends to increase to the point where the upper canopy of extremely old hemlocks sometimes resemble hardwood trees in their form (Fig 4-5). Hemlock trees over 400 years old typically have column-like trunks with pronounced ridges running well into the canopy, and even onto large upper branches.

FIGURE 4. LOW TRUNK TAPER, THICK BRANCHING, BARK RIDGING, AND SINUOSITY IN THE CROWNS OF TWO OLD HEMLOCK TREES

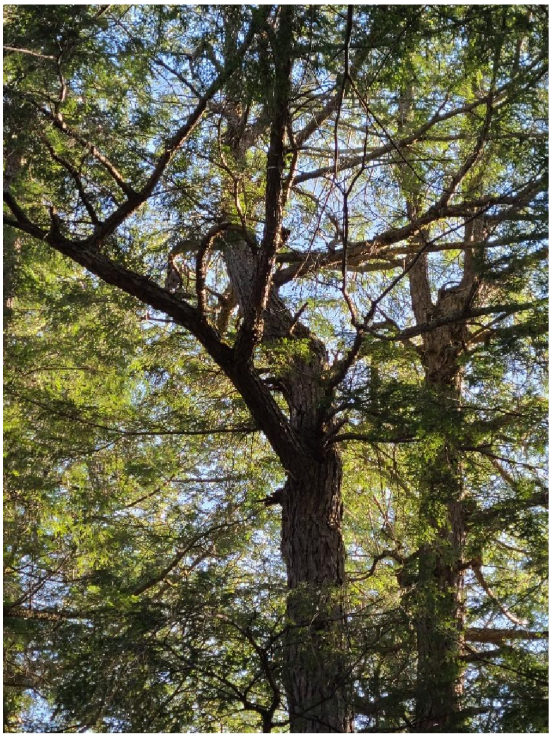


FIGURE 5. THICK BRANCHING AND HIGH BARK RIDGING ON A 425-YEAR-OLD HEMLOCK. NOTE THE DEFLECTION NEAR THE TOP.

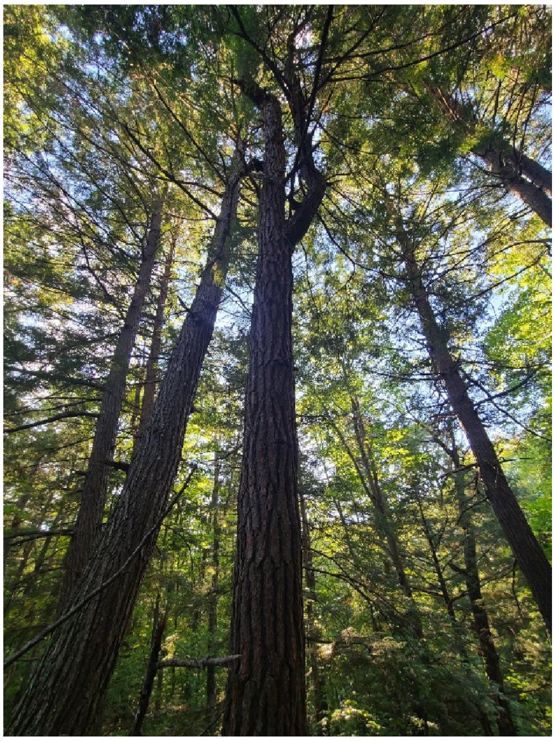
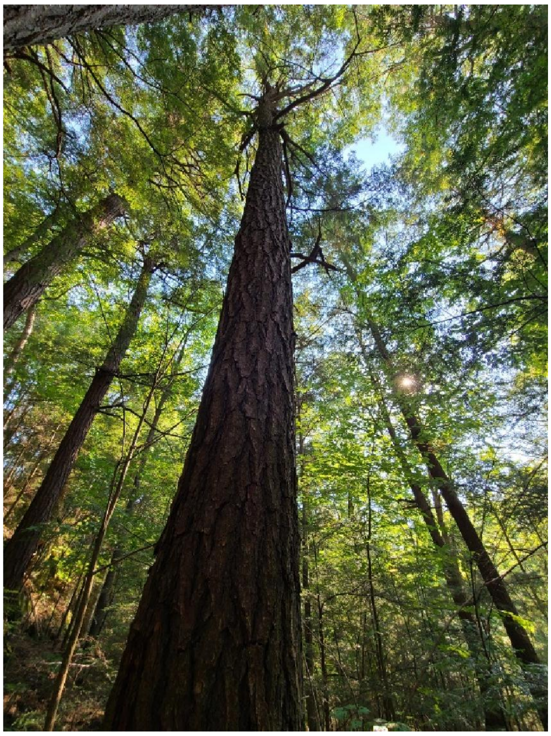


FIGURE 6. LOW TAPER, SINUOSITY ON A 427-YEAR-OLD HEMLOCK (IN PLOT 1)

FIGURE 7. LOW TRUNK TAPER AND HIGH BARK RIDGING ON A 413-YEAR-OLD HEMLOCK



Accuracy of Forest Resource Inventory (FRI) Ages

There are large discrepancies between the most recent FRI stand ages (2008 imagery) and those from the 1987 data, particularly among the oldest age classes; it appears that old-growth ages have consistently decreased across the park in the new inventory data. As a result the 1987 stand ages (updated to 2022) are much closer to the mean age from all tree cores at Cayuga Lake. The 1987 adjusted stand ages where our plots were located range from 171 to 246 years, compared to a mean age of 263 years from plot data. The 2008 FRI data shows almost uniform stand ages of 112 years (in 2021), well under half of our mean stand age of 263 years and much lower than the youngest tree cored.

Table 3 shows field ages from several surveys in Algonquin Park, compared to the 1987 and the 2021 FRI data. The older FRI data is clearly more dependable for locating and describing old-growth forest in Algonquin Park, and likely in other parts of Ontario. The newer FRI data is all but useless in locating the oldest forest stands in Algonquin Park.

TABLE 3 COMPARISON OF AGES OBTAINED FROM INCREMENT BORE TO FOREST RESOURCE INVENTORY STAND AGE

Source	Max age	Mean age	FRI 1987 +35 yrs (% from mean)	FRI 2021 (% from mean)
This study	427	263	246 (-6%)	112 (-57%)
Henry 2023b	338	211	224 (+6%)	143 (-32%)
Henry et al. 2018	408	294	224 (-24%)	112 (-62%)
Henry & Quinby 2018	295	232	210 (-9%)	110 (-53%)

Tree basal area and size class distribution

The average tree basal area from all plots was 36.8 m^2/ha. This is high compared with other studies and literature reviews (see table 4). Keddy and Drummond reviewed 10 studies in old growth forests from 1958-1991 (Table 5) and proposed basal area over 29 m^2/ha as being the normal condition of primary old growth forest, although they recognize that site conditions can have a large influence on basal area. At 36.8 m^2/ha the Cayuga Lake survey area easily fits this criterion for old growth forest.

TABLE 4 BASAL AREA OF OLD-GROWTH FORESTS IN EASTERN NORTH AMERICA

Source	Tree BA (m^2/ha)	Snag BA (m^2/ha)	Location
This study	37	6.2	Cayuga Lake, Northeast Algonquin Park, Ontario
Henry, 2023b	30	3.2	Longboot Lake, southern Algonquin Park, Ontario
Spetich et al. 1999	28	3	12 old-growth sites in IN, IL, MO, and IA
Larson et al. 1999	36		35 heritage (OG) woodlands in southern Ontario
Hale et al., 1999	31		11 OG maple-basswood forests >120 years in MN
Hale et al., 1999	32		10 oak forests >120 years old in MN
Keddy & Drummond 1996	29		Average from 10 studies in eastern North America
Keeton et al., 2007	33	8	10 old-growth forests in Adirondack Park, NY

FIGURE 8 SIZE CLASS DISTRIBUTION

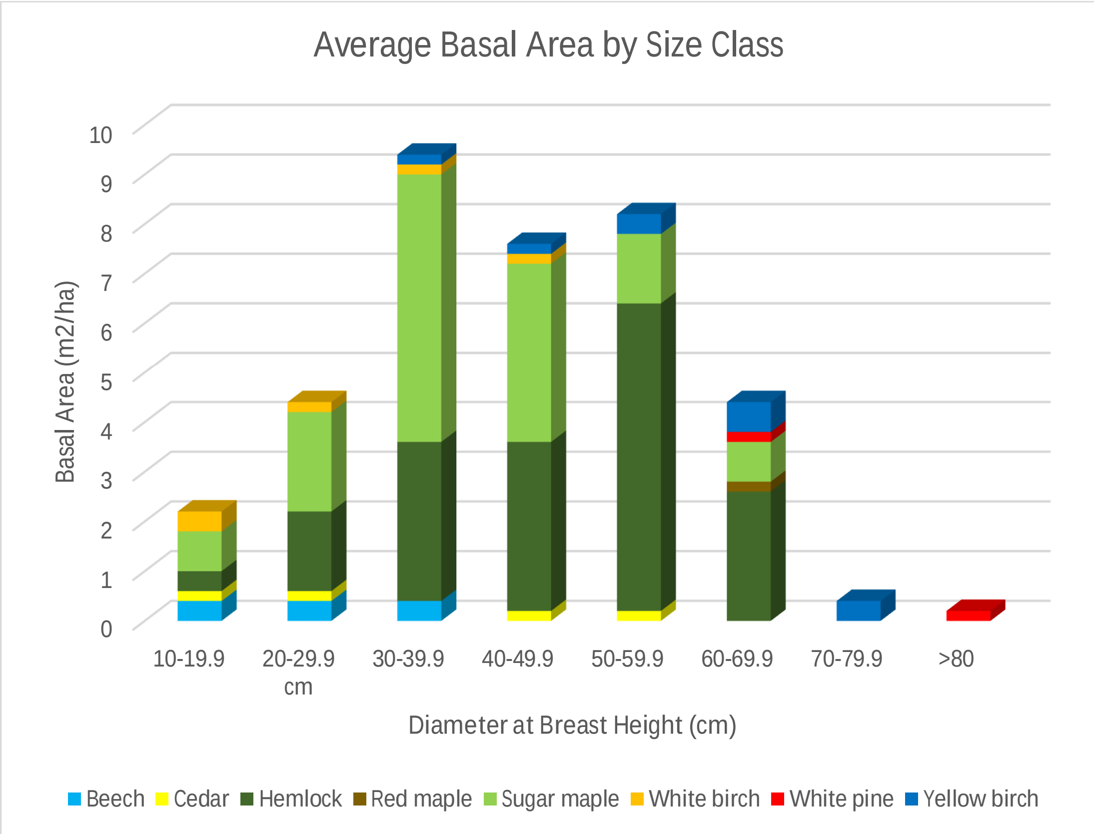


TABLE 5 BASAL AREA OF PRIMARY FOREST STANDS, FROM KEDDY AND DRUMMOND 1996

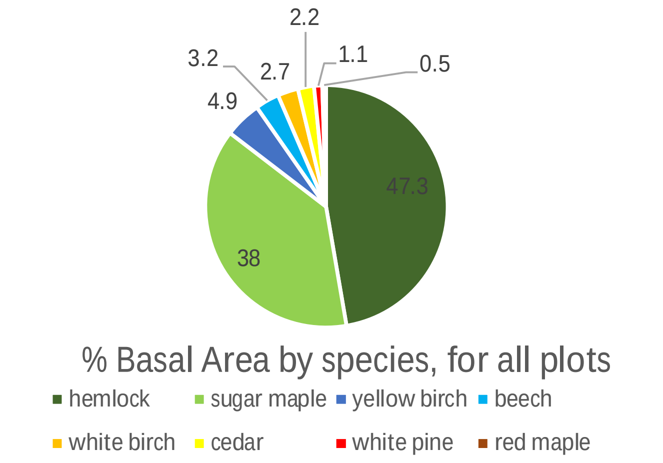
Basal area (m^2/ha)*	Study site†	Forest type	Source
Old-growth stands			
28	Michigan	*Fagus–Acer*	Schmelz and Lindsey (1965)
32	Pennsylvania	*Tsuga–Fagus*	Hough (1936)
40	Ohio	*Acer–Fagus*	Boerner and Cho (1987)
29	Indiana	*Fagus–Acer–Quercus*	Lindsey et al. (1958)
28	Indiana	*Acer–Fagus*	Abrell and Jackson (1977)
26	Indiana	*Fagus–Acer*	Schmelz and Lindsey (1965)
26	Indiana	*Acer*	Schmelz and Lindsey (1965)
23	Indiana	*Fagus–Acer*	Schmelz and Lindsey (1965)
32	Ohio	*Acer–Quercus*	McCarthy et al. (1987)
30	Kentucky	Deciduous	Bougher and Winstead (1974)
($\bar{X}$ = 29, SD = 4)			
Altered sites			
24	New Hampshire	*Fagus–Acer–Betula*	Whittaker et al. (1974) Logged 57 yr before study
21	Tennessee	*Acer saccharum*	Onega and Eickmeier (1991) Nonclimax site
19	Indiana	Upland deciduous	Schmelz and Lindsey (1965) Recently altered forest
($\bar{X}$ = 21, SD = 3)			

* Altered sites' basal areas based on a minimum stem diameter of 10.2 cm, except Boerner and Cho (1987) and McCarthy et al. (1987) used 2.5 cm and Hough (1936) used 9.1 cm. Values have been rounded up to the even number.
† Study sites are listed in the order of ascending latitude.

TREE SPECIES COMPOSITION

Hemlock accounts for 47.3% of the basal area in our plots, and 10-60% of the Forest Resource Inventory stands where the plots are located. Sugar maple makes up a large part of the remainder (see figure 4) in the plot and FRI data.

FIGURE 9 TREE SPECIES COMPOSITION (% OF BASAL AREA) IN PLOTS



Old-growth eastern hemlock forests have high ecological value, and Algonquin Park bears a disproportionate responsibility for their conservation in Ontario and globally. Although Algonquin Park makes up only 1.8% of the productive forest area of Ontario, it contains 60% of the hemlock working group over the age of 140 in the province (Henry & Quinby 2006).

COARSE WOODY DEBRIS

The average volume of logs from all transects was 57.9 m^3/ha. This volume is fairly average for old-growth forests in eastern North America (Table 6), but is lower than expected in these stands since log volume tends to increase with age (Henry, 2023b; Spetich et al., 1999; Tyrrell & Crow, 1994; Susy Svatek Ziegler, 2000).

While any transformation from volume to weight using the limited dataset is bound to be an approximation, it is useful to be able to compare our data to CWD weights in the published literature. We use the green weight of hemlock for this conversion because it is a common component of the logs and it also has an intermediate specific gravity (0.956 Mg/m^3). Adams & Owens (2001) found that across 21 hardwood species, mean specific gravity decreased by nearly 50 percent from decay class 1 to 3, so assuming an average decay class of 3 (the average in our data was 3.4) we use a conversion of 0.478 to transform volume to weight. This gives a very rough approximate weight of 27.7 Mg/ha in this forest, just over the 27 Mg/ha suggested as a minimum for old-growth forests by Keddy & Drummond (1996). One Megagram (Mg) is equivalent to a metric tonne, so there are some 28 tonnes of logs per hectare at the Cayuga Lake West site.

Mean log diameter was 26.4 cm when using large end diameters (as per Bate et al. 2009), which is lower than Larson et al. (1999) with a mean log diameter of 31.7 cm or Henry (2023b) with a mean of 32.7 in southern Algonquin Park.

TABLE 6 COARSE WOODY DEBRIS VOLUME AND DIAMETER IN OLD-GROWTH FORESTS OF EASTERN NORTH AMERICA

Source	Volume (m^3/ha)	Mean Diameter (cm)	Location
This study	57.9	26.4	Northeast Algonquin Park
Henry, 2023b	137	32.7	Southern Algonquin Park
Spetich et al. 1999	60.4		12 old-growth sites in IN, IL, MO, and IA
Larson et al. 1999		31.7	35 heritage (OG) woodlands in southern Ontario
Hale et al., 1999	55 (12-121)		11 OG maple-basswood forests >120 years in MN
Hale et al., 1999	48 (21-68)		10 oak forests >120 years old in MN
Ziegler, 2000	126		12 OG hemlock forests in Adirondack Park, NY
Keeton et al. 2007	163.6		10 old-growth forests in Adirondack Park, NY

STUMP SURVEYS AND HISTORICAL LOGGING

Stumps were noted as we travelled through the stands, and a formal stump count was conducted along the transects. Total transect length was 1350 m in this forest. Any stumps that were visible were tallied, and assuming that visibility was approximately 10 m to either side (average, depending on vegetation) the total surveyed area equates to roughly 2.7 ha.

14 stumps were counted, nearly all of them in a single transect. This equates to an estimate of 5.2 stumps/ha. Seven of the nine transects had no evidence of historical logging, suggesting that this forest is largely pristine old growth.

All the stumps were mid size conifers, likely white pine, decay class 4 or 5 (highly decayed), with an estimated time since logging of 90+ years. Most of the stumps were found in transect one, where there are a few remaining old white pines – a partial core from one 63 cm DBH white pine had 199 rings, suggesting the tree is likely over 300 years old.

CONCLUDING THOUGHTS

Logging of old-growth forest and roadless areas in Algonquin Park clearly undermines the ecological integrity of the park. A strategy for protecting remaining old-growth forest and roadless areas in the park should be included in the next review of the Algonquin Park Management Plan. Adding the remaining unprotected roadless areas and intact old-growth forest to the protected zones of Algonquin Park would likely increase the protected area of the park by only five to six percent, from 35% to around 40%.

A review of the Algonquin Park Management Plan was scheduled for 2018 (ECO, 2014) but has not occurred. When this review occurs a strategy for properly identifying and protecting remaining old-growth forest and roadless areas in the park should be included. Protection of extremely high-quality old growth such as is found at Cayuga Lake West should not be at the discretion of forest managers; this and other high value areas should be identified and incorporated into the protected zones of Algonquin Park.

FIGURE 10 A TREE CORE EXTRACTED FROM A 425-YEAR-OLD TREE IN ALGOQNUIN PARK. THIS TREE IS AVAILABLE FOR LOGGING

ACKNOWLEDGEMENTS

This work would not have been possible without support from the Wilderness Committee, Nadurra Wood Corporation, Ian Jackson, Susan Gibson, numerous small donors, and the work of many fantastic volunteers.

REFERENCES

Adams, M. B., & Owens, D. R. (2001). *Specific Gravity of Coarse Woody Debris For Some Central Appalachian Hardwood Forest Species The Authors*. http://www.fs.fed.us/ne

Bate, L. J., Torgersen, T. R., Wisdom, M. J., & Garton, E. O. (2009). Biased estimation of forest log characteristics using intersect diameters. *Forest Ecology and Management*, *258*(5), 635–640. https://doi.org/10.1016/j.foreco.2009.04.042

Black, B. A., Colbert, J. J., & Pederson, N. (2008). Relationships between radial growth rates and lifespan within North American tree species. *Écoscience*, *15*(3), 349–357. https://doi.org/10.2980/15-3-3149

Brown, P. M., Gannon, B., Battaglia, M. A., Fornwalt, P. J., Huckaby, L. S., Cheng, A. S., & Baggett, L. S. (2019). Identifying old trees to inform ecological restoration in montane forests of the central rocky mountains, USA. *Tree-Ring Research*, *75*(1), 34–48. https://doi.org/10.3959/1536-1098-75.1.34

Environmental Commissioner of Ontario. (2014). *MANAGING NEW CHALLENGES: ANNUAL REPORT 2013/2014*. http://docs.assets.eco.on.ca/reports/environmental-protection/2013-2014/2013-14-AR.pdf

Guyette, R., & Dey, D. C. (1995). Age, size and regeneration of old growth white pine at Dividing Lake Nature Reserve, Algonquin Park, Ontario. *Forest Research Report*, *131*, 1–11.

Hale, C. M., Pastor, J., & Rusterholz, K. A. (1999). Comparison of structural and compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, USA. *Canadian Journal of Forest Research*, *29*(10), 1479–1489. https://doi.org/10.1139/x99-076

Henry, M., & Quinby, P. (2006). A Preliminary Survey of Old-Growth Forest Landscapes on the West Side of Algonquin Provincial Park , Ontario. *Ancient Forest Exploration & Research*, *32*, 1–28. http://www.ancientforest.org/wp-content/uploads/rr32.pdf

Henry, M, & Quinby, P. (2007). *Mapping Threatened Old-Growth Forests of Algonquin Park: The First Step*. *27*. http://www.ancientforest.org/wp-content/uploads/flb27.pdf

Henry, M, & Quinby, P. A. (2018). The Hurdman Creek Old-Growth Forest. *Preliminary Results Bulletin*, *2*. www.ancientforest.org

Henry, M, Torenvliet, N., & Quinby, P. A. (2018). The Cayuga Lake Old-Growth Forest Landscape: An Unprotected Endangered Ecosystem in Algonquin Provincial Park, Ontario. *Preliminary Results Bulletin*, *6*. www.ancientforest.org

Henry, M. (2023a). Old-growth forest survey methods. *Algonquin Old-Growth Forest Project*, *1*.

Henry, M. (2023b). Old-Growth Forest Survey of Longboot Lake, Algonquin Park. *Algonquin Park Old-Growth Forest*

Project, *2*.

Keddy, P. A., & Drummond, C. G. (1996). Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. *Ecological Applications*, *6*(3), 748–762. https://doi.org/10.2307/2269480

Keeton, W. S., Kraft, C. E., & Warren, D. R. (2007). Mature and old-growth riparian forests: Structure, dynamics, and effects on adirondack stream habitats. *Ecological Applications*, *17*(3), 852–868. https://doi.org/10.1890/06-1172

Larson, B. M., Riley, J. L., Snell, E. A., & Godschalk, H. G. (1999). *The Woodland Heritage of Southern Ontario: A Study of Ecological Change, Distribution and Significance*. Federation of Ontario Naturalists. https://books.google.ca/books?id=YA4JAQAAMAAJ

Pederson, N. (2010). External Characteristics of Old Trees in the Eastern Deciduous Forest. *Natural Areas Journal*, *30*(4), 396–407. https://doi.org/10.3375/043.030.0405

Piovesan, G., & Biondi, F. (2021). On tree longevity. *New Phytologist*, *231*(4), 1318–1337. https://doi.org/10.1111/nph.17148

Spetich, M. A., Shifley, S. R., & Parker, G. R. (1999). Regional Distribution and Dynamics of Coarse Woody Debris in Midwestern Old-Growth Forests. *Forest Science*, *45*(2).

Stephenson, N. L., & Demetry, A. (1995). Estimating ages of giant sequoias. *Canadian Journal of Forest Research*, *25*, 223–233.

Thom, D., Golivets, M., Edling, L., Meigs, G. W., Gourevitch, J. D., Sonter, L. J., Galford, G. L., & Keeton, W. S. (2019). The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal–temperate North America. *Global Change Biology*, *25*(7), 2446–2458. https://doi.org/10.1111/gcb.14656

Tyrrell, L. E., & Crow, T. R. (1994). Structural Characteristics of Old-Growth Hemlock-Hardwood Forests in Relation to Age. *Ecology*, *75*(2), 370–386. https://doi.org/10.2307/1939541

Van Wagner, C. E. (1982). Practical aspects of the line intersect method. In *Information Report PI-X-12*.

Vasiliauskas, S. A. (1995). *Interpretation of age-structure gaps in hemlock (Tsuga canadensis) populations of Algonquin Park* [Queen's University]. http://www.algonquin-eco-watch.com/reference-material/Vasiliauskas Study.pdf

Ziegler, Susy S. (2011). Global Ecology and Biogeography. *Global Ecology and Biogeography*, *20*(6), 931–932. https://doi.org/10.1111/j.1466-8238.2011.00723.x

Ziegler, Susy Svatek. (2000). A comparison of structural characteristics between old-growth and postfire second-growth hemlock-hardwood forests in Adirondack Park, New York, U.S.A. *Global Ecology and Biogeography*, *9*(5), 373–389. https://doi.org/10.1046/j.1365-2699.2000.00191.x