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SITE, LEAF AREA, AND PHYTOMASS PRODUCTION IN TREES

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SUMMARY

As the environment becomes harsher, plants allocate proportionally more energy to assure survival and have less to allocate for stem growth. The harshness of an environment for a particular tree species may be assessed by comparing how much stemwood is accumulated per unit of leaf area.

As the environment becomes less favourable for tree growth, canopy leaf area, stand phytomass, and stemwood growth/leaf area decrease predictably. All of these variables may be assessed from growth rings and correlations between sapwood basal area and leaf area.

INTRODUCTION

Trees barely survive at timberline, their limbs torn, their roots exposed on rocky ledges; yet upon flood plains, cathedral groves flourish. Although environments and species vary, could it be that evolution has forged a universal marriage between form and function? From recent studies of forests in western North America, my colleagues and I find striking relationships between phytomass, site, and leaf area. If these findings reflect evolutionary adaptations, they may mirror general functional relationships controlling photosynthesis and the allocation of carbon.

Sapwood Basal Area and Leaf Area

Kline *et al.* (1976) first noted a direct correlation between water flux and conducting area at breast height (1.3 m) while measuring the flow of water through stems. Using data from that study, Grier and Waring (1974), reported a linear relationship between sapwood basal area and leaf biomass (or leaf area) (Fig. 1). More recently, Whitehead (1978) demonstrated that this relationship remains constant for Scots pine *(Pinus sylvestris)* at varying stand densities.

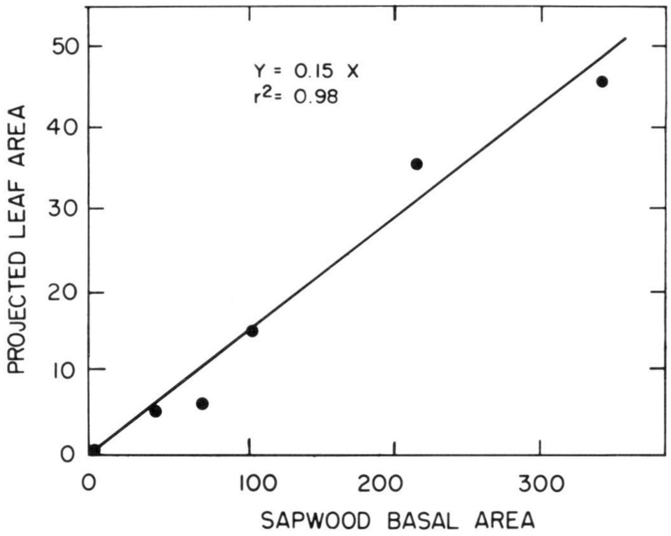

Fig. 1. Leaf area (m^2) of lodgepole pine *(Pinus contorta)* trees in relation to sapwood basal area (cm^2) (R.H. Waring, unpubl. data).

Across a transect from the Pacific coastal forests inland to arid plains east of the Cascade Mountains in Oregon, we find that the ratio of leaf area (square metre projected) to sapwood basal area (square centimetres) varies more than sixfold (Table 1). Those species adapted to more arid and continental environments maintain fewer leaves per comparable amount of conducting tissue than do more maritime species.

TABLE 1: RATIOS OF PROJECTED LEAF AREA TO SAPWOOD BASAL AREA FOR SELECTED CONIFERS OF THE WESTERN UNITED STATES

Species	Environment	Leaf area:sapwood area (m^2/cm^2)
*Picea sitchensis**	humid, maritime	0.44
Pseudotsuga menziesii †	moderate	0.32
Abies procera †	humid, subalpine	0.27
Pinus contorta ‡	continental	0.15
Tsuga mertensiana ‡	continental	0.16
Pinus ponderosa †	semi-arid	0.17
Juniperus occidentalis §	arid	0.07

*D. Whitehead, unpubl. data, Forest Research Institute, Rotorua, New Zealand.

† Grier and Waring, 1974.

‡ R.H. Waring, unpubl. data, Department of Forest Science, Oregon State University, Corvallis, Oregon, United States.

§H.L. Gholz, unpubl. data, Forest Research Lab, Oregon State University, Corvallis, Oregon, United States.

Phytomass and Leaf Area

Using allometric relationships developed by Gholz *et al.* (1979), we can estimate the biomass of stemwood, branches, and other components of trees by measuring stem diameter. Assuming that trees 20 cm in diameter were entirely sapwood (i.e., have a conducting area of 314 cm^2 at breast height), I derived the relationship between leaf area and stemwood biomass presented in Fig. 2. Apparently, trees adapted to progressively harsher environments are shorter and more tapered, a conformation consistent with reduced leaf area.

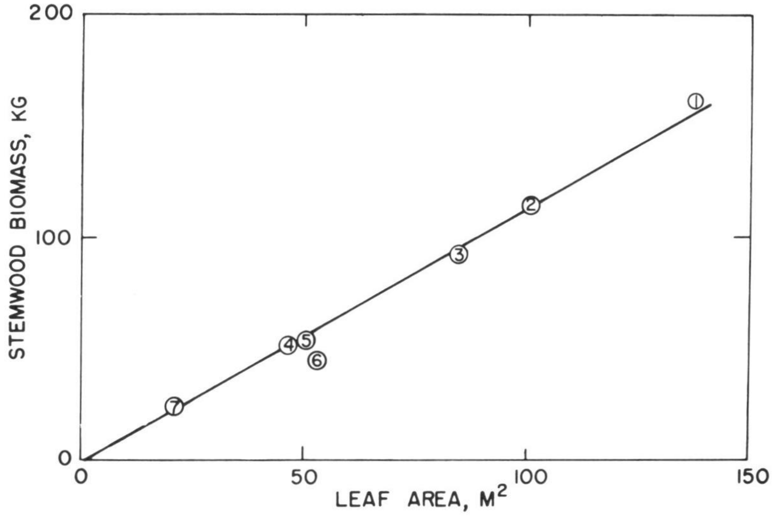

Fig. 2. Relationship between biomass of stemwood and projected leaf area for 20-cm-diameter trees with 314 cm^2 of sapwood basal area. Species are: (1) *Picea sitchensis,* (2) *Pseudotsuga menziesii,* (3) *Abies procera,* (4) *Pinus contorta,* (5) *Tsuga mertensiana,* (6) *Pinus ponderosa,* and (7) *Juniperus occidentalis.* (Conversion from Table 1 and from biomass equations — Gholz *et al.,* 1979.)

Applying the same allometric relationships to forests, my students compared several with mixed compositions and ages (Fig. 3). For very mature forests, the maximum stemwood accumulation (the boundary limit in Fig. 3) increased in proportion to stand leaf area, suggesting that, in spite of variation among species, an upper limit is imposed that keeps respiring and conducting tissue in balance with the carbon-fixing ability of leaves.

Leaf Area and Environment

For the same transect (Pacific coast to inland plain), Grier and Running (1977) developed a simple water budget index incorporating summer rainfall, soil storage, and open-pan

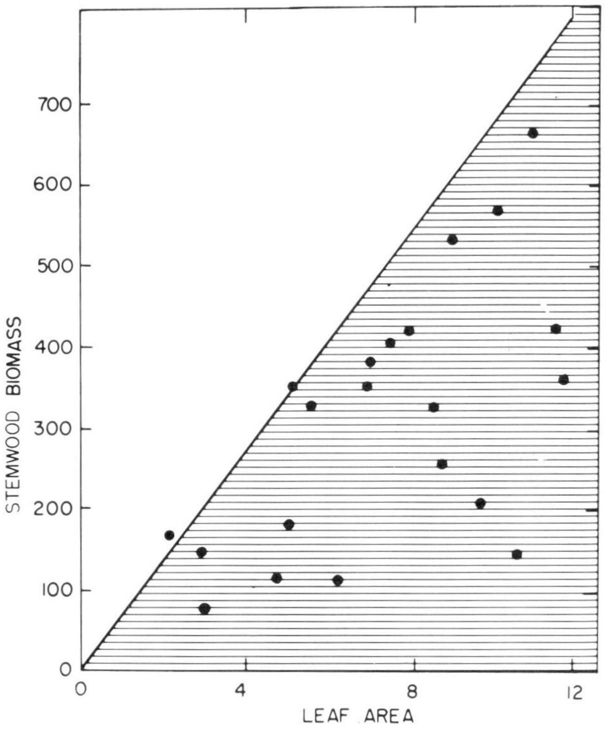

Fig. 3. Maximum biomass accumulation (t/ha) in stemwood is proportional to the development of stand projected leaf area (m^2/m^2) (Waring, 1979).

evaporation. When forests more than 200 years old were sampled and their leaf areas estimated, a strong correspondence was indicated between their water balance index and stand foliage area (Fig. 4). More refined studies by Gholz (1979) suggest that extremely cold winter temperatures play a role in restricting maximum leaf area accumulation on some sites. Waring *et al.* (1978) proposed that interactions between available soil moisture, evaporative demand, and temperature probably explain variations in leaf area in two contrasting mountainous regions of Oregon. Maximum accumulation of foliage occurred on cool, moist sites supporting high phytomass (Fig. 5); however, height growth peaked on warmer, moist sites (Fig. 6). Some sites with infertile soils consistently supported leaf areas and phytomass lower than would otherwise be predicted from their temperature and moisture regimes.

We know that any constraint to photosynthesis will reduce shoot growth, eventually limiting canopy development and phytomass accumulation. Subtle shifts in the environment may favour better adapted species and change the rate of foliage accumulation but, ultimately, maximum canopy development is environmentally controlled.

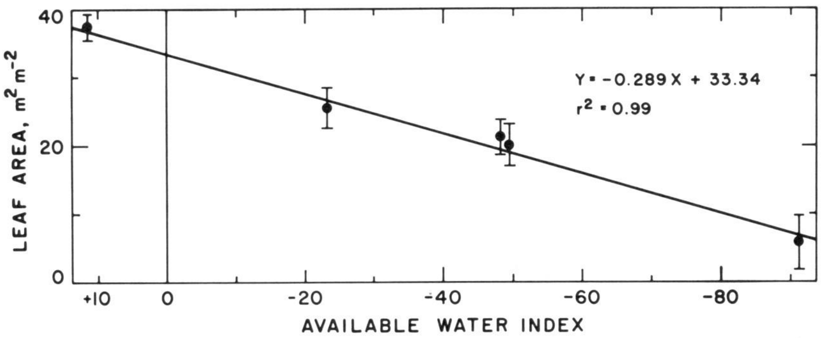

Fig. 4. Relationship between water balance index (computed by adding soil water storage to measured season precipitation then subtracting open pan evaporation) and stand leaf areas (all surfaces) in five forest zones of western Oregon. Zones plotted are, from left to right: *Picea sitchensis*, *Tsuga heterophylla*, *Quercus garryana* (interior valley), east slope mixed conifers, and *Juniperus occidentalis*. Bars show range of observed leaf areas in each vegetation zone (after Grier and Running, 1977).

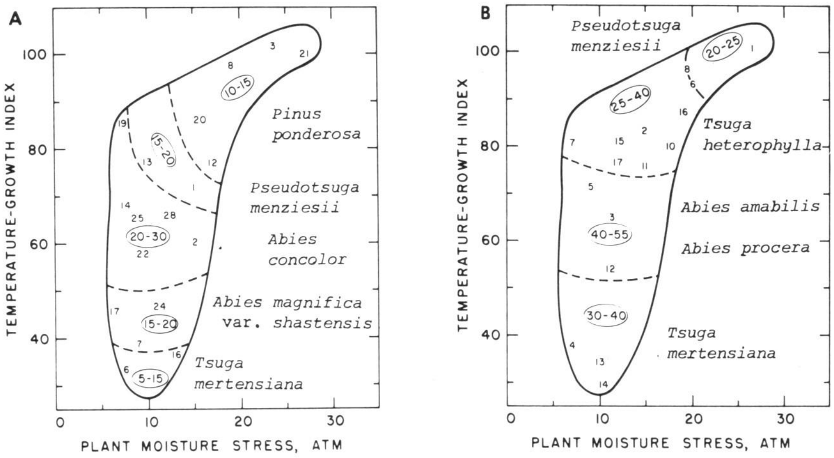

Fig. 5. Comparison between southern (A) and west-central (B) Oregon forests showing dominance of major species in relation to a moisture and temperature gradient. Uncircled numbers refer to undisturbed stands where leaf area (m^2/m^2, all surfaces) was calculated for all tree species (Gholz *et al.*, 1979). The circled numbers represent the range of leaf areas encountered on plots falling within the environments bounded by dotted lines. Note the maximum leaf areas occur where environments are low in moisture stress and moderate in temperature. The harsher climate associated with southern Oregon prevents leaf areas from reaching those common in milder west-central Oregon (Waring *et al.*, 1978). The plant moisture stress gradient reflects the availability of soil water to 1- to 2-m tall conifers after a period of drought (Waring and Cleary, 1967). The temperature-growth index is an accumulative index of how soil temperatures and air temperatures affect the growth of Douglas fir seedlings throughout a growing season of varying length (Cleary and Waring, 1969).

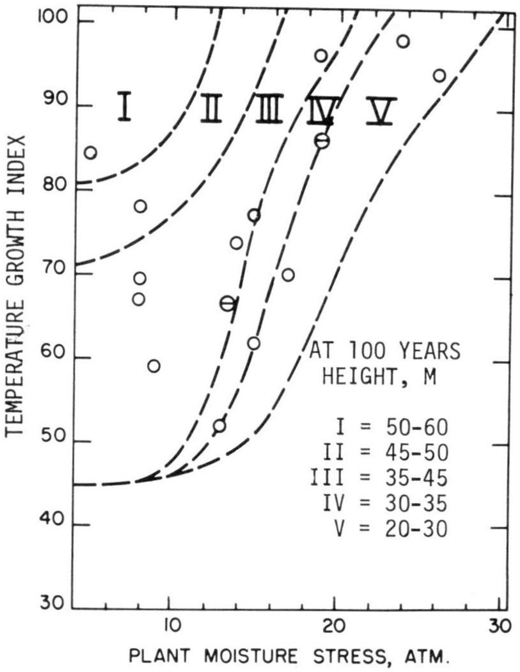

Fig. 6. Douglas fir growth in relation to moisture stress and temperature gradients. Maximum growth occurs on warm moist sites, whereas maximum accumulation of leaf area occurs on cooler sites (Waring, 1970). These data are from southern Oregon but similar patterns are expressed in west-central Oregon.

Stemwood Growth and Leaf Area

How efficiently trees accumulate biomass in relation to their investment in foliage may indicate their carbohydrate balance. Because annual stemwood production is not essential, as evidenced by missing rings common to trees growing on harsh sites, the amount of wood produced is really a measure of reserves left after a tree has met shoot, root, and reproductive commitments, and self-protective requirements (Gordon and Larson, 1968; Eis *et al.*, 1965; Mooney, 1972; Rangnekar and Forward, 1973; Harris *et al.*, 1978). We can estimate wood-producing efficiency by measuring stem diameter, annual ring widths, and sapwood thickness. Knowing these, we can calculate growth of stemwood biomass and leaf area because basal area increment is related to growth in stemwood biomass, and sapwood basal area is related to leaf area. Waring *et al.* (1979) found Douglas fir *(Pseudotsuga menziesii)* trees of varying sizes growing in a natural stand exhibited similar growth efficiencies for the current year and for the last 5 years (Fig. 7).

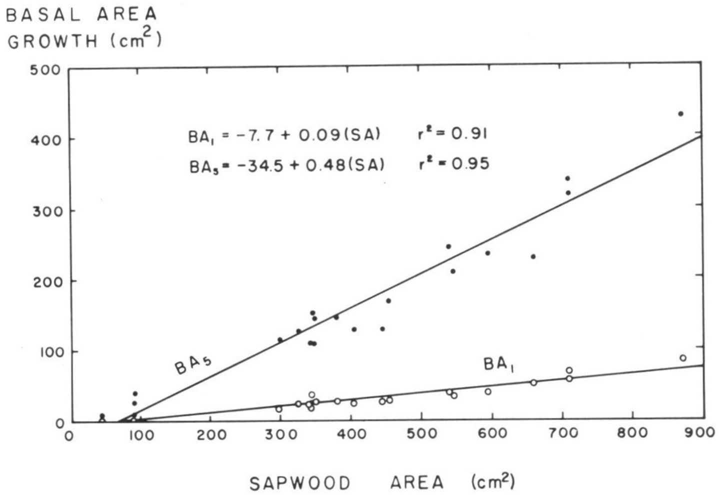

Fig. 7. In a 40-year-old Douglas fir stand, trees of differing sizes and competitive status exhibited similar growth deficiencies, plotted as basal area (BA) increment for the current year (BA_1) and for the last 5 years (BA_5) in relation to sapwood basal area (Waring *et al.,* 1979).

Growth Efficiency and Stand Leaf Area

As a canopy closes, the amount of light reaching shaded branches should decrease exponentially (Fig. 8); however, photosynthesis is strongly inhibited only when light reaching the foliage remains for extensive periods below saturation.

Comparing basal area growth in relation to sapwood area for Douglas fir trees over a range of thinnings, Newman (1979) found that growth efficiency decreased linearly with increasing canopy development (Fig. 9). If this kind of relationship generally applies, we can estimate maximum canopy by extrapolating where basal area growth approaches zero. Further, with suitable conversions, we can compare the efficiency of different species growing in pure or mixed stands across a range of environments. A steeper slope or lower intercept signifies a more severe environment.

Growth Efficiency and Environment

We have only very preliminary data on how growth efficiency actually changes with environment. For two sites differing in height growth (Table 2), at approximately the same leaf area, the better site produced more than twice the biomass and exhibited apparently higher efficiencies in converting carbon assimilate leaf area into stemwood. Although differences persisted between sites, at higher stand leaf areas both efficiency and the rate of biomass accumulation decreased. This is to be expected where high leaf area may

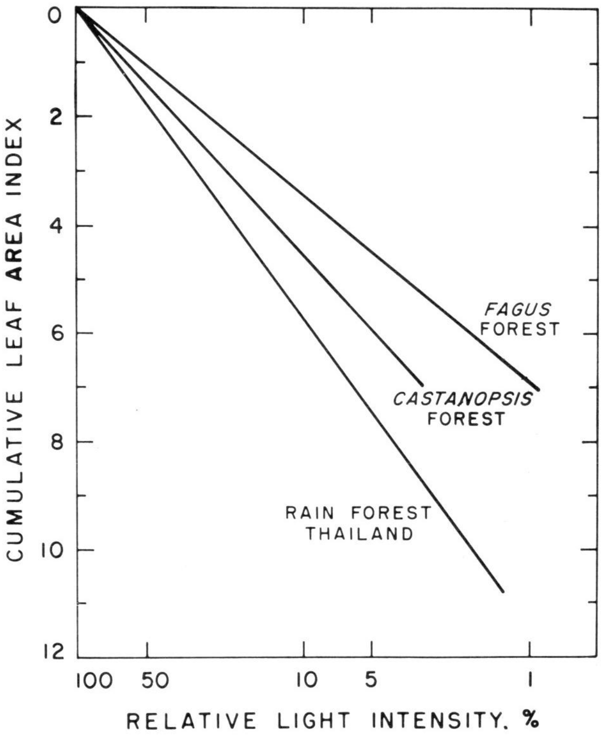

Fig. 8. The amount of light filtering through forest canopies is an exponential function of the amount of projected leaf area (m^2/m^2) (after Kira *et al.,* 1969).

Fig. 9. Growth efficiency (current BA increment per sapwood area) of Douglas fir trees decreases as stand projected leaf areas increase (m^2/m^2). Values are means of 30 trees ± standard error (Newman, 1979).

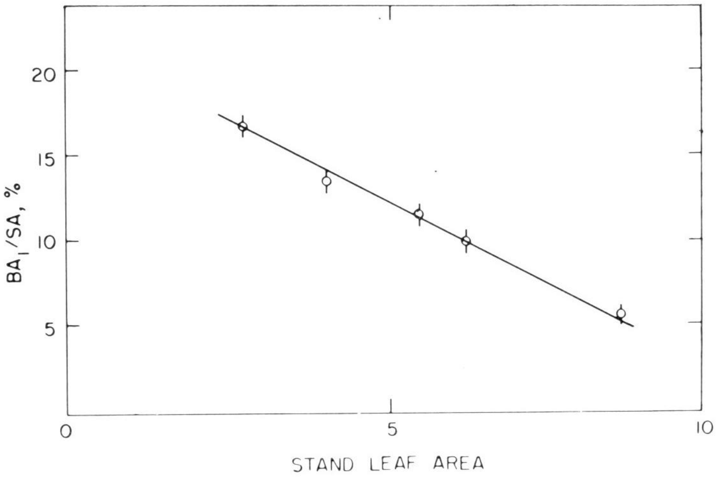

TABLE 2: MEAN PRODUCTION CHARACTERISTICS OF FOUR DOUGLAS FIR STANDS

Stand	Projected height (m) at 100 yr	Stemwood biomass (t/ha)	Stemwood production (kg/ha/yr)
1	52	175	7230
2	52	318	5735
3	27	345	3522
4	27	377	3088

	Leaf area, all surfaces (m^2/m^2)	Stemwood production leaf area ($kg/ha/yr/m^2$)	Growth efficiency BA_5/SA (± SE)* (cm^2/cm^2)
1	12.0	600	0.40 + 0.02
2	17.3	330	0.25 + 0.02
3	11.2	305	0.15 + 0.03
4	18.0	171	0.09 + 0.01

*BA_5 = basal area growth over the past 5 years
SA = sapwood area
SE = standard error

accumulate. In young plantations of conifers (Albrektson *et al.,* 1977) or hardwood forests (Madgwick and Olson, 1974), stemwood production continues to increase with stand leaf area. However, in dense conifer stands, lack of light may become so limiting that even a tenfold increase in number of stems does not prevent decreased wood production per hectare (Fig. 10).

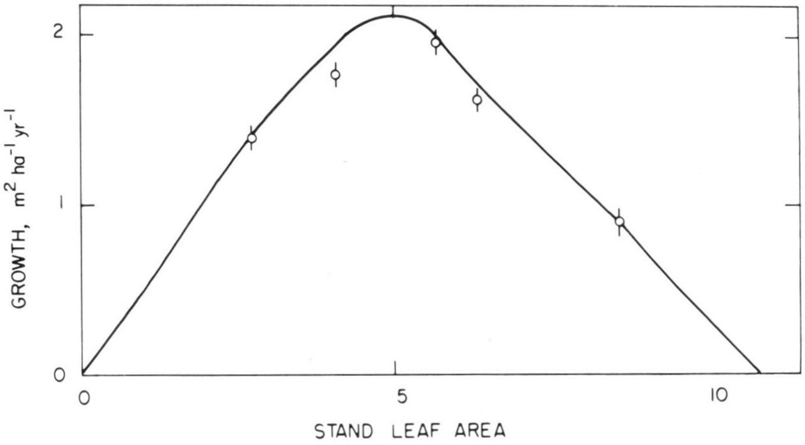

Fig. 10. Basal area growth per hectare peaks at less than maximum stand projected leaf area (m^2/m^2), where very high leaf area may accumulate (Newman, 1979).

CONCLUSION

That a tree's sapwood basal area is closely related to the amount of foliage it supports, provides a promising means of assessing relationships between site and phytomass accumulation. Trees adapted to harsh environments tend to support less phytomass and leaf area per unit of conducting area. Harsh environments not only restrict accumulation — they also reduce the efficiency with which trees accumulate wood per unit of leaf area. This efficiency can be estimated by sampling cores and calculating the percentage of sapwood area laid down in the current year. Such a ratio, when expressed in units of biomass increment per square metre of foliage, permits comparison of relative competitive ability in pure or mixed forests across a range of environments.

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