Tree Physiology 2, 47–59 (1986).

Physiographic, stand, and environmental effects on individual tree growth and growth efficiency in subalpine forests

MERRILL R. KAUFMANN and MICHAEL G. RYAN

USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO 80526, USA

Summary

Annual volume growth of subalpine trees in the central Rocky Mountains was studied in relation to site and stand conditions. Growth of individual trees was most strongly influenced by estimated potential absorbed radiation, which varied with physiographic conditions and tree leaf area. Growth efficiency was estimated by the ratio of annual volume growth to potential radiation absorption by the crown. Growth efficiency was higher in young lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) than in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) or subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). In all species, growth efficiency declined sharply with age, and suppressed and overtopped trees had growth efficiencies equal to the highest efficiencies observed for dominant/codominant or intermediate trees. Lodgepole pine growth was most responsive to site and stand variables, Engelmann spruce was intermediate, and subalpine fir was rather unresponsive.

Introduction

Several approaches have been used to predict the growth of forests. Forest growth models can be characterized by the level at which predictions are made and by the intended use of the model. Predictions about forest growth are made either at the stand level or at the level of an individual tree and then integrated to give stand-level information (see Dale et al. (1985) for a review of individual tree models). Forest growth models have been used to predict stand growth for management purposes (Alexander and Edminster 1980, 1981) or to learn about community dynamics and long-term patterns of growth (Dale et al. 1985, Shugart 1984). The selection of a modeling paradigm depends on the objective for the model, availability of information about the processes involved, and the data available for estimating model parameters.

Most of the models that predict forest growth and yield for management purposes have used the stand-level approach (Joyce and Kickert 1987). These stand models are based on empirical relationships relating stand volume production to easily measured site and stand variables, such as site index, tree height, diameter distribution, and stand density. Because of the limited flexibility of stand models to handle diverse stand structures and environmental conditions and because the lack of tree-level information hinders forest planning efforts, models based on individual trees are becoming more popular.

One problem common to both types of forest models is the reliance on site index (height of dominant/codominant trees at a specified age) to characterize the different growth rates of a species under various growing conditions. Site index is valuable, because it represents the integral of the complex interactions among variables, such as temperature, humidity, irradiance, water availability, soil type and depth, and nutrient availability. However, the use of site index is limited to existing stands because it requires measurement of trees, and site index may not be comparable across species. An additional problem with empirical growth and yield models is that they generally do not incorporate enough information on whole-tree physiology (Dale et al. 1985), and the predictor variables are clearly surrogates for factors that actually influence growth.

An individual tree growth model based upon physiographic, stand, and tree characteristics could resolve most of these limitations. Such a model would be useful for simulating tree growth for a wide range of stand configurations and sites, regardless of the stand now occupying the sites. Furthermore, if such a model is based upon plant processes and conditions influenced by site and environmental conditions, it could be combined with other process models, such as a transpiration model (Kaufmann 1984*a*, 1984*b*), more readily than could an empirical model of growth.

There are several approaches for developing an individual tree growth model. One is to incorporate all of the processes related to carbon, nutrients, and water into a physiological model for estimating growth (a 'bottom up' approach) (Penning de Vries 1983, Reynolds et al. 1980). This approach is very complex and requires a thorough understanding of the physiological processes and their relation to environmental conditions. Once developed, such a model would require extensive data because of the large number of parameters that need to be estimated.

Another approach is to measure individual tree growth and relate it to measured site, stand, and tree characteristics (a 'top down' approach) (e.g., Blyth and MacLeod 1981, Tennent 1982). This approach may be totally empirical, with a model developed using statistical techniques to identify the variables most highly correlated with growth. Such an empirical model has the same limitations found in an empirical stand growth and yield model, although it may be easier to create a model that encompasses a broader range of conditions than for a stand model.

A third approach is to develop a phenomenological model of individual tree growth, in which growth is predicted using variables and relationships carefully selected on the basis of their effects on physiological processes involved in growth. This approach lies between the process and empirical approaches and uses elements of each. The advantage of a phenomenological approach is that empirical data are used, but their use is based upon the physiology of growth.

This paper examines several relationships that might be useful in the development of a phenomenological individual tree growth model. Particular attention is given to potential radiation input as a driving variable for tree growth (Atkinson 1984, Doley 1982) and factors affecting the efficiency of converting radiation into volume growth (Jarvis and Leverenz 1983, Linder 1985).

Materials and methods

All observations were made at the Fraser Experimental Forest (FEF) near Fraser, Colorado. The FEF is located in the subalpine forest zone of the central Rocky Mountains, with elevations ranging from 2700 m to about 3500 m at treeline. This region is characterized by a short growing season, with growth limited by low temperatures. Precipitation is uniformly distributed throughout the year, averaging 50 to 60 mm per month, much of it falling as snow. Summer precipitation comes primarily from thunderstorms; however, since the snowpack remains until May or June and summer precipitation supplies a moderate amount of moisture, summer droughts are uncommon.

The subalpine forests in this region are comprised of four species: Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), and quaking aspen (*Populus tremuloides* Michx.). The three coniferous species occur together throughout most of the experimental forest. Engelmann spruce and subalpine fir are more common at higher elevations and on the wetter sites. Lodgepole pine is more common on drier sites and at lower elevations where logging occurred around 1910. Aspen is uncommon on the FEF and is generally found at low elevations in patches opened by logging. For a complete description of the study area, see Alexander et al. (1985).

This study was confined to the three species of conifers. Individual trees were selected without bias from stands along the FEF road network. An effort was made to sample trees over a wide range of physiographic conditions and for a wide range of age, diameter, and competitive position in the stand. Tree measurements included age at breast height, height, diameter at breast height (dbh), 5-year height and radial growth increments (1979–83), sapwood area at breast height (measured on bole cross-sections), crown depth, and the crown position within the canopy. Individual trees were assigned a crown class number based on their position within the canopy as follows: dominant/codominant (1), intermediate (2), suppressed (3), and overtopped (4).

Some characteristics of the forest stand around the sample tree were also measured. These included the diameter of each tree in a 0.005 ha plot centered on the study tree, and basal area by species of the surrounding stand estimated with a variable radius plot using a basal area factor of 1 m^2 ha^{-1}. A leaf area competition estimate (leaf area of the study tree/leaf area of the study tree and all other trees on the 0.005 ha plot) was derived from these data. Mean annual volume increment was estimated from past and present tree diameter and height using appropriate form factors (Myers 1964, Myers and Alexander 1972, Myers and Edminster 1974). The projected leaf area of the study tree and of all trees in the 0.005 ha plots was estimated from basal area, assuming random needle orientation, by using equations given in Kaufmann et al. (1982).

Physiographic measurements included elevation, azimuth (defined here as the departure in degrees from due south exposure), slope, position on the slope, profile of the horizon, and proximity of the study tree to a local water supply. Position on slope was rated numerically from 0 (top of slope) to 9 (bottom of slope) based on topographic maps. Proximity to water supply was rated for each study tree based on such factors as distance to saturated soil or stream, litter depth, amount of exposed mineral soil, and location on a bench, in a depression, or on a knob or outcropping (the water supply rating ranged from +2 to −2, with average conditions being 0).

An index of irradiance was obtained for the period from May to October for each study tree. This index accounted for the effects of slope, aspect, and horizon obstruction on incoming direct beam irradiance above the canopy (Kaufmann and Weatherred 1982), but not the effects of attenuation by the atmosphere or by the canopy. The relative magnitude of the irradiance index reflects differences in visible irradiance among the individual tree sites.

The product of the irradiance index and the projected leaf area is used as an index of potential radiation absorption for each tree. Interception of the available irradiance for each tree is affected by crown position within the canopy and by self-shading of foliage, both of which result in attenuation of radiation. We have not yet estimated overall attenuation effects, but for these analyses we have adjusted the relative irradiance for the trees based on their position in the canopy. Irradiance for each study tree was obtained by multiplying the site irradiance by a factor arbitrarily selected for each crown class: dominant/codominant (1.0), intermediate (0.9), suppressed (0.8), and overtopped (0.7).

Trees were sampled over a wide range of sites known to vary in site index, from near streams to the tops of ridges, from low elevations to treeline, and on slopes of varying steepness and aspect. The range of physiographic settings for individual trees was similar for all species (Table 1). The irradiance index varied from 24 to 48 and elevation ranged from 2700 to 3400 m, although spruce and fir were sampled at slightly higher elevations than pine.

Results and discussion

Multiple regression was used to identify variables that appeared to influence tree growth. Results of the multiple regression analysis relating tree volume growth to tree and physiographic characteristics are presented in Table 2. These regression equations are not presented as predictive equations, but rather as summaries of the data and an indication of the amount of variability in tree volume growth that can be accounted for by tree, stand, and physiographic factors.

For spruce and fir, potential absorbed irradiance is an important factor influencing annual growth. Azimuth and elevation also affected spruce volume growth, and growth decreased curvilinearly with increasing age in both spruce and fir. For pine, availability of water, a leaf area competition estimate, elevation, and crown class were important. For spruce and fir, both shade-tolerant species, there is little evidence in these data of stand factors affecting growth. In contrast, for the shade-intolerant pine, both the leaf area competition index and position of the study tree

Table 1. Descriptive statistics for individual tree data.

	Engelmann spruce (n = 84)				Subalpine fir (n = 71)				Lodgepole pine (n = 80)			
Variable	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
Site characteristics												
Elevation *m*	3001	16	2798	3395	2985	17	2780	3389	2926	13	2722	3194
Azimuth from south *degrees*	97.0	6.1	2	178	91.1	6.6	0	180	98.4	5.5	8	172
Relative irradiance	38.37	0.5	24.8	46.0	38.9	0.6	24.6	45.9	40.2	0.4	31.6	46.0
Stand characteristics												
Basal area $m^2\ ha^{-1}$	30.17	1.15	1.00	50.00	26.44	1.21	3.00	46.00	28.03	1.19	1.00	50.00
0.005 ha plot leaf area m^2	410.0	47.1	0	2406.9	419.9	44.7	12.3	2010.8	289.6	26.8	0	992.6
Tree characteristics												
DBH *cm*	31.0	1.9	5.4	76.4	23.3	1.5	3.9	52.9	25.4	1.6	5.4	63.7
Height *m*	18.6	1.0	4.1	40.2	14.8	0.9	3.1	29.9	16.3	0.7	2.9	28.8
Age *y*	171	10	15	433	114	7	13.0	234	149	12	10	315
Projected leaf area m^2	95.0	10.5	2.2	438.9	47.4	5.2	1.0	190.6	22.0	2.4	0.8	105.9
Height growth $m\ y^{-1}$	0.083	0.006	0.014	0.246	0.113	0.007	0.017	0.309	0.102	0.013	0.007	0.433
Radial growth $mm\ y^{-1}$	0.75	0.05	0.10	2.06	0.84	0.06	0.12	2.34	0.74	0.08	0.06	3.26
Volume growth $\times\ 10^{-3}\ m^3\ y^{-1}$	8.92	0.91	0.26	39.98	6.93	0.77	0.14	26.64	4.13	0.39	0.32	19.36

crown in the canopy were important.

Physiologically, growth should be related to the absorption of solar irradiance by the tree crown (see Jarvis and Leverenz 1983, for a comprehensive review). Potential absorbed irradiance varies with leaf area of the tree and also with physiographic setting. The relationships between growth and the product of relative irradiance and projected leaf area (potential radiation absorption) are shown in Figures 1 to 3. The relationships between these two variables can be considered as an estimate of growth efficiency (Jarvis and Leverenz 1983). Trees with the highest growth rate at a given potential radiation absorption (steepest slope of line from a data point to the origin) are most efficient at converting absorbed irradiance into volume production. Trees with efficiencies lower than the maximum convert less of the potential irradiance into volume because of environmental stress, differences in respiration or allocation of photosynthate, or because of the structure and properties of the leaves and canopy themselves (Jarvis and Leverenz 1983).

For all species and crown classes, annual volume growth increased with increasing potential radiation absorption. However, growth efficiency varied greatly below an upper limit (maximum efficiency) in the dominant/codominant and intermediate crown classes. In contrast, the suppressed and overtopped trees all had efficiencies approaching the most efficient overstory trees. The goodness-of-fit for the relationship between leaf area and volume growth was as good or better than the relationship between potential radiation absorption and volume growth. This indicates that projected leaf area alone is a good estimator of potential radiation absorption.

Further analyses indicated that growth efficiency was strongly influenced by tree age (Table 3). In spruce (Figure 4) and fir (Figure 5), growth efficiency at an age of 200 years was only about half that of young trees, and growth efficiency was

Table 2. Multiple regression equations relating annual volume growth to potential absorbed irradiance (PAI), azimuth (Azim), elevation (Elev), crown class, age, proximity to water supply (Water Sup), and leaf area competition (LA Comp). Independent variables are given in the order of appearance in a stepwise analysis, and all variables are significant ($P = 0.05$); $\vec{b}_i$ is a vector of coefficients for use with categorical variables.

Engelmann spruce

$$\text{Ann Vol Gr} = 0.044 + 0.168 \times 10^{-5}(\text{PAI}) + 0.299 \times 10^{-4}(\text{Azim}) - 0.153 \times 10^{-4}(\text{Elev}) - 0.43 \times 10^{-7}(\text{Age})^2$$

$r^2 = 0.64$

$S_{y \cdot x} = 0.0051$

Subalpine fir

$$\text{Ann Vol Gr} = 0.0018 + 0.344 \times 10^{-5}(\text{PAI}) - 0.580 \times 10^{-7}(\text{Age})^2$$

$r^2 = 0.78$

$S_{y \cdot x} = 0.0031$

Lodgepole pine

$$\text{Ann Vol Gr} = 0.044 + \vec{b}_1(\text{Water Sup}) + 0.0043(\text{LA Comp}) - 0.117 \times 10^{-4}(\text{Elev}) - \vec{b}_2(\text{Crown class})$$

$r^2 = 0.51$

$S_{y \cdot x} = 0.0026$

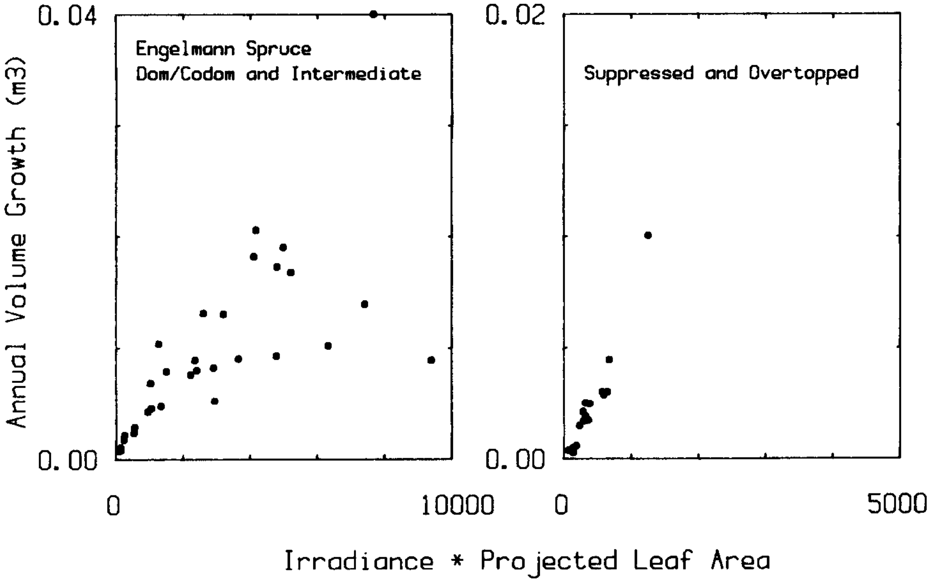

Figure 1. Mean annual volume growth of Engelmann spruce as a function of potential radiation absorption by the crown.

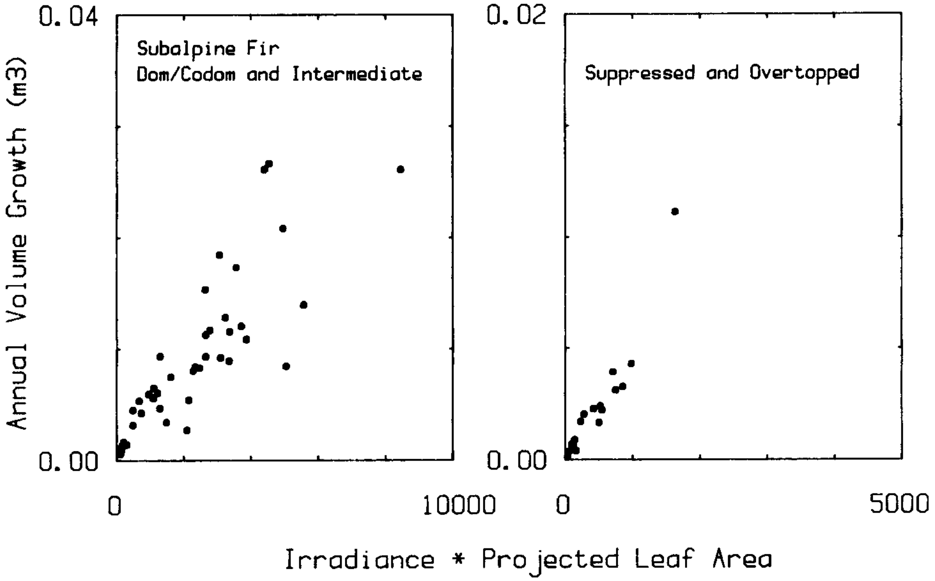

Figure 2. Mean annual volume growth of subalpine fir as a function of potential radiation absorption by the crown.

similar for the two species. Growth efficiency was much higher for young pine trees (Figure 6) than for spruce and fir, and the efficiency decreased very strongly as trees aged. Efficiency was also influenced by azimuth in all species, and by

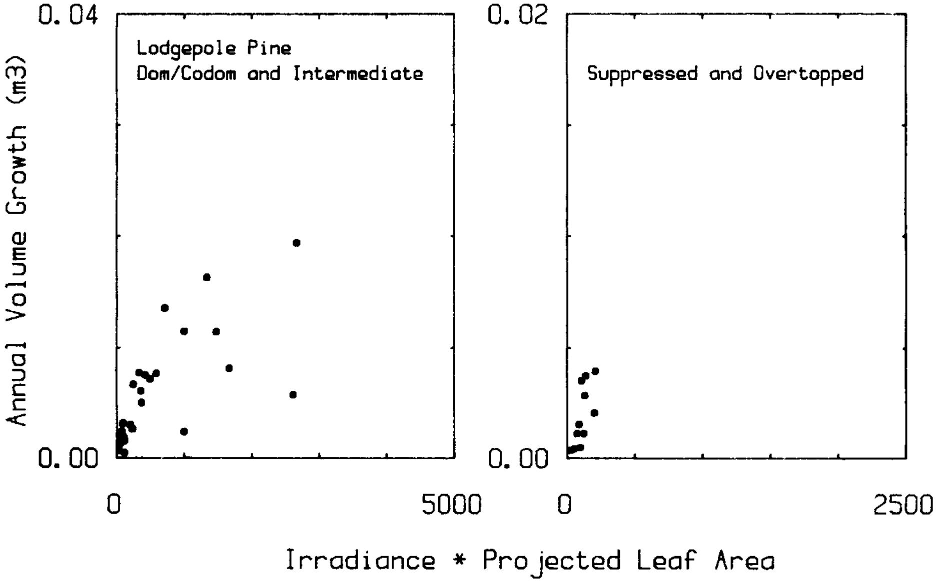

Figure 3. Mean annual volume growth of lodgepole pine as a function of potential radiation absorption by the crown.

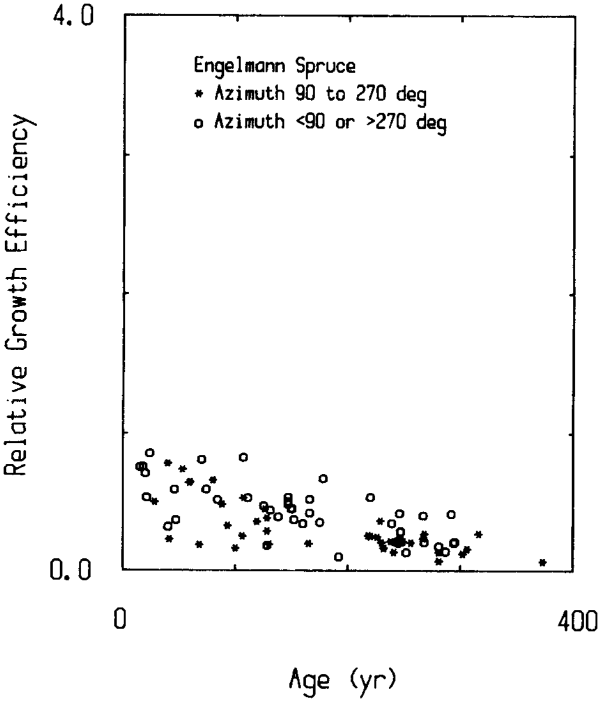

Figure 4. Relative growth efficiency (× 10^5) of Engelmann spruce as a function of tree age at breast height.

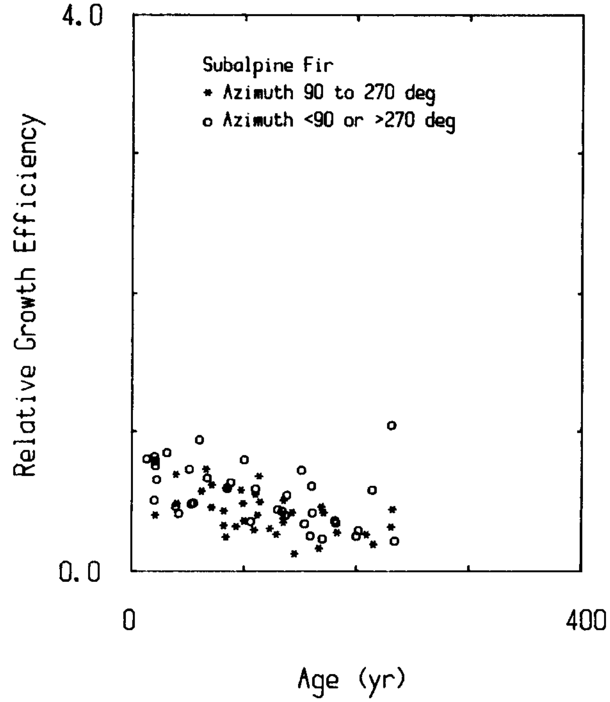

Figure 5. Relative growth efficiency (× 10^5) of subalpine fir as a function of tree age at breast height. The 231-year-old tree having a high growth efficiency was located low on a quite steep, north-facing slope where the estimated irradiance was low.

elevation in lodgepole pine. A plot of the data in Figures 4 to 6, stratified according to azimuth, indicated that azimuth affected growth efficiency uniformly at all ages.

Although we have not conducted a thorough analysis of the role of various physiographic, stand, and tree factors in the physiological processes of growth, several conclusions seem obvious. First, radiation input has an extremely important effect on annual volume growth, and undoubtedly this is related to net carbon gain from photosynthesis. Linder (1985) summarized data from a number of experiments and reached a similar conclusion. Thus, an individual tree growth model for subalpine species will probably require an estimate of potential radiation absorption. The importance of radiation input indicates that we should give additional attention to actual irradiance interception by individual tree crowns. The estimates of radiation absorption can be improved by increasing the precision of the estimates of leaf area, by better estimating absorption of radiation by tree crowns at all levels of the canopy (Oker-Blom 1985), and perhaps by better defining the effective growing season for individual sites.

Second, species differ in their responsiveness to site conditions. Volume growth of subalpine fir is strongly correlated with potential radiation absorption (Table 2). When this irradiance term was adjusted for effects of slope and azimuth, no

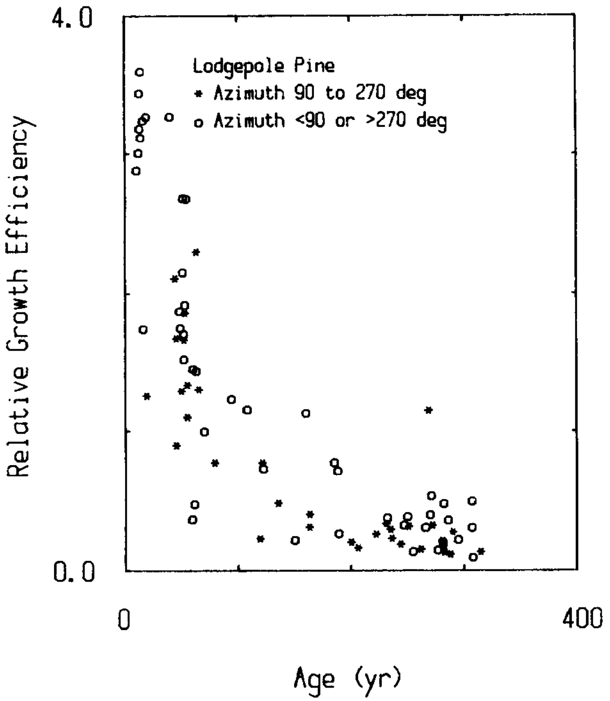

Figure 6. Relative growth efficiency (× 10^5) of lodgepole pine as a function of tree age at breast height. The 269-year-old tree having a high efficiency had been badly suppressed for more than 100 years, but its size and growth rate at the time of sampling were similar to that of much younger trees.

Table 3. Multiple regression equations relating growth efficiency (volume growth/potential absorbed irradiance) to age, azimuth (Azim), and elevation (Elev). Independent variables are given in the order of appearance in a stepwise regression, and all variables are significant ($P = 0.05$).

Engelmann spruce

$$\text{Growth Efficiency} = 0.053 - 0.147 \times 10^{-3}(\text{Age}) + 0.912 \times 10^{-4}(\text{Azim})$$

$r^2 = 0.54$

$\bar{x} = 0.37 \times 10^{-5}$

$S_{y \cdot x} = 0.37 \times 10^{-5}$

Subalpine fir

$$\text{Growth Efficiency} = 0.054 - 0.146 \times 10^{-3}(\text{Age}) + 0.122 \times 10^{-3}(\text{Azim})$$

$r^2 = 0.35$

$\bar{x} = 0.48 \times 10^{-5}$

$S_{y \cdot x} = 0.16 \times 10^{-5}$

Lodgepole pine

$$\text{Growth Efficiency} = 0.100 - 0.218 \times 10^{-2}(\text{Age}) + 0.440 \times 10^{-5}(\text{Age})^2 + 0.286 \times 10^{-3}(\text{Azim}) + 0.123 \times 10^{-3}(\text{Elev})$$

$r^2 = 0.80$

$\bar{x} = 1.09$

$S_{y \cdot x} = 0.46 \times 10^{-5}$

---

additional physiographic factors tested proved significant. Engelmann spruce was somewhat more responsive to azimuth and elevation. Lodgepole pine was responsive to water availability and elevation, but stand features, such as leaf area competition and crown position in the canopy, were also important. The sensitivity of pine to these stand competition factors is consistent with the intolerance of this species to shade. Over the range of physiographic conditions at the FEF, however, volume growth of subalpine fir and Engelmann spruce appears to be much less sensitive to environmental factors than does volume growth of lodgepole pine.

Third, the efficiency of converting potential absorbed radiation into bole volume is much higher in pine than in spruce and fir, particularly in younger trees. Pine typically reaches 1.37 m height 8 to 10 years after clearcutting, whereas spruce and fir generally require 20 to 40 years to reach the same height. More rapid growth of pine during these years may result from higher efficiency at this stage, as found for slightly older trees above breast height (Figure 6).

The decline in growth efficiency with age may be related largely to increased maintenance respiration requirements as the amount of living biomass increases, but other factors may also be important. For example, Grier et al. (1981) observed that as trees aged, a greater proportion of net primary production was allocated to roots. Also, as tree height increases, leaf water potential decreases to overcome the effect of gravity on water transport. This could have a negative effect on midday photosynthesis when environmental conditions are unfavorable. Accordingly, growth efficiency could be reduced in proportion to height increase over time. Lower growth efficiencies on southern exposures may be related to higher temperatures and perhaps to reduced water supply and intermittent tree water stress.

Suppressed and overtopped trees have high growth efficiencies (Figures 1 to 3), but annual growth rates and potential radiation absorption are low. Trees in these crown classes typically have a lower foliage density (leaf area per unit crown volume), and this improves light interception efficiency because of reduced self-shading. However, the high apparent efficiency may reflect the relatively small size of suppressed trees, since small trees have the highest growth rate per unit leaf area. This could be related to the percent annual growth increment of small trees or to lower maintenance requirements for smaller trees.

The growth efficiency of these trees is related to leaf area and site conditions in much the same way as is transpiration (Kaufmann 1984*a*, 1984*b*, 1985*a*). Lodgepole pine, the species with the highest growth efficiency, is also the species that transpires the least water for a given tree diameter, and lodgepole pine has nearly twice as high a water use efficiency as that of Engelmann spruce (Kaufmann 1985*b*). Changes in species composition of these stands may alter both volume growth and stand water balance (Kaufmann 1986).

Although the results presented here are insufficient to develop a functioning individual tree growth model, it appears that consideration of irradiance effects and certain site factors likely to affect physiological process will be valuable in determining the final form of such a model.

Acknowledgment

Drs. P.G. Jarvis and J.J. Landsberg provided helpful suggestions during the analysis of data, and their contributions are gratefully acknowledged.

References

Alexander, R.R., and C.B. Edminster. 1980. Management of spruce-fir in even-aged stands in the central Rocky Mountains. USDA Forest Service, Rocky Mtn. For. and Range Exp. Sta. Res. Paper RM-217, 14 p.

Alexander, R.R. and C.B. Edminster. 1981. Management of lodgepole pine in even-aged stands in the central Rocky Mountains. USDA Forest Service, Rocky Mtn. For. and Range Exp. Sta. Res. Paper RM-229, 11 p.

Alexander, R.R., C.A. Troendle, M.R. Kaufmann, W.D. Shepperd, G.L. Crouch, and R.K. Watkins. 1985. The Fraser Experimental Forest, Colorado: research program and published research 1937–1985. USDA Forest Service, Rocky Mtn. For. and Range Exp. Sta. Gen. Tech. Rep. RM-118, 46 p.

Atkinson, C.J. 1984. Quantum flux density as a factor controlling the rate of growth, carbohydrate partitioning and wood structure of *Betula pubescens* seedlings. Ann. Bot. 54:397–411.

Blyth, J.F. and D.A. MacLeod. 1981. Sitka spruce (*Picea sitchensis*) in north-east Scotland. I Relationships between site factors and growth. Forestry 54:41–62.

Dale, V.H., T.W. Doyle, and H.H. Shugart. 1985. A comparison of tree growth models. Ecol. Modelling 29:145–169.

Doley, D. 1982. Photosynthetic productivity of forest canopies in relation to solar radiation and nitrogen cycling. Aust. For. Res. 12:245–261.

Grier, C.C., K.A. Vogt, M.R. Keyes, and R.L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can. J. For. Res. 11:155–167.

Jarvis, P.G. and J.W. Leverenz. 1983. Productivity of temperate, deciduous and evergreen forests. *In* Physiological Plant Ecology IV, Encyclopedia of Plant Physiology, Vol. 12D. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler. Springer-Verlag, Berlin. pp 233–280.

Joyce, L.A., and R.N. Kickert. 1987. Applied plant growth models for grazing lands, forests, and crops. Ed. K. Wisiol and J.D. Hesketh. *In* Plant Modeling for Natural Resource Management, Chapter 2. CRC Press, Boca Raton, Florida. (in press).

Kaufmann, M.R. 1984*a*. A canopy model (RM-CWU) for determining transpiration of subalpine forests. I Model development. Can. J. For. Res. 14:218–226.

Kaufmann, M.R. 1984*b*. A canopy model (RM-CWU) for determining transpiration of subalpine forests. II Consumptive water use in two watersheds. Can. J. For. Res. 14:227–232.

Kaufmann, M.R. 1985*a*. Annual transpiration in subalpine forests: large differences among four tree species. For. Ecol. and Manage. 13:235–246.

Kaufmann, M.R. 1985*b*. Species differences in stomatal behavior, transpiration, and water use efficiency in subalpine forests. *In* Crop Physiology of Forest Trees. Eds. P.M.A. Tigerstedt, P. Puttonen, and V. Koski. Univ. Helsinki, Finland. pp 39–52.

Kaufmann, M.R. 1986. New silvicultural options for timber and water yield in the Rocky Mountains. *In* Foresters' Future: Leaders or Followers? Proc. Soc. Amer. For. Natl. Conv., Fort Collins, CO. pp 237–242.

Kaufmann, M.R., C.B. Edminster, and C.A. Troendle. 1982. Leaf area determinations for subalpine tree species in the central Rocky Mountains. USDA Forest Service, Rocky Mtn. For. and Range Exp. Sta. Res. Paper RM-238, 7 p.

Kaufmann, M.R. and J.D. Weatherred. 1982. Determination of potential direct beam solar irradiance. USDA Forest Service, Rocky Mtn. For. and Range Exp. Sta. Res. Paper RM-242, 23 p.

Linder, S. 1985. Potential and actual production in Australian forest stands. *In* Research for Forest Management. Eds. J.J. Landsberg and W. Parsons. CSIRO, East Melbourne, Victoria, Australia. pp 11–35.

Myers, C.A. 1964. Taper tables, bark thickness, and diameter relationships for lodgepole pines in Colorado and Wyoming. USDA Forest Service, Rocky Mtn. For. and Range Exp. Sta. Res. Note RM-31, 6 p.

Myers, C.A. and R.R. Alexander. 1972. Bark thickness and past diameter of Engelmann spruce in Colorado and Wyoming. USDA Forest Service, Rocky Mtn. For. and Range Exp. Sta. Res. Note RM-217, 2 p.

Myers, C.A., and C.B. Edminster. 1974. Conversion of tree-volume equations to the metric system. USDA Forest Service, Rocky Mtn. For. and Range Exp. Sta. Res. Note RM-261, 2 p.

Oker-Blom, P. 1985. Photosynthesis of a Scots pine shoot: simulation of the irradiance distribution and photosynthesis of a shoot in different radiation fields. Agric. For. Meteorol. 34:31–40.

Penning de Vries, F.W.T. 1983. Modeling of growth and production. *In* Physiological Plant Ecology IV, Encyclopedia of Plant Physiology Vol. 12D. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler. Springer-Verlag, Berlin. pp 117–150.

Reynolds, J.F., B.R. Strain, G.L. Cunningham, and K.R. Knoerr. 1980. Predicting primary productivity for forest and desert ecosystem models. *In* Predicting Photosynthesis for Ecosystem Models. Vol II. Eds. J.D. Hesketh and J.W. Jones. CRC Press, Boca Raton, Florida. pp 169–207.

Shugart, H.H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York. 278 p.

Tennent, R.B. 1982. Individual-tree growth model for *Pinus radiata*. N.Z. J. For. Sci. 12:62–70.