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BALSAM FIR ON ISLE ROYALE: EFFECTS OF MOOSE HERBIVORY AND POPULATION DENSITY¹

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Abstract. Balsam fir (*Abies balsamea*) population parameters were analyzed in Isle Royale National Park, Michigan, to assess moose (*Alces alces andersoni*) herbivory in relation to the population density of both fir and moose. Fir population parameters were determined at nine study sites, each representing a different combination of relative fir and moose density (high, medium, and low levels, respectively). In general, moose suppression of fir height growth and recruitment to the canopy increased with increasing moose density and decreasing fir density. Where fir densities were low, sapling heights were restricted to <1 m regardless of moose density. In such sites, sapling growth suppression has been continuous since a peak in the moose population in the late 1920s. Canopy fir trees at most sites established prior to arrival of moose on Isle Royale around 1910. At high fir density release from growth inhibition was common following a period of low moose numbers from the mid-1970s to early 1980s. Here this release should facilitate recruitment of fir and effect replacement of canopy losses due to senescence. In other areas, however, continuing canopy losses and lack of recruitment due to intensive herbivory by moose will greatly reduce the fir component of the canopy, effectively preventing any return to the fir-dominated forests of the past.

Key words: *Abies balsamea*; *Alces alces*; balsam fir; boreal; browsing; conifer; foraging; herbivory; Isle Royale; moose.

INTRODUCTION

Balsam fir (*Abies balsamea* (L.) Mill.) is an important component of the winter diet of moose (*Alces alces andersoni* Peterson) wherever moose and fir coexist (Murie 1934, Peterson 1955, Pimlott 1965, Brassard et al. 1974, Peek 1974, Risenhoover 1987). Repeated browsing of apical buds and side branches reportedly can kill saplings (Bergerud and Manuel 1968) or suppress height growth and recruitment of saplings into the canopy (Snyder and Janke 1976, Risenhoover and Maass 1987).

Other coniferous species are also affected by large mammalian herbivores. American yew (*Taxus canadensis* Marsh.) is highly susceptible to damage in areas inhabited by moose (Murie 1934, Bergerud and Manuel 1968, Krefting 1974), while white-tailed deer (*Odocoileus virginianus* Zimm.) can severely limit growth and regeneration of eastern hemlock (*Tsuga canadensis* (L.) Carr.) in some northern mixed deciduous forests (Anderson and Loucks 1979, Frelich and Lorimer 1985). During the last half century the distribution of

fir in Austria was reduced by 50% because of ungulate foraging (Dzieciolowski 1980), and in some regenerating forests in the Soviet Union, 60–70% of young pine saplings were reportedly heavily damaged by moose browsing (Dinesman 1967).

In recent years concepts from animal population dynamics and predator–prey relationships have been increasingly applied to plant–herbivore interactions (Noy-Mier 1975, Caughley and Lawton 1981). One fundamental characteristic of predator–prey relationships is that the density of both predator and prey populations affects the intensity of pressure on the prey species (Taylor 1984). Continuing investigation of moose and wolf populations on Isle Royale has demonstrated these effects (e.g., Mech 1966, Peterson 1977, Peterson et al. 1984) and interactions between moose (predator) and balsam fir (prey) may also be considered in this manner.

Moose damage to balsam fir and other browse species on Isle Royale has been widely reported (Murie 1934, Hickie 1936, Aldous and Krefting 1946, Krefting 1974, Janke et al. 1978), although most studies have merely reported the occurrence of browse damage. Snyder and Janke (1976) observed significant foraging effects on fir in a study limited to areas of relatively high fir density. In heavily browsed areas in Newfoundland, Bergerud et al. (1968) reported a reduction in moose damage to balsam fir after hunting reduced moose density. Thus, herbivore density can be expected to influence the extent of plant damage, but no studies have examined

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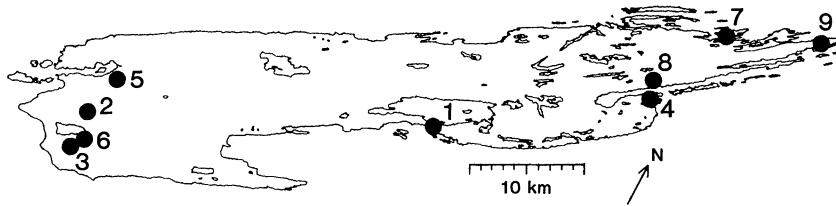


FIG. 1. Location of the study areas (sites 1–9) on Isle Royale.

the simultaneous effects of moose and fir density on the severity of moose browsing of fir populations.

Densities of both fir and wintering moose range widely throughout Isle Royale. This experiment utilized this natural island-wide diversity to compare characteristics of balsam fir demography across coexisting gradients of both moose and fir density. Earlier studies, confined to high fir density areas, may have underestimated the overall impact of moose foraging on fir in this ecosystem. Variations in the relative density of both fir and moose populations can be expected to produce a range of severity of foraging effects on fir. The following questions were addressed: (i) At a constant fir density will browse damage increase as moose density increases? (ii) At a given moose density will foraging damage decrease as fir density increases? (iii) Do effects on individual fir stems and overall stand demography vary across the gradients of moose and fir density? (iv) If fir density and moose density both emerge as important influences on fir demography, what are the implications for the future of balsam fir in this ecosystem?

STUDY AREA

Isle Royale National Park (47°55' N, 89° W) is a 544-km² archipelago lying in northwestern Lake Superior 24 km southeast of the Canadian mainland. The island consists of a series of parallel ridges and valleys formed by uptilted layers of basaltic lavas interspersed with softer layers of sandstone and conglomerate (Huber 1973, 1975). Glacial action has deepened valleys producing numerous lakes, swamps, and streams and has left wide variations among upland soils. Temperature and climate are greatly moderated by Lake Superior.

Boreal species common throughout the island include balsam fir, white spruce (*Picea glauca* (Moench) Voss), white birch (*Betula papyrifera* Marsh.), and quaking aspen (*Populus tremuloides* Michx.). Sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton) dominate smaller areas at higher elevations in the island's interior where warmer and drier conditions prevail in summer (Linn 1957). Historical surveys of the 1840s, prior to the arrival of moose, indicate that balsam fir was one of the most abundant canopy trees on Isle Royale (McKaig 1978). However, a history of human-caused fires has today produced a patchwork of forest cover types of varying size and age. Burned areas are rapidly colonized by

white birch and aspen followed, in ≈ 100 yr, by the invasion of balsam fir and other shade-tolerant species (Janke 1984). No balsam fir are found in large areas in the middle of the island that were burned in this century.

Moose colonized Isle Royale sometime between 1905 and 1913 (Murie 1934). Absence of predators and abundant forage facilitated a rapid increase in population until the early 1930s, when numbers reached 2000–5000 animals or densities of ≈ 4 –10 moose/km² (Murie 1934, Hickie 1936). Coincident with this rise in population was increasing evidence of damage to balsam fir and other forage species due to heavy overbrowsing (Murie 1934, Hickie 1936). American yew, a predominant understory species on much of the island, was nearly eliminated (Brown 1935, Slavik and Janke 1987). Numerous moose deaths due to malnutrition were noted in the winter of 1933–1934, and the population rapidly declined (Hickie 1936, Krefling 1951, Mech 1966). Numbers gradually rebounded until the late 1940s when deaths due to malnutrition were again reported (Krefling 1951). Following the arrival of wolves (*Canis lupus* L.) in 1948, the moose population stabilized somewhat, reaching a peak of ≈ 1400 or ≈ 3 moose/km² in the late 1960s before declining to ≈ 600 or ≈ 1 moose/km² by 1977. The population began to increase again in the early 1980s (Peterson et al. 1984). Moose are the only large browsing herbivores currently on Isle Royale.

METHODS

Nine areas with different combinations of moose and fir density were selected for study (Fig. 1). Four zones of varying moose density (absent, low: ≈ 0.8 moose/km², medium: ≈ 2.5 moose/km², high: ≈ 5.0 moose/km²) were delineated based on annual winter moose censuses from aircraft between 1979 and 1984 (R. O. Peterson, *personal observation*). Balsam fir density zones (absent, low, medium, high) were delineated from maps of vegetative cover, LANDSAT data, aerial photographs, and direct aerial observations in early 1985. Fir density of potential study areas was measured before selection of a representative study area from each of the nine combined zones (cells) of moose and balsam fir density. Zones without moose or fir were excluded. Sites were selected based on densities of moose and balsam fir alone. Every attempt was made to reduce confounding effects although the possibility

TABLE 1. Densities (stems per hectare) of balsam fir populations in each study area and mean densities for each fir density zone.

		Low moose density	Medium moose density	High moose density	\bar{X}
		Site 1	Site 2	Site 3	
Low fir density (stems/ha)	seedlings	1 900	400	1 200	
	saplings	1 200	2 080	1 700	
	trees	160	45	70	
	total	3 260	2 525	2 970	2 900
		Site 4	Site 5	Site 6	
Medium fir density	seedlings	4 200	2 000	800	
	saplings	5 680	9 250	6 880	
	trees	67	130	110	
	total	9 947	11 380	7 790	9 700
		Site 7	Site 8	Site 9	
High fir density	seedlings	111 800	11 300	4 800	
	saplings	12 100	17 400	29 930	
	trees	2 110	910	450	
	total	126 010	29 610	35 180	63 600

of some unknown factor influencing density could not be explicitly excluded in this natural system.

All sampling was carried out from May through mid-July of 1985. Preliminary inspection of balsam fir density for each of the study sites was made by counting individuals in a 3 m wide band along a 200-m transect. Once a site was selected and the perimeter of the stand was determined, a minimum of four sampling points was systematically placed at intervals along one or more transects running the length of the stand. At each point three nested circular plots were used to sample trees (200 m²), saplings (100 m²), and seedlings (50 m²).

Following Snyder and Janke (1976), trees were defined as individuals with a dbh (diameter at breast height) ≥ 5.0 cm. Saplings were individuals < 5.0 cm dbh and ≥ 50 cm tall. Individuals < 50 cm tall that had been apically browsed were included in the sapling class. Unbrowsed stems < 50 cm tall were classified as seedlings. Fir density (stems per hectare) was calculated as the total number of fir stems from all size classes in plots at each study site. Heights of most saplings were measured directly, while height measurements of taller saplings and all trees were made with a Suunto clinometer.

Age was estimated for all trees and every fourth sapling encountered on a plot, either from cores taken by increment borer or from cross sections at the base of stems. Ages from cores and sections were determined in the field with the aid of a hand lens. Trees with rotten or hollow centers were cored farther up the stem until an age could be recorded or until out of reach. No age correction was applied to cores taken above the base so all tree ages should be considered as minimums. Ages were determined for seedlings and some saplings by counting external terminal bud scars along the stem.

Fir stems exhibited browse damage ranging from cropped side branches to severe stunting due to re-

peated apical browsing of terminal stems. To assess impact, saplings were assigned to one of four browse damage classes: 0: unbrowsed, 1: side branches browsed only, 2: apically browsed once, 3: apical leader browsed twice or more. All browse damage was attributed to moose effects. Individuals that exhibited no signs of having been browsed in the past 5 yr were considered released from growth inhibition due to browsing.

An analysis of height growth over time was performed on two systematically selected saplings in each plot, yielding eight analyses for each of the nine combinations of moose and fir density. Cross sections were made at regular intervals along the stem (Shea and Aramson 1972). Interval distance varied from 2 to 30 cm for saplings, depending on the individual's total height. By recording the number of growth rings of each section and the height above the ground, height-age curves were constructed to document height growth of individual saplings over time. Similar analyses of mature trees were made for comparison on eight individuals from recent windfalls (six from the southwestern end of Isle Royale and two from the northeastern end).

In order to investigate differences along density gradients, an unbalanced (unequal sample size) two-way analysis of variance was performed on the log-transformed sapling heights (Montgomery 1984) using moose and fir population densities as the grouping variables. Also, a Student-Newman-Keuls pairwise comparison test was used to compare the mean sapling heights of the nine cells ($P < .05$). Statistical methods followed Zar (1984).

RESULTS

Balsam fir population density

Density classifications for fir primarily reflected the relative abundance of saplings and seedlings (Table 1).

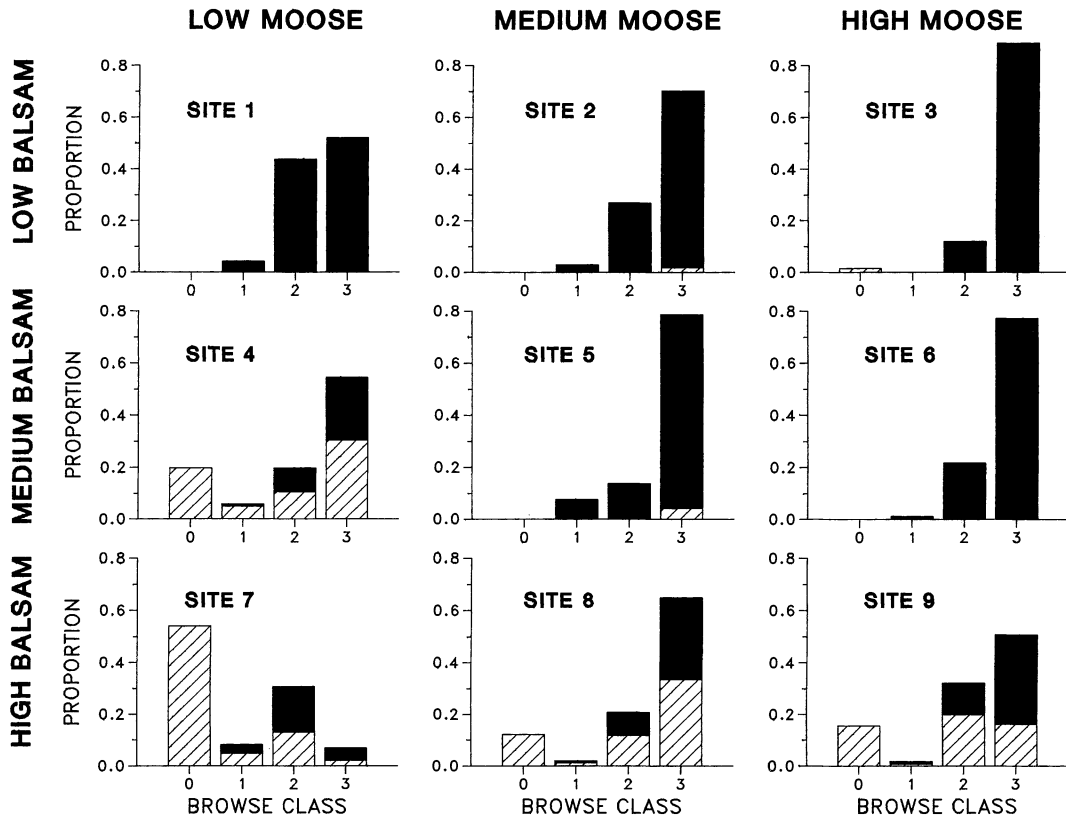


FIG. 2. Extent of moose foraging damage to balsam fir saplings (proportion browsed). Browse damage classed in four categories (0 = no damage to 3 = repeatedly browsed). In each category the proportion exhibiting release from foraging pressure is indicated (hatched).

Except in site 7, seedlings <1 yr old were uncommon. Postfire successional stands (site 8, high fir, medium moose) had, as expected, numerous saplings and seedlings but no canopy trees. Balsam fir density exhibited more than a 10-fold range, averaging from ≈ 2900 stems/ha on low density sites to $\approx 63\,600$ stems/ha in high density sites, although the density of seedlings in site 7 affects the overall mean for high density stands.

Extent of foraging impact

Moose browsing damage to balsam fir saplings was extensive. At low fir density (sites 1, 2, and 3; Fig. 2), all individuals exhibited height growth suppression even at low moose population density. Many of these saplings persisted as stunted, pruned individuals. Similar conditions were found at medium fir density (sites 4, 5, and 6) except at site 4 where 20% of measured saplings were never browsed and 57% of remaining saplings exhibited no sign of browse damage in the last 5 yr. High fir density areas (sites 7, 8, and 9) also showed evidence of past browse damage, although release from browse damage was common. Site 7 (high fir, low moose) had the highest proportion of unbrowsed saplings (54%) and the lowest number of saplings that had been repeatedly browsed (7%).

Sapling and tree height

Effects of moose herbivory were most evident when the height structure of balsam fir populations were compared among study sites. Sapling heights differed significantly among fir density levels (ANOVA: $F_{(2,27)} = 78.34$, $P < .0001$) and moose density levels ($F_{(2,27)} = 3.39$, $P < .05$). The interaction between these effects was also significant ($F_{(4,27)} = 8.37$, $P < .0002$).

Generally, as fir density increased mean sapling height increased, especially at low moose densities (Fig. 3). In sites with low fir density, mean sapling height was <50 cm regardless of moose density. However, at high fir densities there was a reduction in mean sapling height as moose density increased.

Study sites could be divided into four groups based on mean sapling heights (Student-Newman-Keuls pairwise comparison, $P < .05$, Table 2). Sites 1, 2, 3, 5, and 6, located in the middle and southwestern end of Isle Royale, had mean sapling heights of <60 cm, while sites 4, 7, 8, and 9, on the northeastern end of the island, had mean sapling heights >1 m.

Saplings in plots within low fir density zones (sites 1, 2, and 3) did not exceed 1 m in height (Fig. 4). Even where moose density was not high (sites 1 and 2) all individuals encountered had been browsed, often re-

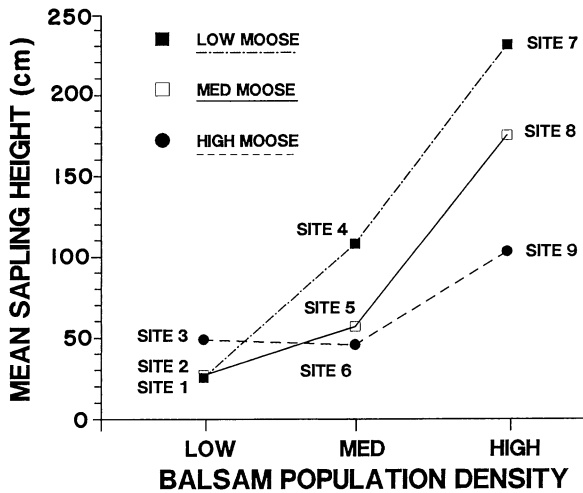


FIG. 3. Influence of balsam fir density and moose density on average height of balsam fir saplings at each study site.

peatedly, and mean sapling height was <30 cm. At medium (sites 4, 5, and 6) and high (sites 7, 8, and 9) balsam fir densities there was a reduction in the range of sapling heights as moose density increased (Fig. 4). At medium fir density, maximum sapling height decreased from 2.85 m (site 4) to 1.45 m (site 5) to 0.88 m (site 6) as moose density increased. Similarly, at high fir densities, maximum heights decreased from 7.50 m (site 7) to 4.90 m (site 8) to 2.81 m (site 9), again with increasing moose density.

The artificial nature of the 5.0 cm dbh distinction between saplings and tree classes was most apparent at high fir density. Height distributions of saplings and trees in sites 7 and 8, where moose density was not high, completely overlapped. Such a stand development pattern is typical of balsam fir (Bakuzis and Hansen 1965, Hett and Loucks 1976). In all other sites, however, no overlap in the height distribution between tree and sapling classes was observed and a gap, centered around 4 m, was present (Fig. 4). For a given moose density, the width of this gap decreased as fir density increased, with the discontinuity ranging from 3–5.5 m in site 9 (high fir, high moose) to 1–13.5 m in site 3 (low fir, high moose).

The discontinuity in the height distribution reflects poor recruitment of young fir trees into the canopy. At most plots in low and medium fir density sites, apical browsing by moose appears to have restricted height growth to <1.5 m. Apparent gaps in the distribution at greater heights reflect the relatively small number of canopy trees measured in the plots at each site and the narrow width (0.5 m) of the bars used to generate the histogram.

Balsam fir growth rates

Height growth patterns of saplings indicate substantial growth inhibition in some study sites (Fig. 5). Though some individuals were >40 yr old, in plots

with low balsam fir density (sites 1, 2, and 3) all saplings were <1 m tall. Even in shade, balsam fir saplings typically reach 1.5 m in height in <25 yr (Bakuzis and Hansen 1965). By comparison, height growth analysis of mature trees, established prior to arrival of moose on Isle Royale, did not reveal any clear evidence of growth suppression in the first 25–40 yr of life.

Height growth at medium balsam fir density was also suppressed where moose density was high (site 6) and no saplings reached heights ≥1 m. Saplings reached nearly 1.5 m in height in medium moose density plots (site 5) while, at low moose density (site 4), fir began to show release between 1975 and 1980 from growth inhibition due to browsing. Here some individuals had reached heights of 2–3 m by 1985.

Likewise, at high fir densities growth rates were inversely related to increasing moose density. Height growth suppression was most evident at high moose density (site 9), although, since the mid-1970s, some individuals had been released from inhibition. Fir stands in plots at low and medium moose density (sites 7 and 8) were crowded and generally even-aged. At low moose density (site 7), unbrowsed saplings of the same age differed by as much as 3 m in height.

Height vs. age distributions

Scatter plots of height vs. age for both trees and saplings suggest a gap in the age distribution that is similar to that in the height distribution (Fig. 6). Where moose foraging was intense, as evidenced by suppressed height growth, measured saplings rarely exceeded 40 yr in age. Older, repeatedly browsed saplings may have succumbed to continual foraging pressure, although no direct evidence of sapling mortality was observed in the study sites. The absence of 40–70 yr old fir is not due to lack of a seed source since many existing trees were present in the canopy throughout this period. Historic photographs and writings from the early 1930s all suggest an abundance of fir in the canopy of undisturbed sites.

In high fir density zones with low-to-medium moose

TABLE 2. Mean fir sapling height (cm) for study sites and statistical groupings based on a Student-Newman-Keuls pairwise comparison test. Sites with a common designation (A–D) are statistically similar ($P < .05$).

	Low moose density	Medium moose density	High moose density
Low fir density	Site 1 25.8 D	Site 2 27.4 D	Site 3 49.0 C
Medium fir density	Site 4 108.0 B	Site 5 57.0 C	Site 6 45.8 C
High fir density	Site 7 230.8 A	Site 8 175.0 A	Site 9 103.3 B

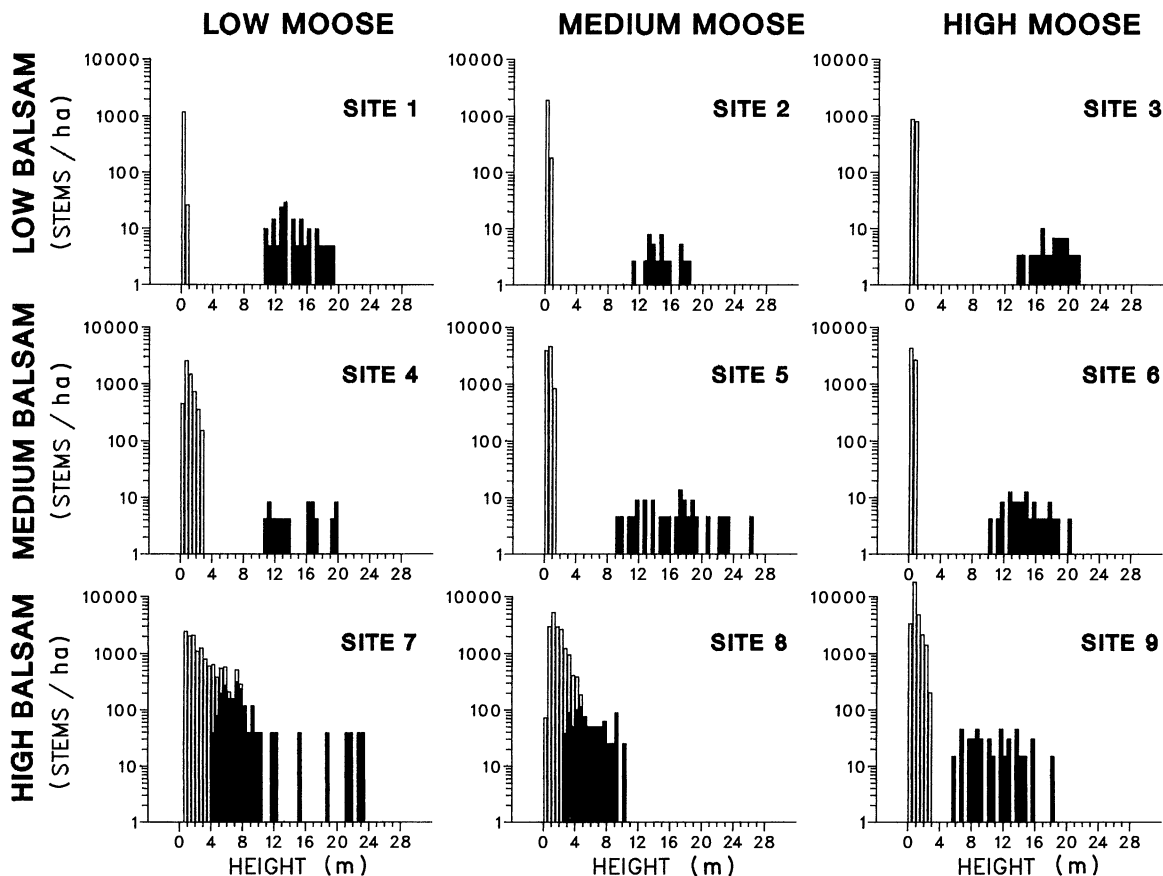


FIG. 4. Height distributions of balsam fir saplings (open bars) and trees (solid bars) for each study site. Heights were pooled in 0.5-m intervals.

density (sites 7 and 8) the overlap of age distributions (Fig. 6) again reflects the artificial designation of tree and sapling classes. At high fir and low moose density (site 7), the plots were dominated by even-aged stands of fir that established 20–40 yr ago. Such stands are common on the north shore of the island following extensive windthrow mortality (Cooper 1913, K. L. Risenhoover, *personal observation*). Site 8 (high fir, medium moose density) was burned \approx 1840 (McKaig 1978). Fir began to appear in the understory there \approx 50 yr ago, following a typical pattern of postfire succession.

DISCUSSION

Both moose and balsam fir density were significant determinants of the impact of moose on fir growth and population structure. Foraging damage to balsam fir was greatest where moose density was high and/or fir density was low. However, the relative influence of moose and fir density did not appear to be equivalent. The growth release of fir at all moose densities in high-fir density zones and the absence of such release in all low-fir density sites suggests that there was no consis-

tent relationship between browse damage and moose density independent of fir density. Given this interaction, fir density appeared more important in determining foraging impact, probably because of the greater range of density present and because of fluctuations in moose density with time.

Browsing effects on growth and stand structure

In all but site 7 (high fir, low moose density) many saplings were repeatedly browsed (Fig. 2) and height growth was suppressed. Stem analysis of sapling growth (Fig. 5) demonstrated continuing periods of little or no vertical growth in areas where incidence of browse damage was high (sites 1, 2, 3, 5, and 6; Fig. 2). Maximum height of saplings was $<$ 1.5 m in these sites (Fig. 4).

For a given moose density, maximum height attained by saplings increased as fir density increased. At high fir density, for example, many individuals appear to have been released from foraging pressure since the moose population decline of the 1970s. Similarly, at a given fir density, height growth inhibition was most

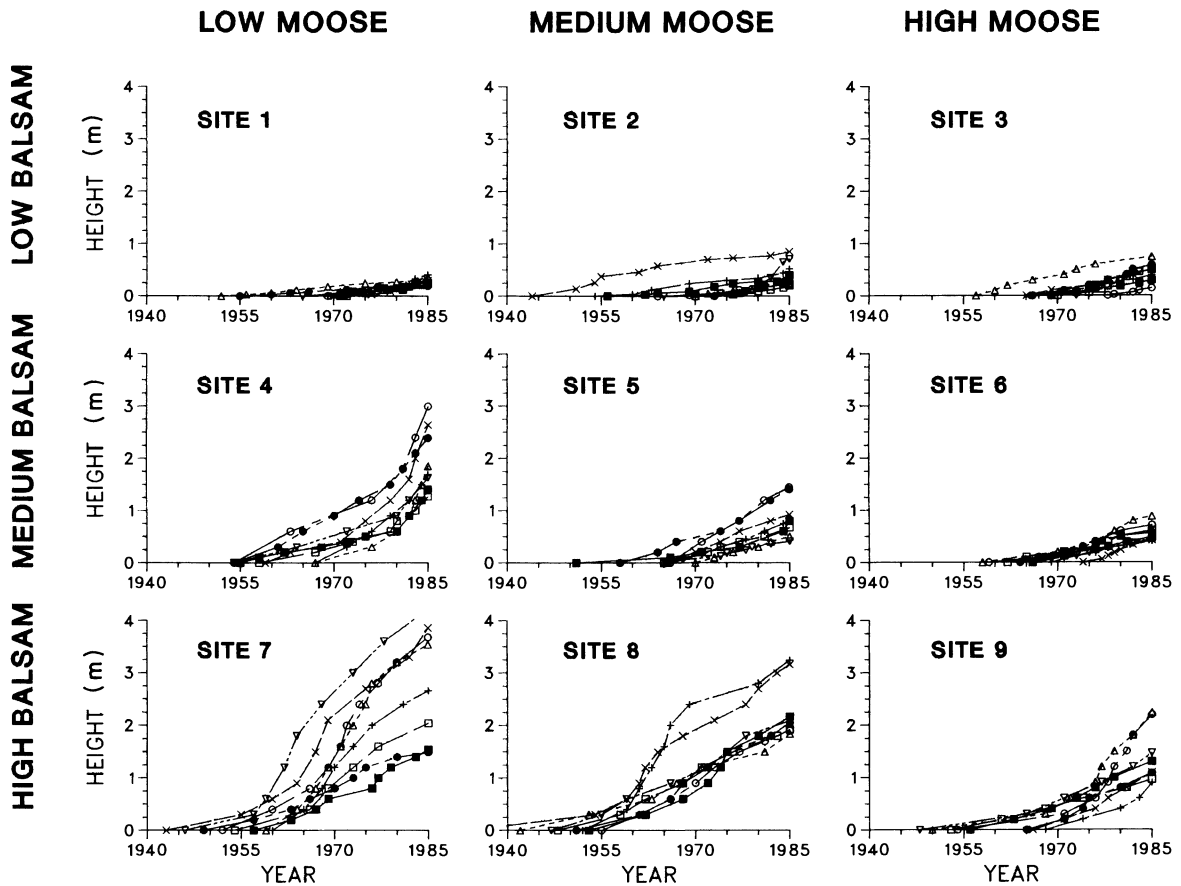


FIG. 5. Representative fir sapling height growth for each study site. Each curve is an individual balsam fir stem.

pronounced at the highest moose density. This trend was clear at high and medium fir densities (Fig. 4), while at low fir density growth suppression was complete regardless of moose density.

Previous investigations of the effects of moose on fir (Bergerud and Manuel 1968, Snyder and Janke 1976) did not address foraging effects across gradients of fir and moose density. Snyder and Janke's (1976) study of moose browsing on several boreal species was conducted on Isle Royale following a period of high moose numbers. They sampled only in areas of high fir density and, in 1973, found no evidence of sapling recruitment into the tree class since the arrival of moose on the island. Currently the substantial number of fir that have been released from browsing effects should facilitate recruitment of trees if recovery continues. The fact that low density fir sites are still experiencing complete growth suppression suggests that damage to young fir may have been even greater in the past when moose numbers were higher.

At most sites, the height structure (distribution) of fir stands contained a marked discontinuity that has apparently been maintained by browsing since moose arrived on the island in the early 1900s. Similar bimodal size distributions are typical in unbrowsed fir

stands when sampling is confined to a limited area, however the distribution troughs would tend to move toward larger sizes as the stands mature (Mohler et al. 1978, Moloney 1986). This was not observed on Isle Royale where the same height classes were consistently absent across the island (Fig. 4). Current canopy trees at most sites established prior to colonization by moose and were tall enough to have escaped apical browsing at that time.

Effects on fir demography

Ability of suppressed saplings to persist over long periods of time may reduce the ability of moose to affect fir density. Little direct evidence of moose-caused mortality (i.e., standing dead saplings) was observed in any of the study sites. Although saplings in this study were rarely >45 yr old, Risenhoover and Maass (1987) found some browsed saplings <3 m tall that were >50 yr old. Field estimates of sapling ages may be lower than actual ages by as much as 10–20 yr since growth rings were nearly microscopic and hand lens readings were often difficult. Some of the oldest suppressed saplings encountered may have persisted since the initial moose peak in the early 1930s, indicating that inhi-

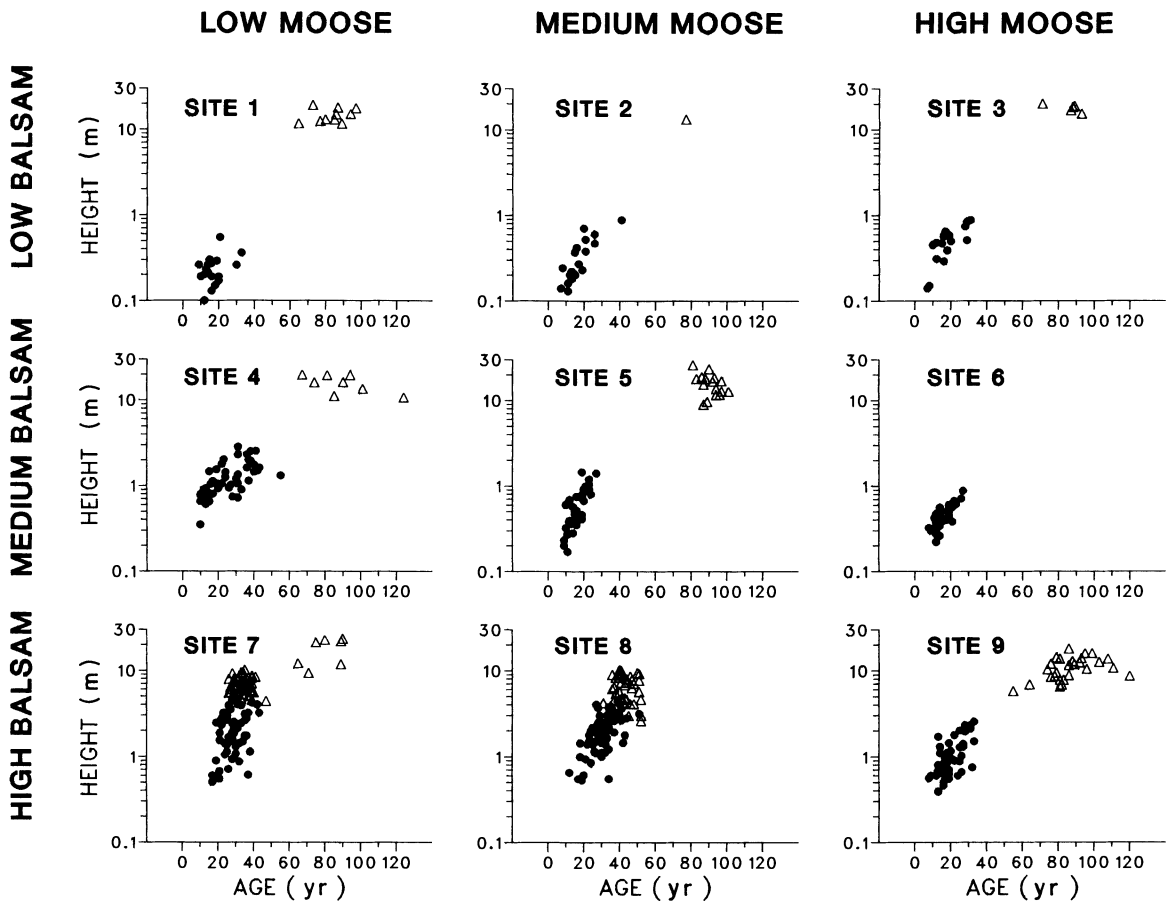


FIG. 6. Height vs. age plots for balsam fir saplings (●) and trees (Δ) in each study site. In many sites (e.g., site 6) trees had hollow or rotten cores and ages could not be determined.

bition has been continuous since that time. In contrast, mortality of saplings due to moose browsing has been reported in Newfoundland studies. Bergerud and Manuel (1968) induced mortality by clipping fir foliage to simulate moose foraging and reported earlier studies recording 66% dead stems in heavily browsed logged areas.

Old trees in the canopy are near the maximum (≈ 100 yr) life-span for this species (Bakuzis and Hansen 1965, Mohler et al. 1978). Many already exceed this age, while recorded ages of others may underestimate actual age by 10–30 yr. Growth of shade-tolerant saplings is highly variable so no age correction was made for cores taken above the base (e.g., unbrowsed saplings of the same age in site 7 differed by > 3 m in height). In some areas most trees cored had hollow or rotten centers. Windfalls were frequently encountered. Fir seed dispersal distances are short and old trees provide the sole seed source for fir. No cone production was observed on any browse-stunted sapling in the study sites. As trees succumb to rot and windfall, the density of canopy-size fir trees will be greatly reduced in many areas of the island. Fir in such forests will be represented only by nonreproducing, repeatedly browsed saplings.

How long individuals can persist in this condition is not known.

Seedlings were relatively uncommon in most study sites (Table 1) and several factors may have played a role. Although seedling plots were carefully inspected, some seedlings may have been overlooked in the leaf litter. Freshly germinated seedlings, encountered in relative abundance on mats of fallen needles in some areas (sites 7 and 8), were scarce in other plots. It is possible that germination had not yet occurred at those sites since sites 7 and 8 were sampled last, in mid-July. Variations in seed production and/or small mammal predation may also have contributed to low seedling numbers. Bergerud and Manuel (1968) reported seedling mortality due to uprooting and ingestion by foraging moose in Newfoundland, but this has never been observed on Isle Royale. However, in some potential study areas almost no saplings or seedlings were found, although canopy fir was abundant. Absence of seedlings and saplings in such stands, if not directly caused by moose, may be attributed to the effects of moose on deciduous understory species (Risenhoover and Maass 1987) and the competition these fast-growing species provide young fir.

The future of balsam fir

Effects of moose herbivory on the demography of fir continue on Isle Royale. The depression of moose numbers in the 1970s resulted in a wave of release from growth inhibition for fir in some areas; however, as the moose population rebounds, height growth of these saplings might again be halted before recruitment into the canopy. This suppression could continue until moose numbers decline again. Release and recruitment after reductions in moose numbers can occur (Bergerud et al. 1968), but only if moose populations remain at reduced levels. In the study sites, there was little evidence of previous waves of recruitment of saplings to the canopy during past lows in moose numbers (e.g., 55 yr olds from the early 1930s or 35 yr olds from 1950). Waves of recruitment, when encountered, could be attributed to flushes after windfall in dense stands (site 7) or typical postfire successional patterns (site 8).

The colonization of Isle Royale by wolves in the late 1940s is a relatively recent development when considered against the long time scale for forest growth. However, the fact that wolf predation maintained the moose herd at low numbers for several years (1975–1983) (Peterson et al. 1984) may help explain why some fir populations are apparently showing recruitment now but not at previous moose population lows.

Original Isle Royale forests were predominantly fir (McKaig 1978), but numerous man-caused fires have eliminated most of those forests, producing the aspen and birch stands that are now fairly common. Subsequently, the role of balsam fir as a component of the island's forests has been reduced. The loss of canopy fir due to age and windfall will magnify this trend although young fir should continue to survive in an inhibited state. The effects of continued moose browsing have been to keep island forests in these earlier successional stages (Risenhoover and Maass 1987), but the intensity of this foraging pressure on fir stands varies at different densities. Long-lived, browse-tolerant fir will persist on Isle Royale, but may never again produce the dominant forests of the past.

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LITERATURE CITED

- Aldous, S. E., and L. W. Krefting. 1946. The present status of moose on Isle Royale. *Transactions of the North American Wildlife Conference* 11:296–308.
- Anderson, R. C., and O. L. Loucks. 1979. White-tailed deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *Journal of Applied Ecology* 16:855–861.
- Bakuzis, E. V., and H. L. Hansen. 1965. Balsam fir: a monographic review. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bergerud, A. T., and F. Manuel. 1968. Moose damage to balsam fir–white birch forests in central Newfoundland. *Journal of Wildlife Management* 32:729–746.
- Bergerud, A. T., F. Manuel, and H. Whalen. 1968. The harvest reduction of a moose population in Newfoundland. *Journal of Wildlife Management* 32:722–728.
- Brassard, J. M., E. Audy, M. Crete, and P. Grenier. 1974. Distribution and winter habitat of moose in Quebec. *Naturaliste Canadien* 101:62–80.
- Brown, C. A. 1935. Ferns and flowering plants of Isle Royale, Michigan. 15th United States Department of the Interior, Emergency Conservation Field Survey, University of Michigan Herbarium, Ann Arbor, Michigan, USA.
- Caughley, G., and J. H. Lawton. 1981. Plant–herbivore systems. Pages 132–166 in R. M. May, editor. *Theoretical ecology: principles and applications*. Second edition. Sinauer, Sunderland, Massachusetts, USA.
- Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. I. *Botanical Gazette* 55:1–44.
- Dinesman, L. G. 1967. Influences of vertebrates on primary production in terrestrial communities. Pages 261–266 in K. Petruszewicz, editor. *Secondary productivity in terrestrial ecosystems*. Volume 1. Panstwowe Wydawnictwo Naukowe, Warszawa, Poland.
- Dziociolowski, R. 1980. Impact of deer browsing upon forest regeneration and undergrowth. *Ekologia polska* 28:583–599.
- Frelich, L. E., and C. G. Lorimer. 1985. Current and predicted long term effects of deer browsing in Michigan, U.S.A. *Biological Conservation* 34:99–120.
- Hett, J. M., and O. L. Loucks. 1976. Age structure models for balsam fir and eastern hemlock. *Journal of Ecology* 64:1029–1044.
- Hickie, P. F. 1936. Isle Royale moose studies. *Proceedings of the North American Wildlife Conference* 1:396–399.
- Huber, N. K. 1973. Glacial and postglacial geologic history of Isle Royale National Park, Michigan. *Geological Survey Professional Paper 754-A*. United States Government Printing Office, Washington, D.C., USA.
- . 1975. The geologic story of Isle Royale National Park. *United States Geological Survey Bulletin* 1309.
- Janke, R. A. 1984. The flora and vegetation ecology of Isle Royale National Park. Report to United States National Park Service. Isle Royale National Park, Houghton, Michigan, USA.
- Janke, R. A., D. McKaig, and R. Raymond. 1978. Comparison of presettlement boreal forests on Isle Royale National Park. *Forest Science* 24:115–121.
- Krefting, L. W. 1951. What is the future of the Isle Royale moose herd? *Transactions of the North American Wildlife Conference* 16:461–470.
- . 1974. The ecology of the Isle Royale moose with special reference to the habitat. *Forestry Series 15*. University of Minnesota Agricultural Experiment Station Technical Bulletin 297.
- Linn, R. M. 1957. The spruce–fir, maple–birch transition in Isle Royale National Park, Lake Superior. Dissertation. Duke University, Durham, North Carolina, USA.
- McKaig, D. M. 1978. Past and present forests of Isle Royale National Park. Thesis. Michigan Technological University, Houghton, Michigan, USA.
- Mech, L. D. 1966. The wolves of Isle Royale. *United States National Park Fauna Series 7*. United States Government Printing Office, Washington, D.C., USA.

- Mohler, C. L., P. L. Marks, and D. G. Sprugel. 1978. Stand structure and allometry of trees during self thinning of pure stands. *Journal of Ecology* **66**:599–614.
- Moloney, K. A. 1986. Wave and nonwave regeneration processes in a subalpine *Abies balsamea* forest. *Canadian Journal of Botany* **64**:341–349.
- Montgomery, D. C. 1984. Design and analysis of experiments. Second edition. John Wiley & Sons, New York, New York, USA.
- Murie, A. 1934. The moose of Isle Royale. University of Michigan Museum of Zoology Miscellaneous Publication **25**.
- Noy-Meir, I. 1975. Stability of grazing systems: an application of predator graphs. *Journal of Ecology* **63**:459–481.
- Peek, J. M. 1974. A review of moose food habits studies in North America. *Naturaliste Canadien* **101**:195–215.
- Peterson, R. L. 1955. North American moose. University of Toronto Press, Toronto, Ontario, Canada.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph Series 11. United States Government Printing Office, Washington, D.C., USA.
- Peterson, R. O., R. E. Page, and K. Dodge. 1984. Wolves, moose and the allometry of population cycles. *Science* **224**:1350–1352.
- Pimlott, D. H. 1965. Influence of deer and moose on boreal forest vegetation in two areas of eastern Canada. *Transactions of the Congress of the International Union of Game Biologists* **6**:105–116.
- Risenhoover, K. L. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Dissertation. Michigan Technological University, Houghton, Michigan, USA.
- Risenhoover, K. L., and S. A. Maass. 1987. The influence of moose on the structure and composition of Isle Royale forests. *Canadian Journal of Forest Research* **17**:357–364.
- Shea, S. R., and K. A. Aramson. 1972. Stem analysis of jack pine (*Pinus banksiana* Lamb.): techniques and concepts. *Canadian Journal of Forest Research* **2**:392–406.
- Slavik, A. D., and R. A. Janke. 1987. The vascular flora of Isle Royale National Park. *Michigan Botanist* **26**:91–134.
- Snyder, J. D., and R. A. Janke. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. *American Midland Naturalist* **95**:79–92.
- Taylor, R. J. 1984. Predation. Chapman and Hall, New York, New York, USA.
- Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.