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Estimating Forest Growth and Efficiency in Relation to Canopy Leaf Area

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I. INTRODUCTION

Major processes controlling forest growth have been intensively studied and integrated into mechanistic models in the last decade (Sievanen, 1980; Promnitz, 1975). Unfortunately, the predictive reliability of these models is generally less than that obtained by more empirically based approaches (Stage, 1977; Mitchell, 1975). Two major factors contribute to this situation. First, detailed environmental data are required to predict accurately the photosynthesis, respiration, growth and necrosis of tissues. Generally, such data are not available. Second, the allocation of carbohydrates to build and maintain tissues is often proportioned in fixed ratios. Yet in times of stress, the way in which plants allocate resources is known to change drastically

(Rangnekar and Forward, 1973; Ericsson, Larsson and Tenow, 1980; Davidson, 1969a,b).

Perhaps classical growth analyses in concert with careful experimentation can unlock the rules by which carbohydrates are distributed. It is my objective in this review to demonstrate that two structural properties of plant communities—(1) canopy leaf area and (2) growth efficiency, measured as the ratio of stemwood production per unit of leaf area—when analysed together, may provide some insight. The product of these two variables estimates production. These same, or closely related, variables have proven valuable in agriculture to compare efficiencies and yields of various cropping systems and genetic varieties (Williams, 1946; Watson, 1952; Watson, 1958; Mitchell, 1970). However, the experimental base from which to draw examples in forestry is at present very small; until recently, simple means of estimating tree canopy leaf area were not available. Where results are known, growth analyses seem to mirror experiences in agriculture. Thus, wherever possible, I will compare findings of both.

This review is organized to develop four basic premises: (1) that canopy leaf area can be related to competition for light, (2) that growth efficiency is responsive to canopy leaf area and other identified environmental factors, (3) that potential productivity or site capability can be estimated from knowing maximum canopy leaf area, and (4) that canopy leaf areas for trees or stands can be non-destructively estimated by determining sapwood cross-sectional area at a convenient reference height.

II. CANOPY LEAF AREA

A. An Index for Growth

As a means of comparing plants of differing size, growth analyses are generally expressed in relative terms, for example, weight increase as a fraction of total weight (Newbould, 1967; Blackman, 1919). For trees with a large proportion of their total weight in non-respiring tissue, a more sensitive growth index may be non-photosynthetic tissue as a proportion of photosynthetic tissue (Jordan, 1971), referred to as “net assimilation rate” (Briggs, Kidd and West, 1920). Because foliage weight may vary from the top to the bottom of the canopy as well as seasonally, leaf area rather than leaf weight is often chosen as a base reference. Chlorophyll or protein concentrations may also serve as a basis for calculating growth efficiency (Jarvis and Šesták, 1971; Williams, 1946).

Canopy leaf area is conventionally expressed as projected surface area. The total surface area of flat leaves is twice the projected surface area whereas that of needle-shaped leaves averages about 2.5 times the projected surface area

(ranging from 2 for flat needles to 3.14 for those circular in cross-section). Because the canopy may consist of more than one layer of leaves, projected leaf surface values ranging from 0–20 may be supported above a given unit of land surface. When canopy is expressed in this manner, the term “leaf area index” (L) is applied (Watson, 1947). A forest canopy whose projected leaf area is $10\,000\text{ m}^2\text{ ha}^{-1}$ thus has an L of 1 m^2 of leaf area m^{-2} ground surface.

B. An Index of Competition for Light

As canopy density increases, the mean absorption of diffuse or direct solar radiation by the canopy may be predicted by Beer-Lambert's law:

$$I_z/I_0 = \exp(-K\Sigma L)$$

where

I_z = intensity of light at increasing canopy depth

I_0 = intensity of light above the canopy

K = slope of the relationship

ΣL = cumulative L from the top of the canopy down to the reference height, z

When plotted on a semi-log scale, this relationship is a straight line for any particular type of vegetative cover (Fig. 1). The slope of the line (the extinction coefficient) may vary somewhat with the angle and intensity of solar radiation (Isobe, 1962) the orientation of leaves (Kira, Shinozaki and Hozumi, 1969) and (or) branches (Honda and Fisher, 1978) and the amount of nonphotosynthetic tissue (Swank and Schreuder, 1974). For a particular vegetation type, however, a predictable relationship between cumulative leaf area and the fraction of light still received (I_z/I_0) at a particular height can be derived (Andersson, 1966; Andersson 1969; Monsi and Saeki, 1953). Further, if different vegetation types can be calibrated, an estimate of L can be translated into comparable units of irradiance (Fig. 1).

III. GROWTH EFFICIENCY

Growth efficiency (E) for trees will generally be expressed in grams of wood produced per square meter of projected leaf surface area. Occasionally, the index will be in units of volume or, when trees are compared with agricultural crops, in grams of dry matter production per square meter of leaf area.

A. Relation to Canopy Leaf Area

Growth efficiencies can be effectively contrasted in experiments where leaf

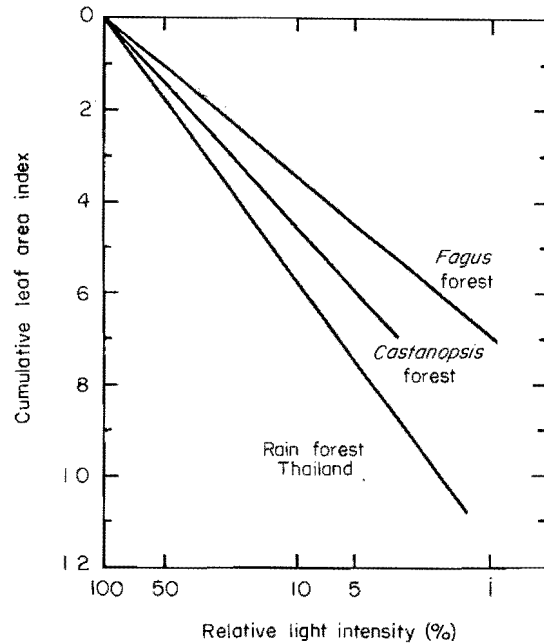


Fig. 1. The amount of light filtering through forest canopies is an exponential function of the cumulative leaf area. Adapted from Kira *et al.* (1969).

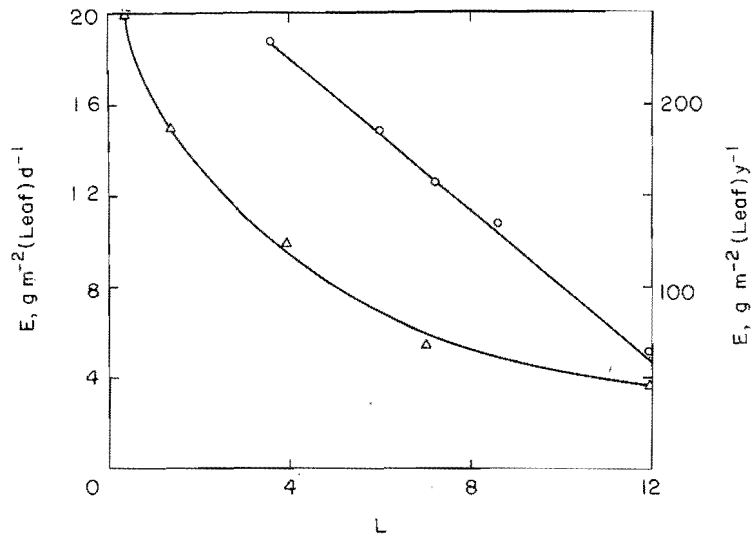


Fig. 2. As light decreases exponentially with increasing canopy leaf-area index (L), growth efficiency (E) decreases for both Douglas fir, O (Waring *et al.*, 1981) and maize, Δ (Williams, Loomis, and Lepley, 1965).

area is selectively maintained at different levels. In Fig. 2 such a comparison is presented for a field of maize (*Zea mays* L.) and a 36 year old stand of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees ranging in stocking from less than 200 to nearly 2000 stems ha^{-1} . In both cases, plants growing under less competition for light, indicated by lower values of L, exhibit higher values of E. At still higher levels of L (not shown), the relationship for Douglas fir also becomes curvilinear as the amount of live canopy is reduced but that remaining is concentrated at the top as reported for two species of spruce (Kramer, 1966). Similar changes in E have been reported as canopy leaf area increases on individual trees (Sato, Kunugi and Kumekawa, 1956). Shading experiments have demonstrated that wood production decreases per unit of leaf area (Rangnekar and Forward, 1973) because photosynthetic efficiency is reduced and because stemwood production has a lower priority than the growth of many other tissues (Kellomaki and Kanninen 1980, Ericsson *et al.*, 1980). In fact, under extreme conditions, no annual rings may be laid down at all in the lower bole of trees.

B. Relation to Water Stress

In forestry, very few studies have been reported in which the amount of soil water has been experimentally varied and the resulting plant growth response expressed in terms of E and L. Barrett (1970) initiated a thinning experiment in ponderosa pine (*Pinus ponderosa* L.) growing in an arid zone receiving about 60 cm of precipitation annually. In one set of experimental treatments, in which development of all understory vegetation was controlled, vegetation removal significantly affected E only when pine canopy L was relatively low (Fig. 3). Once higher values of L were achieved, stores of water were fully utilized by the overstory of trees. Because the tree canopy grew faster without the understory vegetation improvement in E could only be clearly recognized by interpreting the response over a range in L. Unfortunately, most forestry experiments have not been designed with this insight. A treatment that initially dramatically improved growth could increase L so substantially that mortality levels attributed to self-thinning and shading could decrease E and net wood production (Westoby, 1977; Waring, Newman and Bell, 1981).

C. Relation to Mineral Nutrition

Because many forests are situated on relatively infertile land, adding fertilizer should increase both photosynthesis and E. Further, because trees can store mineral reserves in twigs and older evergreen foliage (Sollins *et al.*, 1980; Wells and Metz, 1963; Luxmore, Grizzard and Strand, 1981; Woodwell, 1974; Bormann, Likens and Melillo, 1977) thus, improving their nutritional status by a single application of fertilizer is apt to have a prolonged effect (Miller *et*

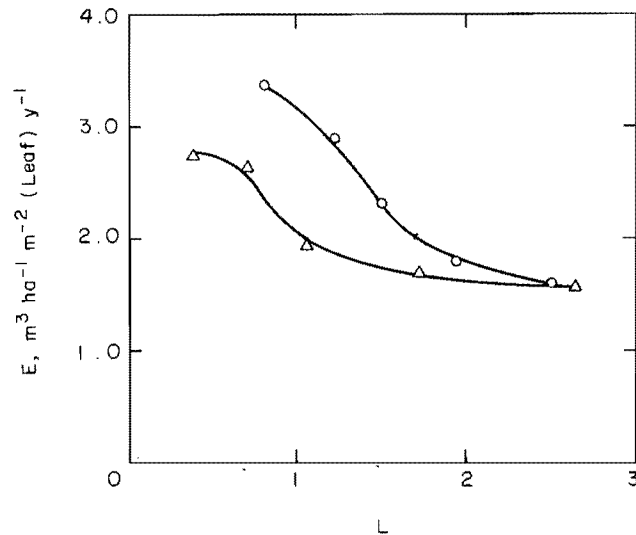


Fig. 3. When understory shrub cover was removed (O) from an arid zone Ponderosa pine forest, the growth efficiency (E) significantly increased over that observed with understory vegetation present (Δ), at least up to a pine canopy leaf-area index (L) of 1.5. At higher L values, all available water was utilized by the trees. Recalculated from Barrett (1970).

al., 1979). Forests usually are fertilized infrequently, causing nutrient availability to increase abruptly, then decrease slowly after fertilizer has been added. Only a few experiments have been reported in which differing levels of fertilizers were applied annually and changes in growth and canopy leaf area documented (Albrektson, Aronsson and Tamm, 1977; Aronsson and Elowson, 1980). In one such study, a Norway spruce (*Picea abies* L.) plantation in Sweden was supplemented with increasing levels of nitrogen and phosphorus. In striking contrast to the relationship depicted earlier in Fig. 2, amendments of nutrients permitted the spruce trees to maintain a high E even as L rose to 6 (Fig. 4). Eventually, however, as the canopy approached its maximum, efficiency decreased (Tamm, 1979). For shade-intolerant species such as pine, E begins to decrease at levels below 4 even with fertilization (Miller and Miller, 1976).

What physiological adjustments might explain the differing responses of E to increasing L observed in Figs. 2 and 4? Improved nutrition has been shown to increase photosynthetic efficiency, in some cases as much as 5-fold (Linder, McDonald and Lohammar, 1981). For many coniferous species however, only a modest increase in efficiency (~ 10 – 25%) can be expected (Linder and Ingestad, 1977; Brix, 1972). Yet this kind of change would be more than offset by the exponential decrease in irradiance associated with increasing L (Fig. 1).

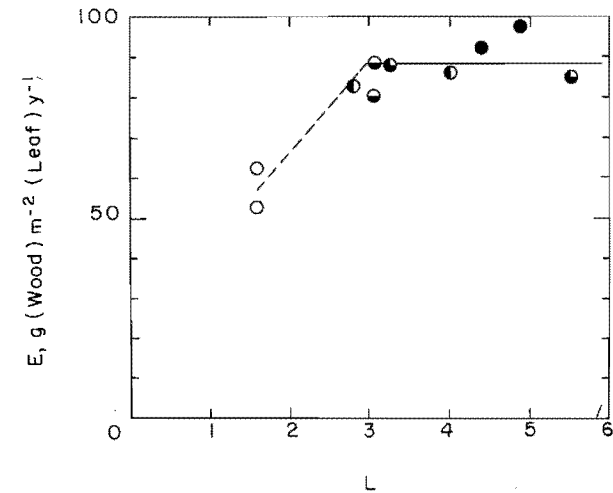


Fig. 4. In a Norway spruce plantation where increasing levels of nitrogen and phosphorus fertilizer were applied annually (O N_0P_0 , \bullet N_1P_1 , \circ N_2P_0 , \bullet N_3P_1), growth efficiency (E) increased and was maintained as leaf-area index (L) increased from 1 to 5.5. At higher values of L, E begins to decrease abruptly. After Albrektson *et al.* (1977) and from unpublished data of C. O. Tamm, University of Uppsala, Sweden.

Recently, the Swedish Coniferous Forest Project reported a unique long-term experiment in which researchers irrigated, fertilized, and combined these two treatments in a young plantation of Scots pine (*Pinus sylvestris* L.) to evaluate photosynthesis, respiration, and allocation to various components, including the ephemeral fine-root structure (Agren *et al.*, 1980; Aronsson and Elowson, 1980; Axelsson, 1981). The amount of photosynthate allocated to root production changed from nearly 70% of the total to less than 50% as the nutritional flux to roots increased. Tree water stress is normally of short duration because the sandy soils are deep and summer showers frequent. Irrigation probably increased decomposition and prolonged the life of small-diameter roots. Persson (1980) reported that production of roots less than 2 mm in diameter during the growing season was similar for all treatments, about 1.8 m tons ha^{-1} . However, the young forest had not yet reached its maximum canopy leaf area, and L varied from approximately 0.5 in the control to 1.25 in the combined fertilizer and irrigation treatment. Thus, when E was calculated in reference to the control, root production per unit of leaf area decreased progressively with irrigation, fertilization, and the combined treatment (Fig. 5). As carbon allocation to roots decreased, the proportion allocated to stemwood simultaneously increased (Fig. 5). This response seems analogous to that observed when levels of fertilization were increased for

Norway spruce (Fig. 4). Because wood production is the product of E and L, the combined treatment increased yields per hectare more than 3-fold, suggesting that nutrition, not temperature, is the primary limiting variable for native boreal tree species such as spruce and pine.

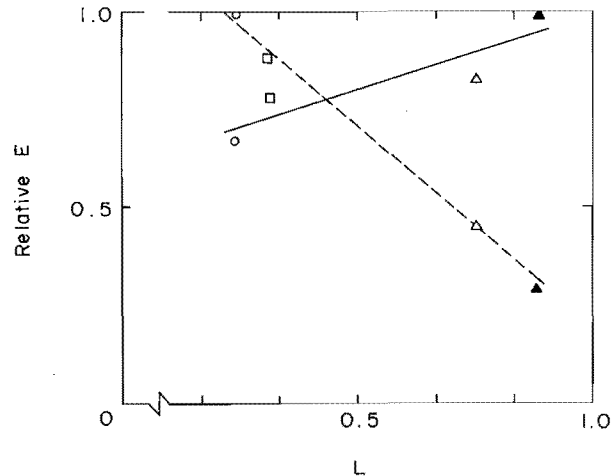


Fig. 5. In a young Scots pine plantation in Sweden where one site was left untreated (O), another irrigated every day (□), another fertilized annually (Δ), and the last fertilized and irrigated daily during the growing season (▲), the relative allocation of carbohydrates per unit of leaf area (E) decreased to roots (---) while increasing to stemwood (—) even though the canopy leaf-area index (L) increased from about 0.4 for the control to 1.0 in the combined fertilizer and irrigated treatment. Preliminary data furnished by A. Aronsson and others in the Swedish Coniferous Forest Project (1980) as part of a consulting review by R. H. Waring; report on file. Also see Alexsson (1981).

Changes in allocation may be expected to vary according to the inherent plasticity of the plant (Chapin, 1980). Some pasture plants have the capacity of varying carbohydrate allocation between roots and shoots by 8-fold as soil temperature and other factors change (Davidson, 1969a,b). Hydroponic experiments with tree seedlings also support the supposition that stress attributed to an unfavourable below ground environment increases the proportion of carbon allocated to roots (Linder and Ingestad, 1977). The opposite might be expected as a response to air pollution (Mann, McLaughlin and Shriner, 1980).

Recently, Grier *et al.* (1981) compared sub-alpine forests of different ages and concluded that older forests allocate substantially more carbon to roots than younger forests. They speculated that reduction in the supply of available

nutrients might contribute to increasing the carbon allocation in both absolute and relative terms to small diameter roots. In 120 year old lodgepole pine (*Pinus contorta* Loud.) forests, fertilization coupled with thinning to increase light significantly increased wood production per unit of leaf area (R. H. Waring, unpublished data). But no one has yet evaluated the E of root response to repeated fertilization of mature forests.

Keyes and Grier (1981) compared two 40 year old Douglas fir stands growing on sites with high and low fertility. Both showed similar total production but allocation varied; the stand on the poor site invested more than 50% of its dry matter production into roots whereas the other stand invested less than 25% into that category. These examples all serve to confirm that carbohydrate allocation patterns are strongly dependent upon a tree's environment.

D. A General Index of Vigor

When compared at similar levels of L, E may give clues to the relative importance of various environmental factors. Where different genetic stock is growing in a similar environment and at similar L or light levels, E can also provide a measure of difference in productive capacity. Nordmeyer (1980) used this approach to demonstrate that the native mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole) in the sub-alpine zone of New Zealand was less than half as efficient as the introduced North American conifer, lodgepole pine.

Using E as an index has even wider applications. Evidence is accumulating that stressed trees, even those limited by nutrients, may be more palatable to animals than unstressed trees (Bryant and Kuropat, 1980; Mattson, 1980; McLaughlin and Shriner, 1980) and more susceptible to disease as well (Schoeneweiss, 1975). Although a number of factors may increase the palability or susceptibility of stressed plants, a reduction in protective chemicals is certainly likely (Mooney and Chu, 1974; Mooney, 1972). These chemicals are often constructed largely of carbon; if reserves were exhausted, production of compounds such as resins, monoterpenes, and tannins would likely be reduced (Wright, Berryman and Gurusiddaiah, 1979). Apparently, wood production is reduced somewhat proportionally; where an epidemic of mountain pine beetles (*Dendroctonus ponderosae* Hopkins) was observed to be killing lodgepole pine, fatal attack densities and E were linearly related (Fig. 6). A similar relationship has recently been observed with a defoliating pine sawfly (*Neodiprion sertifer* Geoffr.) in Sweden (personal communication, S. Larsson and O. Tenow, University of Uppsala).

To summarize, growth efficiency, as estimated by wood production per unit of leaf area, seems a sensitive indicator to environmental stresses. At equivalent canopy leaf areas, E may be used to quantify the relative

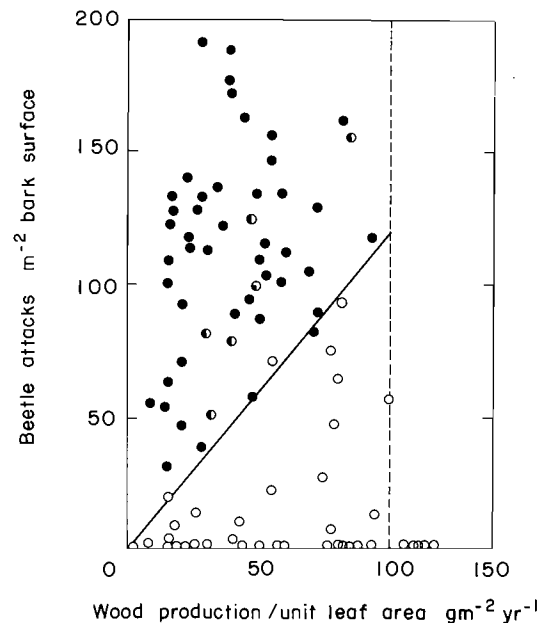


Fig. 6. Interrelationship between tree vigor (X-axis), the density of bark beetle attack (Y-axis) and the degree of mortality observed (blackness of circles) on lodgepole pine. Solid line represents the predicted attack level required to kill lodgepole pine of a specified vigor (after Waring and Pitman 1980). The dotted line indicates the threshold above which attacks by the beetle are unlikely to cause mortality. From R. H. Waring and G. B. Pitman, manuscript in review.

importance of various environmental factors upon growth or the genetic adaptation of different populations. Alone, E may serve as an index of vigor for the proportion of carbohydrates allocated to wood production decrease in parallel with a tree's resistance to insect attack and production of protective compounds.

IV. PRODUCTIVITY

A. Relation to Stocking

As previously noted, trees growing at low canopy leaf areas had little competition for light and were more efficient than those competing at higher canopy densities. However, if only a small fraction of the land is occupied by efficiently growing trees, the actual production may be less than when the canopy is more fully developed, even though individuals grow more slowly. As

long as canopy leaf area increases more rapidly than E decreases, productivity will increase with L (Fig. 7).

Numerous examples of relationships similar to that presented in Fig. 7 have been reported (Madgwick and Olson, 1974; Miller and Miller, 1976; Boyer, 1968). All of these, however, represented forests with relatively low (usually < 6) Ls. Where forests develop higher canopy leaf areas, gross production often reaches a plateau at about half the maximum L (Fig. 8); this response also has been reported for some agricultural species that can develop high canopy leaf areas, as for maize in Fig. 8. However, growth efficiency of the Douglas fir forest decreased 20 g m^{-2} (leaf) for each increase in a unit of L and varied similarly for maize (Fig. 2).

A number of published reports suggest that dry matter production of, for instance, alder (Zavitkovski, Isebrands and Crow 1974), pasture grasses (Pearce, Brown and Blaser, 1965; Donald, 1961), and oil palm (Rees, 1963) should peak at less than maximum L. In forests where stand mortality has been carefully monitored over a period of years, net wood production can be calculated by assuming that the biomass in dead stems is lost. When this approach was followed for the Douglas fir forest in Fig. 8, net productivity peaked at approximately half the maximum L and then decreased as increasing losses from mortality offset small growth increments by a large number of stems (Fig. 9). This is a significant point. When measurements of forest growth are made over short periods or trees cored to determine incremental growth, full mortality losses are not taken into account. From an

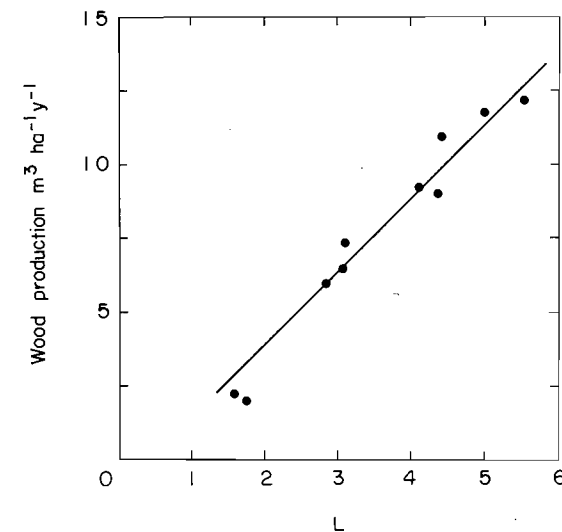


Fig. 7. Forest productivity increased linearly with increasing canopy leaf-area index (L) in a plantation of Norway spruce. Adapted from Albrektson *et al.*, 1977.

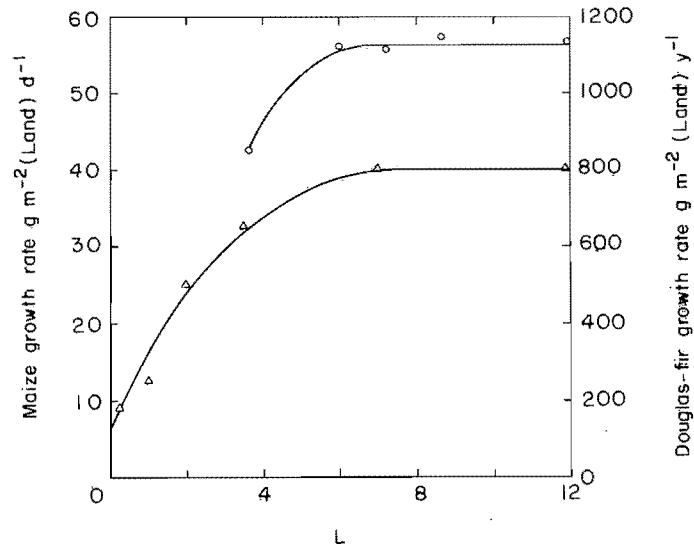


Fig. 8. When gross dry-matter production is plotted in relation to leaf-area index (L) for a stand of Douglas fir (O) or a field of maize (Δ), a plateau is reached above which production does not increase. Adapted from Waring *et al.* (1981) and from Williams *et al.* (1965).

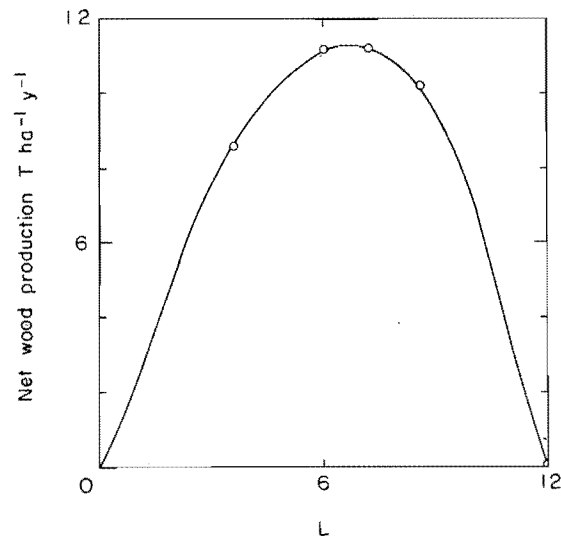


Fig. 9. When losses from mortality of more than 200 trees $\text{ha}^{-1}\text{y}^{-1}$ were subtracted from gross wood production at the highest canopy density (L), net wood production approached zero. The general response is a parabolic curve rather than an asymptotic one, as illustrated in Fig. 8. Adapted from Waring *et al.* (1981).

ecosystem standpoint, carbon stored in necromass is still counted as part of net primary production, along with leaves, twigs, and small-diameter roots that may be produced and die within the same season. In forestry and agriculture, however, the concept of production is generally limited to harvestable material and often excludes losses from mortality.

Gross above ground productivity or net ecosystem primary production may, in fact, decrease as maximum canopy leaf area is approached (Gholz, 1982). Certainly, foresters have long recognized a condition of stagnation in which height growth is inhibited at high levels of stocking on relatively poor sites (Smith, 1962; Daniel, Helms and Baker, 1979). There is evidence that under such conditions the canopy becomes restricted to the upper portion of the stem and that the actual canopy leaf area is reduced somewhat below the maximum obtained at lower stocking (Bormann, 1981).

B. Relation to Vertical Canopy Distribution

Although the maximum reported L_s are similar for crops of short stature, such as *Gladiolus* (Kira *et al.*, 1969), and those of giant stature, such as Douglas fir (Waring and Franklin, 1979), the productivity of dry matter is generally much higher for plants with elongated crowns than for those with compressed growth forms when grown in appropriately favourable environments (Kira and Shidei, 1967). Most trees have foliar densities of between 0.2–0.4 m^2 leaves m^{-3} air whereas agricultural crops have values an order of magnitude higher (Kira *et al.*, 1969). The advantage of having an elongated crown is that diffuse light can penetrate more efficiently, and direct solar radiation from angles below the zenith is better absorbed (Jahnke and Lawrence, 1965; Jarvis, 1981).

The greater efficiency associated with elongated crowns along with tolerance to low light levels help explain why many tree species are able to grow up through and replace shrubs and herbaceous cover that can reach the maximum L for the environment in periods of months (Ewel, 1977) or years (Marks and Bormann, 1972). In some regions, such as the Pacific Northwest of the United States, the dominant forests can develop a two- or three-storied canopy rising vertically more than 70 m. Under such circumstances, maximum L is not approached for at least 40 years after a forest is established (Waring and Franklin, 1979), although considerable mortality may be observed in the initial developing tree canopy.

The productivity of forest stands is then in part controlled by the extent to which the canopy is distributed vertically (Ford, 1975). In addition, the distribution of canopy on individual trees in relation to their total heights affects their growth efficiency and ability to respond to an improved environment after competing canopy leaf areas have been reduced. Foresters have long recognized this by identifying trees with low ratios of live crown to

bole length and, where economical, removing these from a stand. In developing models to predict stocking and growth in coastal Douglas fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests, P. Schroeder and R. H. Waring (manuscript in review) have significantly improved precision ($r^2 \geq 0.95$) by using estimates of E, total depth of canopy, and live crown ratio to predict stocking density.

C. Maximum Leaf Area and Equilibrium Biomass

Even when forests are allowed to grow without disturbance, they do not continue to accumulate biomass indefinitely. Eventually, the canopy reaches a maximum height in balance with the genetic potential of the vegetation and its maintenance cost in a given environment (Kira and Shidei, 1967). This was clearly demonstrated in 1000 year old redwood (*Sequoia sempervirens* Endl.) forests of northern California where trees on the alluvial floodplain reached heights of over 100 m while those on upper slopes never exceeded 30 m (Waring and Major, 1964). The leaf areas were not reported but, on the basis of allometric regressions with stem diameter, should vary in proportion to the maximum canopy height (Fujimori, 1977).

In the Pacific Northwest, graduate foresters estimated canopy leaf area and stem biomass using allometric equations (Gholz *et al.*, 1979) for a range of forests varying from arid zone pine to rain forest Sitka Spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock. Stands varied in age from 100 to more than 500 years. When accumulated stem biomass was plotted against estimated L, an upper boundary limit was approached in direct proportion to the maximum L (Fig. 10).

In a different region, with different genetic stock and environment, maximum accumulation of biomass in relation to canopy leaf area would differ (Waring *et al.*, 1978). The ratio of maximum biomass to maximum L should increase, however, with improving environment. For this reason, the ratio might serve as a sensitive indicator of how increasing carbon dioxide levels affect production.

D. Relation to Environment

If maximum rates of forest production are viewed across the United States (Fig. 11), certain geographical correlations are obvious. Productivity increases southward from the Canadian border to the Gulf Coastal Plain in the eastern United States, decreases westward from the Mississippi River into the Great Plains, and increases again due to the maritime influence of the Pacific Ocean, but, overall, is constrained by chains of north- to south-oriented mountain ranges.

In the mountainous western United States, as in other regions with high relief and few meteorological stations, it is difficult to evaluate climate

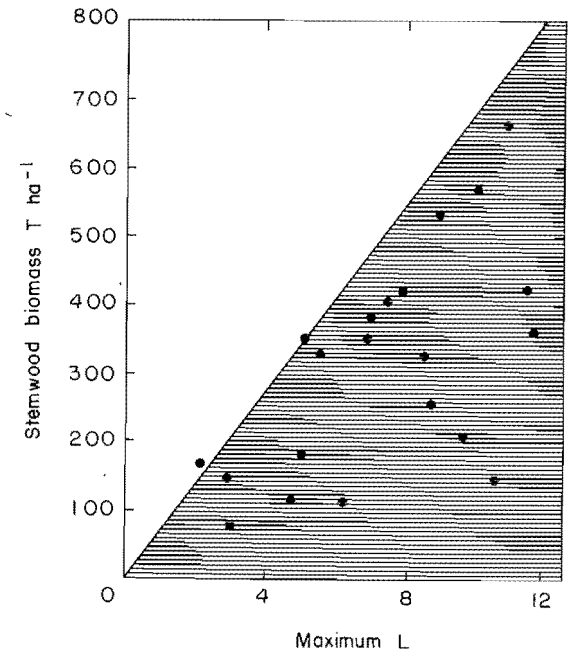


Fig. 10. In one part of the Pacific Northwest region of the United States, the accumulated stemwood biomass in older aged forests approached an upper limit (drawn by eye) in proportion to the maximum leaf-area index (L). Adapted from Waring (1980).

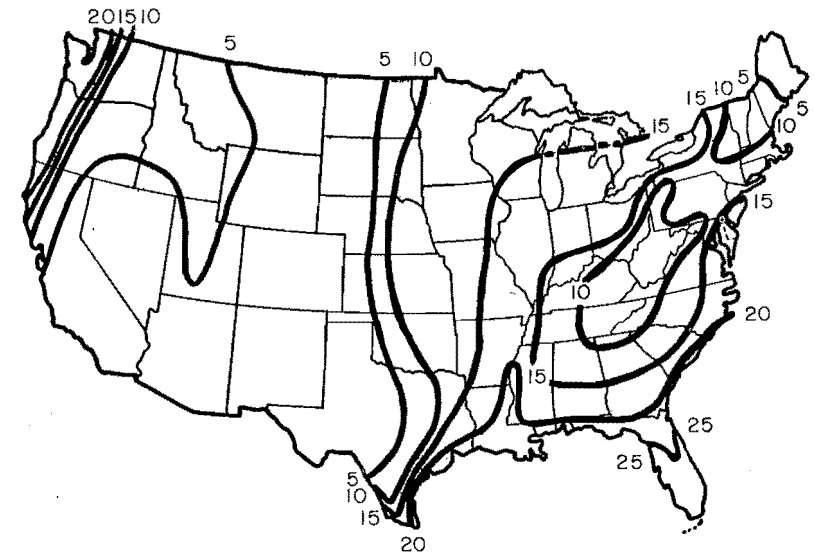


Fig. 11. Estimated maximum woody biomass production in the United States, $T ha^{-1} y^{-1}$. After Ranney (1979).

accurately. Therefore, a considerable effort has been made to correlate structural features such as maximum canopy leaf area directly with productivity. Within one small region of central Washington, precipitation varied from the crest of the mountains to the valley from >2500 to <250 mm annually (Franklin and Dyrness, 1973). Correlations of maximum L with forest productivity reflect changes in this climatic gradient (Fig. 12). Grier and Running (1977) reported a similar range in leaf area was correlated with precipitation or evaporation across a transect of the Oregon Cascade mountains immediately to the south of the Washington study (Fig. 13). Gholz (1982) reported that net primary production generally increased along the same transect in relation to increasing maximum L but eventually reached a plateau at high levels of L. Gholz also demonstrated that extremely cold

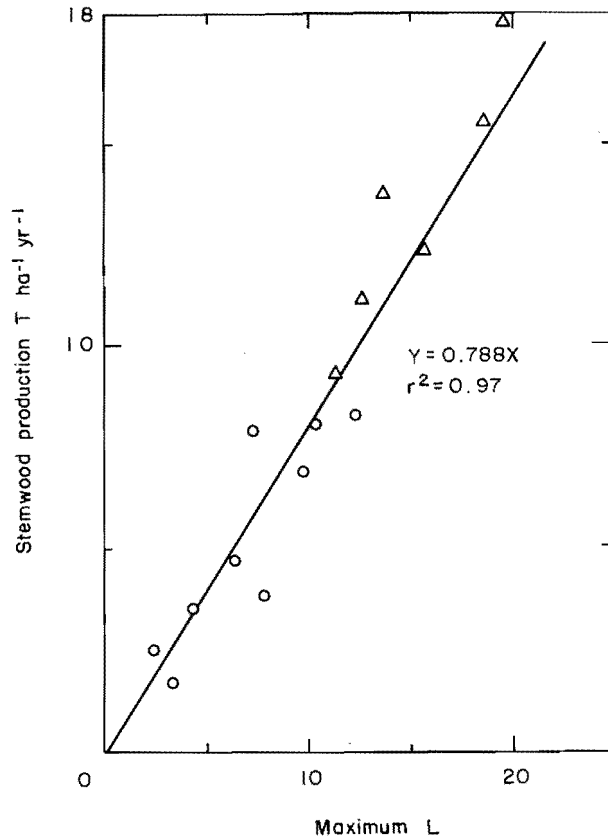


Fig. 12. In two adjacent regions (Δ and O) of east-central Washington, a linear relationship between gross wood production and maximum leaf-area index (L) was reported. Adapted from Schroeder *et al.* (1982).

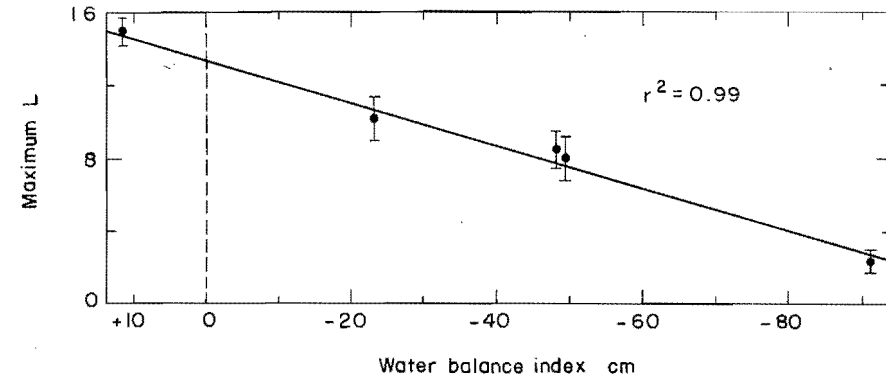


Fig. 13. Along a transect from Pacific coast forests of Sitka spruce inland to shrub-covered deserts, maximum leaf-area index (L) decreased with increasing evaporation and decreasing summer precipitation and soil-water storage. Bars indicate ranges observed in L. Adapted from Grier and Running (1977).

winter temperatures had an impact on reducing productivity, which agrees with other regional studies reported by Waring *et al.* (1978).

Kira and Shidei (1967) made the simple assumption that gross primary production should be related to L and length of growing season (S), and a fair correlation was developed for a number of temperate and tropical wet-forest regions (Fig. 14). In the eastern United States, where maximum canopy leaf area is quite uniform, mean annual temperature or length of growing season correlates with gross production (Leith and Whittaker, 1975).

In regions where soil drought, infertile soils, or mild winter climates predominate, no simple correlation with either L or growing season should be expected. In a small, environmentally diverse portion of western Oregon, data on solar radiation, temperature and plant water stress gathered through the year were used to estimate net photosynthesis per unit area of leaves for four distinctly different environments dominated by Douglas fir (Emmingham and Waring, 1977). Although canopy leaf areas varied only slightly, productivity ranged from about $250\text{--}500\text{ t ha}^{-1}\text{y}^{-1}$, in direct proportion to the simulated annual net photosynthesis. During the dormant season from October through April or May, the proportion of carbon uptake predicted ranged from 30% at the highest elevation site to 55% in an inland valley, demonstrating that environmental correlations for evergreen species must often extend throughout the year.

Although canopy leaf area may be locally related to forest productivity, a general model would seem to require knowledge of detailed processes that take into account environmental constraints upon photosynthesis, respiration, growth, storage reserves or carbohydrates, and seasonal necrosis of

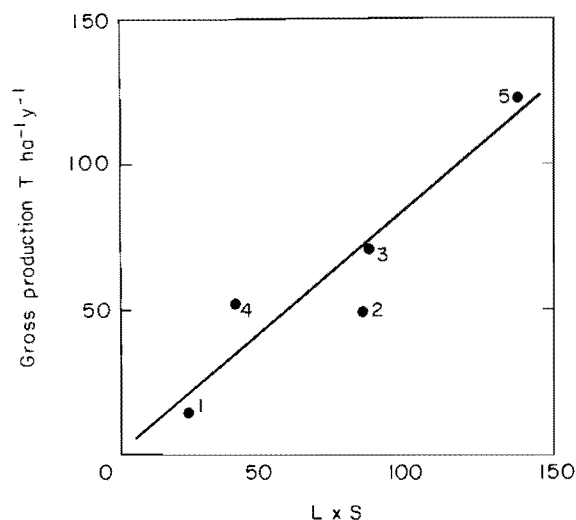


Fig. 14. Gross production was reported to increase as the product of canopy leaf-area index (L) and number of months of growing season (S) increased. The numbered points refer to forests exclusively in wet temperate or tropical regions: (1) *Fagus* forest in Denmark, (2) *Castanopsis* forest in Japan, (3) broad-leaf forests in Japan, (4) tropical humid forests of the Ivory Coast in Africa, and (5) tropical forests of southern Thailand. Adapted from Kira and Shidei 1967).

various tissues (Specht, 1981). Toward that goal, experiments that demonstrate the relative importance of specific environmental factors upon E at comparable Ls will be useful.

V. ESTIMATING CANOPY LEAF AREA FROM SAPWOOD CONDUCTING AREA

The previous sections underline how important an accurate estimate of canopy leaf area and its vertical distribution can be. The widely applied correlations between tree diameter at breast height (1.37 m) and foliage mass or area (Kira and Shidei, 1967; Whittaker and Woodwell, 1968) are not adequate for experiments with canopy manipulations because trees of the same diameter will differ both in the amount and distribution of their foliage (Whitehead, 1978).

An improvement in predicting canopy leaf area on individual trees over that usually obtained with such parameters as basal area is founded on functional relationships with conducting wood cross-sectional area. Observing that foliage weight and sapwood conducting area in the crown were linearly

related, Shinozaki *et al.* (1964a,b) drew the analogy of a pipe system, which suggested that the area of functioning conducting cells might be used to estimate canopy leaf area. Large trees have an interior core of heartwood which provides physical support but no longer conducts water (Zimmermann, 1971). A correction for the change in foliage weight was required because specific leaf weight varies with the amount of light available at different levels in the canopy (Kira *et al.*, 1969; Tadaki, 1970; Kellomaki and Oker-Blom, 1981). The "pipe" was extended from the base of the crown down to breast height. Although good linear correlations were reported for a number of species (Grier and Waring, 1974; Waring *et al.*, 1977; Dixon, 1971; Whitehead, 1978; Rogers and Hinckley, 1979), most of the analyses had been made on small trees with limited lengths of branch-free boles or on trees with comparable proportions of live crowns.

On large trees, the amount of conducting area at the base of the crown and at breast height can differ by more than 50% (Morikawa, 1974). Within a particular stand, the taper in sapwood area can be accurately estimated by felling some trees and cutting out sections at the base of the crown, at breast height, or elsewhere. Cores might also be extracted at various heights along the bole to determine the change in conducting area. Within the crown itself, however, the taper in sapwood area seems directly proportional to changes in the canopy leaf area (Fig. 15). This makes it possible to accurately describe canopy distribution in a single tree (Fig. 16) or by suitable sampling a forest stand (Long *et al.*, 1981).

The above observations imply that a number of parallel changes in the conducting properties of sapwood must occur. The simplest possibility is that the conductivity of wood in the bole decreases from the crown to the ground as the area of conducting wood increases. It is well known that denser and older wood exhibits poorer conducting properties than recently formed wood in rapidly growing sections of a tree (Gregory, 1977; Comstock, 1965; Booker and Kininmouth, 1978). Whether the actual conducting properties of a cross-section remain constant or are offset by variation in water potential gradients and fluctuation in water content is not known. Only very recently have methods been developed to determine the conducting efficiency of whole cross-sections (Booker, 1977; Edwards, 1980). Preliminary results suggest that the saturated conductivity of wood in the crown may not be a constant (Edwards, 1980). The tree crown, however, is known to rarely maintain a saturated condition; thus, the effective conductivity may well reflect the assumed relationship (Whitehead and Jarvis, 1981).

Table 1 presents coefficients that may be useful for preliminary estimates of canopy leaf area where the named species grow. In general, species well adapted to arid climates or to the colonization of exposed habitats appear to have lower ratios of foliage per unit of conducting sapwood area than those adapted to more favourable environments (Waring, 1980).

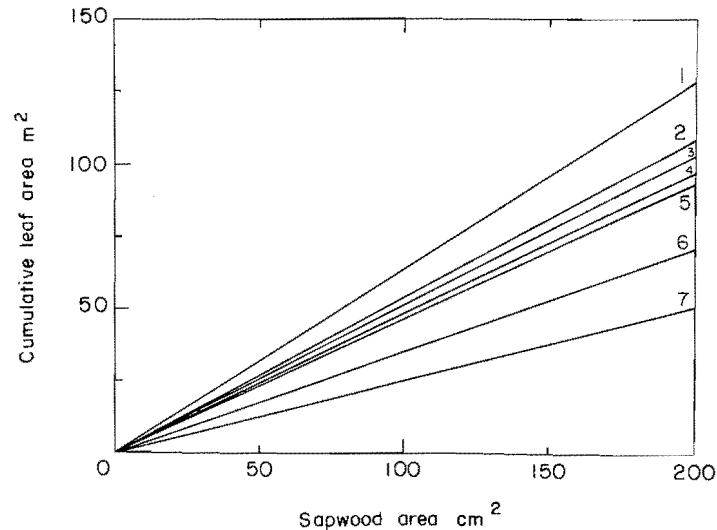


Fig. 15. Cumulative leaf area is closely related to the cross-sectional area of conducting sapwood in the crowns of sampled western United States conifers. Each regression line is based on a sample of five trees ranging in diameter from 5–25 cm. Each crown was sampled in quarters, providing a total of 20 points for each regression (1) *Abies amabilis* (Dougl.) Forbes $r^2=0.96$, (2) *Pseudotsuga menziesii* $r^2=0.97$, (3) *Sequoia sempervirens* $r^2=0.97$, (4) *Abies grandis* Lindl. $r^2=0.98$, (5) *Tsuga heterophylla* $r^2=0.96$, (6) *Picea engelmanni* (Parry) Engelm. $r^2=0.99$, (7) *Pinus ponderosa* $r^2=0.94$. From Waring *et al.* (1982).

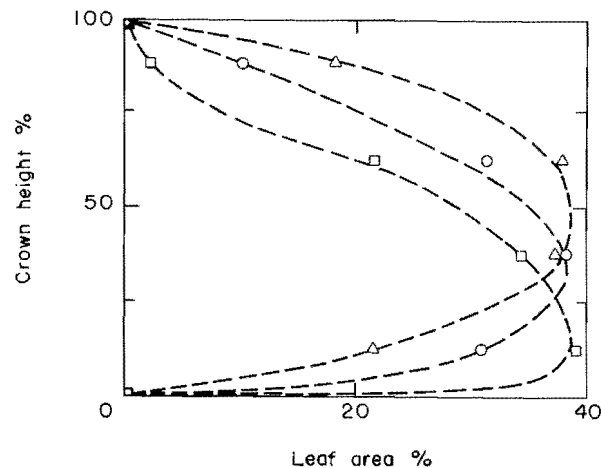


Fig. 16. With the regressions furnished in Fig. 15, it is possible to describe the distribution of canopy leaf area vertically in the crown. Data in this case represent averages from five trees for each of the three species: (Δ) Douglas fir, (O) ponderosa pine, and (□) grand fir. From Waring *et al.* (1982).

Table 1

Ratios of projected leaf area to sapwood cross-sectional area for selected conifers

Species	Leaf area : sapwood area $\text{m}^2 \text{ cm}^{-2}$
<i>Abies amabilis</i> (Dougl.) Forbes	0.64 ^a
<i>Abies grandis</i> Lindl.	0.48 ^a
<i>Abies lasiocarpa</i> (Hook.) Nutt.	0.75 ^b
<i>Abies procera</i> Rehd.	0.27 ^{*c}
<i>Juniperus occidentalis</i> Hook.	0.18 ^d
<i>Picea engelmannii</i> (Parry) Engelm.	0.35, ^a 0.29 ^b
<i>Picea sitchensis</i> (Bong.) Carr.	0.45 ^e
<i>Pinus contorta</i> Dougl.	0.15, ^{*a} 0.18, ^b 0.17 ^{*c}
<i>Pinus nigra</i> var. <i>maritima</i> (Ait.) Melv.	0.15 ^{*f}
<i>Pinus ponderosa</i> Dougl.	0.25 ^a
<i>Pinus sylvestris</i> L.	0.14 ^{*g}
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	0.54 ^a
<i>Tsuga heterophylla</i> (Raf.) Sarg.	0.46 ^a
<i>Tsuga mertensiana</i> (Bong.) Sarg.	0.16 ^{*a}

* Coefficient determined at 1.37 m above ground level rather than at base of crown.

^a Waring *et al.* (1982).

^b Kaufmann and Troendle (1981), converted to projected area by dividing by 2.5.

^c Grier and Waring (1974), converted from biomass to leaf area in Waring (1980).

^d H. L. Gholz (1980).

^e Whitehead (1981).

^f J. M. Roberts, unpublished data, Inst. of Hydrol., Wellingford, England.

^g Whitehead (1978).

VI. SUMMARY AND CONCLUSIONS

In specific regions, maximum L is a good estimator of the productive capacity of native vegetation in different environments as well as an index to maximum biomass accumulation. As the environment becomes more favourable, locally or regionally, maximum L should increase in concert with E and forest productivity. More research is needed to relate how atmospheric and edaphic factors combine to influence forest canopy development and growth.

Canopy leaf area and its vertical distribution can now be accurately estimated through correlations with conducting sapwood area throughout the crown. Species within the same genera have widely differing ratios of leaf area to sapwood area, with those adapted to exposed and arid environments carrying sometimes only a third the foliage per unit of conducting area of those growing in less harsh situations. To estimate canopy leaf area on large trees, the linear taper in sapwood area from breast height (1.37 m) to the base of the crown must be determined. However, the extent to which taper varies with stocking density and environment is not known.

Experiments designed to compare tree growth efficiency (E) over a range of canopy leaf areas (L) provide a means of assessing the relative importance of various factors upon productivity at a given reference point. At high canopy densities, light is often limiting; thus, for forests supporting canopies with potential Ls ranging from 10–20, comparison is recommended at half the maximum canopy leaf area—the point at which productivity should reach a plateau. As the environment for a particular population of plants becomes more favourable and the vertical distribution of foliage more optimally displayed, wood growth per unit of leaf area should increase as a result of improved photosynthetic efficiency and a reduction in the relative allocation of carbon to roots.

E also may indicate the susceptibility of trees to native insects because the production of protective chemicals is reduced in parallel with wood growth. Thus, an individual tree or entire forest may be ranked with regard to risk from attack. More research is required to ascertain whether different insects attack at similar thresholds of tree vigor.

Although pieces of scientific puzzles are scattered throughout the literature, I am moved to reflect that framing the picture's outline was most effective where groups of scientists gathered to focus their talents. For the future, small research teams may prove to be essential in completing the picture of how trees and forests grow.

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