Modeling Aspen and Red Pine Shoot Growth to Daily Weather Variations

Donald A. Peralta
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MODELING ASPEN AND RED PINE SHOOT GROWTH TO DAILY WEATHER VARIATIONS

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Many investigators have attempted to correlate parallel measurements of shoot growth and meteorological variables (Ashton 1975, Cremer 1976, Dahl and Mork 1959, Hiley and Cunliffe 1923, Lanner 1964, Worrall 1973, among others). Hari et al. (1977) were especially successful and developed a dynamic model with good predictive value when applied to shoot growth of a number of plants.

Shoot growth models have a number of potential uses in forestry. By screening out microclimatic variation, they could be used to (1) bring into focus the annual rhythm of shoot growth—one of the best indicators of genetic climatic adaptation (Dietrichson 1971); (2) compare provenance and tree breeding trials over widely separated plantings and over different years (Hari and Leikola 1974, Parviainen 1974); and (3) define climatic provinces suitable for growing exotic or genetically improved trees. Also, reference models might aid in classifying sites and in evaluating silvicultural practices prescribed to modify forest microclimates such as competition control, nurse crops, topographic site selection, and regeneration systems. Herbicide testing and prescription could be improved by predicting plant metabolic activity, and hence sensitivity to herbicides (Aberg 1964), from local meteorological observations.

Development of shoot growth models has been hindered by (a) inadequate measurement frequency and accuracy, (b) complex interactions between environmental variables and plant requirement needs with maturity, (c) lag and displacement of plant response to environmental stimulus, (d) complex energy exchange between plants and environment, and (e) high correlation between meteorological variables (Ford 1980, Idso et al. 1966, Kramer and Kozlowski 1979). In the strictest sense, growth can never be unequivocally related to meteorological variation because natural environments are out of the control of the experimenter. On the other hand, the principles of plant growth are well established (Kramer and Kozlowski 1979) so that carefully interpreted empirical studies may provide theoretically sound working models for testing, refinement, and use.

This paper presents some equations that estimate shoot growth of juvenile quaking aspen (Populus tremuloides Michx.) and red pine (Pinus resinosa Ait.) from daily meteorological records. The underlying objectives of the study were to determine (1) if shoot growth measurement techniques and local standard climatological data could provide analytically usable data sets; (2) the usefulness of data gathered over daily and longer intervals; and (3) whether standard multiple linear regression of the data sets and transformations would provide coherent and theoretically sound shoot growth equations. The equations are by no means definitive because the data sets were limited and because of other weaknesses. On the other hand, they demonstrate that meteorological data may be much more useful than is generally conceded.

"Shoot growth" as used here means the difference between successive measures of shoot length and may include reversible changes due to hydration as well as irreversible changes due to tree growth (Cremer 1976, Milne et al. 1977).

METHODS

Shoot growth data were gathered near Grand Rapids, Minnesota, for two growing seasons (1978-1979) from planted red pine and for three seasons (1977-1979) from naturally regenerated aspen suckers (table 1). All trees were on level terrain and open-grown
Table 1.—Characteristics of aspen and red pine measured for shoot growth

<table>
<thead>
<tr>
<th>Measurement year</th>
<th>Age(^1)</th>
<th>Stocking</th>
<th>Total height(^1)</th>
<th>Seasonal shoot growth</th>
<th>Duration of growth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Years</td>
<td>1,000 stem/ha</td>
<td>m</td>
<td>mm</td>
<td>Days(^2)</td>
</tr>
<tr>
<td>1977</td>
<td>1</td>
<td>93</td>
<td>1.12–2.08</td>
<td>1,124–2,083</td>
<td>81</td>
</tr>
<tr>
<td>1978</td>
<td>2</td>
<td>72</td>
<td>1.94–2.50</td>
<td>667–991</td>
<td>71</td>
</tr>
<tr>
<td>1979</td>
<td>3</td>
<td>48</td>
<td>2.52–2.96</td>
<td>437–583</td>
<td>54</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Year</th>
<th>Age</th>
<th>Stocking</th>
<th>Total height</th>
<th>Seasonal shoot growth</th>
<th>Duration of growth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>13</td>
<td>1.1</td>
<td>1.93–2.82</td>
<td>487–777</td>
<td>59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>14</td>
<td>1.1</td>
<td>2.50–3.56</td>
<td>566–795</td>
<td>61</td>
</tr>
</tbody>
</table>

\(^1\)At end of measurement year. Red pine age is total age from seed (planted as 3–0 stock).

\(^2\)First and last 5 percent of growth excluded.

with little or no mutual shading. The pines were separated from the aspen by 200 meters. The climate is continental—July temperatures average 20°C, annual temperatures average 4°C, and total annual precipitation averages 630 mm with about half falling during the growing season (May–August) (Aakre 1966). The soil is an unnamed silt loam having 5 percent gravel by weight and good internal drainage (table 2).

Terminal shoot growth of 10 quaking aspens and 10 red pines were measured mostly daily, however, in 1978 and 1979 up to 3 or 4 days and in 1977 up to 8 days occasionally lapsed between measurements. Measurements to the nearest mm with a steel tape were begun usually at 1400 hours, local standard time, but occasionally as late as 1530 hours. Maximum reading error was 1 mm based on spot checks. Measurements were indexed to a permanent mark of India ink (red pine) or current year bud scale scar (aspen) and made to the meristematic tip or new terminal bud. The apical meristem of aspen was usually hidden by unfolding leaves during early growth. Meristem position was estimated with little loss of precision after gaining some experience by dissecting adjacent unmeasured shoot tips.

Several shoots were broken, injured by disease or insects, or had unusually slow or short periods of growth. These data were discarded, leaving as few as three aspens with usable data for 1979 (table 1). Accumulated shoot growth (Si) was averaged to the nearest 0.1 mm and for aspen in 1978 and red pine in 1979, by groups having similar growth duration. Periodic shoot growth (ΔS) is simply the difference between mean Si on successive measurements.

Maximum and minimum daily temperatures and daily precipitation were obtained from an official weather station located about 1.3 km from the study site (U.S. Department of Commerce 1977–1979); daily wind speeds were obtained for Hoyt Lakes located 105 km northeast of Grand Rapids (U.S. Department of Commerce 1977–1979); and daily solar radiation and relative humidity for Grand Rapids were provided by the University of Minnesota.

The following variables were derived from these data:

\[ \text{Tmax} - \text{Daily maximum air temperature, to nearest 0.1 } \text{C}^\circ. \]

\[ \text{Tmin} - \text{Daily minimum air temperature, as above.} \]

\[ \text{Tgm} - \text{Geometric mean daily air temperature, } \sqrt[\text{Days}]{(\text{Tmax})/(\text{Tmin})}, \text{ as above.} \]

Table 2.—General description of the soil on the study site

<table>
<thead>
<tr>
<th>Horizon</th>
<th>Depth (cm)</th>
<th>Texture</th>
<th>Roots</th>
</tr>
</thead>
<tbody>
<tr>
<td>A2</td>
<td>0–16</td>
<td>Silt loam</td>
<td>Abundant</td>
</tr>
<tr>
<td>B2</td>
<td>16–26</td>
<td>Sandy clay loam</td>
<td>Common</td>
</tr>
<tr>
<td>B3</td>
<td>26–36</td>
<td>Sandy clay loam</td>
<td>Common</td>
</tr>
<tr>
<td>C</td>
<td>36+</td>
<td>Sand</td>
<td>Few</td>
</tr>
</tbody>
</table>

\(^3\)Special appreciation goes to Drs. D. G. Baker and D. K. Wildung for making these data available.
Daily soil moisture balance in a 66 cm rooting profile (depth of A2 + B2 + B3 + 30 cm of C soil horizons) estimated according to Thornthwaite and Mather (1955). Calculated maximum moisture retention summed for the profile is 100 mm. Water held at greater than 15 atmospheres is assumed to be unavailable to plant growth, 18 mm in this case (Brady 1974). Expressed in mm minus 18, to nearest mm.

Current day incoming solar radiation, to nearest cal/cm²/day (Langley's/day).

Previous day incoming solar radiation, as above.

Free surface evaporation, to nearest mm/day. Calculated according to a modified Penman equation (Gray et al. 1970),

\[ E = \frac{\Delta H + \gamma E_a}{\Delta + \gamma} \]  

Where \( \Delta \) = slope of the saturation vapor pressure-temperature curve at mean air temperature; 
\( \gamma \) = a constant (0.49 mm Hg per °C) to keep units consistent; 
and \( H = W_o \) a conversion of solar 59 radiation into mm of evaporated water.

(Evaporation power of the air, mm/day) is calculated:

\[ E_a = 0.35 \left( e_s - e_o \right) (1 + 0.54 \mu_2), \]  

where \( e_s - e_o \) is the saturation vapor pressure deficit. \( e_o \) was determined from List (1966, table 94); \( e_s \) from Brown (1973, fig. 9), based on daily mean air temperature and relative humidity (RH); and \( \mu_2 = \) wind speed in m/sec. Mean RH was determined by excising the area between measurements under the hygrograph chart trace, weighing, and dividing by the weight of the 100 percent chart.

Each meteorological variable (Xi) associated with daylight hours—Tmax, Wo, and \( \mu_2 \)—was apportioned to the current and succeeding measurement period according to the portion of the solar day (Brown 1973) elapsed at measurement time. The synthesized variable (Xi) representing the measurement period was calculated:

\[ X_i = \frac{P_i \left( X_{i_1} \right) + (1 - P_i) X_{i_1}}{P_i + (1 - P_i)} \]  

where "P" is portion of solar day and "o" and ".1" are subscripts for current and preceding day, respectively. W-1, Tmin, and M needed no adjustment. For measurement intervals of 2 or more days, mean daily Xi (or Xi) and their transformations were determined by averaging.

Dummy variables (0, 1) were used to identify different groups or measurement years within regressions.

To accommodate the variation in length of measurement period, the term ln DAYS was introduced. DAYS is simply the total minutes in the measurement period divided by 1440 min/day, to the nearest 0.01 day.

\( \Delta S \) for each species-group was fitted over the independent climatic and derived variables using backward stepwise multiple linear regression. The general model was:

\[ \ln \Delta S = b_0 + b_1 \ln X_1 + b_2 X_1 + \ldots + b_m \ln X_m + b_{Xm} \]  

This model was chosen because it is interactive, is adaptable to a wide variety of nonlinear relations (Freese 1964), and enforced minimal preconceived constraints on the relations between shoot growth and the environment. With each run, the least significant variable was omitted, with the restrictions that dummy variables were retained throughout and \( \Delta S \) variables were not omitted until the last run. This process was iterated until an equation with the smallest standard error was obtained. If plots of residuals over Xi (or Xi) revealed a trend, a new transformation was added to the maximum model and the entire stepwise procedure repeated until only random residuals remained.

During the analysis it became apparent that the beginning and ending 5 percent of growth were insensitive to environment—a common experience
RESULTS AND DISCUSSION

Environment and inherent growth rhythm accounted for 91 to 98 percent of the diurnal variation in shoot growth with 13 percent or less arithmetic standard error (table 3). With only two exceptions, terms in the final equations were significant at least at P <0.05. Shoot growth was similar among species and ages in response to all environmental variables except soil moisture (figs. 1-3). None of these responses were necessarily inconsistent with currently understood principles of plant growth.

\textbf{Sc/Sf (Cumulative Shoot Growth/Final Shoot Measurement)}

Red pine had a stronger inherent growth rhythm than aspen (fig. 1). The rhythm for red pine has been noted before (Baldwin 1931, Cook 1941, Farnsworth 1955, Kienholz 1941, Kozlowski and Ward 1961, Kramer 1943) and is similar to that of Scotch pine, \textit{Pinus sylvestris} L. (Vuokko \textit{et al.} 1977).

Kienholz (1941) found a moderate growth rhythm for quaking aspen saplings but its real magnitude is questionable without accounting for the influence of microclimate. Hari and Leikola (1974) observed that European white birch, \textit{Betula verrucosa} Ehrh., after a period of growth acceleration and after accounting for air temperature had a long period of stable growth. Quaking aspen appears to have a similar rhythm.

\textbf{W-1 (Previous Day Incoming Solar Radiation)}

The most consistent shoot growth response was to previous-day solar radiation (fig. 1). Response was strongly positive with no indication of approaching an upper asymptote. Shoot growth response to W-1 is partly due to photosynthate production, which is needed for metabolism and cell structure (Kramer and Kozlowski 1979), and partly due to soil warming, which is needed for root growth (Barney 1951) and absorption and uptake of nutrients and water (Kramer and Kozlowski 1979). Most of the fine feeder roots of aspen and red pine are found in the upper few centimeters of soil (Alban \textit{et al.} 1978) where diurnal temperature may fluctuate up to 15°C or more (Cochran 1969).

\textbf{M (Daily Soil Moisture)}

Shoot growth response was least consistent with Thornthwaite estimates of available soil moisture (fig. 1). The theoretical response curve should consist of three zones: (1) a zone of rapidly increasing growth over increasingly available M from the wilting coefficient at 18 mm to about 40 mm; (2) an optimum zone from 40 mm to perhaps 80 mm available M; and (3) a zone of reduced growth from 80 to 100 mm because of impeded aeration by excess gravitational M (Brady 1974, Kramer and Kozlowski 1979). It appears that the red pine response is entirely in zone 1, third-year aspen in zones 1 and 2, second-year aspen in zone 2, and first-year aspen entirely in zone 3.

The reason for response displacement is related to errors in estimating M due to the unavailability of water use coefficients for adjusting differences in evapotranspiration between species and ages and to errors in estimating soil volume exploited by tree roots. Evapotranspiration is much less in regenerating aspen stands than in mature stands (Johnston 1970, Verry 1972) and at least 10 years are required before full canopy development and hence maximum evapotranspiration is regained (Ohmann \textit{et al.} 1978). This would cause overestimates of soil moisture depletion in young stands. At age 13, red pine already has attained maximum rooting depth (Fayle 1975) so soil moisture depletion may have been underestimated. Soil warming rate is inversely related to soil moisture content (Cochran 1969) which would also slow shoot growth as discussed earlier.

\textbf{Tmax and Tmin (Daily Maximum and Minimum Temperatures)}

Some of the independent variables were highly correlated so it would be inappropriate to depict shoot growth response over one without considering another (table 4). Such is the case with maximum (day) and minimum (night) temperature. Additionally, Tgm was a significant variable for second- and third-year aspen.

Red pine shoot growth increased asymptotically with day temperature, and in third-year aspen, high day temperatures even became limiting in combination with high night temperatures, probably due to excessive respiration (Kramer and Kozlowski 1979).
Table 3.—Equation coefficients (with statistics) to predict terminal shoot growth of aspen and red pine
(In mm/day (ln units))

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Variable form</th>
<th>Quaking aspen</th>
<th>Red pine, years 13 and 14</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Year 1</td>
<td>Year 2</td>
</tr>
<tr>
<td>Tmax</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>lnX</td>
<td></td>
<td>2.025(7.3)</td>
<td>5.206(3.5)</td>
</tr>
<tr>
<td>X²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tmin</td>
<td>lnX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>e-.18X</td>
<td></td>
<td>.01263(2.2)</td>
<td></td>
</tr>
<tr>
<td>Tgm</td>
<td>lnX</td>
<td></td>
<td>-8.761(-3.4)</td>
</tr>
<tr>
<td>M</td>
<td>lnX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wo</td>
<td>lnX</td>
<td></td>
<td>1.580(3.6)</td>
</tr>
<tr>
<td>X</td>
<td>.002296(1.6)</td>
<td></td>
<td>.004671(-3.7)</td>
</tr>
<tr>
<td>W-1</td>
<td>lnX</td>
<td></td>
<td>.8469(3.5)</td>
</tr>
<tr>
<td>X</td>
<td></td>
<td></td>
<td>.001835(5.8)</td>
</tr>
<tr>
<td>E</td>
<td>lnX</td>
<td>-1.571(-3.2)</td>
<td></td>
</tr>
<tr>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X⁻¹</td>
<td></td>
<td>1.997(2.2)</td>
<td></td>
</tr>
<tr>
<td>Sc/Sf</td>
<td>lnX</td>
<td>.2296(2.4)</td>
<td>.6523(6.3)</td>
</tr>
<tr>
<td>X</td>
<td>.007385(-3.0)</td>
<td></td>
<td>.01466(-4.4)</td>
</tr>
<tr>
<td>Constant¹</td>
<td></td>
<td>-6.08(6.4)</td>
<td>-11.162(4.2)</td>
</tr>
<tr>
<td>Standard error:</td>
<td></td>
<td>.0590</td>
<td>.1288</td>
</tr>
<tr>
<td>ln</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent²</td>
<td></td>
<td>5.9</td>
<td>13.0</td>
</tr>
<tr>
<td>Overall F</td>
<td></td>
<td>103</td>
<td>148</td>
</tr>
<tr>
<td>n³</td>
<td></td>
<td>20</td>
<td>41</td>
</tr>
<tr>
<td>R²: Total equation⁵</td>
<td></td>
<td>.99</td>
<td>.98</td>
</tr>
<tr>
<td>Net equation⁶</td>
<td></td>
<td>.95</td>
<td>.91</td>
</tr>
</tbody>
</table>

¹ Corrected for logarithmic bias according to Baskerville (1972).
² Also adjusted for mean ln days (see text).
³ Of arithmetic mean Y.
⁴ Number of observations.
⁵ Including ln DAYS and dummies (see table 5).
⁶ Variation remaining after reduction by ln DAYS and dummies.
Evaporation and Current Day Solar Radiation

The range of shoot growth was consistently widest over E and Wo, followed in order by air temperature, W-1, and M. Other research has shown that air temperature is the major factor governing shoot growth (Ashton 1975, Dahl and Mork 1959, Lanner 1964; Mitscherlich et al. 1973, Worrall 1973). Indeed Hari and Leikola (1974) needed only growth rhythm and air temperature to predict from 91 to 96 percent of the variation in shoot growth of Scots pine in Finland. Adding other environmental variables to their model improved predictive ability less than 1 percent. They reasoned that soil moisture and solar radiation were not as limiting in boreal climates as they might be elsewhere.

E and Wo (Free Surface Evaporation and Current Day Solar Radiation)

The correlation between these variables is high because current-day solar radiation is the dominant variable in calculating free surface evaporation (Eq. 1) (table 4).

Red pine and third-year aspen shoot growth were similar—growth increased greatly with decreasing E and Wo (fig. 3). The reflexed isopleths in the region of high E and Wo indicates that growth increases slightly with increasing E. This is inconsistent with growth theory. The theoretical response should be a “flat” region of minimum growth. Likely this is a fault of the model induced by the size and precision of the data set. The fault is not serious if the low magnitude of growth is kept in perspective with the greatly increased shoot growth for the rest of the range.

The first-year aspen were unique in that shoot growth increased over the entire range of increasing Wo (given constant E), perhaps due to their dependence on warm soils for metabolism of stored root carbohydrates. Second-year aspen response pattern was intermediate. In all regressions, maximum growth was in the range of 100 to 200 Langleys per day and about 1.5 mm daily evaporation.

Figure 1.—Diurnal shoot growth of red pine and first-, second-, and third-year quaking aspen in response to seasonal growth rhythm (Sc/Sf), previous-day incoming solar radiation (W-1) and Thornthwaite soil moisture. In these and subsequent figures, the fixed variables are held constant at their means (Wo and W-1 = 387, M = 80, Tmax = 25.8, Tmin = 11.3, E = 5.0, and Sc/Sf = 50).
Cremer (1976) attributes decreased growth of giant eucalyptus, *Eucalyptus regnans* F. Muell., and especially Monterey pine, *Pinus radiata* D. Don, on hot sunny days at least in part to shrinkage due to dehydration caused by high evaporative demand. The rate of shrinkage was greatest before noon and caused an early afternoon depression in measured shoot length. He found no mid-day depression on rainy days. Milne *et al.* (1977) observed similar shrinkage in Sitka spruce, *Picea sitchensis* (Bong.) Carr. Such shrinkage is reversible overnight. It is questionable whether we would have found such large shoot growth responses to E and the growth anomaly at high E and W if we would have taken the measurements early in the morning.

**In DAYS and Dummy Variables**

In DAYS served three purposes: to account for variations in length of measurement period; to evaluate the effect of handling growing shoots; and to evaluate the suitability of long remeasurement periods.
Table 4.—Simple correlation matrix between independent and dependent variables in the ln form

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Dependent variables (ΔS)</th>
<th>P. tremuloides</th>
<th>P. resinosa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Year 1</td>
<td>Year 2</td>
</tr>
<tr>
<td>Tmax</td>
<td>1</td>
<td>0.86</td>
<td>0.71</td>
</tr>
<tr>
<td>Tmin</td>
<td>1</td>
<td>0.62</td>
<td>0.59</td>
</tr>
<tr>
<td>M</td>
<td>-0.06</td>
<td>0.01</td>
<td>0.11</td>
</tr>
<tr>
<td>Wo</td>
<td>0.74</td>
<td>0.74</td>
<td>0.34</td>
</tr>
<tr>
<td>W-1</td>
<td>0.19</td>
<td>0.17</td>
<td>0.53</td>
</tr>
<tr>
<td>E</td>
<td>0.22</td>
<td>0.31</td>
<td>0.42</td>
</tr>
<tr>
<td>Sc/Scf</td>
<td>1</td>
<td>0.02</td>
<td>0.50</td>
</tr>
</tbody>
</table>

1Coefficients between independent variables are for years 1977-1979 combined.

Figure 3.—Diurnal shoot growth of red pine and quaking aspen in response to free surface evaporation and current-day incoming solar radiation. The dashed curve encloses the range of observed independent variable combinations.
for growth analyses. The first purpose could have been met just as well with ln (ΔS/DAYS) as the dependent variable.

Shoot growth apparently was not altered by handling because the coefficients for ln DAYS for three of the four regressions were not significantly different from 1 (table 5). A coefficient significantly greater than 1 would be interpreted as a reduction in growth due to handling assuming shoots would recover from handling disturbance during longer measurement periods. Coefficients less than 1 would indicate a stimulus by handling.

The significant coefficient for ln DAYS for first-year aspen means that long measurement periods are less suitable than short periods for analysis. (Handling effects can be ruled out because these aspens had the longest remeasurement intervals.) A wide range in DAYS tends to increase its significance as a predictor variable at the expense of other variables. Extreme observations are diminished in averages, narrowing the statistically useful range of variation. The constant for this regression has been adjusted for mean DAYS by adding the contribution for the mean ln DAYS term (table 3).

The dummy variables showed that red pine grew nearly 10 percent more in year 13 and that groups of pine and aspen differed in growth by about 5 and 8 percent, respectively (table 5). This much intra-specific and inter-year variability is common.

CONCLUSIONS

This study demonstrated that sufficiently accurate measures of shoot growth can be easily taken and quantitatively related to meteorological variation. The equations are credible because they were derived independently and because they depict growth generally consistent with expected plant-environment interaction. Some weaknesses in method disclosed by the analysis are not insurmountable. Empirical shoot growth models integrate a number of competing and complementary processes whose net sum is expressed as growth, and so they do not provide much insight into the complexity of plant-environment interaction. On the other hand, their simplicity and adaptability to application are critical to their usefulness.

NEEDS AND RECOMMENDATIONS

The greatest need for improvement is in estimating the water balance. Zahner (1967) showed that soil moisture under forest cover could be accurately estimated according to Thornthwaite and Mather (1955) in soils with good internal drainage. The problem is to estimate the volume of soil exploited by roots, the amount of water available to plants in that volume, the relative importance of each textural horizon, and the amount of water evaporated. These will vary with species and the age of the stand. Crop/age water use coefficients could be determined empirically with concurrent instrumentation of soil moisture.

Thornthwaite and Mather's (1955) calculation of soil moisture depends on estimates of evapotranspiration based on air temperature. Their method has a distinct advantage because it is easy to apply and temperature is the most common meteorological information available. On the other hand, evapotranspiration is more properly estimated from solar

Table 5.—Additional equation coefficients for terms needed for analysis but not for predicting shoot growth (t-value in parentheses)

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Aspen</th>
<th>Red pine</th>
<th>Years 13 and 14</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Year 1</td>
<td>Year 2</td>
<td>Year 3</td>
</tr>
<tr>
<td>Year Dummy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group Dummy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ln DAYS¹</td>
<td>1.155(2.52)</td>
<td>1.076(1.77)</td>
<td>1.004(0.09)</td>
</tr>
</tbody>
</table>

¹Dummy coefficients are in arithmetic units and are interpreted as a ratio of the greater over the lesser.
²Year 13 greater than year 14 (by 10 percent).
³Average DAYS are 4.06, 2.34, 1.51, and 1.74, respectively. t-values are computed as deviation from 1.000
radiation and evaporative power of the air (Eq. 1). The modified Penman approach (Gray et al. 1970) should be evaluated to determine if significantly improved estimates of evapotranspiration and therefore soil moisture are possible.

Small but significant improvements should be made in shoot growth measurement procedures. Remeasurement should be near sunrise to eliminate the problems of diurnal shrinkage (Cremer 1976, Milne et al. 1977). At 45°N latitude, less than 3 percent of a clear June day’s solar radiation is elapsed by 0800 hours local daylight savings time (0700 hours local standard time), so the need to partition data associated with the solar day is eliminated. Measurement intervals should seldom exceed one day, both to gain advantage of data extremes and to provide as many observations as possible. Measurement precision could be improved to ±0.1 mm (at least for pines) by setting a reference pin in the lower stem and by using a vernier scale (Farnsworth 1955, Hari and Leikola 1974). Automatic recorders (Milne et al. 1977) would be ideal but not necessary. Ten to 20 trees should be measured, both to assure a complete seasonal data base and to minimize measurement errors by averaging.

Excising and weighing a thermograph trace would provide reasonably fast and highly accurate expressions of mean temperatures or hourly temperature sums. Temperature sums have been useful in predicting shoot growth in other studies (Hari and Leikola 1974).

Nonlinear and dynamic (Hari and Leikola 1974) models should be tested in future modeling efforts. Models fitted around the concept of leaf temperature/transpiration relations (Idso et al. 1966) need to be explored. Certainly the biggest need is for long term regional growth data for a wide range of climates, soils, species, and ages.

LITERATURE CITED


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Modeling aspen and red pine shoot growth to daily weather variations.
Quantifies daily shoot growth of quaking aspen and red pine in response to daily variation in air temperature, soil moisture, solar radiation, evapotranspiration, and inherent seasonal plant growth rhythm. Discusses potential application of shoot growth equations to silvicultural problems related to microclimatic variation. Identifies limitations and areas for improvement.

KEY WORDS: Populus tremuloides, Pinus resinosa, air-temperature, soil-moisture, solar-radiation, evapotranspiration.