

AN ABSTRACT OF THE THESIS OF Ram Oren for the degree of Doctor of Philosophy in Forest Science presented on September 25, 1984.

TITLE: Leaf area index and specific leaf weight: keys to interpreting canopy photosynthesis and stand growth.

Abstract approved: Signature redacted for privacy.  
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#### ABSTRACT

Two physiological factors are of major importance to tree and stand growth: (1) the photosynthetic rate of foliage and (2) the amount of foliage. If carbohydrate allocation patterns remain constant, stand growth should be related directly to total canopy photosynthesis. From a literature analysis I assess methods of relating photosynthetic rates to biochemical, anatomical, and structural characteristics of foliage. A number of these foliage characteristics were found to be interrelated. Specific leaf weight was shown to be a valuable index for comparing photosynthesis by various parts of a tree canopy

over a season or throughout an entire year. Mean annual photosynthetic rate in five separate portions of a spruce canopy was directly proportional to observed differences in specific leaf weight ( $r^2 = 0.99$ ). Annual carbon uptake was a function of total foliage biomass ( $r^2 = 0.96$ ). When foliage biomass at each crown segment was adjusted for differences in specific leaf weight, reflecting differences in photosynthetic rates, the predictive equation further improved ( $r^2 = 0.99$ ). Specific leaf weight is recommended as an index for comparing the relative effects of various silvicultural treatments on photosynthesis.

I then evaluated how stand growth and canopy leaf area were related by analyzing 24 years of growth records from a Pinus ponderosa (Laws.) experiment. The experiment included a wide range in initial stocking and partial control of understory vegetation (Barrett 1982). I found that treatment effects on tree growth can be evaluated at low values of stand leaf area from comparison of growth efficiencies (wood produced per unit leaf area) among plots of similar canopy leaf area. By comparing stand growth with stand leaf area, I concluded that the major effect of removing understory vegetation was to

speed the development of the canopy. This interpretation was also supported by a comparison of the rate of leaf area development on plots with and without understory vegetation at comparable levels of canopy leaf area. Comparing stands at a similar canopy leaf area is advised for assessing how treatment affects stand development. This is a valuable alternative to analyzing treatment effects at one point in time and helps to explain the results of many fertilization experiments.

Leaf Area Index and Specific Leaf Weight:  
Keys to Interpreting Canopy Photosynthesis  
and Stand Growth

by

Ram Oren

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Signature redacted for privacy.

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For: Ram Oren

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"I learnt from all my teachers, and from my students I learnt even more."

(Ancient Hebrew Proverb)

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An Indian proverb says "Nothing is so strong as gentleness, nothing so gentle as real strength." Three people taught me so by example: Susan Stafford, Paul Adams and John Tappanior. Susan listened and encouraged me during times of dissolution with the ways of science, and helped in channeling anger into learning and constructive criticism. Paul, apart from providing most helpful suggestions for improving the quality of this thesis, drew my attention to research fields other than my own and widened the scope of my interest. John was able to ask questions which made me think about the actual, not only the theoretical, meanings of my results. John also taught me that even scientists can separate ego from ideas, thus

not allowing the ego to stand in the way of free discussion of ideas.

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# LEAF AREA INDEX AND SPECIFIC LEAF WEIGHT: KEYS TO INTERPRETING CANOPY PHOTOSYNTHESIS AND STAND GROWTH

## INTRODUCTION

Forest production is dependent upon 1) total photosynthesis by all trees in a stand and 2) the fraction of photosynthate that is allocated to stemwood. Maintenance respiration by living tissue drains a large amount of photosynthate away from stemwood production.

Total stand photosynthesis is the product of the amount of foliage and the photosynthetic rate per unit of foliage. Amount of foliage can be estimated indirectly by a variety of non-destructive techniques (Kira and Shiedi 1967, Waring et al. 1982). Photosynthetic rate is difficult to measure directly, however. In general, photosynthetic rates can be expected to decline with increasing canopy density as less light, water, or nutrients are available per unit of foliage. Within a single tree, more exposed foliage absorbs more radiation and has higher photosynthetic rates than shaded foliage.

A variety of biochemical, anatomical, and structural characteristics of leaves have been correlated with



photosynthetic activities in agricultural crops and tree seedlings (Tsel'niker 1979, Kallis and Tooming 1974). In Chapter I, I review these studies and analyze data gathered on various tree species in search of a seasonal index of photosynthetic rate. By multiplying the amount of foliage in various layers of a tree or forest canopy by an index of photosynthetic rate, annual carbon uptake may be estimated.

Photosynthate is allocated differentially amongst roots, foliage, and stemwood depending upon whether or not water or nutrients are limiting (Axelsson 1981, Waring 1983). Because stem growth has relatively low priority compared to foliage and feeder roots, the ratio of stemwood produced per unit of foliage from a given amount of photosynthate is a good measure of variation in photosynthate partitioning (Waring 1983). By applying an index of canopy photosynthesis developed in Chapter I, I evaluate in Chapter II how pine forests maintained at various densities differ in their allocation of photosynthate to stemwood.

The amount of living tissue in a tree, and therefore its maintenance respiration increase as trees grow larger. The amount of living tissue in the stem is closely related

to the volume of sapwood present. For a given amount of sapwood, maintenance respiration increases exponentially with temperature (Waring and Schlesinger in press). In a given environment, the effect of maintenance respiration on production is related directly to the amount of sapwood present in a tree or stand.

In Chapter II, I estimate the amount of foliage present in pine stands, growing with and without understory vegetation, as the stands developed over a 24 year period (Barrett 1982). Even without an estimate of canopy photosynthesis, the total amount of carbohydrates allocated to stemwood can be calculated from knowledge of the amount of foliage present in the stands and the growth of stemwood per unit of foliage (Waring et al. 1981). Further, by analyzing the trends in the rate of foliage development and changes in stemwood production per unit of foliage, I project future stand wood production.

CHAPTER I.

INDIRECT MEASURES OF CANOPY PHOTOSYNTHESIS

by

R. OREN

## Indirect Measures of Canopy Photosynthesis

### Abstract

Canopy photosynthesis is difficult to measure directly on trees with large and seasonally changing canopies. Most models that predict photosynthesis require detailed knowledge of environmental and canopy characteristics. In this paper, I review progress in relating measurements of photosynthesis to various biochemical and structural characteristics of leaves in search of an indirect integrator of seasonal and annual net photosynthetic rate.

A number of leaf chemical and structural characteristics vary in concert with photosynthesis. The amount of photosynthetic enzymes can change in a matter of hours, the number of chloroplasts may respond in days, and specific leaf weight fluctuates seasonally. The slower response characterized by specific leaf weight is advantageous for seasonal or yearly estimation of mean annual photosynthetic rate. An analysis comparing variations in photosynthetic rate to variations in specific leaf weight showed excellent correlation in

hardwood and conifer tree canopies. Annual carbon uptake reflects both the photosynthetic rate and the amount of foliage biomass.

Annual carbon uptake of different segments in a mature spruce crown was closely related to leaf biomass ( $r^2 = 0.96$ ); the relationship was further improved when leaf biomass of each segment was weighted by that segment's specific leaf weight ( $r_2 = 0.99$ ). When the product of foliage biomass and specific leaf weight is expressed on a relative basis, it may serve as a sensitive index to the effects of natural disturbances and silvicultural practices upon canopy photosynthesis.

## CHAPTER 1

### INDIRECT MEASURES OF CANOPY PHOTOSYNTHESIS

Ram Oren

#### Introduction

Many natural disturbances and silvicultural practices in forests affect stand growth largely as a result of modifying canopy photosynthesis. Canopy photosynthesis, expressed for example as annual carbon uptake, is dependent to a significant extent upon the amount of foliage present and its photosynthetic efficiency.

Foliage biomass or leaf area may be estimated by a number of non-destructive techniques (Kira and Sheidi 1967; Kaufmann and Troendle 1981; Waring et al. 1982). However, photosynthetic rates in forests has been difficult to measure or to model because the seasonal and spatial variation associated with carbon uptake in large trees requires intensive sampling. Fortunately, certain biochemical and structural characteristics of leaves have been found to vary with photosynthetic rates (Mahon et al. 1983; Boardman 1977). I will briefly review some of the

interrelations among structure, composition, and photosynthesis in search of a sensitive and convenient measure of seasonally integrated photosynthesis for a part or for all of a tree canopy. I will provide evidence from an analysis of published data that a structural index, specific leaf weight, averaged for the entire canopy, is an indirect measure of mean annual photosynthetic rate. Leaf biomass can then be multiplied by specific leaf weight to provide an index of canopy photosynthesis that generally fulfills the aforementioned criteria.

### Discussion

#### A. Biochemical properties

Concentrations of a number of leaf enzymes and pigments involved in photosynthesis vary as leaves are placed under different conditions (Doehlert and Walker 1981; Tsel'niker 1979; Lewis 1972). Among the most important are the carboxylation enzyme, RuBP carboxylase, and the chlorophyll pigments (Schnyder et al. 1984; Sampath and Kulandaivelu 1983). Chlorophyll and RuBP carboxylase contents are usually higher in more exposed foliage and in

environments more favorable for photosynthesis (Berry and Downton 1982; Louwarse and Zweerde 1977; Lewandowska and Jarvis 1977). Although the relationships between photosynthesis and concentration of carboxylation enzyme or chlorophyll are strong (Louwarse and Zweerde 1977; Tsel'niker 1977), the concentration of these materials respond rapidly to changing environmental conditions; i.e. within seconds to days (Lewandowska and Jarvis 1977; Gross 1982). So rapid are the changes that sampling requirements are too high for most ecological studies focused on integrated measures of seasonal or annual photosynthesis.

## B. Structural indices

Under stable conditions leaf structure also correlates well with photosynthetic rates, however, structural characteristics vary little compared with the variations in enzyme and pigment concentrations (Boardman 1977). For example, the ratio of internal (mesophyll) area to external surface area correlates well with chlorophyll content and carboxylation enzyme levels in

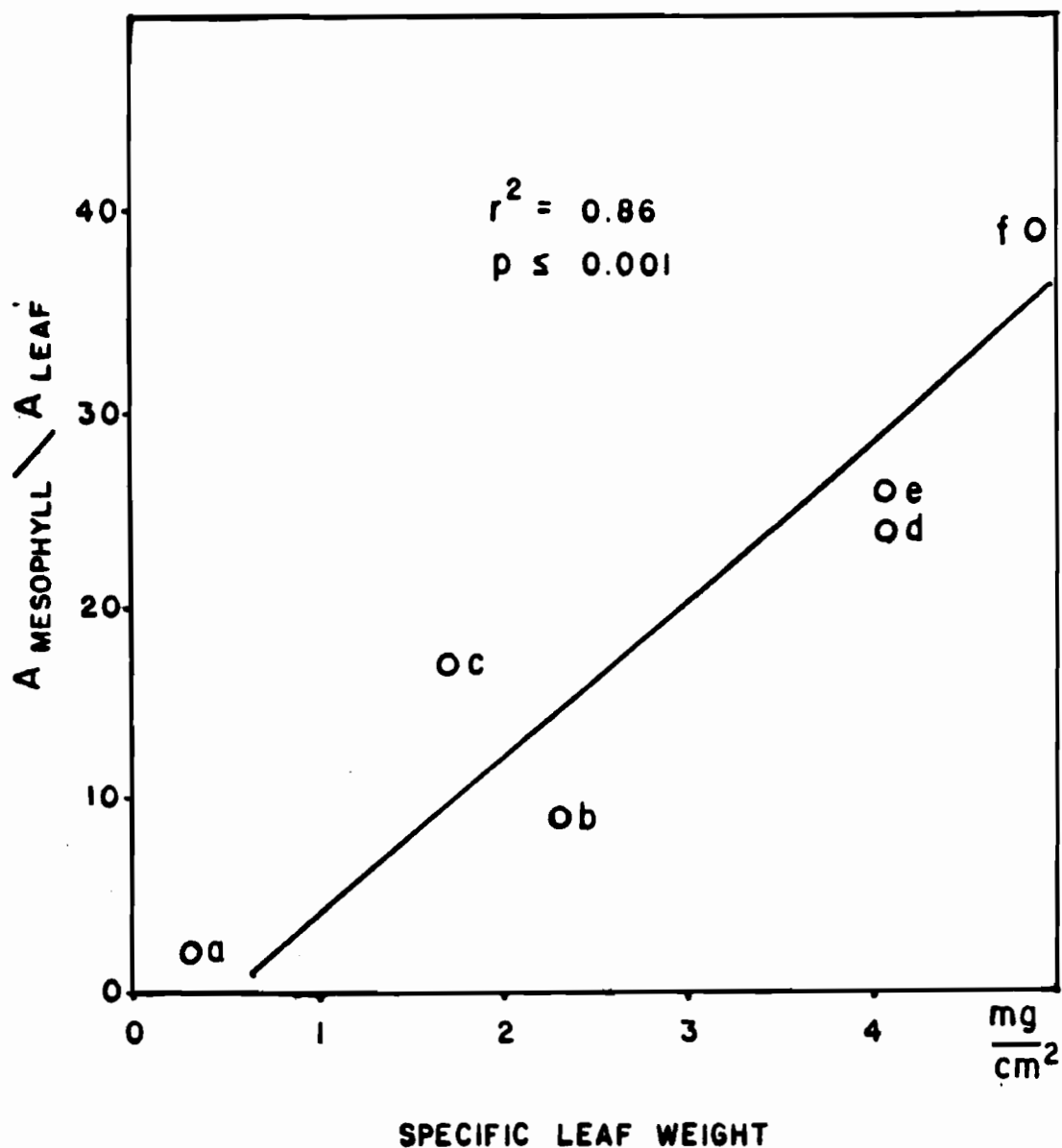


leaves exposed to stable environments (Nobel 1976). This ratio also varies directly with photosynthesis because it reflects the total photosynthetically active radiation around the leaf (Nobel et al. 1975; Nobel 1977, 1980; Lewis 1972). In the changing environments experienced by trees, however, the internal/external area ratio changes little (Louwerse and Zweerde 1977; Boardman 1977), reflecting conditions at the time of leaf formation and not changing thereafter.

Another structural index, the ratio of leaf thickness/leaf width, decreases in more shaded environments (Aussenac 1973; Brehmer 1981) because shaded leaves have fewer layers of parenchyma cells than leaves in more exposed environments (Nobel 1976; Louwerse and Zweerde 1977). Because the additional layers of parenchyma cells contribute to both leaf thickness and to mesophyll area, leaf thickness correlates well with the ratio of internal/external leaf area (Turrell 1936; Nobel et al. 1975; Nobel 1976, 1977). As an index of photosynthesis, however, leaf thickness has the same drawback as the internal/external area ratio; it does not change much with variation in the environment subsequent to leaf formation (Ewers 1982; Loach 1967; Nobel 1976).

Specific leaf weight (SLW), expressed as dry mass per unit of projected leaf surface area, correlates well with both the ratio of leaf thickness/leaf width and with internal/external leaf area (Dornhoff and Shibles 1976; Nobel et al. 1975), at least during the first growing season (Fig. 1). Moreover, seasonal changes in SLW can account for variations in storage carbohydrates that are accumulated during periods favorable for photosynthesis and are depleted during unfavorable periods (Ericsson 1979; Chatterton 1972; Smith et al. 1981). Changes in SLW have also been correlated with ambient irradiance (Tucker and Emmingham 1977; Drew and Ferrell 1977; Del Rio and Berg 1979).

From this survey, I conclude that SLW may be an appropriate measure of seasonal variation in photosynthetic rate. Indeed, photosynthetic rate in annual crops is highly correlated with SLW (Pearce et al. 1969; Kallis and Tooming 1974; Dornhoff and Shibles 1976; Louwerse and Zweerde 1977).

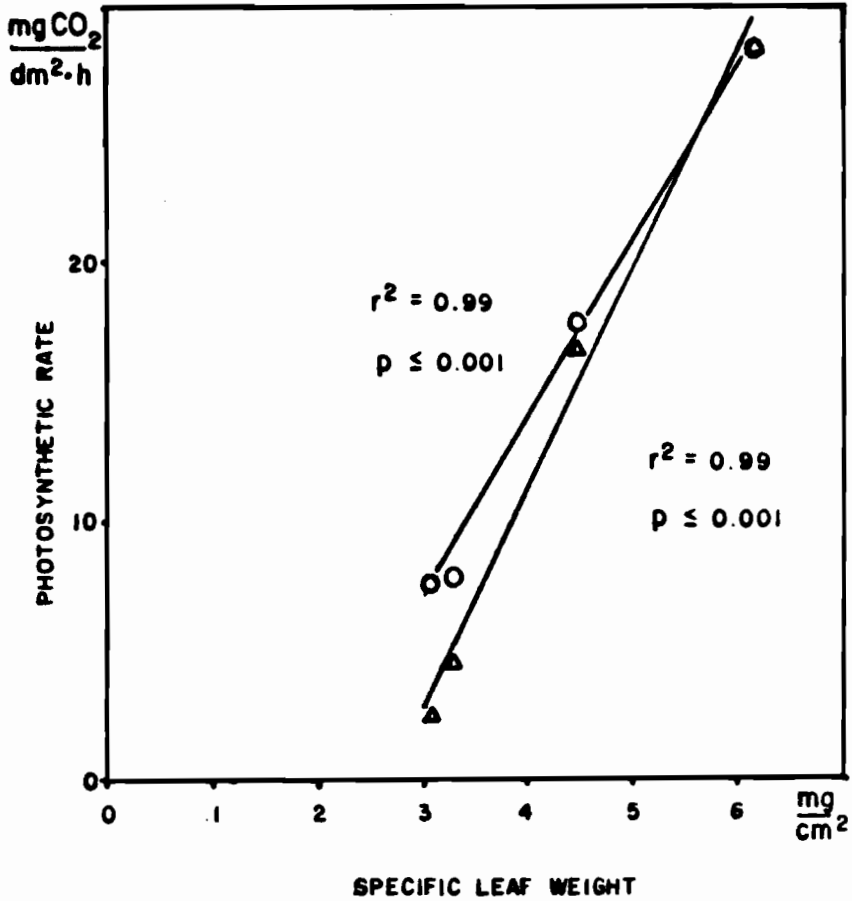


- I. 1. Relationship between mesophyll area per unit leaf area ( $A_{\text{mesophyll}}/A_{\text{leaf}}$ ) and specific leaf weight among plants differing in growth form and leaf morphology. Symbols: a = Mnium ciliare, b = Plectranthus parviflorus, c = Beta vulgaris, d = Hyptis emoryi, e = Encelia farinosa (well watered), f = E. farinosa (under water stress). Recalculated from Nobel (1980).

### C. Correlation between specific leaf weight and photosynthesis in trees

A literature search provided data from which I could calculate SLW and evaluate the relationship between photosynthetic rate and SLW in tree species. In silver birch (Betula pubescens Ehrh.) and in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) seedlings grown under various light levels, photosynthetic rate was related to ambient light conditions and SLW (Nygren and Kellomaki 1983, Fig. 2; Brix 1967). Photosynthetic rates at light saturation increased proportionally for all specific leaf weights (Fig. 2). Similarly, Alnus glutinosa L. seedlings grown under high illumination developed leaves with two-fold greater SLW and showed photosynthetic rates 2.5 times greater than leaves from plants growing in shade (Gordon and Wheeler 1978).

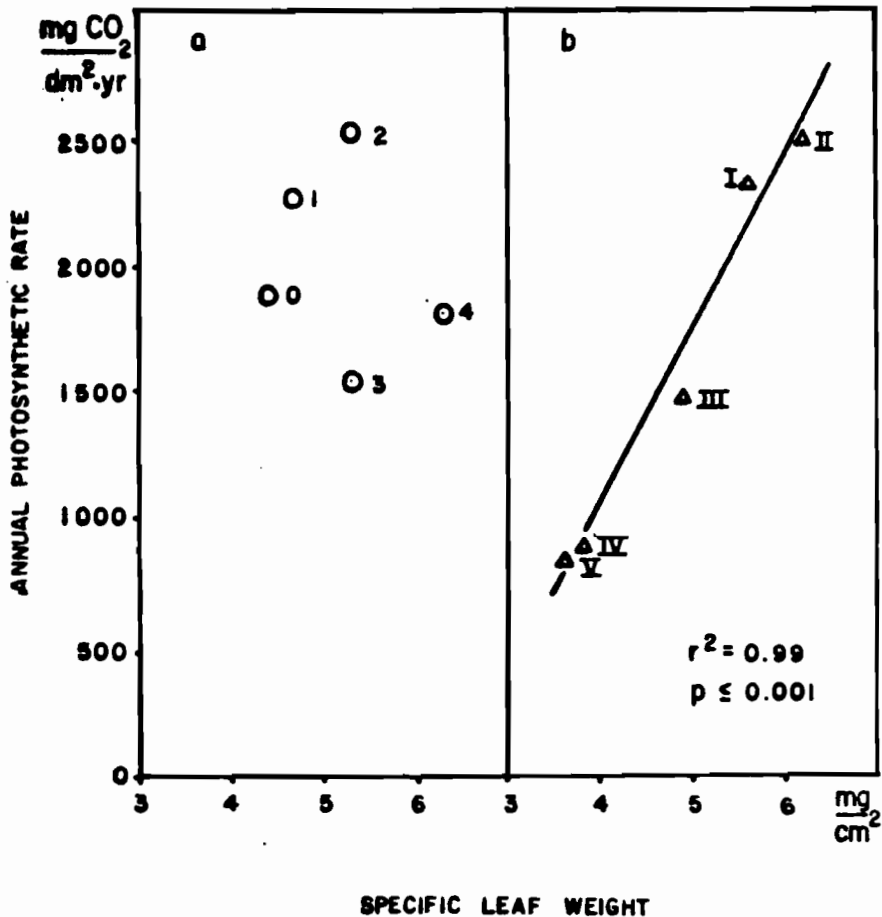
With large trees, only a few studies report data for both photosynthetic rate and SLW. For a mature beech (Fagus sylvatica L.), a broad-leaved deciduous species, specific leaf weight of sun foliage increased two and a half fold over that of shade foliage; this increase was



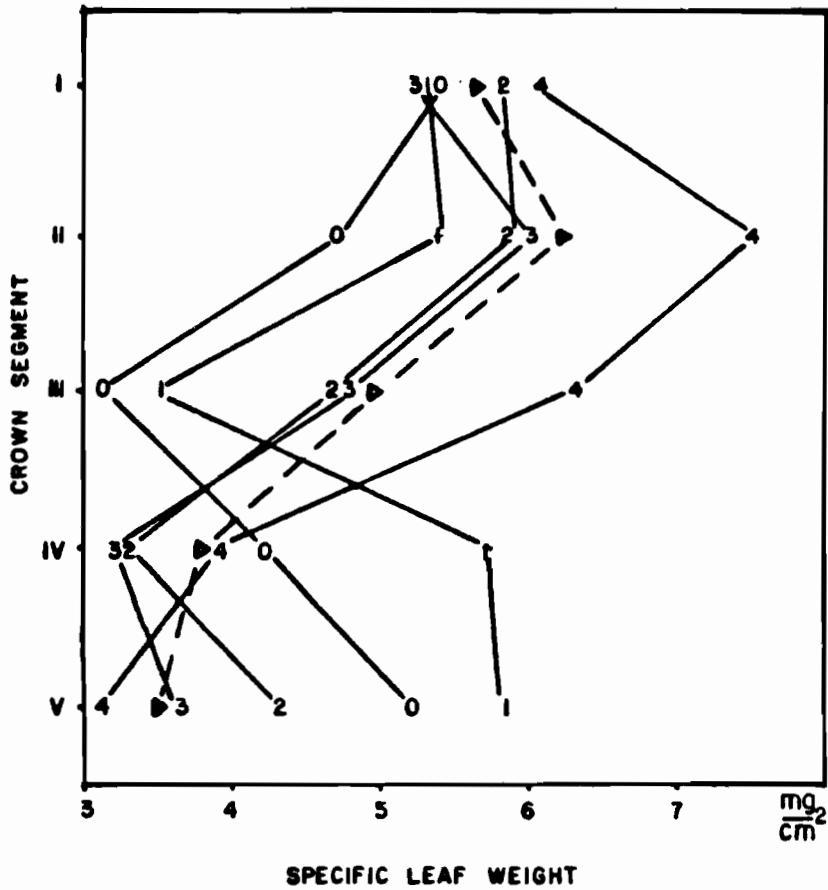
- I. 2. Relationship between photosynthetic rates at light saturation (O) and at ambient light intensity ( $\Delta$ ) and specific leaf weight in Betula pendula seedlings. Recalculated from Nygren and Kellomaki (1983).

accompanied by a similar change in photosynthesis (Schulze 1970).

Evergreen trees present a special problem both because their leaves experience progressively more shaded environments as new branches continue to grow, and because the capacity of foliage to photosynthesize decreases with age (Helms 1970; Teskey et al. 1984). Only one study, on Norway spruce (Picea abies), has been published with data on photosynthesis, leaf area, and leaf biomass throughout the crown (Schulze et al. 1977a). From analysis of these data I found that annual net photosynthesis per unit of leaf area was generally higher progressing from current to 2-year-old needles, in close correlation with an increase in SLW (Figs. 3a and 4). Three and four-year-old foliage appeared to break this pattern, however, with four-year-old foliage photosynthesizing at rates similar to current needles, despite differences in specific leaf weights of more than 40% (Fig. 3a). Some differences in SLW may be attributed to annual increments in phloem tissue (Ewers 1982) and to accumulations of inorganic or organic compounds other than storage carbohydrates (Berg and Staff 1980; Berg et al. 1980). These changes would tend to make older foliage appear less efficient when photosynthesis is



- I. 3. a. Relationship between net annual photosynthesis and specific leaf weight of various age classes of Norway spruce needles (0 = current through 4 years old). b. Relationship between net annual photosynthesis and specific leaf weight of a Norway spruce (averages for 5 crown segments). Each segment represent 20% of the crown length; uppermost segment is indicated as (I) and the others are numbered progressively downward. Calculated from Schulze et al. (1977a).



I. 4. Distribution of mean specific leaf weight of different age classes of Norway spruce foliage (0 = current to 4 = 4-year-old) in five equal length segments of the crown (I = uppermost, V = lowermost,  $\Delta$  = weighted mean for each segment). Calculated from Schulze et al. (1977b).



expressed per mass rather than per unit area of foliage. This is not apparent from this study (Fig. 3a).

Although the photosynthetic rates of current and 4-year-old foliage may be similar, these age classes of foliage are not distributed evenly throughout the crown. The majority of new foliage is located on branch tips and near the top of the tree whereas most of the old foliage is located in the interior of the crown and on branches along the lower portion of the tree (Schulze et al. 1977a). When various sections of a tree crown are compared, the mean SLW is highest just below the upper third of the crown, corresponding to the point at which maximum photosynthetic rate occurs (Woodman 1971, also see Fig. 3b). The relationship between photosynthetic rate and SLW is almost reversed when photosynthesis is expressed per unit of leaf weight; the maximum is at the base of the crown (Schulze et al. 1977b).

#### D. Canopy photosynthesis

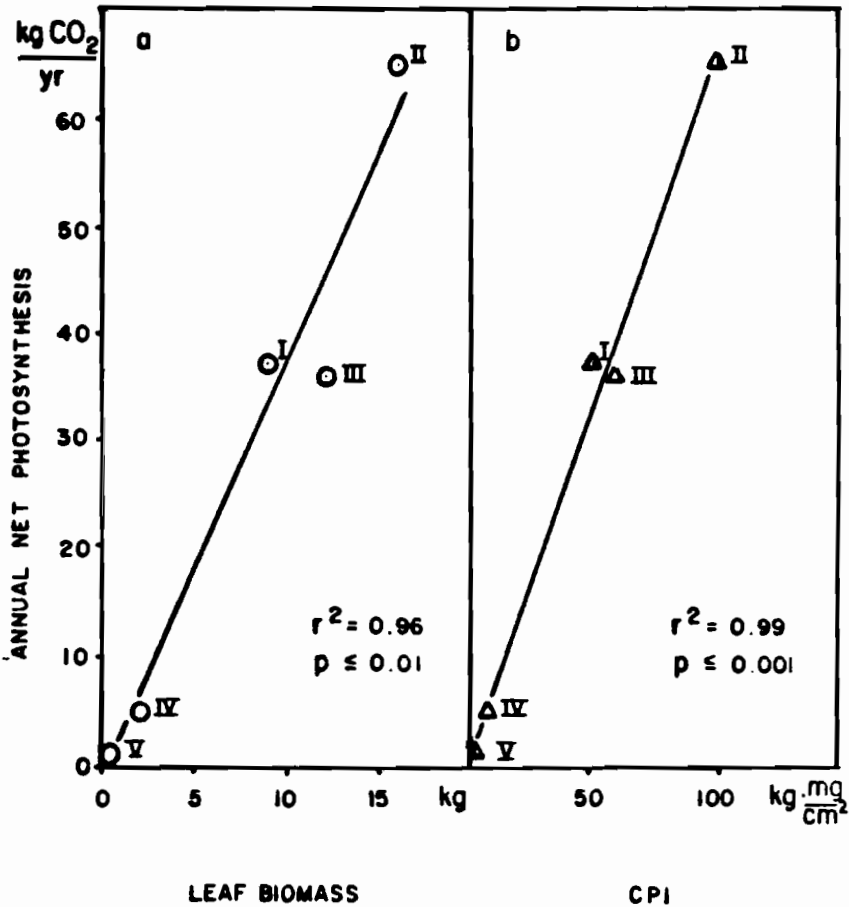
Schulze et al. (1977a) found a correlation between the distribution of foliage biomass and annual net photosynthesis ( $r^2 = 0.96$ ,  $P < 0.01$ ) in five crown zones

(Fig. 5a). The correlation with leaf area was not as good ( $r^2 = 0.88$ ,  $P < 0.05$ ). Close inspection of the relationship indicates that the more exposed part of the crown near the top and that in the mid-zone each contributed about a quarter of the annual net photosynthesis. The mid-zone, however, carries 34% more needle biomass and 52% more foliage area than the uppermost zone of the tree crown. The discrepancy emphasizes the importance of accounting for photosynthetic rate in addition to foliage biomass when estimating annual photosynthesis.

Because of the close correlation between SLW and photosynthetic rates, the product of foliage biomass and SLW for a given portion of the crown should serve as an index of seasonal or annual net photosynthesis.

Canopy Photosynthetic Index = Leaf Biomass x SLW

In fact, a close relationship ( $r^2 = 0.99$ ,  $P < 0.001$ ) emerges when annual photosynthesis is related to this index (Fig. 5b). This canopy photosynthetic index (CPI) had a lower bias according to the Cp criteria and lower mean square error (Neter et al. 1983) than the correlation with needle biomass alone. Moreover, when both photosynthesis and the canopy photosynthesis index were expressed in relative

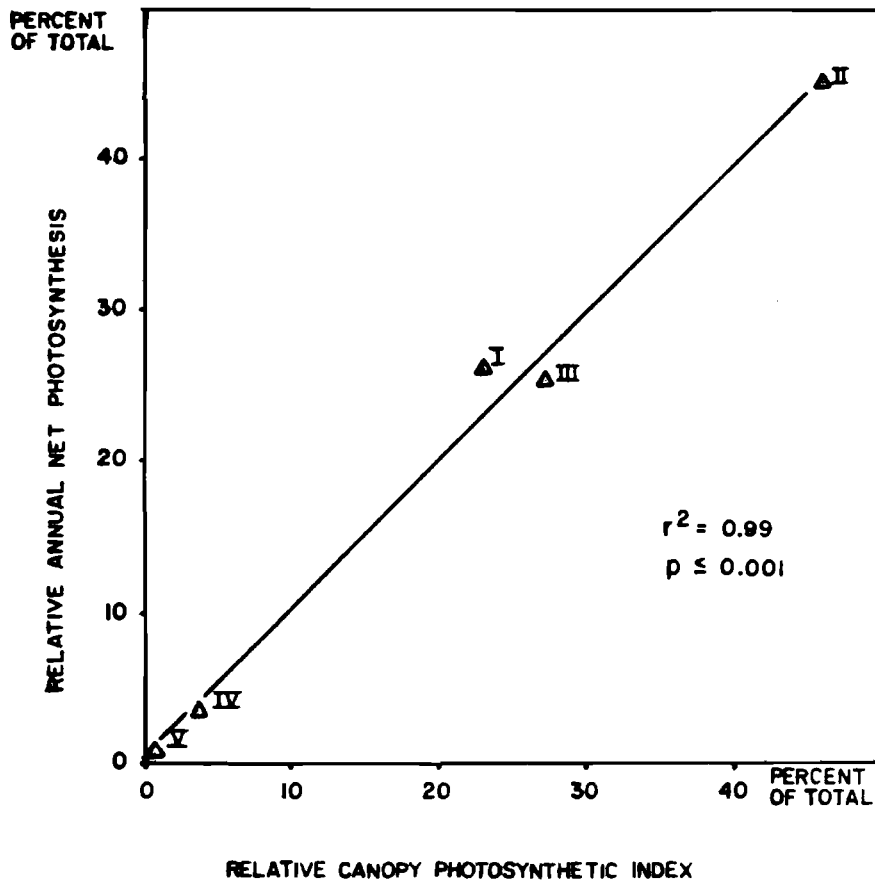


- I. 5. Annual net photosynthesis by 5 equal length segments of a Norway spruce crown (I = uppermost, V = lowermost portion). a. in relations to leaf biomass. b. in relations to canopy photosynthetic index (CPI). Calculated from Schulze et al. (1977a).

units, the slope of the correlation was closer to unity ( $b = 0.99$  vs.  $1.07$ ) than the correlation with relative canopy biomass (Fig. 6).

When predictions for total canopy photosynthesis are compared, the needle biomass correlation overestimated measured values by 6% whereas the canopy photosynthesis index was within 3% of that measured. This agreement is well within the variation associated with sampling error (20 percent) of photosynthesis (Woodwell and Botkin 1970).

The canopy photosynthetic index can be used to estimate annual net photosynthesis. Even where direct measurements of photosynthesis are not available for calibration, the index may be considered a good relative measure of photosynthesis under variable stand conditions and for various portions of the canopy (Fig. 6). For example, if the spruce tree referred to in earlier analysis had a canopy representative of the photosynthetic activity of an entire stand, then removal of all foliage in the lower 40% of the live canopy, either by pruning or by removing the smaller size classes of trees, would result in reducing the stand's carbon uptake by only 3%. The lower 40% of the canopy represents only about 5% of the total foliage biomass.



- I. 6. Relative contributions of five crown segments of Norway spruce to annual net photosynthesis (I = uppermost, V = lowermost). Calculated from Schulze et al. (1977a).

### E. Estimates of canopy biomass or area

Our interest in forestry research and management extends from the canopy of individual trees to entire stands. If we are to use the CPI on a stand basis, we must have accurate estimates of Leaf Area Index, an expression denoting the projected canopy cover per unit of ground space. A Leaf Area Index (LAI) of 1.0 represents a projected canopy area equal to ground area.

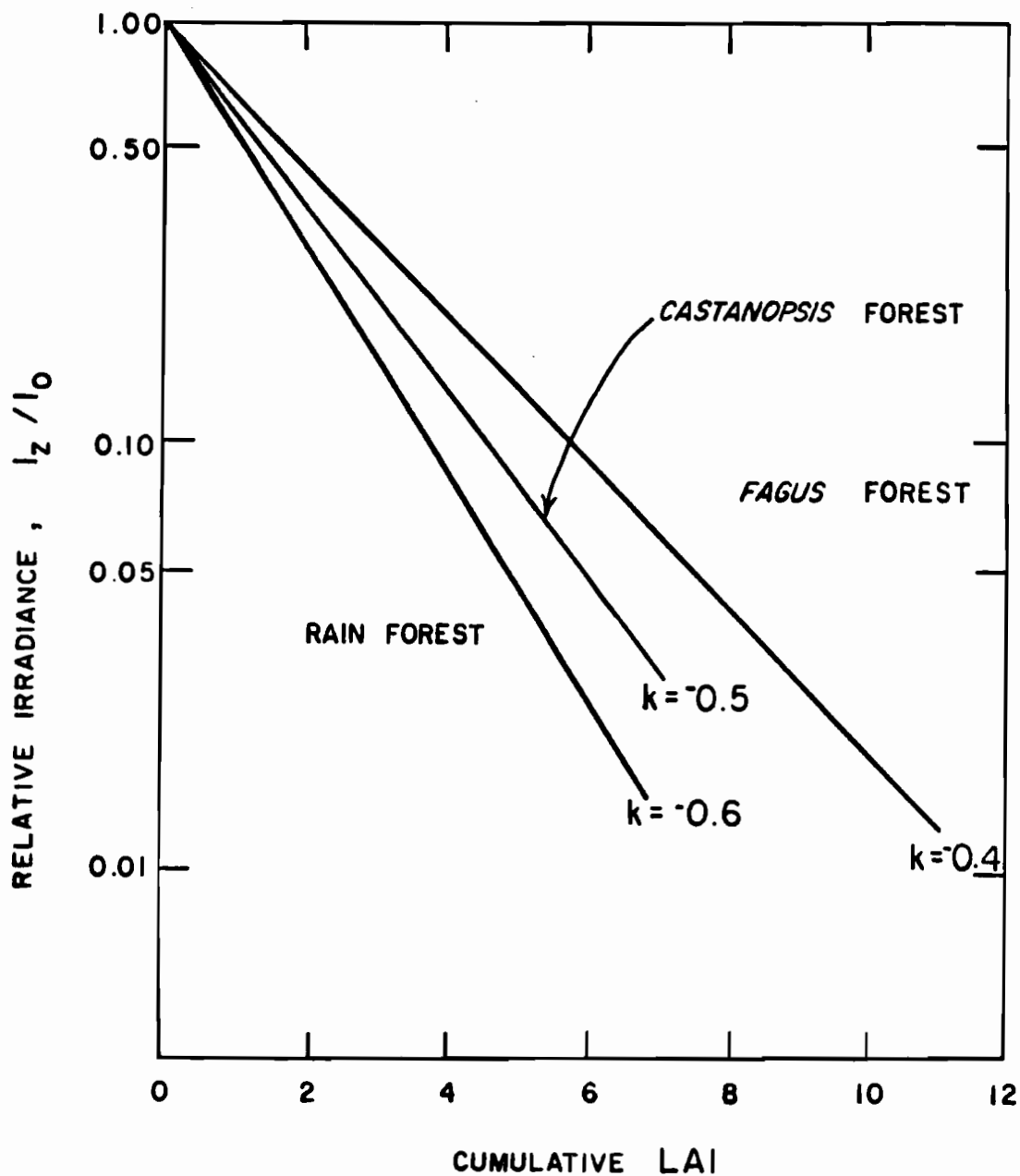
Sapwood cross-sectional area at breast height or at the base of the live crown has been found to correlate well with foliage mass or area displayed near the end of the growing season. These relationships have been demonstrated for a variety of conifers and hardwood species (Waring et al. 1982; Rogers and Hinckley 1979; Grier and Waring 1974; Snell and Brown 1978; Kaufmann and Troendle 1981) although variations between sites were also reported (Albrektson 1984; Brix and Mitchell 1983).

Although either mass or area of foliage may be estimated from sapwood area measurements, leaf area estimates appear more consistent from site to site (Waring 1983). Leaf area, however, does vary seasonally. To evaluate seasonal changes in canopy LAI the irradiance

under the canopy may be monitored and estimates of LAI predicted from the Beer-Lambert Law and knowledge of light extinction coefficients (Jarvis and Leverenz 1983). Irradiance at different heights in canopies, resulting in various levels of cumulative LAI are demonstrated in Fig. 7 for a typical rain forest, an evergreen hardwood canopy of Castanopsis, and a deciduous beech (Fagus) forest. A reduction in LAI from 6 to 3 would correspond to an increase in relative irradiance under the canopy of beech from 5% of incident radiation to 22%.

It is particularly important to follow seasonal changes in LAI in forests. A drought or insect defoliation may reduce the canopy far below normal. Of course, differences in length of the growing season also play an important part in determining forest production. For example, gross primary production (total carbon uptake) by hardwood forests of the northeastern United States was only about half that reported for a forest with similar LAI in the southeastern United States (Whittaker et al. 1974; Harris et al. 1975) where the growing season was over 60% longer (180 vs. 110 days).

The consideration of leaf duration (LAI x months growing season) has provided an index to gross primary

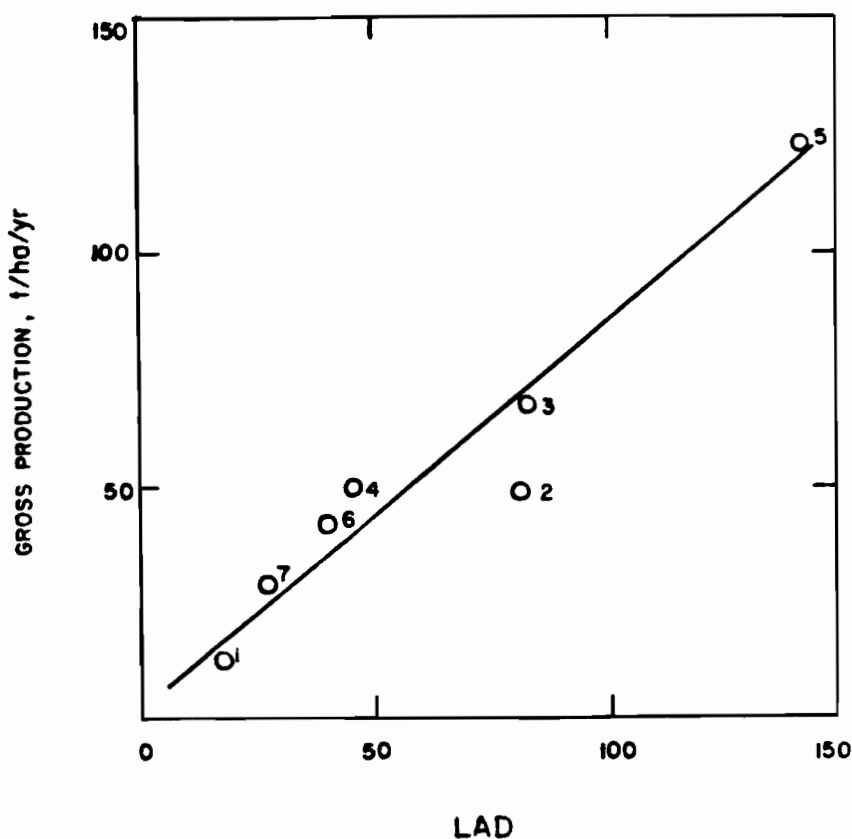


- I. 7. Relationship between cumulative leaf area index and relative irradiance, including extinction coefficients ( $k$ ) for different forest types.  $I_0$  = irradiance in open,  $I_z$  = irradiance below various levels of cumulative leaf area index. After Kira and Shidei (1967).



production in a wide variety of evergreen and deciduous hardwood forests (Fig. 8). How much improvement this Leaf Area Duration (LAD) index might receive by consideration of canopy photosynthetic index is not known.

Correlations between sapwood area and leaf area may be quite variable among closely related species and some variation is likely even for the same species grown in different environments (Albrektson 1984; Brix and Mitchell 1983; Waring et al. 1982). Nevertheless, good correlations are obtainable by sampling within environmentally homogeneous areas.



- I. 8. Gross primary production (total  $\text{CO}_2$  uptake) in a wide range of broad-leaf forests in relation to the product of Leaf Area Index and number of months in the growing season. This latter index is termed Leaf Area Duration (LAD). The numbered points refer to (1) Fagus forest in Japan, (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 (Kira and Shidei 1967). Point number (6) is a Liriodendron forest in southeastern United States (Harris et al. 1975) and (7) is a mixed hardwood forests from the northeastern United States (Whittaker et al. 1974).

## CONCLUSION

The canopy photosynthetic index reflects seasonal and annual net photosynthesis. The index should be sensitive to silvicultural practices such as thinning, fertilizing, and pruning since there is good evidence that such treatments change the photosynthetic efficiency of the canopy (Linder and Axelsson 1982; Waring 1983). Like photosynthesis, however, the index is not directly related to aboveground forest production. Production is affected not only by photosynthesis but also by allocation patterns of photosynthates into various organs and by maintenance respiration (Waring 1983; Jarvis and Leverenz 1983). Nonetheless, canopy photosynthesis is one important aspect of stand production and the relative effects of various silvicultural practices upon photosynthesis can, using the canopy photosynthetic index, now be more widely assessed.

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CHAPTER II

ANALYSIS OF 25 YEARS OF PONDEROSA PINE GROWTH IN  
RELATION TO CANOPY LEAF AREA AND UNDERSTORY COMPETITION

by

R. OREN

Analysis of 25 Years of Ponderosa pine Growth in relation  
to Canopy Leaf Area and Understory Competition

Ram Oren

Abstract

From an experiment in which initial stocking and understory vegetation were controlled, the hypothesis that stand growth is a function of canopy leaf-area index was evaluated. This hypothesis was generally supported from the analysis. Stands without understory vegetation developed canopy leaf area faster than those with an understory present. Further, stands without an understory grew more efficiently in terms of wood produced per unit of foliage than stands without understory control up to a canopy leaf-area index of 2.0.

From comparisons of published soil water depletion data, I found that complete exhaustion of available water in the rooting zone occurred when leaf area index exceeded 2.0, even with understory vegetation absent. Growth efficiency remained stable for both treatments at leaf area indices above about 2.5. Below a leaf area index of

2.0, however, trees in stands without understory vegetation may allocate less carbohydrates to roots because water remains available longer in a given horizon. In addition, trees growing in stands with low leaf area indices and without understory vegetation may have more available nutrients relative to trees growing at high leaf area indices with an understory present.

The initial differences in growth efficiency observed at low leaf area indices resulted in more rapid biomass accumulation on plots without understory vegetation. Differences in stand growth persisted at later stages in stand development due to greater canopy leaf area. The major effect of removing understory vegetation in this water-limited system was to speed the development of canopy leaf area. This response may be comparable to the effects of adding fertilizer at a similar stage in stand development where nutrients are limiting.

## Introduction

Silviculturalists have experimented with various techniques to increase or redistribute stand growth by controlling stocking and by improving the availability of limiting soil resources. Recent physiological studies suggest that the improved growth resulting from silvicultural practices can be interpreted by analyzing how canopy leaf area and carbon allocation patterns are changed (Jarvis and Leverenz 1983; Waring 1983).

A long-term study initiated by Barrett (in 1959) in ponderosa pine stands in south-central Oregon demonstrated that major alterations in stand growth resulted following control of stocking and understory vegetation (Barrett 1982). I visited the experiment in 1981, 22 years after its initiation and made specific measurements to estimate present canopy leaf area and a canopy photosynthetic index (see Chapter I). The fact that in this stand stemwood was essentially all sapwood permitted me to estimate individual tree and total canopy leaf area from stand densities and tree diameters in the past as well as in the present (Waring et al. 1982). Sapwood area at the base of the crown is linearly related to leaf area (Waring et al.

1982). The historical analysis was further simplified because essentially no natural tree mortality had occurred (Barrett 1970).

The study provided a unique opportunity to separate the influence of stocking on growth from that of understory competition for water on growth. Published records indicated that the major change in water use occurred more than a decade ago (Barrett 1970). Since that time most available water in the rooting zone has been depleted every year by the end of the growing season in all treatments. Changes in the availability of soil water are known to affect both photosynthesis (Whitehead and Jarvis 1981) and the pattern of carbon allocation between roots and shoots (Linder and Axelsson 1982; Waring 1983).

Major changes in canopy photosynthesis can be related to variation in specific leaf weight because more exposed foliage has more mesophyll tissue and greater photosynthetic capacity than shaded foliage. Moreover, when water and nutrients are adequately supplied, leaves receiving similar irradiance accumulate more starch compared with water - or nutrient-deficient foliage (Berry

and Downton 1982). Thus heavier foliage in general indicates high rates of photosynthesis (see Chapter I).

Stand wood production is dependent upon the net carbon uptake, losses in respiration, and the fraction of photosynthate allocated to wood. In a particular stand, maintenance respiration per unit of living biomass is generally quite uniform, being related to temperature (Penning de Vries 1975). Estimation of total losses to respiration were beyond the scope of this study, however.

Carbohydrate allocation may be altered significantly, depending upon the silvicultural treatment. For example, with irrigation, Scots pine (Pinus sylvestris L. ) increased shoot / feeder root production by 50% (Axelsson 1981). When only above ground production is known, estimates of canopy photosynthesis are required to evaluate treatment effect on carbon uptake. Growth differences not attributed to variation in canopy photosynthesis can then be assumed related to changes in carbohydrate allocation.

The approach followed in this study illustrates how allocation patterns can be interpreted if compared at the same canopy leaf area. A historical analysis was required because stands without understory vegetation grew faster

and achieved high leaf areas earlier than stands with understory vegetation remaining.



## Methods

### Study area

The study, located in the Pringle Falls Experimental Forest, 55 km southwest of Bend, Oregon, was installed by J.W. Barrett in a pure ponderosa pine stand with about 50 old-growth trees per ha above a dense understory (averaging 17,000 per ha) of 40-70 year-old suppressed smaller trees (Barrett 1982). The small trees averaged 5.0 cm in diameter and 2.5 m in height. Ground vegetation consisted mainly of purshia tridentata (Pursh) DC., Ceanothus velutinus Dougl. ex Hook., and Arctostaphylos patula Greene.

Study plots were on an east-facing slope at 1350 m elevation. Mean annual precipitation is 60 cm, 85 percent of which falls between October and April. From January to March the ground is commonly covered with a snowpack of about 60 cm. Soils, developed from dacite pumice, average 80 cm in depth to a buried soil profile developed in an older ash layer (See Barrett 1982). Site index estimates for this area project ponderosa pine growth to reach 24 m in height at 100 years (Barrett 1982).

## Experimental design

Thirty rectangular 0.073 ha plots, each surrounded by a 10 m wide buffer strip, were laid out in 1957. In 1958 all of the large pines were removed and five spacing levels, each replicated six times, were established at: (1) 2470, (2) 1235, (3) 618, (4) 309, and (5) 153 trees per ha. All treatments were randomized and extended into the surrounding buffer strip. Within each stocking treatment, half the plots were maintained clear of understory vegetation by herbicides and mechanical means throughout the 24 year experiment.

Beginning in the fall of 1959, and at every 4th growing season thereafter until 1979, diameter at breast height (dbh), total height, and height to the base of the live crown were measured (Barrett 1982). In the summer of 1983, I measured dbh and height to the base of the live crown on all trees and total height on at least 12 trees per plot at low stocking (153 and 309 trees per ha), and on not less than 25 percent of the trees at higher levels of stocking.

## Leaf area and specific leaf weight calculations

Leaf area was estimated by assuming a linear relationship between sapwood cross-sectional area at the base of the live crown and leaf area (Waring et al. 1982; Larsson et al. 1983). In 1981, I confirmed from increment cores that less than 3 percent of the total wood cross-section in any treatment consisted of heartwood. This permitted me to estimate leaf area on all trees from diameter measurements, correcting for bark thickness, at each of the five measurement periods beginning at the time when the treatments were established (1959-1979). My last sampling of wood cores in 1983 showed a similar high percentage of sapwood but the leaf area estimate for each plot at the last measurement period (1980-1983) was reduced according to the mean sapwood percentage of the plot.

Ponderosa pine exhibits marked taper in the lower bole. The taper between dbh and the base of the live crown I determined from data on 120 trees sampled 20 km northeast of this study area and covering the full range of size classes represented in this experiment (Cochran

1979). Analyses of these data resulted in the following predictive equation:

$$D = 10^{(0.258+0.168(\text{DBH})-0.324(\text{HT})+0.266(\text{L}/\text{HT})) \times L^{0.937}}$$

$$r^2 = 0.97, P < 0.001$$

where: D = diameter inside bark (cm) at point L, where L = a known distance from the top of the tree (m), HT = total height (m).

At the base of the live crown, a  $\text{cm}^2$  of sapwood cross sectional area supports  $0.25 \text{ m}^2$  of projected pine needle area (Waring et al. 1982). At periods between the 4-year measurements, tree leaf areas were estimated by linear interpolation. Canopy leaf area for each plot was determined by summing leaf area of individual trees. This value was divided by the plot area to obtain canopy leaf area index, the projected surface area of needles above a unit area of ground.

Specific leaf weight, shown in Chapter I to be correlated with photosynthesis, was determined in 1984 on 1-year-old foliage collected from the bottom and mid-crown portions of 5 trees in each plot. Foliage was not collected from the top of the trees because differences in specific leaf weight among treatments would be minimal at

the top of the crowns. If large differences occur among treatments they would be found lower in the canopy. Samples were maintained at 3°C until leaf area could be determined (less than 1 week) on a Licor 3100 area meter. Samples were then oven dried at 70°C for 48 hours and their dry weight determined. Specific leaf weight was obtained by dividing dry weight by needle area.

Stand leaf biomass was calculated by multiplying canopy leaf area per hectare by specific leaf weight. Canopy photosynthetic index (CPI) (Chapter I) was calculated as the product of specific leaf weight and leaf biomass.

#### Growth

Tree volume was calculated for each tree from an equation developed for this experiment (DeMars and Barrett, unpublished, U.S. Forest Service, Bend Silvicultural Lab., Bend, Oregon). Growth in volume was determined by the difference between two consecutive measurements and interpolated for periods in between. Tree height was required to estimate volume. Because in 1983 heights were not measured on all trees, local

equations were developed for each combination of stocking level and understory vegetation conditions to predict height from diameters on each plot. The  $r^2$  values of these local equations were between 0.70 and 0.85 and were significant in all cases ( $p < 0.001$ ). The equations were based on 35 to 175 trees.

Growth in biomass was determined in each plot by multiplying, volume growth by wood specific gravity (ranging from 0.26 to 0.31 gm/cm<sup>3</sup>) sampled from cores, taken from 5 to 19 trees per plot, depending on stocking. To estimate how efficiently stemwood was produced per unit of foliage, the increment in volume or biomass was divided by the estimated leaf area on each tree. An average growth efficiency was then determined for each plot.

Stand stem growth was calculated by summing the growth of individual trees in a given plot and then converting to growth per ha.

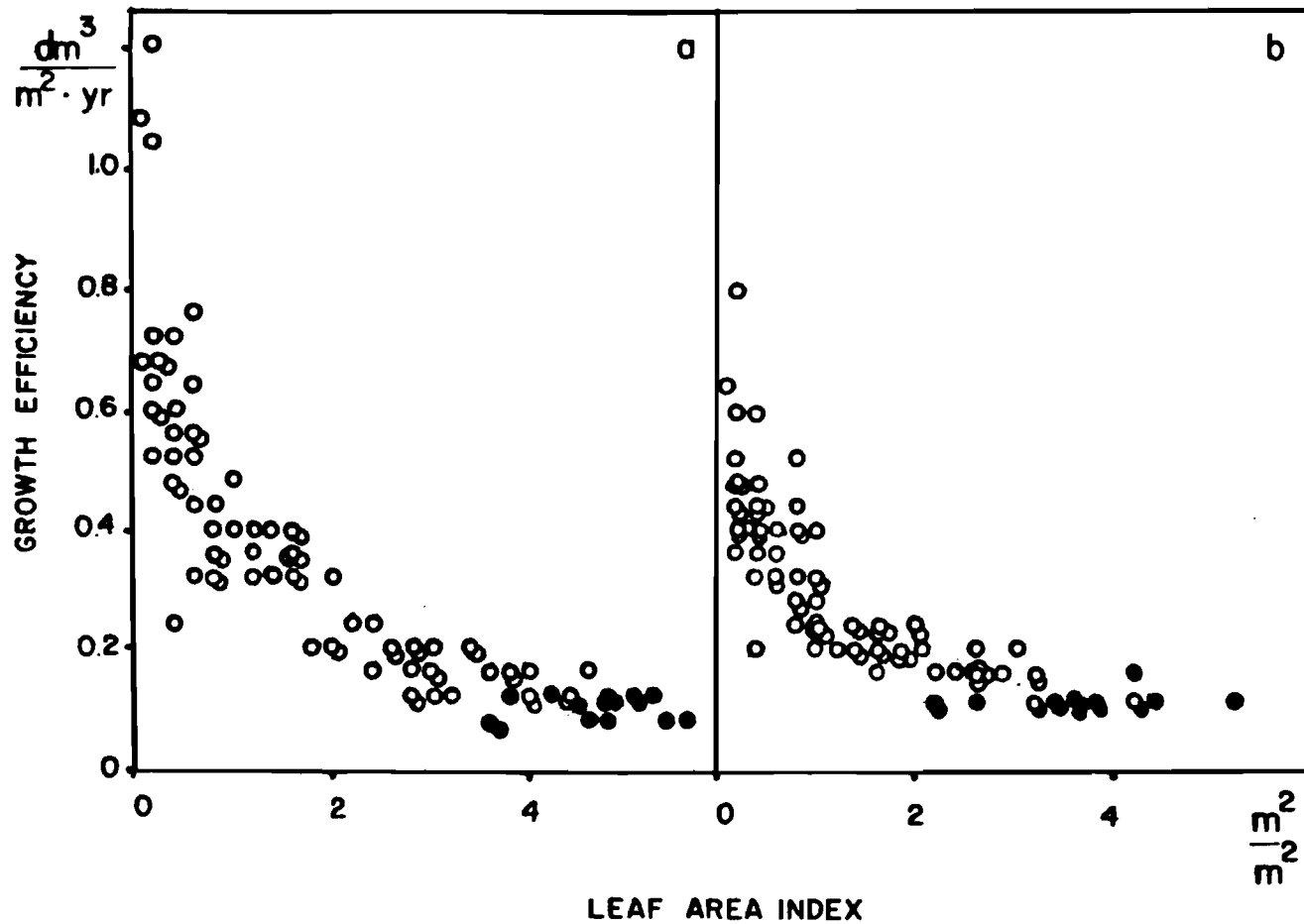
## Results

Over the 24 years of the experiment, mean dbh increased from 7 to 12 cm in the highest stocking level

and to 26 cm in the lowest in plots with understory present. The basal area in these plots increased from an average of 5.1 to 31.5 m<sup>2</sup>/ha and from 0.35 to 8.8 m<sup>2</sup>/ha for the two stocking levels respectively. Mean dbh in plots with understory absent increased over the same period from 8 to 13 cm in the highest stocking level and to 32 cm in the lowest. In the absence of understory, basal area increased from 3.8 to 33.5 m<sup>2</sup>/ha and from 0.35 to 12.9 m<sup>2</sup>/ha in the two stocking levels respectively.

When specific leaf weight was compared across all plots during the last sampling period (corresponding to leaf area index between 2.5 to 6), no significant differences were found ( $P < 0.05$ ). This suggested that photosynthetic rate of trees among plots was similar and that differences in canopy photosynthesis was in this case a simple function of total leaf area or leaf biomass.

In Figs. 1a and 1b, growth efficiency is shown to decrease rapidly to a canopy leaf area index (LAI) of



II. 1. Growth efficiency (stem volume produced/unit of foliage area) in relation to stand leaf area index. Data are for six measurement periods made at 4 year intervals. Last period denoted by filled circles. (a) with understory absent, (b) with understory present.



about 2.0 and to decrease slowly thereafter<sup>1</sup>. Note that understory removal allowed the pines to reach higher growth efficiency at leaf area indices of less than 2.0 (approximately 30 percent at LAI of 1.0) but that efficiencies were similar with or without understory vegetation present at higher LAI's.

To make the relationship illustrated in Fig. 1 more linear, and therefore simpler to analyze statistically, the reciprocal of growth efficiency was used. This transformation resulted in a linear relationship with LAI with  $r^2$  above 0.87 (Table 1). The analyses are performed on the complete data set (n=90) as well as for the period up to the last measurements (n=75). This permitted me to check estimates of growth and canopy development using equations derived from earlier measurements against observed values in the last sampling.

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1. The relationship between growth efficiency and LAI (Fig. 1) can be described by a modified Michaelis-Menten equation (Reed and Webb 1972) as:

$$GE_i = (GE_{\max} - GE_{\min}) \left( 1 - \frac{1}{1 + [(K_L - a)/(LAI_i - a)]} \right) + GE_{\min}$$

where:

$GE_i$  = growth efficiency at  $LAI_i$

$GE_{\max}$  = maximum growth efficiency

$GE_{\min}$  = minimum growth efficiency

$K_L^{\min}$  = LAI at which GE is 1/2 ( $GE_{\max} - GE_{\min}$ )

$a$  = LAI at  $GE_{\max}$

Table 1. Stemwood growth efficiency (GE), relative rate of leaf area accumulation (LAI), stand stemwood growth (G) in relation to canopy leaf index (LAI), and mean leaf area / tree (LA) in ponderosa pine stands. All relationships are significant at  $P < 0.001$ .

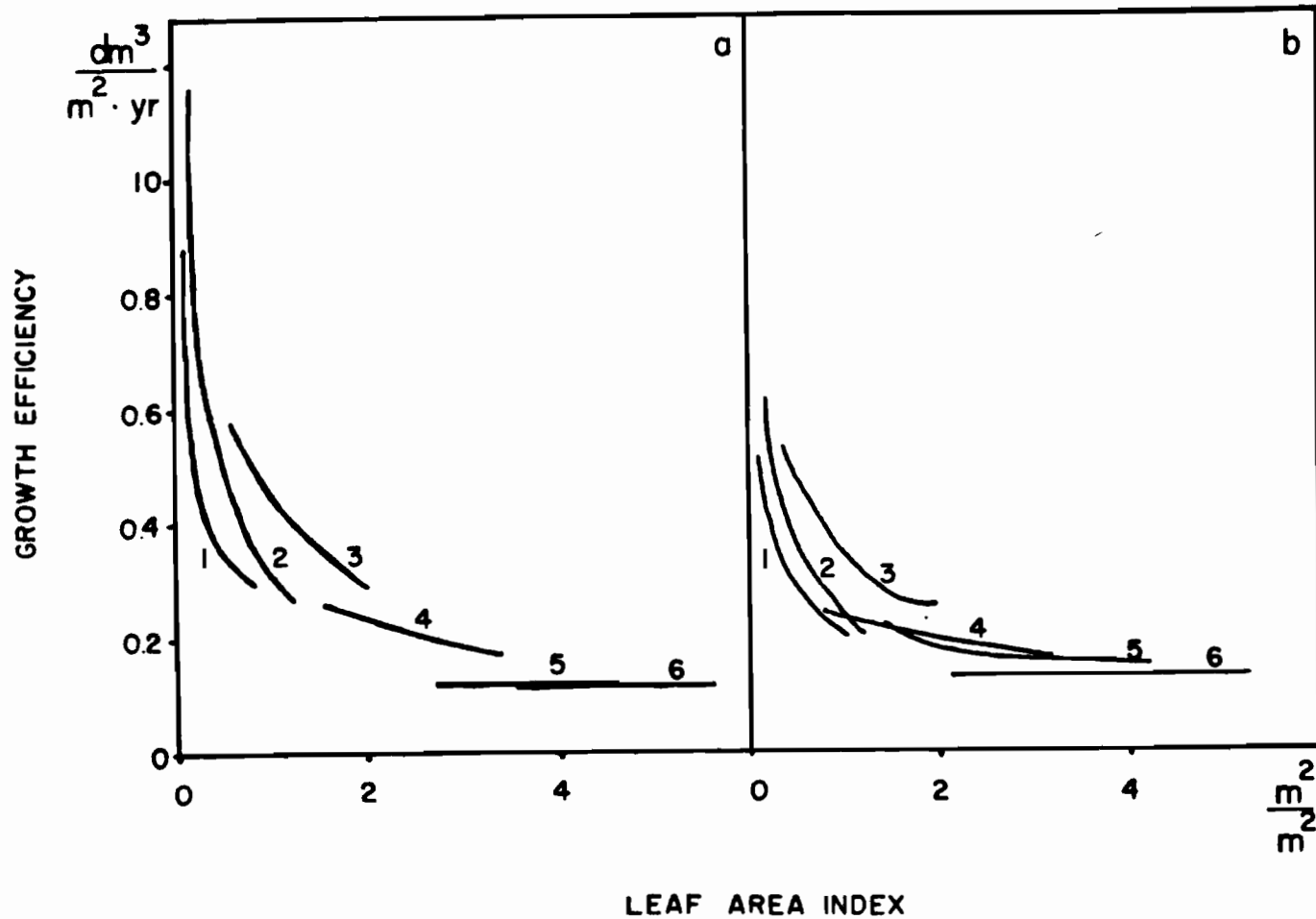
Dependent Variable	Units	Ground Vegetation	Independent Variables			LA	n	Adj. $r^2$
			Intercept	LAI	LAI <sup>2</sup>			
1/GE	dm <sup>3</sup> /m <sup>3</sup> .yr	+	2.12***	1.39 <sup>NS</sup>			75	0.79
		-	1.19	1.50 <sup>NS</sup>			75	0.87
		+	2.04**	1.61 <sup>NS</sup>			90	0.80
		-	1.05	1.67			90	0.87
1/GE	kg/m <sup>2</sup> .yr	+	7.16***	5.45 <sup>NS</sup>			75	0.77
		-	4.33	5.58 <sup>NS</sup>			75	0.85
		+	7.18**	5.87 <sup>NS</sup>			90	0.77
		-	3.96	6.11			90	0.86
1/GE	dm <sup>3</sup> /m <sup>2</sup> .yr	+	3.06***	1.28 <sup>NS</sup>		0.02***	75	0.88
		-	2.29	1.45 <sup>NS</sup>		0.01	75	0.91
		+	1.77***	1.36 <sup>NS</sup>		0.02***	90	0.90
		-	0.95	1.45		0.01	90	0.92
1/GE	kg/m <sup>2</sup> .yr	+	10.29***	4.98 <sup>NS</sup>		0.09***	75	0.85
		-	8.34	5.35 <sup>NS</sup>		0.03	75	0.91
		+	6.06**	4.85 <sup>NS</sup>		0.09**	90	0.89
		-	3.61	5.35		0.04	90	0.90
LAI	m <sup>2</sup> /m <sup>2</sup> .yr	+	0.0002 <sup>NS</sup>	0.1649***	-0.0259***		75	0.83
		-	0.0012	0.2205	-0.0386		90	0.73
		+	0.0096 <sup>NS</sup>	0.1420***	-0.0187***		90	0.82
		-	0.2420	0.1706	-0.0256		90	0.69
G	m <sup>3</sup> /ha.yr	+	0.41**	1.65 <sup>NS</sup>	-0.14 <sup>NS</sup>		75	0.94
		-	0.80	1.68 <sup>NS</sup>	-0.17 <sup>NS</sup>		75	0.91
		+	0.55**	1.38 <sup>NS</sup>	-0.08 <sup>NS</sup>		90	0.93
		-	0.93	1.49	-0.12		90	0.90

G	T/ha.yr	+	0.11**	0.50 <sup>NS</sup>	-0.06 <sup>NS</sup>		75	0.90
		-	0.23	0.44 <sup>NS</sup>	-0.04 <sup>NS</sup>		75	0.91
		+	0.16**	0.39 <sup>NS</sup>	-0.02 <sup>NS</sup>		90	0.89
		-	0.27	0.37	-0.03		90	0.89
G	m <sup>3</sup> /ha.yr	+	0.41***	1.93 <sup>NS</sup>	-0.20 <sup>NS</sup>	-0.008 <sup>NS</sup>	75	0.96
		-	0.76	1.92 <sup>NS</sup>	-0.20 <sup>NS</sup>	-0.005 <sup>NS</sup>	75	0.93
		+	0.51***	1.73 <sup>NS</sup>	-0.14 <sup>NS</sup>	-0.008 <sup>NS</sup>	90	0.97
		-	0.87	1.71	-0.15	-0.006	90	0.94
G	T/ha.yr	+	0.11***	0.60**	-0.08***	-0.003***	75	0.94
		-	0.22	0.50 <sup>NS</sup>	-0.05	-0.001	75	0.92
		+	0.14***	0.50 <sup>NS</sup>	-0.04**	-0.003***	90	0.93
		-	0.26	0.43	-0.03	-0.001	90	0.92

n = 75 is representative of the first 5 measurement periods  
n = 90 is representative of the first 6 measurement periods  
\*\*, \*\*\*, indicate statistically significant differences  
between plots with (+) and without (-) understory  
vegetation for each independent variable and the  
intercept at the 0.01, and 0.001 level, respectively.  
ns indicates no significant differences at the 0.05 level.

I attempted to analyze the relationship between the reciprocal of growth efficiency and canopy leaf area for each measurement period separately. Significant differences ( $P < 0.01$ ) were found among relationships from different measurement periods, but there were no systematic changes and pooling the data for the entire experiment seemed justified (Fig. 2a and 2b). Some of the variation may be a result of climatic differences between measurement periods.

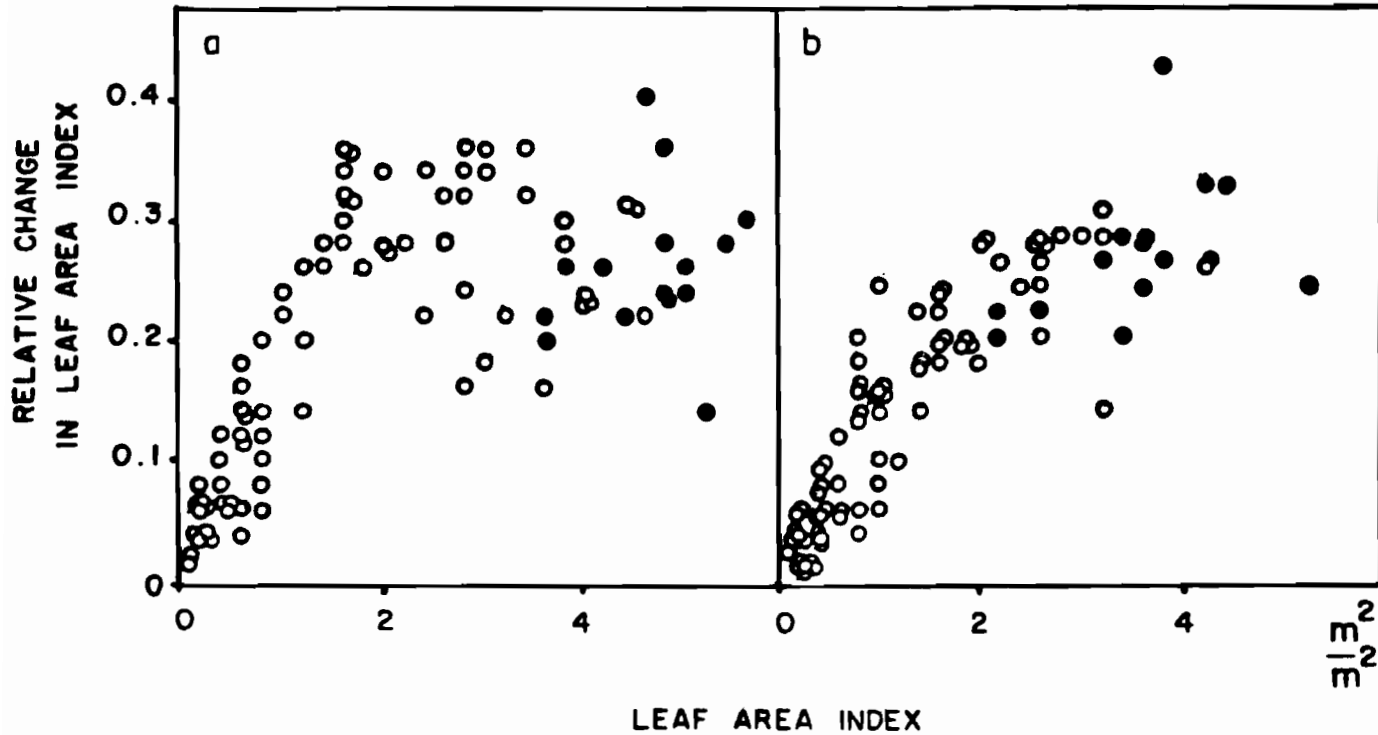
Differences in mean stem biomass/tree and in mean leaf area/tree among plots were then added to the regression equation. A significant improvement resulted with the addition of mean leaf area/tree, but not with stem biomass (Table 1). Stem biomass/tree and leaf area/tree were closely correlated because live crown ratios varied little (0.72-0.83) and because both stem biomass and leaf area were calculated from stem diameter. The stepwise regression technique selected tree leaf area second after canopy leaf area index, and no further gain in explained variation in  $1/\text{growth efficiency}$  then resulted by adding stem biomass ( $r^2$  improved less than 0.01, and  $P$  for inclusion less than 0.05).



II. 2. Least square fit of growth efficiency (stand volume produced/unit of foliage area) in relation to stand leaf area index. Six measurement periods are represented by separate lines (1 = 1st, to 6 = last period). (a) with understory absent, (b) with understory present.

When comparing reciprocal growth efficiency (in terms of volume or biomass increment) on plots with and without understory vegetation, LAI accounted for most of the variation and slopes of the lines were similar (Table 1). The intercepts were significantly higher, however, on plots where understory vegetation was not controlled. This confirmed that growth efficiency at low LAI were significantly higher when understory vegetation was controlled than when it was not (Figs. 1 & 2). When the analysis was done for each measurement period separately, the intercepts of the two earliest periods only were significantly different ( $P < 0.01$ ) between plots with and without vegetations, and none of the slopes was different ( $P < 0.05$ ). With the addition of mean leaf area/tree, the regressions were further improved. For a given increase in tree leaf area, the effect upon growth efficiency was significantly more negative when trees were growing with understory vegetation than without (Table 1).

Because LAI is so important in predicting growth efficiency, the ability to predict the rate of increase in LAI in relation to current LAI was analyzed. A curve appearing as a parabolla resulted (Figs. 3a and 3b) which is expected to be best described with a peaking (bell)



II. 3. Relative rate of change in canopy leaf area index in relation to current leaf area index. (a) with understory absent, (b) with understory present. Data are from measurement periods defined in Figure 1.

function if LAI accumulate over time in a sigmoid fashion. With limited data at high LAI, a parabolic function was used (Table 1) although this function is of limited value at either end of a bell-shaped curve<sup>2</sup>. In general, the rate of increase in leaf area index was highly predictable up to an LAI of about 2.0. Above an LAI of 2.0, the relationship became more variable. Following the rate of change in LAI of individual plots suggested that site differences such as plant available soil water may account for some of the variation but that stocking plays no role. The only important difference found between plots with and without understory vegetation was that the rate of change in LAI was higher on plots without understory vegetation (Fig. 3; Table 1).

2. An example of peaking function for describing change in LAI. The function was fit to the entire data set (Jensen and Homeyer 1970):

$$\Delta LAI_i / \Delta LAI_{max} = \frac{e^{-\left| \frac{(LAI_i / LAI_m) - 1}{.9} \right|^{3.0}} - .2187}{.7813}$$

where:

$\Delta LAI_i$  = relative rate of LAI accumulation at LAI<sub>i</sub>

$\Delta LAI_{max}$  = maximum relative rate of LAI accumulation

$LAI_{max}$  = LAI at  $\Delta LAI_{max}$

$r^2_m$  = 0.81 with understory present,  $r^2$  = 0.69 without understory present.



Contrasting the analyses made with and without the last set of measurements indicated changes in the development pattern of the stands (Table 1). I used measurements made during the last period of measurement to evaluate predictions made with equations developed from all measurements save the last. Predictions included the rate of change in leaf area index, growth efficiency, LAI, and stand growth (Table 1). Stand growth was predicted in two ways: (1) by continuous accumulation of growth calculated as the product of predicted LAI and predicted growth efficiency, and (2) by an equation describing the relationship between stand growth and LAI (Figs. 3a, 3b and Table 1) using predicted LAI for the end of the last (1980-1983) measurement period.

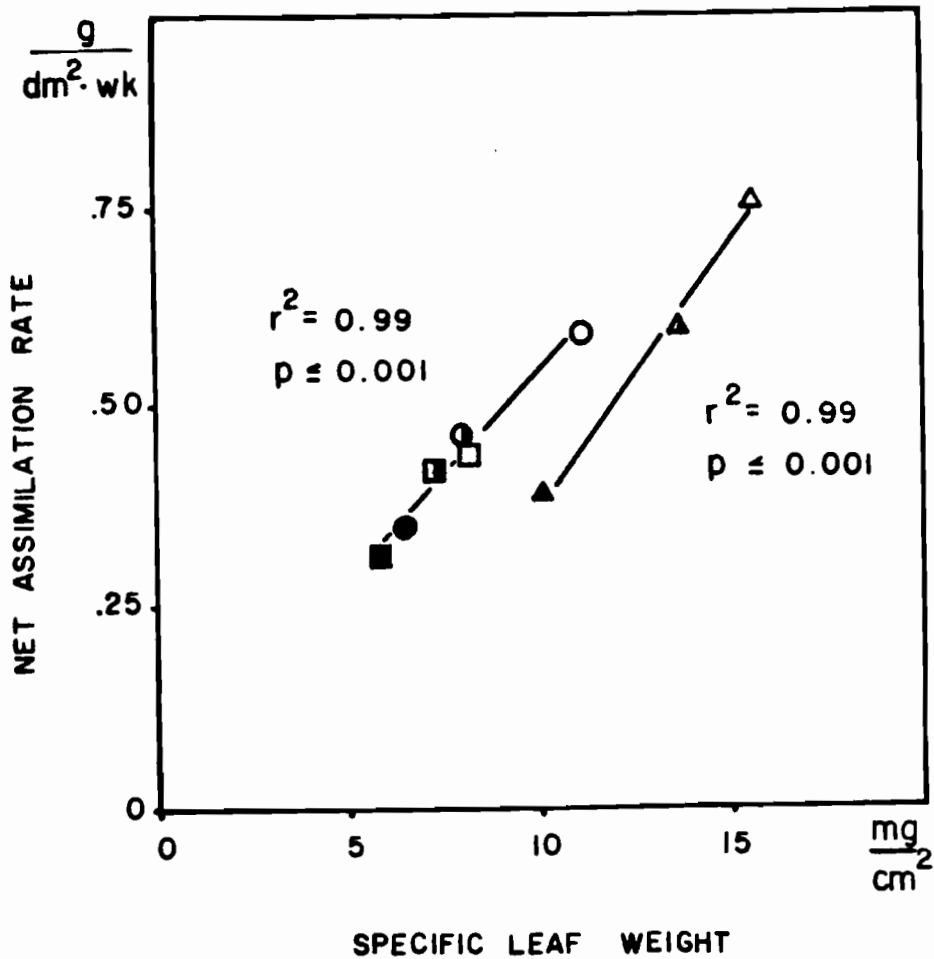
The estimated change in LAI during the last measurement period generally agreed within 30%, with an understory absent and within 45% in stands with understory vegetation present. This degree of variation is not surprising considering the variation illustrated in Figs. 3a and 3b. Growth efficiency, in terms of volume or biomass, agreed with observed values within 20% and 30%, respectively. Leaf area index agreed within 15%. Using the first estimation procedure, stand growth in volume and

in biomass agreed within 20% and 30%, respectively. Using the second estimation procedure, predicted stand volume and stand biomass growth were within 10% of observed values.

## Discussion

In Chapter I, photosynthesis was shown to be closely correlated with specific leaf weight. Here I will consider how specific leaf weight relates to production. In theory, if total plant respiration expressed per unit of leaf area is proportional to the net photosynthesis per unit of leaf area then the net assimilation rate, or the rate of dry matter production per unit of leaf area, should also correlate closely with specific leaf weight. On an individual seedling basis, Brix (1967) provided data from which a linear relationship between specific leaf weight and net assimilation rate (total dry matter produced per unit of foliage) was derived (Fig. 4). The relationship shifted, depending upon whether plants were grown at 13°C or at higher temperatures.

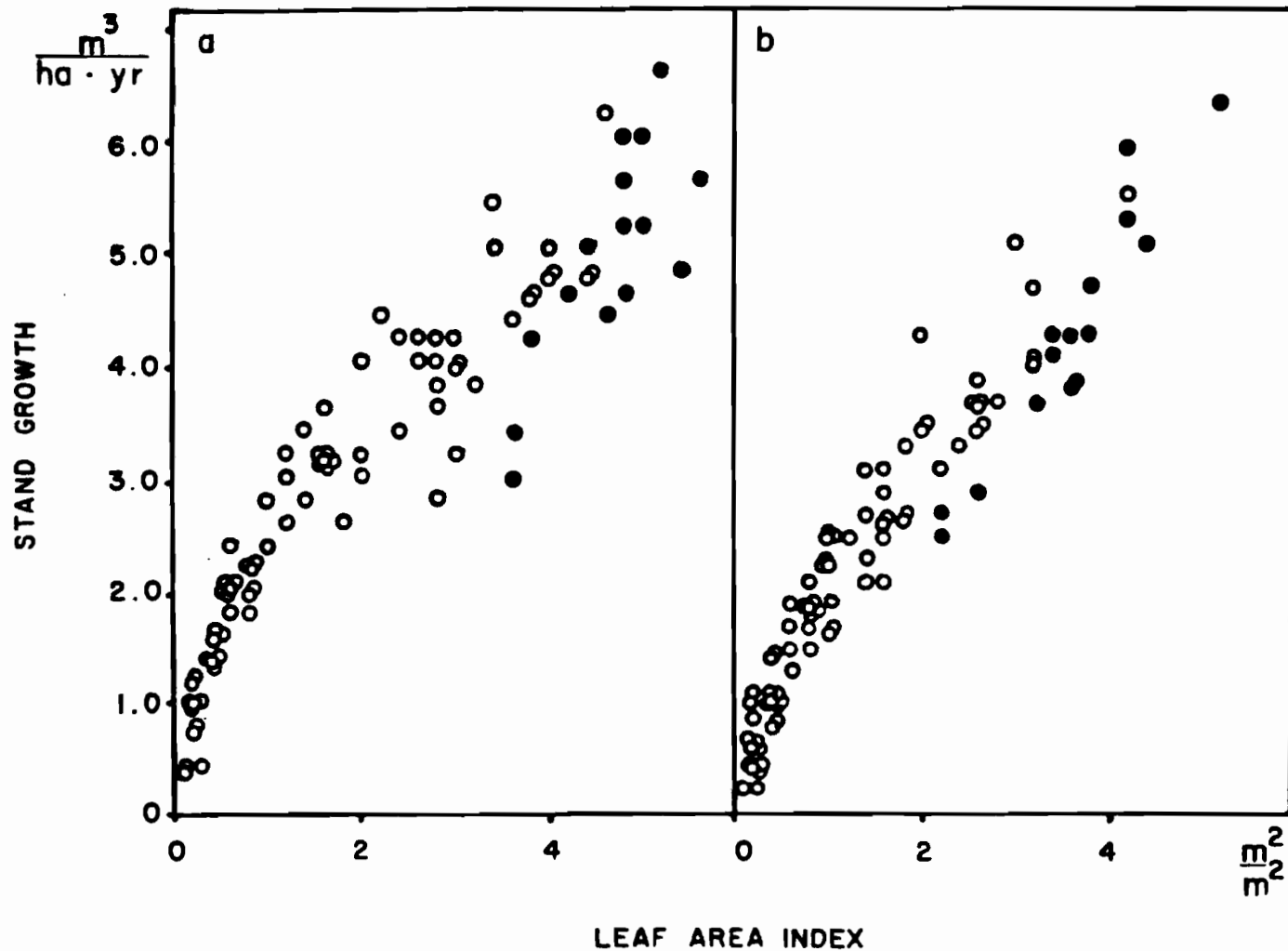
Specific leaf weight can, theoretically, correlate with growth efficiency if the proportion of the net assimilation which is allocated to stemwood production remain constant over a range of net assimilation rates. In my study, specific leaf weight was only determined during the last period and did not differ significantly among plots. Growth efficiency also did not vary



- II. 4. Net assimilation rate (total dry weight produced/unit of leaf area) of Douglas-fir seedlings grown under different illumination and temperature in relation to specific leaf weight. Light levels were 1800 ft-c. (open symbols), 1000 ft-c. (half-filled symbols), 450 ft-c. (filled symbols). Temperature at 13 $^{\circ}C$  ( $\Delta$ ), 18 $^{\circ}C$  (O), 24 $^{\circ}C$  ( $\square$ ). Recalculated from Brix (1967).

significantly among plots in the last period of measurements. Similar specific leaf weights suggest comparable photosynthetic rates per unit of leaf area. Comparable photosynthetic rates could help account for a linear increase in stand growth over the range in LAI between 3.5 and 6.0 (Fig. 5a and 5b).

Growth efficiency rapidly decreased as leaf area index approached an LAI of 2.0 and remained relatively constant at higher LAI. At the lower values of LAI, it is unlikely that changes in light penetration would cause a major decline in photosynthetic rates. What therefore might explain the abrupt decrease in growth efficiency with small increments in LAI? Initially, roots from the overstory and dense (17,000 trees/ha) understory probably fully occupied the soil. In the process of eliminating the overstory and drastically thinning the understory, a large volume of soil was left unoccupied by roots. In this water limited environment, reduction in root density provides more water, and perhaps more nutrients, to the few remaining trees. Available water and nutrients in the proximity of surviving root systems increased in relation to reductions in stocking density and with the removal of



II. 5. Stand volume growth in relation to leaf area index. (a) with understory absent, (b) with understory present. Data are from measurements defined in Figure 1.

understory vegetation. The effect was most pronounced during the first two periods (Fig. 2).

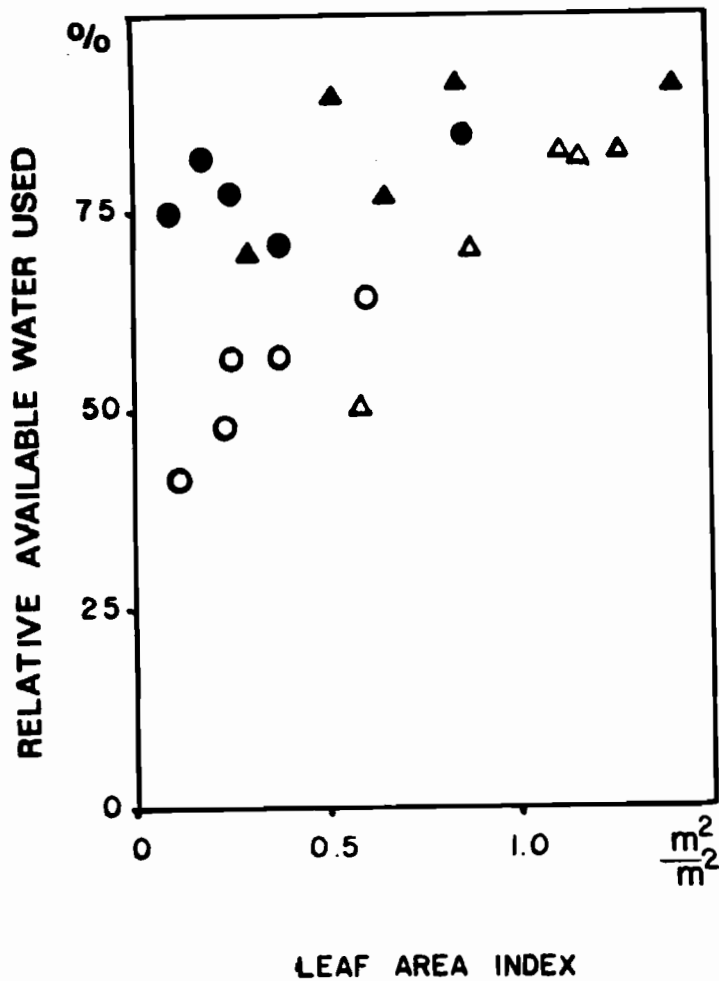
The increase in growth efficiency observed between the first and second period, at comparable or increased LAI, I interpret to reflect slow reoccupation of the soil by roots growing in pumice soils. Pumice soils, similar to the soil in this study, contain particles that are bridged together and present major barriers to rapid root growth (Youngberg and Cochran 1980; Hermann and Peterson 1969, Hermann 1969). A relative large amount of water and nutrients available per unit of foliage is likely to permit near maximum rates of photosynthesis and result in greater growth efficiency once roots are better established (as observed here during the 2nd period).

The rapid decrease of growth efficiency with increasing leaf area index has been demonstrated previously from thinning experiments in Douglas-fir (Waring et al. 1981), lodgepole pine (Mitchell et al. 1983), and ponderosa pine (Larsson et al. 1983). In experiments in which the supply of water and nutrients were controlled, Scots pine showed similar decreases in growth efficiency over time as LAI increased (Waring in press).

In this study available water supply was nearly used by the end of the growing season, as compared to what appears to be a complete water use by the adjacent uncut stand, when LAI approached 1.5 (Fig. 6). Nevertheless, total production continued to increase with increasing LAI (Fig. 5). If production of roots stabilize when all water is used and photosynthetic efficiency does not decrease demonstrably between LAI of 2.5 to 6.0, then increased stem wood production may reflect improved water use efficiency (carbon uptake per unit of water). In stands with high LAI much of the photosynthesis may take place early in the growing season when water is not limiting and when evaporative demand is low. Further, much of the foliage is sufficiently shaded and so probably loses less water than does more exposed foliage in stands with lower LAI. The shaded foliage is also likely to have higher water use efficiency (Troeng 1982).

Based on initial signs of density-related mortality (up to 2% of the smallest size classes in the densest stocking levels) and based on the reduction in the rate of net accumulation of leaf area, the stands appear to be reaching their maximum LAI. Because stand growth is a function of both growth efficiency and LAI, and because





- II. 6. Relative available soil water used by the end of the growing season, as compared with water used by adjacent uncut stand, in relation to canopy leaf area index on ponderosa pine plots without understory vegetation (open symbols), and with understory vegetation (filled symbols). Circles represent data obtained two years after initiation of the experiment and triangles represent data obtained 8 years following initiation of the experiment. Calculated from Barrett (1970).

both of these variables appear to be approaching constants, stand growth is approaching a plateau. Stand growth will eventually decrease as maintenance respiration increases (Whittaker 1976; Assmann; Waring and Schlesinger in press) and tree mortality reduces the rate of growth. Extrapolation of equations describing changes in growth rates, leaf area index, and other variables (Table 1) based on earlier measurement periods did not include the changes in growth patterns observed in the last period where growth efficiency plateaus. In the future, equations incorporating data from the last measurement period are expected to better describe the relationships and to result in smaller error estimates.

From experimental work with Scots pine and from this study one important principle emerges. The effect of treatments upon growth efficiency can best be assessed by comparing growth efficiency at a similar and relatively low LAI. This usually requires an annual assessment of growth and LAI over a sufficiently long period to assure that comparable values of LAI can be obtained. Another important observation derived from this study is that differences in stand growth attributed to treatment usually, but not always (Brix 1981), ignore the fact that

leaf area development is enhanced initially by the treatment. Production rates/unit of leaf area may then be very similar once stands reach high values of LAI. This point was recognized by Miller (1981) in his interpretation of the effects of periodic fertilization upon stand growth and development. Only in those cases where a treatment is sustained might the maximum LAI in a particular environment be expected to increase (Waring 1983; Axelsson 1981).

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