THINNING STRATEGIES FOR ASPEN: A PREDICTION MODEL

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Quaking aspen (*Populus tremuloides* Michx.) occurs extensively in the Lake States, the northeastern United States, and the Rocky Mountains, as well as over most of Canada. Aspen characteristically regenerates from root sprouts (suckers) following a disturbance such as fire or timber harvest. It typically forms dense, more or less pure stands that grow rapidly and are relatively short-lived (pathological rotation ca. 40 to 70 years in the east). Yields exceed 50 tons per acre (ovendry basis) in above-ground biomass at 30 years on good, fully-stocked sites (Perala 1977). Because tree diameters in dense stands are small, aspen is grown primarily for fiber; it supports a large paper-making industry.

Compared with pulpwood yield, aspen sawtimber and veneer yield is low, but demand for aspen saw logs has increased following a recent decision to grade aspen lumber under softwood rules (Brinkman and Roe 1975). The present supply of aspen saw logs and veneer bolts is limited to overmature stands where cull due to decay by *Phellinus igniarius* is high. Future sawtimber supplies will decline as more aspen is grown on 30- to 35-year pulpwood rotations. However, yield of sawtimber and veneer bolts could be increased by intermediate thinnings that would concentrate growth on select trees, and by shortening rotations to minimize decay losses.

Many analyses of aspen growth are available (Bella 1972, Day 1958, Hubbard 1972, Schlaegel 1971, 1972, Schlaegel and Ringold 1971, Sorensen 1968, Steneker 1964, 1969, 1974, Steneker and Jarvis 1966). Most are for unthinned or once-thinned stands, and are not well-suited to analyzing aspen growth response following multiple thinnings to various stand densities. A model is needed to help prescribe economically and silviculturally sound thinning strategies to assure a future supply of aspen sawtimber and veneer bolts.

The model presented here is for site index 80 quaking aspen; it includes equations for stand growth in basal area, height, and sawtimber and veneer bolt volumes. Stand density in basal area and number of trees, stand age, and thinning effects are the primary independent variables. The impacts of growing season variation in rooting zone soil moisture and maximum air temperature, and defoliation by forest tent caterpillar (*Malacosoma disstria* Hubner) were also quantified.

STUDY AREA

A thinning demonstration in a uniformly dense (4,250 stems, 48 square feet basal area per acre), 13-year-old quaking aspen sucker stand was installed in March 1936 on the Pike Bay Experimental Forest, Minnesota (47° 20′N, 94° 30′W). The soil is a Warba very fine sandy loam with clay-loam subsoil—a good site for aspen. Elevation is 1,310 feet and topography is nearly level, with less than 2 percent slope. The climate is continental with a mean annual precipitation of 24 inches and mean July temperature of 68° F.

METHODS

Six 0.6-acre plots were thinned at three or four different times to maintain a full range of stem densities (table 1). Plots were remeasured during the dormant season at 5-year intervals over 40

Table 1.—*Summary of residual basal area and number of trees after repeated thinning in aspen*

	Age at thinning (years)							
	13		**23**		**28**		**33**	
Plot	Basal area	Trees per acre	Basal area	Trees per acre	Basal area	Trees per acre	Basal area	Trees per acre
	ft^2 /a		ft^2 /a		ft^2 /a		ft^2 /a	
207	30.1	1,717	58.2	1,100	[1] 76.9	[1]900	77.8	463
208	25.8	1,675	64.9	1,242	[1] 81.9	[1]1,000	78.9	493
210	21.2	1,216	54.2	775	58.5	558	62.4	385
212	18.8	975	57.8	677	63.0	450	67.6	275
211	14.2	544	53.0	383	61.3	272	63.4	200
213	9.5	396	28.5	221	40.8	183	49.6	155

[1] Not thinned at age 28.

years of growth. Each tree was classed as poor risk, secondary growing stock, or primary growing stock.[1] This was the ordered priority for removal in thinnings and provided the equation data for residual basal area after thinning (equation 6, table 3). Diameter of each live tree was measured at 4.5 feet (d.b.h.) with a steel diameter tape to the nearest 0.1 inch. Trees that died were not remeasured; their diameters at the beginning of the growth period were used for computing gross and mortality basal areas. Basal area was computed by (d.b.h.)^2 summation expanded to a per-acre basis. Initially, about 50 trees per plot representing the diameter range were measured for height to the nearest foot with an Abney level. This number declined by half for the last remeasurement. Mean stand height was determined at each measurement and after each thinning by regressing measured tree height over *l*n (natural logarithm) d.b.h. and solving for the tree of mean basal area. It should be stressed that any event that increases mean stand d.b.h., such as thinning or mortality of small trees, also increases mean stand height.

Summaries of monthly climatological data (U.S. Department of Commerce 1926-1975) for May-August at an official weather station in Cass Lake, Minnesota (315°, 5.1 miles from the study) provided the variables (average temperature, average maximum temperature, and total precipitation) needed for the climatic analysis. Soil moisture was assumed to be at field capacity on May 1 and succeeding average monthly soil moisture storage values for May through August of each year were computed according to Thornthwaite and Mather (1955) using average monthly temperature, total precipitation, and a rooting zone of 6.7 feet having maximum soil moisture retention of 14 inches.

The only natural stand disturbance was a forest tent caterpillar outbreak from 1951 to 1953. Yearly defoliation was estimated to average 30, 35, and 38 percent.

Basal area growth was separated for analysis into three components: gross basal area growth, mortality basal area, and mortality mean d.b.h. Gross basal area growth includes basal area growth of surviving trees plus basal area of mortality trees. Since all trees were measured, there was no ingrowth. The height growth component is the difference between mean stand height of live trees only (mortality excluded at remeasurement). All growth is expressed as 5-year growth.

Scatter diagrams of dependent over independent variables helped determine order of independent variable input and equation form. The data were fitted using least squares techniques; the residuals about the equation were plotted against the remaining independent variables, and a new equation term selected. This process was reiterated until no trend of residuals over any stand or environmental variable was detected.

All equation terms are explained in table 2. The final four equations that describe stand growth and two equations that estimate mean stand height and basal area after thinning are given in

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[1] *Primary growing stock: sound, progressive, good form; secondary growing stock: either sound, progressive with poor form, or sound but regressive; poor risk: all defective and suppressed trees with poor crowns.*

Table 2.—*Explanation of independent variables, notations, units, and range of data or limitations for model inputs*

Symbol	Meaning	Units	Range (or limitations)
T	Stand age at beginning of growth period	Decades	1.3-4.8 (1.0-5.5)
T_1	Stand age at end of growth period	Decades	(1.5-6.0)
Tth	Stand age at beginning of growth period immediately following thinning	Decades	(1.0-3.5; enter "0" for all other growth periods)
Td	Time since peak defoliation, including time in current growth period	Decades	(cannot exceed 1.8; "0" otherwise)
Td^y	Time since peak defoliation, including time in current growth period, to the power of y ($y = 1$ for growth period following thinning, $y = (Td)^2$ for other growth periods)	Decades	(Td cannot exceed 1.0; "0" otherwise)
B	Stand live basal area at begining of growth period	ft²/acre	9.5-121.9
B_o	Stand live basal area before thinning	ft²/acre	(<150)
N	Stand number of trees at beginning of growth period	1,000/acre	0.140-1.717
N_o	Stand number of trees before thinning	1,000/acre	(<6.000)
Nth	Stand number of trees after thinning	1,000/acre	(0.090-2.000)
D	Mean stand d.b.h. (of tree of mean basal area at beginning of growth period)	Inches	1.68-11.18
D_1	Mean stand d.b.h. at end of growth period	Inches	(>1.5)
H	Mean stand height (of tree of mean basal area at beginning of growth period)	Feet	24.1-80.7
$M(\ln F)$, $(\ln M)/F$	Five-year mean interaction terms of mean monthly (jn = June, jy = July) soil moisture storage according to Thornthwaite and Mather (1955) and maximum air temperature. Computed as: $M(\ln F) = \frac{\sum_1^5 (M)(\ln F)}{5}$ where means are for current growth period, and $(\ln M)/F = \frac{\sum_1^5 (\ln M)/F}{5}$ where June and July means are for 5-year periods ending 3 and 9 years earlier, respectively, than last year of current growth period.	$F = \frac{F^\circ - 50}{10}$, M = inches	June: 10.63-11.66, July: 11.91-13.74 for $M(\ln F)$; June: 1.022-1.190, July: 0.672-0.845 for $(\ln M)/F$.
P	Mean percent defoliation during a 5-year growth period	Percent	1-26("1" for nonepidemic growth periods)
exp, e	Base of natural logarithms	——	——
$\ln$	Natural logarithms	——	——

Table 3.—*Aspen growth and stand characteristic equations*

Dependent variable	**Independent variables**[1]	**R^2**	**$\bar{Y}$**	**[2]Sy.x**	**[3]N**	**Eq.**
Bg (5-year gross basal area growth, including mortality, ft²/acre)	$B \cdot \exp\{b_o + b_1(\ln T + 2.3)^{-1} + b_2 \ln B + b_3 NT(\ln B) + b_4 [NT(\ln B)]^{-1} + b_5 [M(\ln F)]_{jn} + b_6 [M(\ln F)]_{jy} + b_7 \ln P\}$	0.99	22.6	6.8	48	(1)
Bm (5-year mortality basal area, ft²/acre)	$-1 + \exp\{b_o + b_1(T - 1.73)^2 + b_2 B + b_3 B^{T/D} + b_4 [(\ln M)/F]_{jn} + b_5 [(\ln M)/F]_{jy} + b_6 \ln Tth + b_7 [.097^{eTd} \cdot (e^{Td})^{7.0}]\}$	.76	3.4	54.8	48	(2)
Dm (quadratic mean d.b.h. of mortality, inches)	$\exp\{b_o + b_1 e^{-T} + b_2 \ln Tth + b_3 \ln D + b_4 \ln Bm + b_5 \ln(1 + Td^{y})\}$	.95	4.1	12.0	45	(3)
ΔH (5-year mean stand height growth, feet. Based on tree of mean basal area)	$H \cdot \{\exp[b_o + b_1 \ln \frac{\ln(D_1 + 1)^{T1}}{\ln(D+1)^{T}} + b_2 P]\} - H$	.88	6.2	22.7	48	(4)
H (mean height, feet, of stand or stand component such as mortality or removals)	$\exp\{b_o + b_1 \ln T + b_2 \ln[\ln(D+1)^{T}]\}$	.99	51.9	2.7	54	(5)
B_{th} (stand basal area after thinning, ft²/acre)	$\exp\{\ln B_o + b_o + b_1 [\ln(\frac{100\ Nth}{N_o})]\}$	.99	36.6	11.1	50	(6)

[1] Coefficients are given in table 4.

[2] Sy.x is converted from the logarithmic form to the arithmetic form according to Baskerville (1972) and is expressed as a percent of arithmetic mean Y.

[3] Number of observations.

table 3; equation coefficients are in table 4. The growth equations were checked by comparing predicted values with values observed on other aspen thinning studies on the Pike Bay Forest and elsewhere in northern Minnesota (table 7, Appendix). No independent data were available for testing equation 6 (table 3).

The model was then used to predict how a number of thinning strategies, varying or constant climate, and defoliation would affect stand growth and development. Data from a sucker stand growing nearby on the same soil were used for prethinning densities at age 10. For comparison, Perala's (1973) equations were used to estimate basal area growth and stem survival in unthinned stands aged 10 to 20, and Schlaegel's (1971) equations were used for stands aged 20 to 60.

Volumes were determined from the following stand equations developed by Schlaegel (1974, 1975):

$V_{bw} = exp.(.996\ ln-\ BH - .854)$ (7)

$V_6 = V_{bw}\,[1.056 - 6.476\,(.735^{D})]$ (8)

$V_8 = V_{bw}\,[.889 - 33.261\,(.653^{D})]$ (9)[2]

where:

V_{bw} = total bolewood volume cubic feet/acre, excluding 6-inch stump,

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[2] *Schlaegel developed but did not publish equation (9).*

Table 4.—*Equation ceofficients and significance (in parentheses) as determined by t-test*

Equation[1]	[2]b_0	b_1	b_2	b_3	b_4	b_5	b_6	b_7
(1)	−4.7159 (.001)	+6.3111 (.001)	−0.8921 (.001)	−0.03946 (.001)	−1.186 (.001)	+0.1887 (.001)	+0.3191 (.001)	−0.2419 (.001)
(2)	−2.432 (.3)	+.0593 (.4)	+.00925 (.3)	+.067 (.01)	+4.38 (.02)	−3.22 (.2)	−.235 (.2)	+.353 (.05)
(3)	−1.1635 (.01)	+3.421 (.01)	+.1506 (.01)	+1.372 (.001)	+.0608 (.05)	−.2094 (.1)		
(4)	+.0025 (.6)	+.513 (.001)	−.0025 (.001)					
(5)	+3.084 (.001)	−.17 (.05)	+.618 (.001)					
(6)	−3.324 (.001)	+2.176 (.001)						

[1] To use equations (1), (2), and (4) with average climate and no defoliation assumptions, ignore the climate and defoliation terms and subsititute these values for b_0:

Equation	b_0	Ignored terms
(1)	+5.9369	b_5, b_6, b_7
(2)	−0.1814	b_4, b_5, b_7
(4)	+0.000	b_2

[2] Constant includes correction for logarithmic bias (Baskerville 1972).

V_6 = bolewood volume to a 6-inch top (i.b.), cubic feet/acre,

V_8 = bolewood volume to an 8-inch top (i.b.), cubic feet/acre,

BH = stand basal area (B, square feet/acre) x mean stand height (H,feet), and

D = mean stand d.b.h., inches.

Note that Schlaegel's 7-inch and 9-inch outside bark ratio estimators are used to estimate to inside bark industry standards. Since double-bark thickness of aspen is approximately 0.5 inch, these estimates are somewhat conservative. All volumes are gross volumes without deduction for defect.

A 40-year climate "loop" using the same 5-year mean climate record sequence observed in this study was used to simulate growth response at different ages to varying climate. The "loop" was advanced 5 years at the start of each of eight 40-year growth simulations. The varying climate input was followed in sequence, rather than randomly, to mimic its cyclic nature.

The effect of defoliation on aspen growth was simulated specifying constant average climate. This simulation specified 3 years of defoliation beginning the first year after thinning at age 30 and peaking at 38 percent— similar to what was observed in this study.

RESULTS AND DISCUSSION

Thinning

Most of the stand variables in this analysis are those commonly used in forest growth studies: basal area, number of trees, stand age, and mean stand diameter. Mean stand height (height of tree of mean basal area) is usually not used in growth studies although it is more accurate than dominant height when used in the combined variable, BH (see equation (7)), to estimate stand yields (Schlaegel 1974). Mean stand height, however, requires a large number of observations to develop height/diameter curves, compared with the fewer observations required for dominants and codominants alone. Mean stand height is a more precise integrator of the effects of defoliation and climate on height growth because, as will be pointed out later, these stresses are more pronounced in the lower dominance classes.

Variable forms used here (e.g., logarithms, polynomials) are common to growth studies. Two exceptions are the combined variables incorporating number of trees (N), stand age (T), and stand basal area (B). In equation (1) (table 3), NT(lnB) indicates that gross basal area growth (ΔBg) is maximized with optimum interactions of basal area and number of trees at a given age (climate and defoliation effects excluded). This is biologically sound, since stand growth is limited at low densities by incomplete utilization of the site and at high densities by overcrowding. The combined variable $B^{T/D}$ in equation (2) (table 3) says that mortality basal area (Bm) increases with decreasing mean stand d.b.h. (D) at a given age. This can be interpreted as follows: for stands of the same age and basal area, but with decreasing mean stand d.b.h., there must be a greater number of trees (on a given site) and therefore more intense competition, more trees under stress, and more trees dying.

Although thinning did affect ΔBg indirectly by changing the number of stems, basal area, and their interactions, thinning did not directly affect ΔBg. In contrast, thinning *per se* slightly lowered Bm, presumably because risk trees were removed. However, thinning increased mean d.b.h. of mortality, probably by exposing larger trees to sunscald or by providing favorable conditions for insects or pathogens. Both of these effects lasted only through the first 5-year growth period after thinning, and neither importantly influenced stand growth.

The first simulations identified thinning densities that would maximize volumes of saw logs and veneer bolts at the regeneration cut and before the onset of pathological rotation, usually 50 years. These simulations specified no defoliation and average climate. The strategies included thinning to 2,000, 1,500, 1,000, 750, and 500 stems per acre initially at age 10, with other thinnings to one-half initial stem density at age 20 and one-fourth initial stem density at age 30. At age 50, figure 1a shows that 1,500 and 1,000 stems initially were optimum for basal area growth. Of course, mean stand diameter decreased with increased stocking (fig. 1b). Because merchantable volume is a direct function of stand basal area and mean stand d.b.h. (equations 7-9), 750 stems per acre proved to be the optimum initial density for sawtimber (fig. 1c) and veneer (fig. 1d), followed closely by the 1,000 and 500 initial densities. There is little practical difference over the range of 500 to 1,000 stems initial density in veneer bolt volumes; the 500 density may be preferred because there are fewer, larger stems to handle. Also, milling efficiency is increased with fewer but larger, higher quality bolts and less waste in cores. It is undesirable to thin to densities lower than 500 stems because the site is underutilized and natural pruning of aspen tends to suffer.

After much trial, two other useful thinning strategies emerged; an initial thinning at age 10 to 550 stems per acre with (a) no further thinning or (b) a single repeat thinning to 200 stems per acre at age 30. The single thinning increased merchantable volume but the two-thinning strategy was a great improvement, producing nearly as much 6- and 8-inch material as the highest yield strategies (fig. 2).

Finally, a single commercial thinning to 240 trees per acre at age 30 or 35 was simulated. Compared with no thinning, this thinning improved volume of sawtimber, especially veneer bolts, at age 50 (fig. 2). It must be cautioned that thinnings so late in the rotation risk increased mortality from sunscald, which is not accounted for by the model (see Appendix). Therefore these simulations probably overestimate net thinning response.

Other thinning strategies were simulated, including very light thinnings at 5-year intervals, but these gave at best only slight increases in sawtimber or veneer above the best strategies already described.

The model shows that thinnings can increase the rotation yield of *total* bolewood by as much as 40 percent compared with no thinning (table 5). The 1,000/500/250 thinning strategy was the most efficient in this regard because it salvages mortality (table 5) and maintains the stand closest to optimum density over a greater proportion of the rotation.

The 550/200 stems at ages 10/30 strategy seems most advantageous, since only two thinnings are needed to yield nearly maximum sawtimber, veneer, and total bolewood. However, trees in stands grown with this strategy will average almost 2 inches smaller in d.b.h. at age 50 than those in stands also thinned at age 20. If a larger product is desired, a three-thinning strategy (500/250/125 stems at ages 10/20/30, fig. 1) should be considered.

Table 5.—*Simulated bolewood yield of thinnings and crop trees, and gross production over a 50-year rotation (see figs. 1 and 2 for additional stand structure information)*

Thinning strategy		Mean d.b.h. thinnings	Volume removed					Mortality volume[1,5]	Total gross production[1,5]
				Regeneration cut					
			Thinnings[1]	[2]6-in	[3]6-in	[4]8-in	Total[1]		
trees/acre	*age*	*inches*	*cunits per acre*						
2000/1000/500	10/20/30	1.2/2.6/4.0	1.5/4.9/7.1	16.4	33.5	11.2	63.4	9.9	73.3
1500/ 750/375	10/20/30	1.2/3.0/4.6	2.0/5.2/8.5	11.5	43.3	26.9	70.5	8.2	78.7
1000/ 500/250	10/20/30	1.3/3.5/5.6	2.6/5.1/8.3	5.2	51.8	40.5	73.0	6.5	79.5
750/ 375/188	10/20/30	1.3/3.8/6.2	3.0/4.7/8.0	2.4	52.6	43.2	70.7	5.4	76.1
500/ 250/125	10/20/30	1.4/4.1/6.7	3.5/3.7/6.7	0.5	46.1	38.7	60.5	3.7	64.2
550/200	10/30	1.4/5.7	3.4/11.9	3.3	49.8	40.3	68.4	5.4	73.8
550	10	1.4	3.4	15.5	44.7	23.3	63.6	11.9	75.5
240	30	4.3	15.8	6.4	38.3	27.7	60.5	3.7	64.2
240	35	4.9	15.9	7.2	36.0	24.9	59.1	3.2	62.3
Unthinned		—	—	19.6	31.7	4.6	51.3	—	—

[1] Total bolewood, 6-inch stump to tip of tree.
[2] Total bolewood minus yield to 6-inch top.
[3] Total sawtimber and veneer volume.
[4] Veneer bolt volume.
[5] Excludes mortality prior to thinning (mortality is not modeled in unthinned stands).

Climate

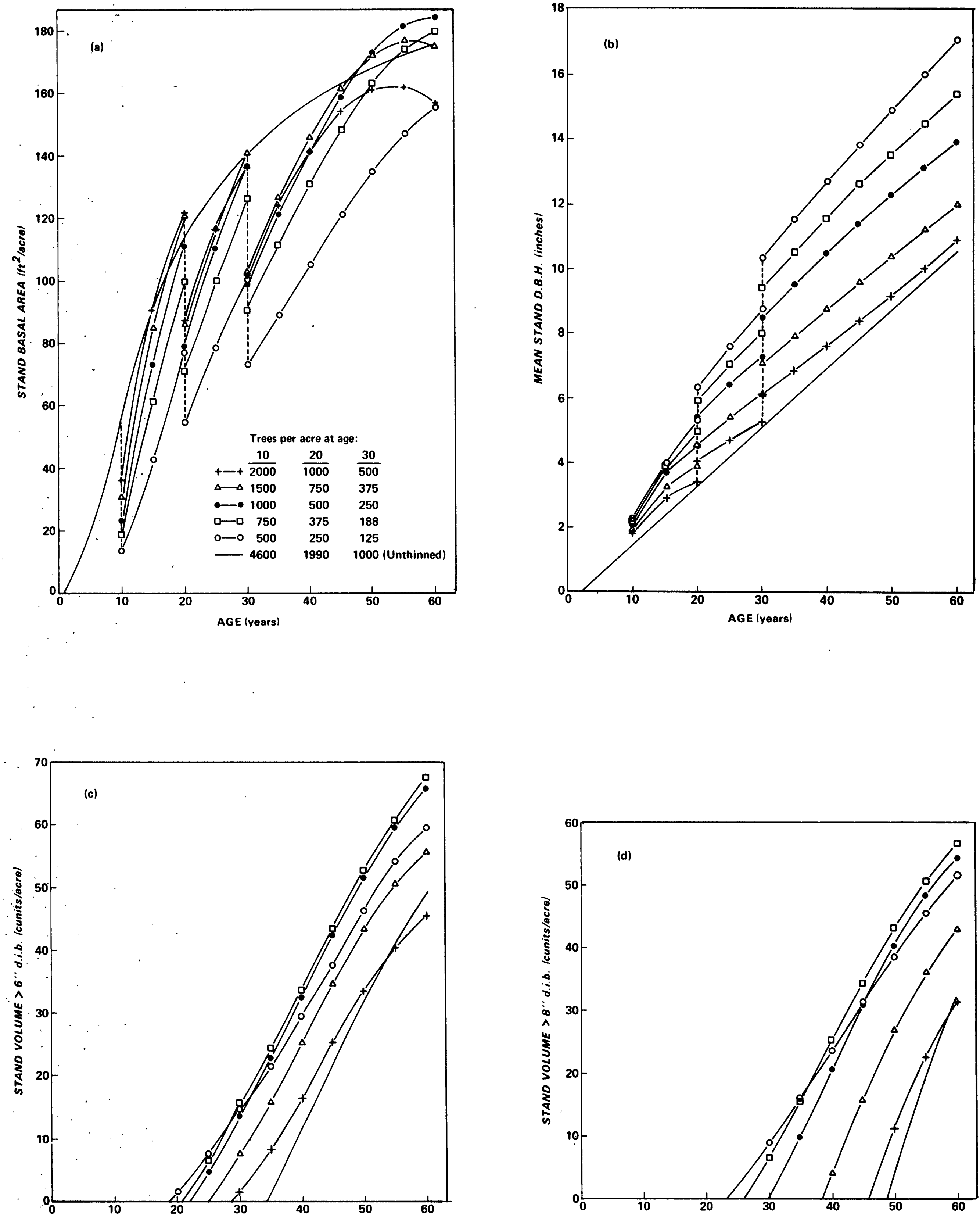
Tree growth is limited more often by internal water deficit than by any other factor (Kramer and Kozlowski 1960). Variations in radial growth with climatic variation are well-documented (Fritts 1976) and are particularly useful for archaeological dating and reconstructing past climate.

Several researchers have shown that radial tree growth responds directly to variation in growing season soil moisture, air temperature, or both (e.g., Bassett 1964, 1966, Fraser 1962, Fritts 1974, Phares and Rogers 1968). Variations in daily maximum temperature, relative humidity, percent of possible sunshine, and wind velocity are also important, but to a lesser degree (Fraser 1956, Fritts 1958, 1966, 1974). Variations in annual height growth with climatic variation are less well-documented. However, temperature and soil moisture (Cantiani 1967, Cremer 1975, Schmidt 1969, Yu 1964) have been correlated with height growth; temperature is apparently more important in the spring and soil moisture more important in the summer.

Quaking aspen has relatively inefficient stomatal control of transpiration (Tobiessen and Kana 1974). It is not surprising, then, that the climatic variables governing evapotranspiration and soil moisture availability—and therefore the water balance—measurably alter aspen growth. The importance of soil moisture is reflected in the rapid improvement of aspen site index with relatively small increases in soil moisture (Stoeckeler 1960, Graham *et al.* 1963).

Climatic variation also affects forest growth by inducing stress that kills trees directly or weakens their resistance to injurious biological agents. In aspen, *Armillaria mellea* causes root rot (Schmitz and Jackson 1927) that may be favored by a series of dry summers (Leaphart 1963). Hypoxylon canker, caused by *Hypoxylon mammatum*, is a common disease in aspen estimated to kill 1 to 2 percent of the crop each year (Anderson 1964). Hypoxylon canker infections seem to be established in a "wave year" pattern (Schmiege and Anderson 1960), although climatic variation is not known to be responsible.

Although the general relations between tree growth and growing season climate have been recognized, I know of no published studies that have included climatic variation in stand growth equations. Climatic data need not come from on-site weather stations because standard climatic records up to 20 miles distant are usable (Fritts


(a)
STAND BASAL AREA (ft^2/acre)
0
20
40
60
80
100
120
140
160
180
AGE (years)
0
10
20
30
40
50
60
Trees per acre at age:
10 20 30
+—+ 2000 1000 500
△—△ 1500 750 375
●—● 1000 500 250
□—□ 750 375 188
○—○ 500 250 125
—— 4600 1990 1000 (Unthinned)
(b)
MEAN STAND D.B.H. (inches)
0
2
4
6
8
10
12
14
16
18
AGE (years)
0
10
20
30
40
50
60
(c)
STAND VOLUME > 6'' d.i.b. (cunits/acre)
0
10
20
30
40
50
60
70
AGE (years)
0
10
20
30
40
50
60
(d)
STAND VOLUME > 8'' d.i.b. (cunits/acre)
0
10
20
30
40
50
60
AGE (years)
0
10
20
30
40
50
60

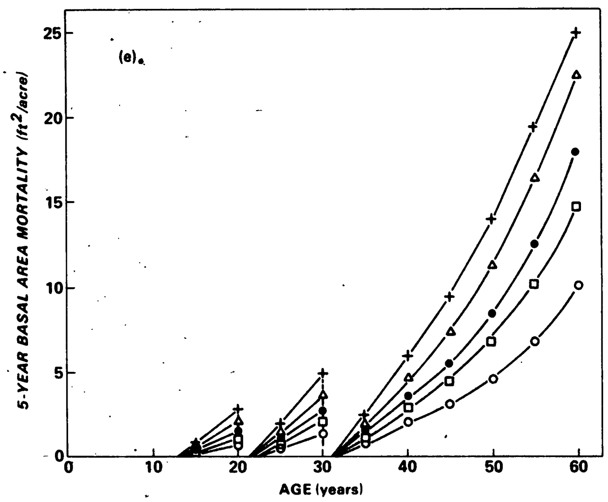
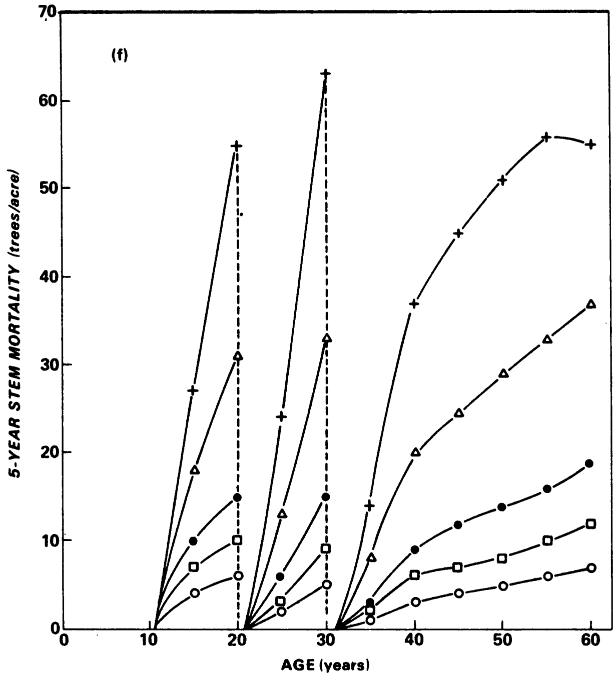


Figure 1.—*The effect of thinning to various stem densities at ages 10, 20, and 30 on (a) stand live basal area, (b) mean stand diameter, (c) volume to a 6-inch top, (d) volume to an 8-inch top, (e) 5-year basal area mortality, and (f) 5-year stem mortality.*



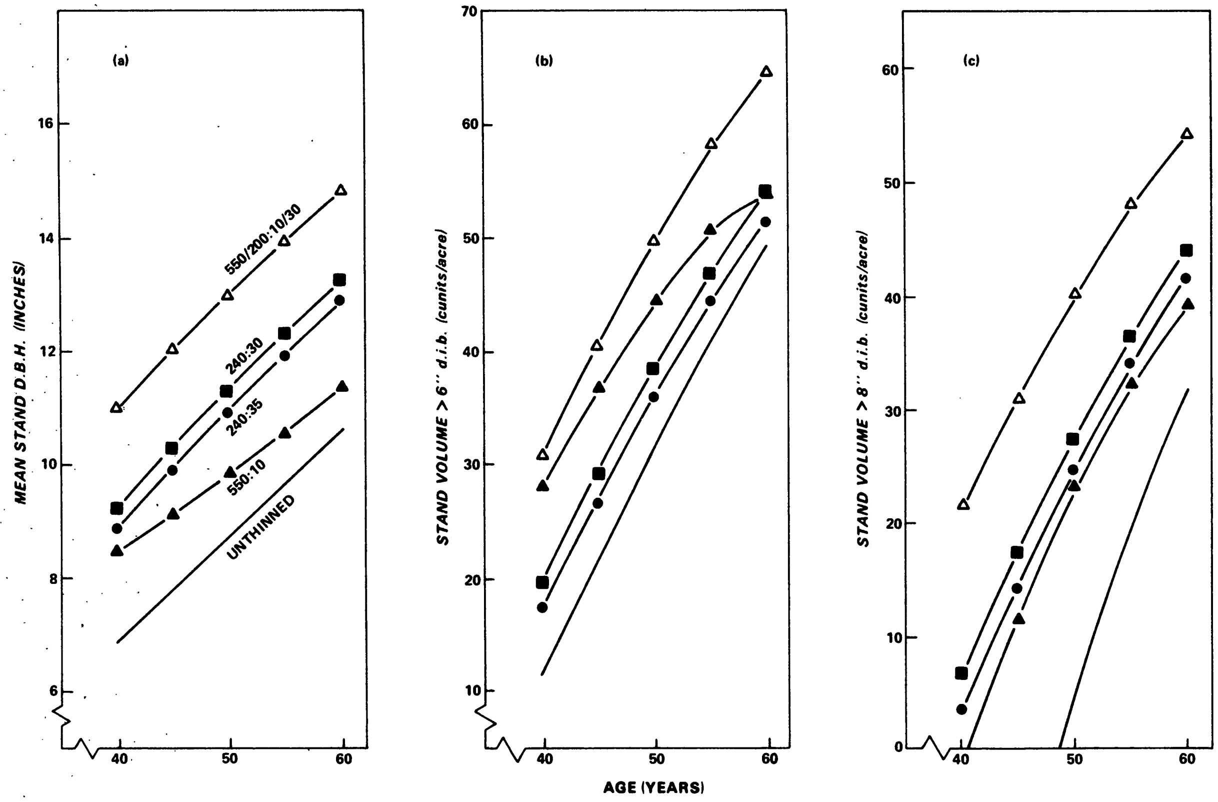


Figure 2.—*The effect of various thinning timings and frequencies on (a) mean stand diameter, (b) volume to a 6-inch top, and (c) volume to an 8-inch top.*

1976). Soil moisture under forest cover can be accurately estimated from Thornthwaite and Mather's (1955) computations if surface infiltration and internal drainage are good (Zahner 1967).

Three assumptions made in this study could lead to errors in computation of soil moisture and its availability to tree growth. First, the assumption that soil moisture is at field capacity by May 1 is not always valid. During a recent record drought, soil moisture under aspen at the Marcell Experimental Forest (20 miles north of Grand Rapids, Minnesota) was only 12 inches in May 1976 and only 8 inches in May 1977, compared with field capacity of 14 inches.[3] In our study, the climatological data (U.S. Department of Commerce 1926-1975) indicated that precipitation over the recharge period was sufficient to bring soil moisture to field capacity for 43 of the 50 years. Complete year soil moisture calculations for the other 7 years revealed that incomplete recharge led to these soil moisture overestimates:

Year:	1928	1931	1932	1934	1935	1956	1961
Overestimate (inches),							
June:	1.26	4.18	1.63	3.00	1.61	0.37	0.56
July:	1.13	3.69	1.45	2.31	1.58	0.33	.48

Because these errors are diluted in 5-year averages, the errors in the computed climate variables are small (0.5 to 5.2 percent overestimates) and do not detract seriously from this analysis. However, the assumption of full soil moisture recharge should not always be accepted outright.

The second assumption, that the rooting zone for aspen remained constant at 6.7 feet during the entire study, could be questioned. Practically nothing is known about changes in aspen rooting with age, but some inferences can be drawn from hydrologic observations. The increased water yield after clearcutting aspen steadily diminishes until stabilizing at about age 8 to mature forest levels.[3] This indicates full occupation of the rooting zone by the sucker stand, and little change would be expected thereafter. Thus, the second assumption appears to be valid.

The third assumption is that the rooting profile of aspen is indeed 6.7 feet. This depth is taken directly from Thornthwaite and Mather (1955) for closed mature forest. Verry[3] has observed soil moisture depletion as deep as 7.5 feet under mature aspen, indicating rooting occurs at that depth. The 6.7-foot assumption is not as important for this study as it would be for a larger study that included sites with different soil textures and moisture capacities. Such a study would need to determine absolute amounts of water available for tree growth on each site.

It should not be inferred that growing season soil moisture and air temperature are the only climatic variables affecting aspen growth. The total effect of climate on aspen growth is underestimated by this model because the growth analysis is restricted to the current season and records of solar radiation, wind, and other climatic variables are not available.

In this study, neither gross basal area growth (ΔBg) nor mortality basal area (Bm) reacted to soil moisture independently from temperature; both responded best to June and July monthly interactions of soil moisture and temperature.

For ΔBg (equation 1, table 3), the combined climatic variable, M(lnF), suggests that aspen growth increases more as a result of increased soil moisture than as a result of increased air temperature. An inspection of the magnitude of the coefficients in equation (1) shows that July is 70 percent more important than June as a growing month (table 4). The same combined climatic variable for August had no additional effect on ΔBg. This agrees with the observations of Fraser (1962), who found that the bulk of radial growth of aspen in Ontario occurs in July and is nearly complete by August.

The best combined climatic variable for Bm (equation 2, table 3) was (lnM)/F, again for June and July only, but for 5-year means 3 and 9 years earlier, respectively. (See table 2 for computation.) The coefficient for June was positive and the coefficient for July was negative (table 4), meaning that mortality increased with a cool, wet June 3 years previous and a hot, dry July 9 years previous. This interpretation has some biological support: the 3-year lag (four growing seasons including current year) response to June climate falls nicely in the range of 3 to 7 years needed by hypoxylon to kill pole-sized trees (Schipper and Anderson 1976). This may be a clue to understanding the infection mode of hypoxylon. The hot, dry summers that favor *Armillaria mellea* root rot may not injure

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[3] *Personal communication with E. S. Verry, Forest Hydrologist, North Central Forest Experiment Station, Grand Rapids, Minnesota, March 2, 1978.*

aspen as seriously, and trees may take longer to die—thus the 9-year lag response to July climate.

Most of the variation in height growth (ΔH, equation 4) was accounted for by increase in mean stand d.b.h., which is dependent on net changes in basal area (from equations 1 and 2) and numbers of trees (from equations 2 and 3). Because both ΔBg and Bm responded to combined climatic variables, ΔH has already responded to climate.

Figure 3 shows the upper and lower bounds and examples of stand basal area net growth and 5-year mortality basal area calculated from equations (1), (2), (3), and (6) using the climate "loop" described in "Methods". Note that the bounds do not represent any single run but rather define the amplitude that can be expected at each 5-years' growth with successive runs having different starting points on the climate "loop". The surprising result is that stand conditions are similar after 40 years of growth regardless of when favorable or unfavorable climatic conditions were introduced. This is not as apparent in figure 3 for mortality, which was plotted as 5-year values for clarity, but when plotted as accumulated values, the pattern is similar to basal area growth.

Basal area growth, 5-year mortality, and mean stand diameter are shown in figure 4 for a stand grown with constant "best", "average", or "worst" climate based on the extremes and mean 5-year soil moisture and air temperature interaction terms calculated from this study. The growth response to the worst climate was not nearly as dramatic as to the best climate. Aspen grown during the worst climate had 19 percent less basal area, 8 percent smaller stand d.b.h., and 26 percent less volume in 8-inch bolts (not shown in figure 4) at age 50 than aspen grown with average climate. Aspen grown during the best climate averaged 4 inches larger in d.b.h. and had nearly twice as much basal area and volume in 8-inch bolts as

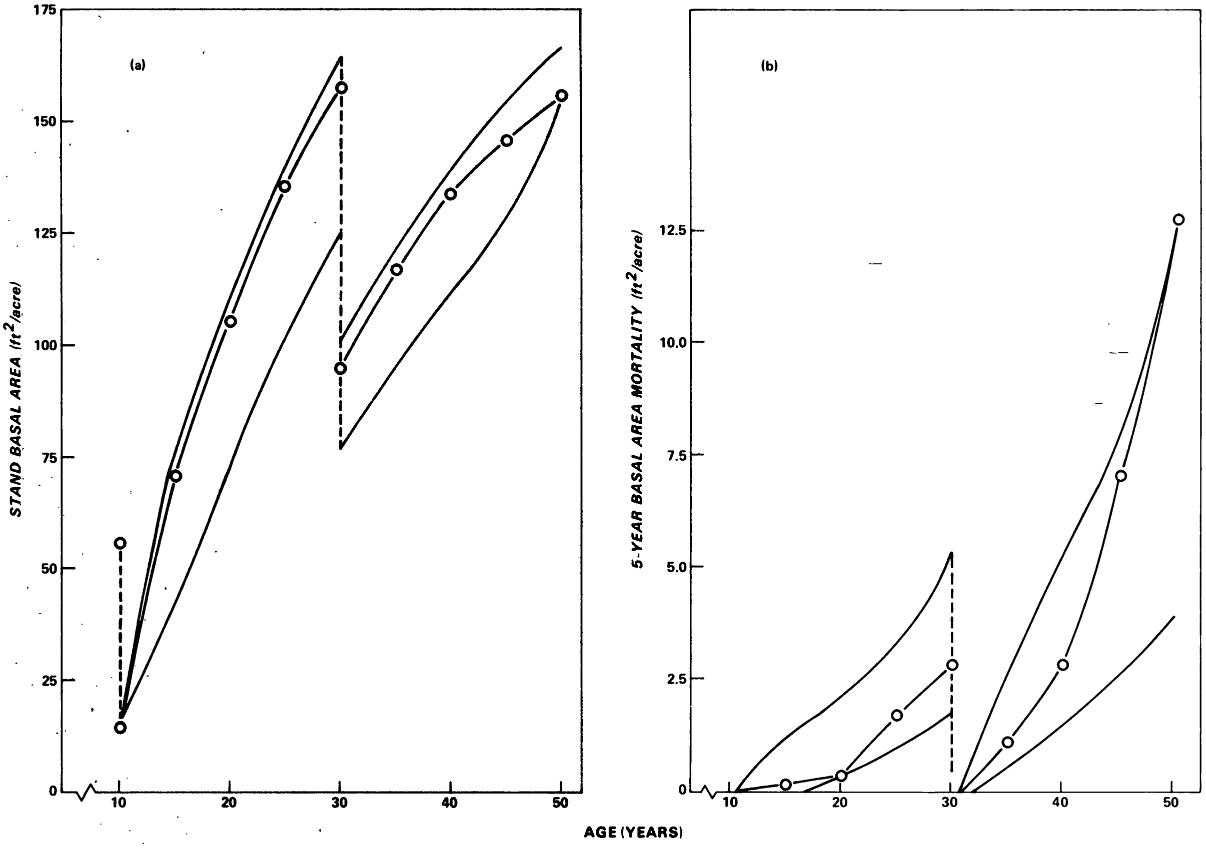

Figure 3.—*The effect of varying 5-year growing season climate on (a) live basal area, and (b) 5-year basal area mortality after thinning to 550 and 200 stems per acre at ages 10 and 30, respectively. See text for details.*

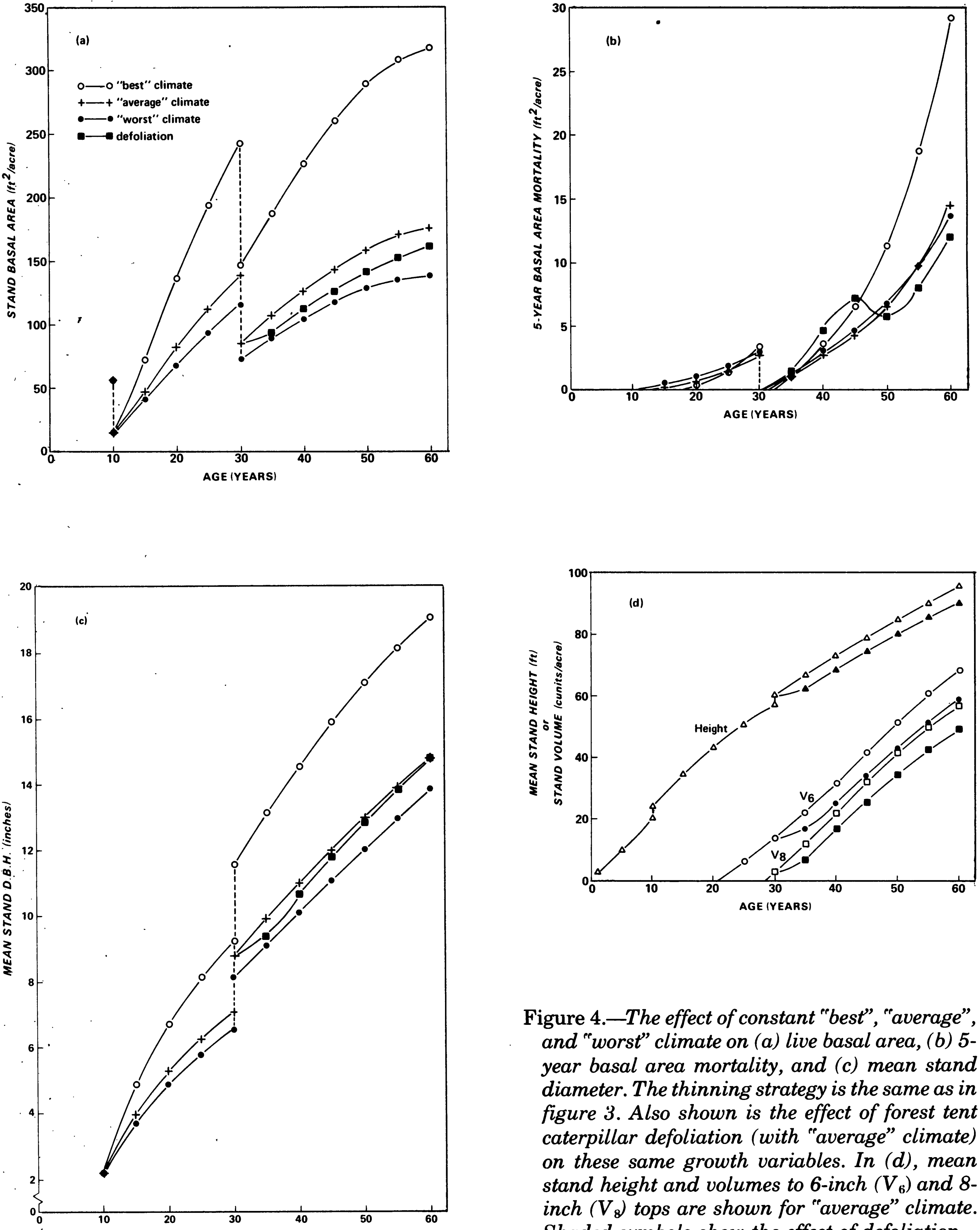

Figure 4.—*The effect of constant "best", "average", and "worst" climate on (a) live basal area, (b) 5-year basal area mortality, and (c) mean stand diameter. The thinning strategy is the same as in figure 3. Also shown is the effect of forest tent caterpillar defoliation (with "average" climate) on these same growth variables. In (d), mean stand height and volumes to 6-inch (V_6) and 8-inch (V_8) tops are shown for "average" climate. Shaded symbols show the effect of defoliation.*

aspen grown with average climate at the same age. Of course, these are extrapolations; continued "best" or "worst" climate could induce unforeseen growth or mortality reactions that would not occur during varying climate.

The main value of these simulations is they show (1) that aspen growth is little affected by combinations of favorable and unfavorable growing years that have the same long-term average; (2) that continued adverse climate (at least within the limits of the past 40 years) does not necessarily present an unacceptably grave risk to aspen management; and (3) that favorable climate could boost aspen growth tremendously. This also suggests the magnitude of aspen growth response to irrigation, since soil moisture is the major contributor to the climate response.

Forest Tent Caterpillar Defoliation

Aspen stands commonly suffer temporary increment loss and mortality from periodic outbreaks of defoliating insects such as the forest tent caterpillar and the large aspen tortrix (*Choristoneura conflictana* Walker). Forest tent caterpillar populations erupt following an increase of annual cyclonic passages (Wellington 1952).

Forest tent caterpillar defoliation was an important variable in all growth equations (equations 1 to 4). Defoliation reduced gross basal area growth (ΔBg) and height growth (ΔH), and increased mortality basal area (Bm) in smaller trees up to 8 years later. This seems realistic because small trees that are suppressed and clearly under stress suffer most from defoliation (Kulman 1971, Witter *et al*. 1975). From 8 to 18 years following defoliation Bm was still elevated, peaking at 13 years (see figure 4), although size of trees dying was no longer affected. This 13-year delay in peak mortality also seems reasonable, because defoliation exerts a stress on the tree that is not immediately fatal but that subtly tips the balance of survival, perhaps much like the stress induced by hot, dry July's discussed earlier. Barter and Cameron (1955) reported increased mortality the first 3 years after defoliation in 60-year-old aspen, but in general, 3 to 4 years of defoliation causes little mortality (Kulman 1971). The increased mortality found in this study was not great and would not have been detected without accounting for the several other variables affecting Bm. In contrast, Witter *et al.* (1975) reported reductions in aspen stem density and basal area of 41 and 27 percent, respectively, after 5 to 7 consecutive years of heavy defoliation.

There is no doubt that defoliation decreases ΔBg (Ghent 1958, Rose 1958), especially after accounting for variation in summer rainfall (Duncan and Hodson 1958). Batzer (1955) reported crown dieback when aspens were repeatedly defoliated by forest tent caterpillars, which could explain the reduction in ΔH by defoliation (equation 4).

Simulated defoliation effects are shown in figure 4. Note the mortality peak during the third 5-year growth period. The total mortality due to defoliation during the four subsequent growth periods was only 30 percent above normal basal area mortality, but 57 percent above normal stem mortality. Since this acted as a thinning from below, mean stand d.b.h. was not affected nearly as much at age 50 as were other parameters. The effect on height growth is particularly important because mean stand height was reduced 5 feet at age 50. Since dominant height is proportional to mean stand height, large errors in measured site index are possible, especially in stands suffering more than one defoliation period. Productive potential of such stands could be considerably underestimated. In this simulation, sawtimber and veneer volume was reduced 17 percent at age 50 by defoliation.

In addition to the 550/200 thinnning strategy, the effect of the same specified defoliation was simulated using the 1,000/500/250 strategy (table 6, Appendix). Defoliation reduced V_8 more than Vbw, and reduced V_8 most, at least initially, in the 1,000/500/250 strategy, which has the greater stand density. Even though defoliation volumes slowly gained parity with no defoliation, the growth loss would not be completely made up prior to pathological rotation.

CONCLUSIONS

The primary objective of thinning is to concentrate growth on crop trees to increase the yield of large-diameter products. Secondary objectives may be to increase the total fiber yield by salvaging anticipated mortality, to bring early financial return from commercial thinnings, to reduce the cost of logging during the regeneration cut, and to improve regeneration conditions for aspen suckers. Another possible objective in aspen is to upgrade the genetic composition of the stand by removing undesirable clones in thinnings.

Even though the model presented here was developed from data from a single site, the proportionate gains (if not absolute gains) in sawtimber and veneer bolts as a result of thinning should be representative for most site index 80 stands. How stands of higher or lower site quality respond to thinning is not known with certainty, although response usually increases with site quality.

Thinnings should be from below except to remove defective and risk trees. The first thinning may deviate from strictly regular spacing in order to keep the best trees. Occasional clumps of close-growing, vigorous trees can be left until a later commercial thinning to provide the widest latitude in crop tree selection. The final thinning, however, should be regularly spaced because of the long wait until the regeneration cut. Great care should be taken during thinning to avoid injury to crop trees. Aspen is extremely sensitive to wounds, which serve as an entry point for defect and decay. The risk of wounding is highest during spring and early summer when the bark slips easily; thus, thinnings should be scheduled during the dormant season. For more thinning information, see Brinkman and Roe (1975) and Perala (1977).

As this analysis has demonstrated, long-term forest growth records and standard local climatological records can be used to partition forest growth response to varying climate and insect defoliation. It must be recognized, however, that the climate response model developed here is limited to stands on very specific soils (see Appendix). Zahner (1967) points out that soils that have considerable storm runoff, receive downslope soil moisture, or have seasonally perched water tables present quite different soil moisture regimes than do soils with good internal drainage and flat topography. Stoeckeler (1960) found that aspen site index varied widely with soil percent silt-plus-clay, depth to water table, internal drainage, slope, and aspect. Moisture availability for tree growth is greatly affected by all these variables and must be accounted for in any modeling attempt involving climatic response.

The stronger response of basal area growth and basal area mortality to the combined climatic variables than to separate soil moisture and air temperature variables implies a synergistic growth response to soil moisture and temperature. A problem with using a combined variable is that much trial and error is needed to find the combination and form of variables that provide the correct response curve, such as M(lnF) and (lnM)/F in this study. Although these interaction terms performed well here, they may be much less adequate for other soils, as suggested in the model tests (see Appendix). Even coding or choosing the units of measure affects the relation with dependent variables when logarithmic and arithmetic units are combined.

It should be possible to develop a map of aspen productivity on well-drained soils throughout its eastern range. A model responding to geographic variation in growing season temperatures, computed soil moisture, and probably latitudinal variation in solar radiation would be needed. This concept has already had some success in Europe (Pardé 1959, Paterson 1959) and the western United States (Jones 1971). Refinements for topographic positions, depth to water table, and other site variables could be added and the confounding factor of aspen clonal variation would need to be resolved (Jones 1971).

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APPENDIX

MODEL RELIABILITY

The equations in the model have high statistical reliability (i.e., high R^2 and low sy.x, table 3), partly because the data are gathered from a single, uniform study area. The repeated measurements have the disadvantage of introducing an unestimable error, usually small, due to autocorrelation (i.e., the error terms are underestimated). On the other hand, the study is unique in providing data over an entire 53-year rotation for thinned aspen. Moreover, many growth remeasurements are necessary to partition the effects of varying climate and defoliation from stand age and density.

Coefficient significances are at least $p<0.05$ in equations (1), (4), (5), and (6), and for all terms in equation (3) except $ln(1+T_d^y)$, which is $p<0.1$ (table 4). Equation (2) contains a number of variables that under usual statistical interpretation (if $p>0.05$) would be deleted. However, one goal in the analysis was to find the combination of variables that would eliminate any trend of residuals about time; this required retaining variables that produce biological responses according to existing knowledge or theory even if they had limited statistical significance. Considering the highly variable nature of mortality and the fact that mortality of individual trees is not incrementally measured (a tree is either dead or alive, which often varies with observer judgment), it was further felt $p<0.05$ was too strict a requirement for this study. The statistical risk of erroneously retaining a given variable in the mortality equation is high, but the practical risk is low, because mortality in multiple thinned aspen is a minor component of stand growth.

One way to evaluate the reliability of these equations is by testing them against independently observed values from other studies.

TESTING THE MODEL

The first step was computing, as described in "Methods," the combined climate variables based on climatological records from the weather station nearest each study. Maximum soil moisture retention for each stand was assumed identical to this study—i.e., 14 inches. Then growth was predicted based on stand parameters and either including or ignoring climatic variability and defoliation. Deviations of observed values from values predicted when ignoring climatic variability or defoliation were then plotted over the contribution predicted for each. Finally, deviations of observed values from predicted values for study H-70 (others did not have enough observations) were plotted over the equation stand variables to detect bias.

Generally, predicted basal area growth was closest to growth observed in stands thinned at ages 7 to 15 (table 7). Deviations of basal area and height growth from observed values were usually consistently biased within a stand, rather than random, when climate was included. In contrast, when climate was ignored the deviations were random.

Gross basal area growth (ΔBg) comparisons were available from studies H-70, NC-93, DM, and BC (table 7). In H-70, ΔBg was consistently overestimated by 13 to 35 percent (4 to 5 square feet/acre/5 years) with climate included. The check of deviations with climate-ignored over climate-predicted response showed a strong 1:1 positive slope, indicating the same climatic response as in the primary study on the same soil nearby. The site index for H-70 is about 7 feet less than in the primary study, which could account for the consistent overestimate. There was no trend of deviations over observed stand parameters in H-70.

ΔBg for study DM was greatly overestimated for the first growth period after thinning, but was estimated perfectly for the second growth period. A great deal of bark splitting and poplar borer (*Saperda calcarata* Say) injury was noted at the first 5-year remeasurement after thinning, indicating stress in the stand. The equation-predicted climatic effect was more favorable in the first growth period than in the second, so some other unknown factor is probably responsible.

In younger stands, ΔBg was predicted closely in NC-93. In study BC, ΔBg was unexplainably overestimated at age 7 and underestimated at ages 12 and 17. These low estimates are probably due to the higher site index of study BC and, at age 17, an additional error from overestimating growth reduction by forest tent caterpillar defoliation. Defoliation was nearly 100 percent during one year but no defoliation was observed during the other years. This probably has less effect on radial growth than three successive years of much lighter defoliation, as was experienced on the primary study. Five-year climate during these three growth periods varied little and presumably did not account for any of this variation.

In constrast with ΔBg, predicted basal area mortality (Bm) and stem mortality (Nm) varied widely from observed values (table 7). In general, mortality was greatly overestimated in studies H-70 and M-371, and greatly underestimated in NC-52i, NC-93, and BC. Since most mortality was by hypoxylon canker and resistance to hypoxylon varies widely among clones (Copony and Barnes 1974), it is not surprising to find wide variation in mortality among stands. The model estimates for mortality are biased consistently within stands, except that mortality is greatly underestimated for the first growth period after thinning stands age 20 or older. Pole-sized aspen can suffer sunscald when suddenly released, but sapling stands apparently are not affected. Because the model was developed from aspen thinned initially as saplings, later pole-sized thinnings did not induce abrupt changes that would increase mortality. In fact, equation (2) predicts less mortality during the first growth period following thinning, because poor risk trees are specified in the thinnings. Thus the model erroneously underestimates mortality in the first 5 years after initial thinning in pole-sized stands.

The test of climatic effects on Bm showed that H-70 responded much like the primary study—i.e., Bm increased with increasing computed contributions by climate. Studies DM and BC showed no logical trend over variation in climate, suggesting that mortality is more strongly controlled by site and genotype than by climate.

Where mortality is inaccurately predicted, it follows that net basal area growth (ΔBn = ΔBg− Bm) is predicted less accurately than is ΔBg. ΔBn was predicted closely only in the studies (BC and PN-3, 8; PN-1, 6; PN-2, 7) that were thinned at ages 7 to 15 (table 7). Although such comparisons are limited to only 12 growth periods, it is encouraging to find these close agreements between predicted and observed values of ΔBn, the variable of most practical interest to the land manager.

Predicted mean stand height growth (ΔH) varied widely from observed values but was consistently biased within a stand (table 7). In H-70 and M-371, the model tended to increasingly overestimate ΔH with age, confirming the difference in site index and suggesting that height growth slowed earlier than in the primary study. The only deviations from this trend are during the defoliation years when the model overestimated reductions in height growth. The other studies have too few observations to determine if a consistent bias is present in estimating ΔH.

In summary, the model is highly specific in respect to thinning strategy, site index, degree of defoliation, and soil moisture characteristics. The model works best for (1) site index 80 stands; (2) stands thinned initially at about age 10; (3) Warba or similar soils; and (4) stands lightly to moderately defoliated (if at all) over a 2- to 4-year period.

This is not as restrictive as it at first seems. Future thinning programs will concentrate on the best aspen sites, of which site index 80 is most common. About 120,000 acres of the Chippewa National Forest, for example, have Warba soils, most of which support site index 75-80 aspen.[4] Extending the model to other areas and soils would show greatest weaknesses in the climate terms, and the mortality and height growth equations. However, the model should serve as a guide to thinning response until a more universal model is developed.

Table 6.—*The effect of defoliation on standing total bolewood (Vbw) and veneer bolt (V_8) volumes by thinning strategy*
(In percent of no defoliation)

Stand	550/200		1000/500/250	
age	Vbw	V_8	Vbw	V_8
30	100	100	100	100
35	83	58	84	47
40	83	77	85	71
45	83	80	85	77
50	84	83	87	81
55	85	85	90	84
60	87	87	90	86

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[4] *Personal communication with Grant Goltz, Soil Scientist, Chippewa National Forest, March 1, 1978.*

Table 7.—*Deviation of model-predicted values minus values observed expressed as a percent of values observed in seven other once-thinned aspen studies (climate and defoliation variables included)*

Study	T	P	ΔB_g	ΔBn[1]	Bm	Nm	ΔH	Remarks
				---------------percent of observed---------------				
H-70	30	1	+33	+93	−78	−71	+63	N[2] = 9. S[3] = 73. Tth = 30. Soil = Warba very fine sandy loam. Located 085°, 0.4 mile from primary study.
	42	14	+35	+15	+115	+90	+26	
	47	1	+13	−24	+144	+104	+94	
	52	1	+25	−98	+124	+55	+97	
	57	1	+22	−58	+108	+60	+294	
M-371	20	1	Na[4]	+5	Na	−42	+2	N = 6. S = 70. Tth = 20. Soil = Warba fine sandy loam. Located 020°, 4.6 miles from primary study.
	35	1	Na	+30	Na	+57	+63	
	40	15	Na	−1	Na	+279	−2	
	45	1	Na	+132	Na	−17	+88	
NC-52i	19	1	Na	+106	Na	−76	Na	N = 20. S = 80. Tth = 10. Soil = Warba very fine sandy loam. Located 200°, 0.9 mile from primary study.
	24	1	Na	+17	Na	−78	Na	
	29	1	Na	+141	Na	−78	Na	
NC-93	16	1	+4	+30	−91	−93	−34	N = 4. S = 60–75. Tth = 1. Soil = Warba very fine sandy loam. Located 340°, 2.0 miles from primary study.
DM	37	1	+70	−90	−91	−90	+180	N = 4. S = 85. Tth = 37. Soil = heavy silt loam. Located 47° 50′N, 93° 40′W and 350°, 7.1 miles from official weather station at Bigfork, Minnesota.
	42	1	0	+23	−35	+23	+34	
BC[5]	7	1	+32	+31	+∞[6]	+∞[6]	Na	N = 2. S = 90. Tth = 7. Soil = loamy sand with clay subsoil. Located 160°, 9.3 miles from official weather station at Indus, MN and 255°, 17.3 miles from International Falls, MN.
	12	1	−9	−6	−86	−90	Na	
	17	18	−20	+3	−66	−67	Na	
PN 4,5[5]	4	1	Na	−78	Na	+50	Na	N = 2. S = 66+. Tth = 4, 7, 10, 15. Soil = variable. Located 48° 10′ – 48° 20′N, 93° 25′ – 93° 35′W
PN 3,8	7	1	Na	−3	Na	+125	Na	
PN 1,6	10	1	Na	+4	Na	−32	Na	
PN 2,7	15	1	Na	+11	Na	−32	Na	

[1] ΔBn=Net basal area growth. Except where noted, other symbols follow tables 2 and 3.
[2] N=Number of plots.
[3] S=Site index, feet at age 50.
[4] Na=Not available.
[5] Data supplied by John W. Hubbard, Management and Research Forester (retired), Boise Cascade Corporation, Big Falls, Minnesota.
[6] Mortality was predicted but none was observed, therefore the infinite deviation.

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