Efficiency of Tree Crowns and Stemwood Production at Different Canopy Leaf Densities

R.H. WARING, KEN NEWMAN and JOHN BELL

School of Forestry, Oregon State University, Corvallis, Oregon, USA 97331

SUMMARY

Variation in the unit leaf rate in trees, i.e. the weight of wood increment per unit of leaf area, arises from disproportionate changes in their rates of net photosynthesis and in the allocation of carbohydrates. Changes in unit leaf rate in response to variations in canopy density were investigated in a thinning experiment established in a 36 year-old Douglas fir forest. Tree growth was estimated from increment cores and leaf area by linear correlation with sapwood basal area. Net assimilation and mean growth of individual trees expressed as basal area and volume decreased in direct proportion to increase in canopy density from 3.6 to 12.0 $m^2 m^{-2}$ of projected leaf area. These relationships were linear with multiple correlation coefficients (r^2) $\geqslant$ 0.97.

Net stand increment, in contrast to unit leaf rate, culminated as projected leaf area approached 6 $m^2 m^{-2}$ and decreased at the higher canopy densities due to mortality. The approach developed in this paper could be applicable in predicting growth in response to various silvicultural treatments.

INTRODUCTION

It is well known that trees released by thinning tend to grow faster and that total wood production often equals or may exceed that observed in unthinned stands. Open-grown trees intercept more sunlight, produce more carbohydrates and allocate proportionally more assimilates to stemwood than trees in shaded canopies. (Mooney 1972; Rangnekar and Forward 1973). As a measure of the efficiency of production of tree crown several authors have estimated increment in terms of stemwood production per unit of leaf weight (e.g. Van Laar 1973, Tadaki 1966, Larson and Isebrands 1972, Halle, Oldeman and Tomlinson 1978). This approach is similar to the traditional techniques developed in agricultural research (Gregory 1918, Briggs, Kidd and West 1920) but although readily applied to tree seedlings (see Hunt 1978, Sestäk *et al* 1971) the application of growth analysis techniques in forestry has been delayed by the difficulty of accurately estimating changes in the leaf canopy of large trees. The recognition that the basal area of conducting tissue in a given tree species has a linear relationship with foliage weight or leaf area has partly removed this difficulty (Dixon 1971, Grier and Waring 1974, Waring *et al* 1978, Whitehead 1978, Rogers and Hinckley 1979).

Stemwood increment is usually estimated from changes in basal area, using local volume tables, so it appears logical to estimate net assimilation rate ($kg\ m^{-2} y^{-1}$)

from the ratio of current growth in basal area to total sapwood basal area (Waring, Thies and Muscato 1980). From a limited comparison of four stands with different canopy densities, they reported nearly proportional relationships between net assimilation rate and canopy leaf area. In their study, volume growth and sapwood basal area were measured from stem analysis on 122 trees of varying sizes and dominance classes.

To test more rigorously and widely how the competing canopy might affect net assimilation rate, a uniform forest previously thinned at different intensities was selected. From an analysis of wood core samples from different treatments and from knowledge of stand density and other stand characteristics, this paper develops an approach for predicting growth responses over a wide range of thinning intensity.

STUDY AREA

The study area is located near Hoskins, Oregon (longitude 123°28′, latitude 44°41′) on the west side of the Coast Range at 300 m elevation. The climate is wet and mild; temperatures rarely fall below freezing and rainfall exceeds 2000 mm annually. Soils are well drained Haplumbrepts (Western Brown Forest Soils) derived from Tyee sandstone.

The naturally established forest of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), 36 years-old at the time of our study, had been selected in 1963 for experimental thinning to nine stand densities (Bell and Berg 1972). Each treatment was replicated three times on 809 m^2 (1/5 acre) plots in a completely randomized design. Stand density has since been maintained by successive thinning in 1966, 1970, 1973 and 1975.

Data for the study were collected after the last thinning from five of the stand densities, including the unthinned control. Stand characteristics after the last measurements in 1978 are given in Table 1.

METHODS

For each density, stand and individual-tree characteristics were assessed. From an annual survey, the number of trees living on each plot and the extent of mortality were known. Height estimates were made by interpolation from measurements of 30 trees from each density in 1975 and in 1978.

Characteristics of individual trees were assessed from 30 trees randomly selected in each stocking density. On each sampled tree, diameter at breast height, 1.37 m, was recorded. Annual increment in 1978 and sapwood thickness were determined from two cores extracted at 180°. From these data, mean tree basal area, diameter, sapwood basal area, and growth in basal area and volume were derived. Stemwood volumes were calculated from an allometric relationship between diameter and biomass established by Gholz *et al* (1979) and to convert from biomass to volume, a wood density of 400 kg m^{-3} was assumed.

Stand characteristics were derived as the product of the number of trees and mean values for all trees. The leaf area index, expressed as square metres of projected

TABLE 1. *Stand Characteristics for five stocking levels after the 1978 growing season. Values are means ± standard error*

Measurement	Treatment 1	Treatment 2	Treatment 3	Treatment 4	Control
Diameter breast height, cm	35.9 ± 0.8	34.2 ± 1.0	28.9 ± 1.2	29.8 ± 0.8	18.3 ± 1.2
Height, m	25.5 ± 0.3	25.6 ± 0.3	25.5 ± 0.4	25.5 ± 0.3	24.0 ± 0.5
Trees, ha^{-1}	173.0 ± 0	304.0 ± 29	477.0 ± 18	593.0 ± 19	1977.0 ± 147
Basal area, m^2 ha^{-1}	17.5 ± 0.8	27.9 ± 1.6	31.3 ± 2.6	41.3 ± 2.2	52.5 ± 6.9
Sapwood basal area, m^2 ha^{-1}	8.3 ± 0.4	13.7 ± 0.7	16.3 ± 1.1	19.5 ± 0.9	27.4 ± 4.0
[1]Stemwood volume, m^3 ha^{-1}	224.7 ± 13.2	348.1 ± 19.7	352.8 ± 38.0	475.0 ± 33.1	451.3 ± 76.8

[1] Stemwood volumes were estimated from a local volume table (Gholz et al. 1979) which did not take into account possible differences in taper related to treatment. Professor Allen Berg, however considers that trees of similar size differ less than 10 per cent in volume in this particular experiment (personal communication).

TABLE 2. *Characteristics of tree growth and stand growth in relation to leaf area of a stand. Means are presented with standard errors*

Treatment	Average tree growth: Basal area m^2 y^{-1}	Average tree growth: Volume m^3 y^{-1}	Average tree growth: Height m y^{-1}	Average stand growth: Basal area m^2 ha^{-1} y^{-1}	Average stand growth: Volume m^3 ha^{-1} y^{-1}	Stand leaf area m^2 m^{-2}	Wood production per unit leaf area g m^{-2}
1	0.0075 ± 0.0003	0.124 ± 0.003	1.00	1.30 ± 0.05	21.4 ± 0.5	3.6 ± 0.2	235 ± 5
2	0.0058 ± 0.0003	0.092 ± 0.005	0.97	1.77 ± 0.09	28.1 ± 1.7	6.0 ± 0.3	185 ± 2
3	0.0041 ± 0.0004	0.059 ± 0.007	1.01	1.95 ± 0.20	28.1 ± 1.3	7.2 ± 0.5	157 ± 6
4	0.0033 ± 0.0003	0.049 ± 0.005	1.01	1.69 ± 0.27	25.6 ± 1.3	8.6 ± 0.4	135 ± 7
Control	0.0009 ± 0.0002	0.010 ± 0.003	0.80	−1.02 ± 0.76	−4.0 ± 2.4	12.0 ± 1.8	66 ± 3

leaf area per square metre of ground surface, was obtained by multiplying sapwood basal area of the stand by 0.44 (Gholz, 1981; Grier and Waring 1974) and then dividing by 10000, the number of square metres in a hectare. Net assimilation rate, expressed as increment in stemwood production per square metre of leaf area, was determined for quadratic mean trees in each treatment from changes in diameter, using allometric equations (Gholz *et al* 1979) and correlations with sapwood basal area and leaf area.

RESULTS

Characteristics of tree and stand growth for each stocking level are summarized in Table 2. Mean basal area growth of trees in the most heavily thinned stands was

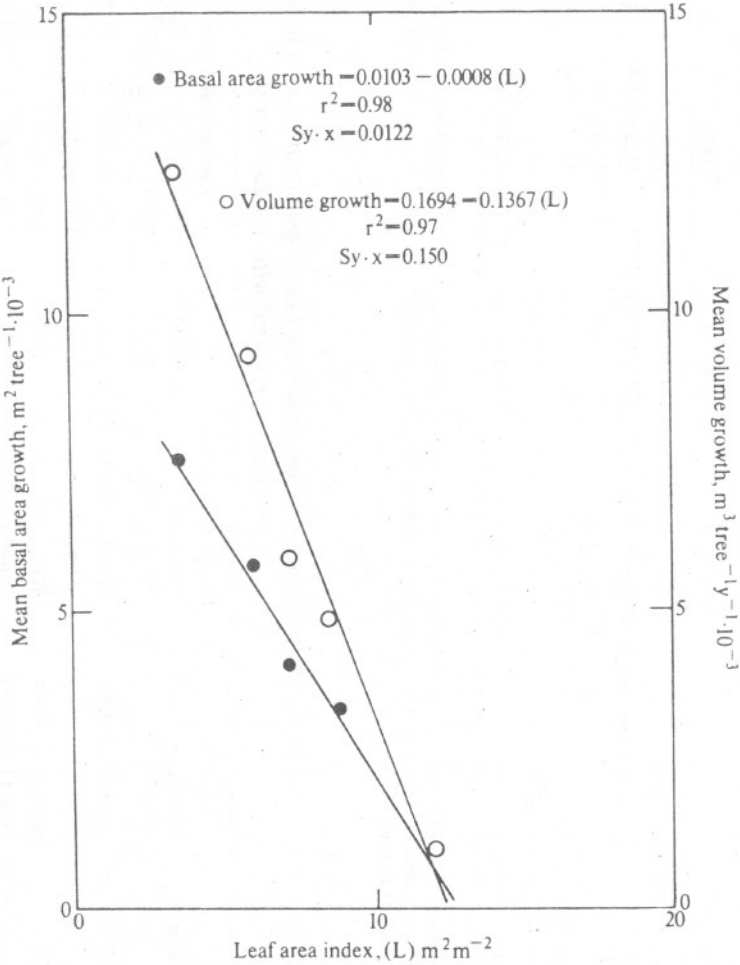

Fig. 1. Mean growth in basal area and volume of individual trees in relation to stand leaf area (L). Error estimates around means are given in Table 2. Sy·x is the standard error of the mean for the regression.

more than eight times that of those in the control stand while volume growth was twelve times and net assimilation rate nearly four times greater.

Three linear relationships between stand leaf area and tree growth characteristics (Figs. 1 and 2) demonstrate that growth in basal area, volume, and net assimilation rate decrease predictably ($r^2 \geqslant 0.97$) as the competing canopy increases in density from 3.6 to 12.0 $m^2 m^{-2}$.

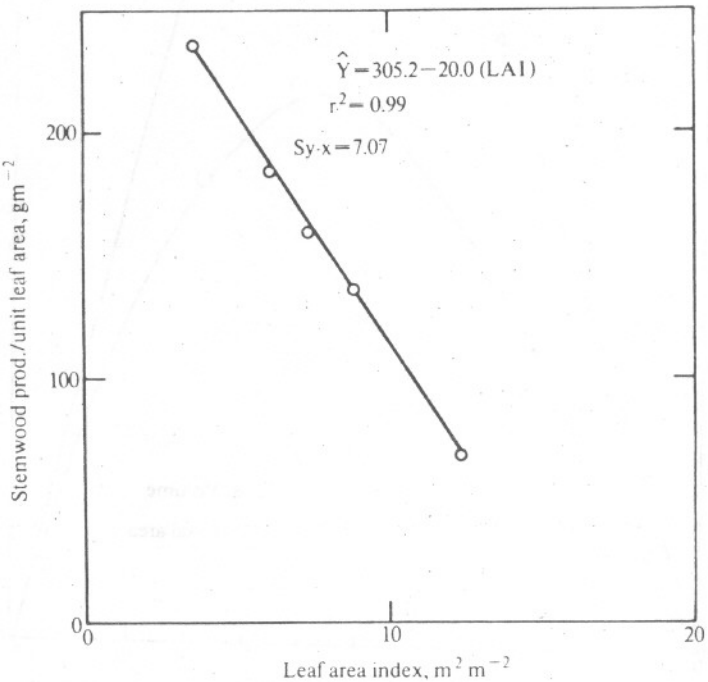

Fig. 2. Net assimilation rate, expressed as stemwood production per unit of leaf area, decreases linearly for Douglas-fir trees as leaf area (LAI) of the canopy increases. Values are means of 30 trees; error estimates are given in Table 2. Sy·x is the standard error of the mean for the regression.

Stand growth, in contrast to tree growth, appears to increase until canopy density reaches nearly half the maximum projected leaf area and then to plateau before decreasing rapidly at the highest stocking level (Fig.3). The abrupt growth decrease in the unthinned stands may be attributed to the 1978 mortality of 111 trees ha^{-1}. The gross basal area production was 1.80 ± 0.40 $m^2 y^{-1}$, not significantly different from all but the most heavily thinned stands. The only other recorded mortality was in stands of Treatment 4, which lost four trees ha^{-1} in 1978

DISCUSSION

The relationship shown in Figures 1 and 2, although linear, should not be extrapolated beyond the range of data. We would expect, for example, that when stand

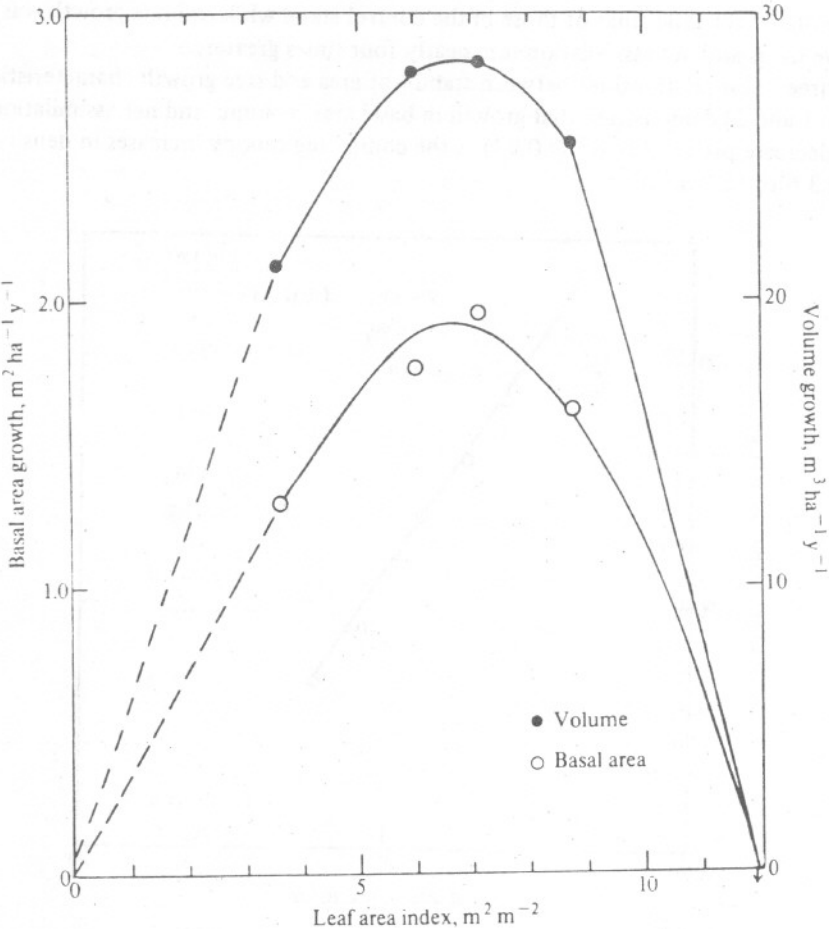

Fig. 3. Net stand growth in basal area and volume reached a peak at canopy leaf areas of 6.0 $m^2 m^{-2}$ of projected surface. Leaf areas of 7.2 and 8.6 $m^2 m^{-2}$ show no significant decrease in yield (Table 2). However, annual mortality was 111 trees ha^{-1} at the highest observed canopy density, 12.0 $m^2 m^{-2}$ leaf area index; so net production, but not gross production, falls to zero or below (-1.02 ± 0.76 m^2 $ha^{-1} y^{-1}$).

leaf areas are between 0.5 and 1.0 $m^2 m^{-2}$, competition would be reduced sufficiently that growth would reach a plateau. Extrapolating net assimilation rates toward zero may also be inaccurate. We have some evidence that growth stagnation at extremely high levels of competition may slightly reduce the stand leaf area. With these qualifications, the linear relationships support our hypothesis that growth of individual trees and net assimilation rate decrease in direct proportion to canopy leaf area, in a given environment.

The stands sampled in this experiment were unusually uniform as evidenced by the small range of variation in diameters and height (Table 1). In unmanaged forests

the range in size classes is normally much greater, often varying two to three fold (Waring *et al* 1980). In such cases the average basal area or volume growth per tree varies considerably. Although trees may vary in size, their net assimilation rates may be similar except for those which are diseased or completely suppressed (Waring *et al* 1980).

Comparable studies of tree growth efficiency are rare because few thinning experiments include estimates of leaf area. From data from a three-level spacing study on *Populus* clones (Larson, Dickson and Isebrands, 1976), we derived a similar linear relationship with net assimilation rate for stand leaf areas ranging from 3.5 to 20.0 m^2m^{-2}.

Recently, Oren (1980), assessing net assimilation in heterogeneous Douglas fir stands by subsampling small homogeneous areas, reported that some natural stands showed linear relationships but that one with extensive root rot did not; only a few trees reached their potential rates across a range of canopy densities. Past stand condition may thus limit the possible response to thinning, at least over a period of a few years.

An obvious question is how these relationships change as stands age. Tadaki (1977) suggests that taller trees with more dispersed canopies permit sunlight to be more efficiently absorbed, which may explain why old forests of tall trees generally have greater leaf areas than young stands of the same species (Waring *et al*, 1978); Gholz, Fitz and Waring 1976).

As trees grow, the amount of respiring tissue continues to increase. If live branches were pruned from most of the bole we would expect a decrease in assimilation rates because of a change in balance between producing foliage and respiring tissue. Waring, Thies and Muscato (1980) reported that, except for suppressed trees, different size classes with comparable crown to bole ratios demonstrated similar net assimilation rates.

Because the relationship appears linear over a wide range of canopy densities, accurate estimates of mean tree growth at intermediate points should be possible. Although a measure of tree net assimilation rate is obviously dependent upon the number of trees as well as the total leaf area of a stand, stand net assimilation rates (wood production per stand leaf area) in this study were comparable to those averaged for 30 trees sampled from each stand across the range of canopy densities, having a correlation with an r^2 of 0.92.

Although canopy leaf area appears to have a direct impact upon tree growth, other factors, such as competition for water, or nutrients, could be expected to interact with the shading effect of the canopy. In our study, moisture was not limiting.

By observing how tree growth responds to changes in canopy leaf area and how various ameliorations further improve growth at a given leaf area, we should be able to more precisely assess interactions and predict stand responses. With additional knowledge of how rapidly the canopy is reestablished following thinning, the essential structural relationships for a more biologically based model of stand growth would be available.

REFERENCES

Bell, J.F. and Berg, A. 1972 Levels-of-growing stock cooperative study on Douglas-fir. Report No. 2. The Hoskins Study, 1963–1970. *U.S. Dep. Agric. For. Serv. Res. Pap. PNW-130*. Pac. Northwest For. Range Exp. Stn., Portland, Oreg. 19 p.

Briggs, G.E., Kidd, R. and West, C. 1920 Quantitative analysis of plant growth. *Ann. appl. Biol.* 7, 202–223.

Dixon, A.F.G. 1971 The role of aphids in wood formation I. The effect of sycamore aphid, *Drephanosiphum platanoides* (Schr.) (Aphidae), on the growth of sycamore. *J. appl. ecol* 8, 165–179.

Gholz, H.L. 1981 Limits on aboveground net primary production, leaf area, and biomass in vegetational zones of the Pacific Northwest. *Ecology* (In press).

Gholz, H.L., Fitz, F.K. and Waring, R.H. 1976 Leaf area differences associated with old-growth forest communities in the western Oregon Cascades. *Can. J. For. Res.* 6, 49–57.

Gholz, H.L., Grier, C.C., Campbell, A.G. and Brown, A.T. 1979 Equations for estimating biomass and leaf area of plants in the Pacific Northwest. *Forest Research Lab., Res. Pap. 41*. Oregon State University, Corvallis. 37 p.

Gregory, F.C. 1918 *3rd Ann. Rept.*, Exptl. Res. Stn. Cheshunt. p. 19.

Grier, C.C. and Waring, R.H. 1974 Conifer foliage mass related to sapwood area. *For. Sci.* **20**, 205–206.

Halle, F., Oldeman, R. and Tomlinson, P.B. 1978 *Tropical Trees and Forests: an Architectural Analysis*. Springer Verlag, Berlin.

Hunt, R. 1978 Plant growth analysis. *Studies in Biology No. 96* Edward Arnold Limited, London. pp. 67.

Larson, P.R., Dickson, R.E. and Isebrands, J.G. 1976 Some physiological applications for intensive culture. In: Intensive Plant Culture. *U.S. Dep. Agric. For. Ser., Gen. Tech. Rep. NC-21*, p. 10–18. St. Paul, Minn.

Larson, P.R., and Isebrands, J.G. 1972 The relationship between leaf production and wood weight in first year sprouts of two *Populus* clones. *Can. J. For. Res.* 2, 98–104.

Mooney, H.A. 1972 The carbon balance of plants. *Annu. Rev. Ecol. Syst.* 3, 315–346.

Oren, R. 1980 Stand sapwood basal area: an indicator of tree vigour. Unpubl. *M.S. thesis*, Oregon State University, Corvallis.

Rangnekar, P.V. and Forward, D.F. 1973 Foliar nutrition and wood growth in red pine: effects of darkening and defoliation on the distribution of ^{14}C-photosynthate in young trees. *Can. J. Bot.* 51, 103–108.

Rogers, R. and Hinckley, T.M. 1979 Foliar weight and area related to current sapwood area in oak. *Forest Sci.* 25, 298–303.

Sestak, Z., Catsky, J. and Jarvis, P.G. 1971 *Plant photosynthetic production. Manual of methods*. D.W. Jank, N.V. Publishers, The Hague. 818 p.

Tadaki, Y. 1966 Some discussion of the leaf biomass of forest stands. Gov. For. Exp. Station. *Tokyo Bull.* **184**, 135–161.

Tadaki, Y. 1977 Forest biomass. *In*: Primary productivity of Japanese forests. Productivity of terrestrial communities. *JIBP Synthesis Vol. 16*. Univ. Tokyo Press, p. 39–64. Tokyo, Japan.

Van Laar, A. 1973 Needle biomass, growth and growth distribution of *Pinus radiata* in South Africa in relation to pruning and thinning. Forschungsberichte, Forstliche Forschungsanstalt Munchen. 258 pp.

Waring, R.H., Emmingham, W.H., Gholz, H.L. and Grier, C.C. 1978 Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. *For. Sci.* 24, 131–140.

Waring, R.H. Thies, W.G. and Muscato, D. 1980 Stem growth per unit of leaf area: A measure of tree vigour. *For. Sci.* 26, 112–117.

Waring, R.H., Gholz, H L., Grier, C.C. and Plummer, M.L. 1977 Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms. *Can. J. Bot.* 55, 14–74.

Whitehead, D. 1978 The estimation of foliage area from sapwood basal area in Scots pine. *Forestry* 51, 137–149.

Reprinted from

Forestry Volume 54, No. 2, 1981

Printed at the University Press, Oxford, England.