SEEING THE FOREST WITH THE TREES: USING DENDROCHRONOLOGY TO INVESTIGATE MOOSE-INDUCED CHANGES TO A FOREST UNDERSTORY

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ABSTRACT: Dendrochronology is presented as a tool for measuring changes in woody plant growth caused by moose damage. The isolation of the moose population in Isle Royale National Park, Michigan, and the availability of annual estimates of its density since 1959 allow analysis of the relationship between moose browsing and tree-ring growth records. Whole-stem and increment-core records of balsam fir (*Abies balsamea*), a winter forage tree, mountain ash (*Sorbus americana*), a year-round forage tree, and white spruce (*Picea glauca*), a non-forage tree, are presented and discussed.

Determination of annual growth in woody plants is often achieved with the use of tree-ring records. Sometimes, insight into past effects of herbivory can be gained from these records. For example, dendrochronology is commonly used to assess insect herbivory (e.g. Jardon *et al.* 1994, Morin and Laprise 1990, Ostaff and MacLean 1995), and it has been used to show damage by snowshoe hares (Sullivan and Sullivan 1986, Sinclair *et al.* 1993). Occasionally the method has been applied to forest interactions with larger mammals like moose (e.g. Roberts 1990).

In Isle Royale National Park, Michigan, a model moose ecosystem, the relationship between annual forage growth rate and moose density has been poorly defined. Discussion of carrying capacity for moose in the island ecosystem has been limited to concern with seasonal changes in forage (Jordan *et al.* 1970), or to changes in moose habitat caused by major disturbances like fire (Peterson *et al.* 1984). Short-term declines in plant productivity caused by leaf and twig removal have been inferred from direct observation of moose browsing (Belovsky *et al.* 1973, Risenhoover 1987). Comparison of vegetation inside and outside moose exclosures (Krefting 1974, Risenhoover and Maass 1987,

McInnes *et al.* 1992, Pastor *et al.* 1993), among offshore islands with different accessibility to moose (Janke 1976, Snyder and Janke 1976), and between transects established before and after the arrival of moose (Janke *et al.* 1978, McKaig 1978) were indirect methods applied to assess long-term changes, primarily in plant community composition, but not in annual forage growth rates. Here, we use ring records from 3 tree species in the Isle Royale understory to investigate the relationship between moose browsing and annual forage growth rates.

STUDY AREA

Isle Royale National Park (48°N, 89°W) is located in Lake Superior, 24 km from the Canadian mainland. The park is an archipelago, with several small islands surrounding a main island of 544 km², about 90 km long on its main, southwest (SW) to northeast (NE) axis. Considerable topographic variation exists on the large island, not only parallel to its main axis, where upturned sedimentary and metamorphic rock layers are alternately exposed, but also in the geologic history of its opposite ends (Huber 1973). The SW end is an area of glacial deposition, where till deposits underlie deeper, well-drained soils,

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and higher elevations support a mixed hard-wood forest. In contrast, the NE end has an eroded, accentuated ridge-and-valley topography, and it supports shallow soil development, interrupted drainage, and a boreal-type forest. The SW and NE end forests are separated by a burn in the central part of the island, dating to a 1936 fire, a 160 km² area still dominated by secondary successional forest. The NE end was extensively burned in the 19th century, whereas the SW end has had no major fires in recorded history (McKaig 1978).

Moose arrived on Isle Royale shortly after the turn of the 20th century. Barred from easy migration to and from the mainland, populations rose exponentially, possibly reaching densities of 6-10 km⁻² in the 1930's (Murie 1934). The arrival of wolves on the island in 1948 and a period of unusually severe winters in the early 1950's coincided with a period of relatively low moose density (Mech 1966, R. O. Peterson, unpubl. data). Aerial observations and counts were made of moose and wolves on Isle Royale beginning in 1958. Predator and prey populations went through 2 successive cycles in abundance of 20-30 years each (Peterson *et al.* 1984, McLaren and Peterson 1994), during which density of moose declined to <1.5 km⁻², while the number of wolves reached a high of 92 per 1,000 km² in 1980. In 1981 and 1982 wolves suffered 2 successive years of high mortality, with the suspected cause an introduced disease (Mech and Goyal 1993), and wolf density has been low (<30 per 1,000 km²) ever since (McLaren and Peterson 1994). Moose density again reached very high levels (3-4 km⁻²) by the late 1980's.

Shoreline forests on Isle Royale include white spruce and northern white cedar (*Thuja occidentalis*). Balsam fir is replaced by these conifers, especially on the SW end, where recruitment of fir is impeded by moose damage to fir saplings (Janke *et al.* 1978,

McKaig 1978, Brandner *et al.* 1990). Accompanying the conifers are lesser amounts of aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*), originating after past fires, or occurring in larger gaps. Mountain ash is a subdominant and rarer shoreline component. Maples (*Acer rubrum, A. saccharum*, and *A. spicatum*) and yellow birch (*Betula alleghaniensis*) are minor components, occurring especially in the understory of the shoreline forests of the SW end of the island. Between January and April, diet composition of 12 radio-collared moose in the mixed SW-end shoreline forest was 69% balsam fir, 7% cedar, 6% mountain ash, and 6% white birch, with minor components of aspen, and shrubs like dogwood (*Cornus stolonifera*) and beaked hazel (*Corylus cornuta*) (Risenhoover 1987). From measurements in a shoreline area of the SW end, it was found that summer woody diet consists of 78% mountain ash, 19% maple, with minor components of yellow and white birch (Belovsky *et al.* 1973).

METHODS
Collection of trees

We chose to study balsam fir as a dominant winter forage tree, mountain ash as a tree consumed year-round, and white spruce as a non-browse species. Following the procedure established in McLaren and Peterson (1994), we randomly selected individual trees from widely-dispersed stands on the SW and NE ends, limiting collection to areas <60 m elevation above Lake Superior. Destructive samples were restricted to 1 stem per 1 mi² (2.7 km²), to obtain representation of as much of the island as possible, and to ensure that past browsing events occurred independently in each tree. Sixteen suppressed balsam fir stems (0.5-2.8 m ht), 8 from the SW end, and 8 from the NE end, were redrawn as individual chronologies, from averaged data presented earlier (McLaren and Peterson 1994). Twelve canopy mountain ash trees (5-10 m

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ht) were collected from 3 sections in the SW end, and 3 similar trees were sampled from the NE end. Ten suppressed mountain ash trees (1.5-3.0 m ht) were collected adjacent to each larger mountain ash tree sampled from the SW end. Distribution of canopy mountain ash on the island was determined during aerial moose surveys in Feb. 1995; immediate identification of canopy trees was possible owing to a peak fruit crop in 1994 which persisted through winter. White spruce canopy trees (10-15 m ht) were destructively sampled, 10 from the SW end, and 10 from the NE end of the island. Three balsam fir and 5 white spruce stems (5-6 m ht) growing together in a subcanopy, self-thinning stand on the NE end of the island were cored at breast-height (1.4 m) using an increment borer.

Calculation of growth indices

Primarily, we analyzed tree-ring records using whole-stem analysis, at a station equipped with a binocular microscope attached to a SONY Magnescale, and to a PC with Lotus as a data-capture tool. Mean ring width was obtained from 4 measurements accurate to 10^{-2} mm on 4 radii of 30-40 sections, taken at 10-30 cm intervals along the base and top, and 1 m intervals along the bole (canopy trees only) of the main stem. For the canopy mountain ash trees, the lateral branch with the largest diameter was deemed the main stem.

Cross-checking was performed by viewing graphs after each radial measurement. Cross-checking along individual radii and sections of the same tree facilitated identification of false rings and missing rings (Fritts 1976). Cross-checking between trees was deliberately avoided, on the assumption that changes in growth rate might be influenced by localized episodes of browsing.

Current annual volume increment (CAVI) was calculated by approximating the stem as a series of stacked conic sections.

That is, the square of the mean radial distance to each annual ring on 2 adjacent sections was multiplied by $\pi \times$ the distance between the sections. The resulting conic volume was subtracted from the conic volume of the previous year. CAVI was then divided by the surface area of the previous season's cambium. The result was annual specific volume increment (SVI) in linear units (mm), proportional to the metabolic growth potential of the tree relative to its foliage in the year of wood accumulation (Duff and Nolan 1957). Essentially, SVI is a weighted average of ring growth throughout a tree's stem. It allows direct comparison of growth rates of trees of different sizes. For the purposes of this analysis, the index captured damage that may have occurred anywhere in the stem due to moose browsing, and allowed the assumption that ring width might vary with changes in the foliar biomass available to moose. This relationship may not be direct and may vary considerably for different forage species. It is beyond the scope of this paper to test the relationship; however, for balsam fir, SVI proved a sensitive and accurate index of defoliation by spruce budworm (Ostaff and MacLean 1995).

Secondarily, we used raw ring-width data from increment-cores. These were averaged for 2 cores collected from each tree. The time taken to sample, mount, prepare, and measure increment-cores was fractional (< 0.1 hr per core) relative to the time taken to cut, prepare, and measure sections with whole-tree analysis (> 5 hr per tree). However, growth at only one point in the tree was measured, and the early part of the trees' chronology was omitted by coring. Chances for cross-checking were also minimal. Thus, increment-cores were a sacrifice in accuracy that nonetheless served as a substitute for the whole-stem records when trees were not to be destroyed, or when time constraints limited research.

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Analysis

Individual tree-ring records were entered as dependent variables in stepwise regressions, whenever record length exceeded 14 yr. Moose density and annual evapotranspiration (AET), taken from McLaren and Peterson (1994), were 2 of the independent variables entered into models. Other independent variables were weather records obtained from seasonal stations monitored on Isle Royale by the Park Service. These included June and July minimum and maximum temperature, and June and July rainfall, for a station specific to each end of the island (SW end: Windigo; NE end: Mott Island). Weather variables were tested unlagged and with 1-yr lags, and moose density was tested unlagged, and with 1- and 5-yr lags. Significance level for entry into the regression was 0.05.

RESULTS

Balsam fir

Balsam fir chronologies displayed a pattern of cyclic suppression (Fig. 1). Individual fir trees may or may not have had im-

proved growth in the "release" periods 1955-1970 and 1976-1989 on the SW end, or in the "release" periods 1955-1975 and 1979-1990 on the NE end, but growth was uniformly suppressed for the years 1971-1975 on the SW end, and the years 1976-1978 on the NE end. Recent suppression, beginning in 1989-1990, occurred in both samples. A lag in NE-end trees was apparent, when the decline in SVI began 3 yr after peak moose density in 1973. The first period of suppression in SW-end trees encompassed peak moose density, and recent suppression also occurred earlier in the SW-end sample than in the NE-end sample.

Mountain ash

Distribution of canopy mountain ash was concentrated on the SW end of the island,
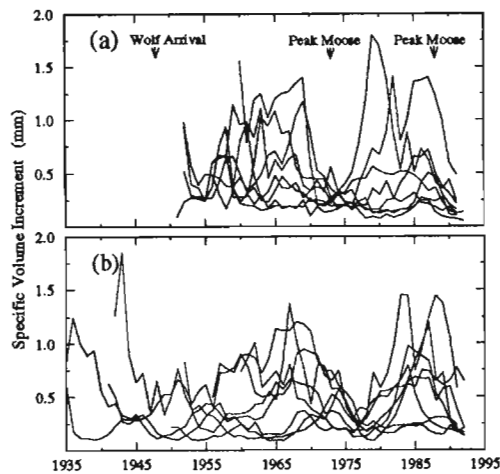

Fig. 1. Tree-ring records from suppressed balsam fir on (a) the SW end, and (b) the NE end of Isle Royale from whole-stem analysis. Each series represents one stem chronology. The captions indicate relevant periods in wolf-moose history on Isle Royale.
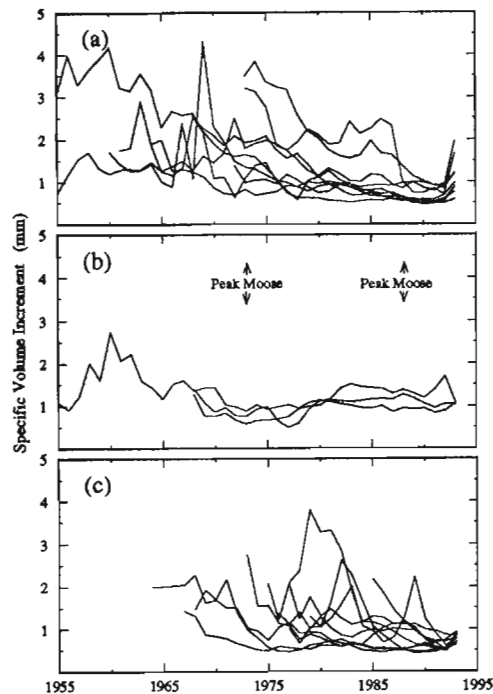

Fig. 2. Tree-ring records from (a) canopy mountain ash from the SW end of Isle Royale, (b) canopy mountain ash from the NE end of Isle Royale, and (c) suppressed mountain ash from the SW end of Isle Royale. Each series represents one stem chronology.

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where 24 of 49 moose survey plots (ca. 1 km²
each) contained mountain ash, compared to
only 3 of 26 plots on the NE end. Individual
canopy mountain ash trees displayed matched
periods of suppression (Fig. 2), even though
at the time of sampling they were beyond the
reach of moose browsing. All SW-end trees
had uniformly depressed SVI beginning in
1989, when they were 5-8 m tall, but showed
no earlier period of suppression. Meanwhile,
NE-end trees had reduced growth in 1972-
1978, when they were 1-2 m tall. Among the
3 suppressed mountain ash stems dating be-
fore 1970, all had slower growth beginning
in 1973. All but 2 of the 7 remaining sup-
pressed-tree chronologies sharply declined
in SVI beginning in 1984.

White spruce

Peak SVI growth on the SW end was
higher than that of the NE end, a trend com-
mon to balsam fir, mountain ash and white
spruce (Figs. 1, 2, 3). White spruce SVI
records had no common periods of suppres-
sion on the SW end, while growth declined
gradually in most NE-end trees beginning
about 1983 (Fig. 3). Certain years showed

characteristically poor growth in most stems,
such as 1967, 1973 and 1983, but this effect
lasted 1 yr only. Like the canopy NE-end
whole-tree spruce sample, the subcanopy
spruce increment cores showed a gradual
decline in growth beginning in the mid-1980's
and continuing into the 1990's (Fig. 4a). In
the matched balsam fir increment-core sam-
ples (Fig. 4b), there was significantly faster
growth (approx. twice as fast) in the 1970's
than after the second peak moose density,
1989-1994 ($t = 8.97$, $P < 0.0001$), a differ-
ence which also occurred in white spruce ($t = 11.48$, $P < 0.0001$). However, in balsam fir,
the decline in growth between 1981 and 1989
levelled off in the 1990's; this pattern did not
occur for white spruce.

Analysis

Results of individual regressions of tree-
ring records are summarized in Table 1. Few
conclusive patterns emerge. Worthy of note
is the trend of inverse correlation of annual
changes in balsam fir ring width with moose
density, particularly when moose density is
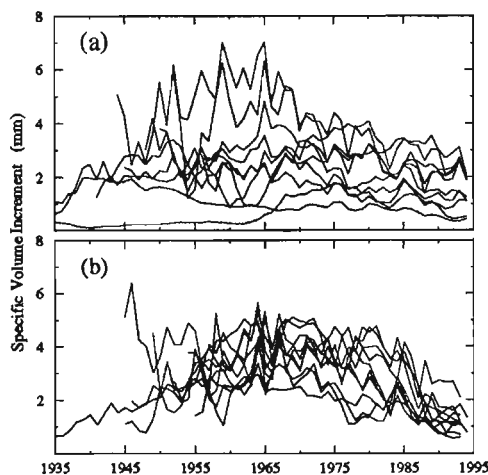lagged 1 or 5 yr. This pattern also exists for

Fig. 3. Tree-ring records from canopy white
spruce sampled in (a) the SW end, and (b) the
NE end of Isle Royale. Each series represents
one stem chronology. Three of the chronolo-
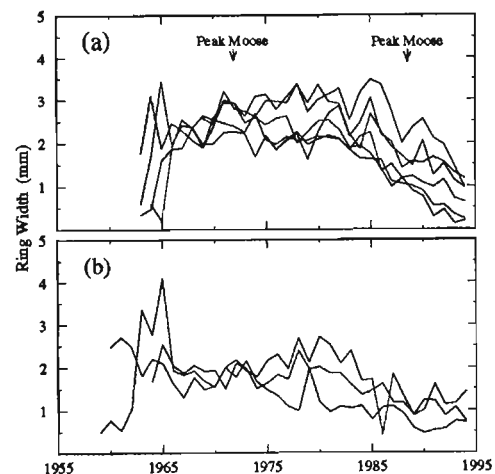gies in (a) date to the 19th century.

Fig. 4. Tree-ring records of (a) white spruce, and
(b) balsam fir, from increment-cores collected
in a self-thinning stand on the NE end of Isle
Royale. Each series represents one stem chro-
nology. Note that the axis for the core samples
is ring width, not SVI.

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Table 1. Positive and negative correlations with individual tree-ring records from Isle Royale for 9 independent variables, including weather and annual moose density estimates. Entries into the table are numbers of correlations in N stepwise regressions of series $n>15$, where n is record length, and $P < 0.05$, where P is the significance level for model entry. The 1st row is the number of positive correlations; the 2nd row is the number of negative correlations; N is the number of individual records or the maximum possible correlations for each species and sample location. For each independent variable, the 1st column is for the unlagged series and the 2nd column is for a 1-yr lag (exception is for SW-end tree-ring records, where moose density is lagged 5 yr in the 2nd column).

Species	Sample Location		Independent Variables[1]								
			1	2	3	4	5	6	7	8	9
Balsam fir (see Fig. 1a)	SW End	+	1 1	0 0	1 2	1 1	0 0	0 0	0 0	0 1	0 0
		-	0 0	0 1	1 0	0 0	0 1	0 0	0 0	0 0	1 4
		N	8								
Balsam fir (see Fig. 1b)	NE End	+	3 2	0 0	2 0	0 0	0 0	2 1	0 0	0 0	0 0
		-	1 0	0 0	0 0	0 0	0 0	0 3	0 0	1 0	1 6
		N	8								
Mountain ash (see Fig. 3a)	SW End	+	0 1	0 0	1 2	0 0	0 0	0 0	0 0	0 1	1 0
		-	1 0	0 1	0 1	1 4	0 1	0 2	0 1	0 0	1 1
		N	9								
Mountain ash (see Fig. 3b)	NE End	+	1 0	0 0	0 2	0 0	0 0	0 0	0 0	0 0	0 0
		-	1 1	0 0	0 0	0 0	0 0	0 1	0 0	0 1	0 1
		N	3								
Mountain ash (see Fig. 3c)	SW End (suppr.)	+	0 0	0 0	0 0	0 0	0 0	0 0	1 0	0 0	2 1
		-	1 0	0 0	0 0	0 1	1 0	0 0	0 0	0 0	1 1
		N	9								
White spruce (see Fig. 4a)	SW End	+	1 0	0 1	0 3	0 1	0 0	0 0	0 0	1 0	0 1
		-	0 0	0 4	0 1	0 0	0 0	1 0	0 0	0 0	3 1
		N	10								
White spruce (see Fig. 4b)	NE End	+	0 0	0 0	0 0	0 0	2 0	0 0	1 0	2 3	0 0
		-	0 2	0 0	0 0	0 0	0 0	1 1	0 0	0 0	2 4
		N	10								
White spruce (see Fig. 5a)	NE End	+	1 0	0 1	0 1	0 0	0 0	0 0	1 2	5 3	0 0
		-	0 1	0 0	0 0	1 0	0 1	0 0	0 0	0 0	6 0
		N	6								
Balsam fir (see Fig. 5b)	NE End	+	0 0	0 0	0 0	0 0	0 0	0 0	0 0	1 3	0 0
		-	0 1	0 0	0 0	0 0	0 0	0 0	0 0	0 0	2 0
		N	3								

[1] Key to independent variables: 1: Actual evapotranspiration (AET); 2: Mean annual temperature; 3: June minimum temperature; 4: June maximum temperature; 5: June rainfall; 6: July minimum temperature; 7: July maximum temperature; 8: July rainfall; 9: Moose density.

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many of the white spruce trees, but for few of the mountain ash trees.

Balsam fir growth had the least consistent relationship with weather variables among the 3 species studied. Balsam fir growth was positively correlated with AET, particularly on the NE end. Canopy mountain ash growth appeared positively correlated with June minimum or negatively correlated with June maximum temperature. White spruce growth was negatively correlated with lagged mean annual temperature in 4 of 10 trees on the SW end, and positively correlated with July rainfall in many trees on the NE end.

DISCUSSION

This paper offers several avenues for speculation of the effect of moose browsing on woody plant growth. The idea that cyclic suppression in ring growth of balsam fir is related to change in moose density brought about by predator regulation is discussed in McLaren and Peterson (1994), and will not be elaborated here. Displaying individual chronologies for fir illustrates that increase in growth rate during moose decline was not ubiquitous. Fir growth can, therefore, be partly influenced even by less frequent episodes of winter foraging, by successional trends that vary by stand, by the location of individual trees relative to their apparency to moose (Brandner *et al.* 1990), or by weather (e.g. NE-end fir growth is often correlated with AET; Table 1). Mountain ash echoes the pattern of fir, with suppression while within the reach of moose occurring in the common peak-moose periods of 1972-1978 (NE end) and 1984-1994 (SW end). While the tree is above the reach of moose, normal growth of canopy mountain ash can still be interrupted by stripping of bark (SW end).

Location of damage by moose on Isle Royale cannot be generalized for fir and mountain ash. For example, while current suppression of fir ring width appears similar on the SW and NE ends of the island (Fig. 1),

suppression of mountain ash ring width appears more severe on the SW end (Fig. 2). One reason for the difference may be the high winter concentration of moose in areas of occurrence of mountain ash on the SW end (R. O. Peterson, annual reports). Alternatively, bark stripping of canopy trees may occur for target individuals that lie in the path of winter travel by moose, so that vulnerability is more a chance event for canopy trees.

Contrary to our expectations, white spruce ring growth rates were not more correlated with weather variation than was the case for the 2 forage species; indeed, several spruce growth series were correlated with variation in moose density. In part explanation, we found that regressions of individual series were not the best approach to understanding variation in growth for any of the species studied. Widely-dispersed stem collection predisposed individual trees to microsite variation that is impossible to predict without site-specific measurement of physical variables. It was for this reason that we chose to limit analysis to averaging chronologies in McLaren and Peterson (1994). In summary, we have decided that the sampling approach we used was appropriate to show the ubiquity of past suppression events, but that the regression approach to dendrochronology would be more suited to trees collected from a single plot. In this analysis, it was possible to suppose that growth of all Isle Royale trees was limited by low temperatures, especially in June, and that NE-end white spruce growth was particularly limited by July drought (Table 1). However, negative correlation of canopy spruce growth with moose density confounded such interpretation. Spruce growth declines may have been caused by successional patterns that were coincidental with changes in moose density, such as stand competition during ingrowth of trees on ridges opened by the 1936 fire. Alternatively, gradual decline in ring width of white spruce may have been

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an indirect effect of moose browsing; that is, they consistently followed cyclic increase in growth of competing fir trees in denser, self-thinning stands, such as in the stand from which the chronologies in Fig. 4 were measured. Collection of cores from trees of varying distance from neighbours and comparison of plant competition indices to ring suppression might have increased our ability to explain suppression in white spruce.

The potential for dendrochronology to explain forest dynamics and to trace changes in stand composition is high. At issue in some of the past literature on moose-forage relationships have been successional trends following fire on the Kenai Peninsula, Alaska (Loranger *et al.* 1991), carrying capacity of cutover areas in Quetico Park, Ontario (McNicol *et al.* 1980), or damage to moose habitat on the Gaspé Peninsula, Québec (Crête and Bédard 1975). None of these papers used dendrochronology, although several key hypotheses offered by the authors could have been tested this way. One of the reasons dendrochronology might have been avoided in past studies of moose ecology is the complication of choosing baseline data to compare with the effects of moose on tree growth. White spruce in our study fails as a baseline species because its growth was apparently influenced by plant competition, or indirectly influenced by moose browsing on Isle Royale. In managed areas, forest harvest renders moose habitat as predominantly secondary successional forest, including species like white birch and aspen, with tree rings that are absent or difficult to distinguish. Changes to understory dynamics caused by overstory harvest probably predominate over moose damage in mainland areas. Isle Royale is a unique system for observing food-chain relationships, because many changes imposed on mainland systems, e.g. by management, can be eliminated as contributing factors. Human harvest of the moose population does not occur, nor does forest harvest change moose habitat.

Tree-ring records that are obtained from moose habitat will always be short and difficult to analyze. Nevertheless, it is hoped that the examples presented in this paper and the potential to address interesting hypotheses with dendrochronology foster further study of tree rings in moose ecosystems. An important area of experimental investigation will be to test directly the effect of forage removal on ring width in a variety of species.

ACKNOWLEDGEMENTS

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