

An index of photosynthesis for comparing forest sites in western Oregon

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An index was developed that takes into account the combined influence of air and soil temperatures, light, and the availability of soil moisture upon photosynthesis by a unit area of fully exposed foliage of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The index is derived from a summation of daily estimates of carbon assimilation (milligrams CO₂ assimilation per decimeter per day) for an entire year. In a comparison of forest environments in western Oregon the index was correlated to a measure of forest productivity ($r^2 = 0.99$). Furthermore, it suggests that much of the annual carbon fixation occurs during the mild winters characteristic of the region. The ability to assess the effects of frost, soil drought, and other variables separately was valuable in explaining differences between coastal, valley, and mountainous sites.

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Les auteurs ont développé un indice qui tient compte de l'influence conjointe des températures de l'air et du sol, de la lumière, et de la disponibilité de l'eau du sol sur l'activité photosynthétique du feuillage du Douglas (*Pseudo. suga menziesii* (Mirb.) Franco). L'indice est dérivé d'une sommation des estimations quotidiennes d'assimilation de carbone (mg CO₂ assimilé dm⁻² jour⁻¹) pour 1 année entière. Une étude comparative de divers milieux forestiers de l'ouest de l'Orégon a révélé que l'indice était corrélé à une mesure de la productivité de la forêt ($r^2 = 0.99$). L'étude suggère de plus qu'une bonne part de la fixation annuelle de carbone a lieu au cours des hivers doux qui sont caractéristiques de la région. Une évaluation séparée des effets du gel, de la sécheresse du sol et autres facteurs a permis d'expliquer des différences entre stations côtières, stations de vallée, et stations de montagne.

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Introduction

Predicting forest growth, changes in composition, and results of silvicultural manipulations are difficult in mountainous regions of the western United States because of marked spacial variation in physical environment. Interpreting microclimatic data through their influence upon important plant responses led to indices that aid in vegetation analysis and in estimating forest productivity (Waring 1969; Waring *et al.* 1972; Reed and Waring 1974).

Zobel *et al.* (1976) found that climax vegetation types (Daubenmire 1968) assigned by Dyrness *et al.* (1974) for the central Oregon Cascades fell along moisture and temperature gradients as defined by Waring (1969). Similar indices in the Siskiyou Mountains of southwestern Oregon, however, did not signify identical vegetation or productivity (Waring *et al.*

1972). For this reason we sought a more integrative general index.

Recent studies (Walker *et al.* 1972; Salo 1974; and John Helms, University of California, Berkeley, personal communication) show that some conifers in the western United States are adapted to photosynthesize at cool temperatures, which are common throughout much of the region during winter. Perhaps the indices developed thus far did not adequately predict differences in productivity because they were restricted to the growing season (Waring *et al.* 1972; Waring and Youngberg 1972; Reed and Waring 1974).

Because carbon assimilation is basic to primary production, an index based on evaluation of forest microclimates as they affect photosynthesis year-round should show a close relation to forest productivity. In addition, assessment of the role of frost, soil drought, and other variables could explain differences in site productivity.

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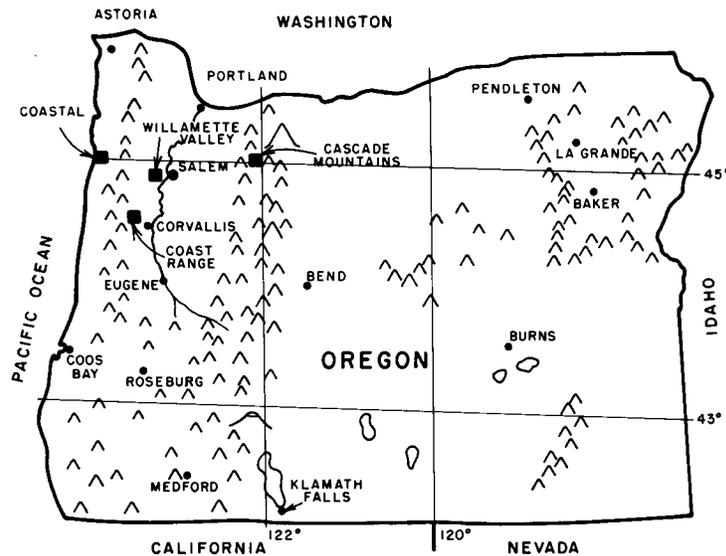


FIG. 1. Location of the four study plots in a transect across western Oregon.

This paper documents assumptions implicit in deriving a photosynthetic index and contrasts simulated photosynthesis at four environments representing a transect from productive coastal forests to sites with summer drought, winter snow cover, or both.

Methods

Study Sites

The four locations compared were a moist coastal site a few kilometres from the Pacific Ocean, a dry interior Coast Range site, a mild lowland site in the Willamette Valley, and a cool site in the Cascade Mountains (Fig. 1).

The coastal site had a gently sloping (20%) west aspect and was situated at less than 100 m elevation. This area receives between 200 and 250 cm of precipitation annually, with fog drip an important supplement to rainfall. The deep, rich Brown Lateritic (Haplohumult) soils support highly productive stands of the *Picea sitchensis* zone (Franklin and Dyrness 1973), where *Picea sitchensis* (Bong.) Carr., *Pseudotsuga menziesii* (Mirb.) Franco, and *Alnus rubra* Bong. are important tree species.

The interior Coast Range location was at 570 m elevation on a 30% east-facing slope. An annual rainfall of 150 cm comes primarily during the winter months. A Reddish Brown Lateritic (Haplohumult) soil of moderate depth does not store enough water to supply a fully vegetated area during the summer, and drought is common. Important tree species include *Acer macrophyllum* Pursh, *Arbutus menziesii* Pursh, *Pseudotsuga menziesii*, and *Abies grandis* (Dougl.) Lindl.

The Willamette Valley study area was at an elevation of 75 m on a 10% southeast aspect. The 100 cm of precipitation is generally confined to the nongrowing season. The deep clay (Xerert) soil is capable of storing large amounts of water, which reduce summer drought.

Plant communities are dominated by *Quercus garryana* Dougl., *Pseudotsuga menziesii*, and *Abies grandis*.

The mountain site was located in the western Cascade Mountains at 1050 m elevation on a 35% north slope. Average precipitation is over 200 cm, and a winter snowpack of 2 to 4 m is common. The soil is a rocky Regosol (Xerumbrept). The site is in the *Abies amabilis* zone, where, in addition to *Abies amabilis* (Dougl.) Forbes, *Pseudotsuga menziesii*, *Tsuga heterophylla* (Raf.) Sarg., and *Abies procera* Rehd. are important tree species (Franklin and Dyrness 1973).

Climatic and Physiological Measurement

Climatic data required for simulations were collected at each site. These included solar radiation and soil and air temperatures from instruments located in forest openings. Data for the coastal site were collected in 1972, and other sites were measured in 1970.

Shortwave incoming solar radiation was recorded with Kipp solarimeters during the spring, summer, and fall at the three interior sites. Daily total radiation was calculated by summing visually estimated, 15-min averages. During the winter, we could not measure radiation, so 5-year average radiation from near Corvallis was substituted for the interior sites (Bates and Calhoun 1969). For the coastal site, solar radiation data from Astoria, Oregon, 96 km to the north, were used.

Temperatures at 20 cm below and 1 m above ground were recorded continuously on 30-day Partlow thermographs. Air temperature records were digitized for computer analysis following the methods of Cleary and Waring (1969). Average day and night temperatures were computed according to the appropriate day length. Average daily soil temperature was taken visually from the chart.

Physiological information needed for the photosynthesis simulation included predawn xylem water potentials and the length of growing season. Xylem water potentials were measured with a Scholander pressure chamber

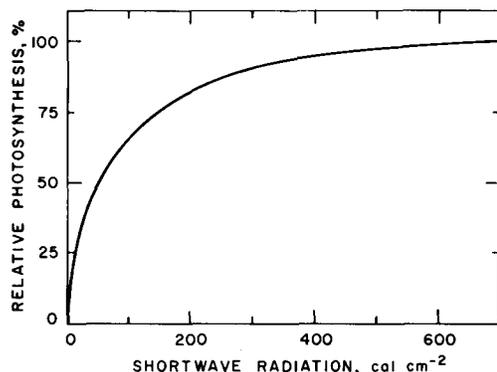


FIG. 2. The light response curve of the photosynthesis model assuming constant temperature and a 12-h day. An efficiency of 1 was arbitrarily assigned at 700 cal cm⁻² day⁻¹ (1 cal cm⁻² min⁻¹ = 69.8 mW cm⁻² min⁻¹).

(Scholander *et al.* 1965; Waring and Cleary 1967) at 10- to 14-day intervals during the growing season. Values for intervening days were estimated by linear interpolation.

Measurements needed to establish the relation between leaf conductance and predawn xylem water potential were taken with a Turner aspirated diffusion porometer (Turner *et al.* 1969) using methods described by Running (1976).

The growing season was defined as that period when the secondary cambium of small Douglas-fir trees was actively dividing (Cleary and Waring 1969). Cambial activity was assessed by periodically inserting pins into the stem and later observing anatomical abnormalities in the xylem (Wolter 1968). The beginning of cambial activity was correlated with warming of the soil (Emmingham 1977). Although the cambium of Douglas-fir may be capable of some activity throughout the winter (Worrall 1971), the growing season was considered over by mid-October, after which cell divisions were infrequent.

Wood Production

Wood production for a 100-year period was estimated from the site index tables generally used in the region (McArdle *et al.* 1961). Site index (height at 100 years) was estimated for each plantation by determining age and height of adjacent stands.

Model Development

To provide a seasonal interpretation of carbon assimilation, we chose to evaluate environmental data at a daily resolution.

To make the model general and to avoid the need for detailed information on stand structure and foliage distribution, the simulation was based on 1 dm² of fully exposed needle area at 1 m height. Douglas-fir was chosen because it is the most widespread and dominant conifer in the region.

Our interest in identifying reasons for varia-

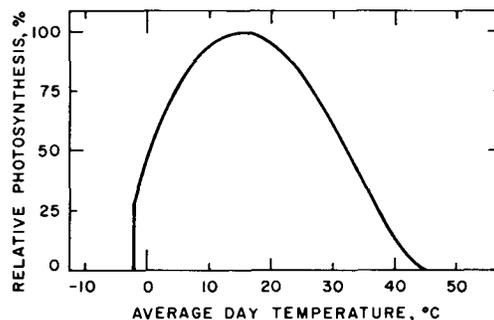


FIG. 3. The temperature response curve of the photosynthesis model assuming constant light and a 12-h day. An efficiency of 1 was assigned at the highest point on the curve.

tion in productivity led to a partitioning of simulation results into 'potential' and 'predicted' photosynthesis. Potential photosynthesis was defined as that possible under prevailing light and temperature conditions assuming no limitation from drought or preconditioning. This should not be confused with potential in the optimum sense. Predicted photosynthesis was defined as that possible after other physiological or climatic limitations such as drought or cold were considered. In other words, it was an estimate of actual carbon assimilation.

We sought to include the major environmental constraints upon photosynthesis, recognizing that all the desired information was not available specifically for Douglas-fir.

Light and Temperature

Basic to any simulation of photosynthesis is the effect of temperature and light (Reed and Webb 1972). Phillip Sollins (Oregon State University, Corvallis, personal communication) adjusted light and temperature curves to fit gas-exchange data taken on 40-year-old Douglas-fir (Salo 1974) by techniques discussed in Sollins *et al.* (1973). The light effect (Eq. 1, part 2) had over 70% efficiency above 2.15 mW (150 cal cm⁻²) per day (Fig. 2). The temperature effect (Eq. 1, part 1) gave optimum carbon uptake between 11 and 18°C and a decrease to zero at -2 and 45°C (Fig. 3). These curves are similar to those derived from other gas-exchange studies (Webb 1972; Larcher 1969; Troughton 1975). Implicit in this model was the assumption that stomata were open ($k_{1a} = 0.13465$) during daylight hours unless other factors, to be discussed later, were limiting.

$$[1] \quad P = [B_1(H_d)(B_2 - T_d)^{B_4}(T_d - B_3)] \cdot \frac{E}{B_5 + \frac{E}{60H_d}} \cdot k_{1a}$$

$P = (\text{Temperature effect}) \cdot (\text{light effect}) \cdot (\text{average leaf conductance}),$

where $P =$ net daily photosynthesis ($\text{mg CO}_2 \text{ dm}^{-2} \text{ day}^{-1}$); $H_d =$ day length (h); $T_d =$ average day temperature ($^{\circ}\text{C}$); $k_{1a} =$ average leaf conductance (cm s^{-1}); $E =$ total radiation ($\text{cal cm}^{-2} \text{ day}^{-1}$) ($1 \text{ cal cm}^{-2} \text{ min}^{-1} = 69.8 \text{ mW cm}^{-2} \text{ min}^{-1}$); $B_1 = 0.0097$ ($\text{mg CO}_2 \text{ h}^{-1} \text{ dm}^{-2} (^{\circ}\text{C} - (B_4 + 1)) \text{ s cm}^{-1}$), a scaling factor; $B_2 = 45$ ($^{\circ}\text{C}$) upper assimilation threshold; $B_3 = -5$ ($^{\circ}\text{C}$) lower assimilation threshold for curve definition; $B_4 = 1.5$ (dimensionless) definition of slope; and $B_5 = 0.1$ ($\text{cal cm}^{-2} \text{ min}^{-1}$) light threshold. Night respiration was calculated from average night temperature and night length (Eq. 2). The results from both equations were added to give net 24-h CO_2 fixation. Hereafter, reference to photosynthesis will be to net daily assimilation

$$[2] \quad R = -B_6 \cdot (24 - H_d) \cdot \exp(B_7 T_n),$$

where $R =$ respiration in leaf at night ($\text{mg CO}_2 \text{ dm}^{-2}$); $T_n =$ average night temperature ($^{\circ}\text{C}$); $B_6 = 0.1$ ($\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$) adjustment factor; and $B_7 = 0.2$ ($^{\circ}\text{C}^{-1}$).

Other restrictions on CO_2 assimilation were modeled as they affected leaf conductance, a strategy suggested by Brown (1969). All leaf conductances were computed with total rather than projected leaf area.

Drought

Because drought is common in forest ecosystems of western Oregon (Waring 1969; Zobel *et al.* 1976) and has a direct effect on photosynthesis in Douglas-fir (Cleary 1971), its effect on leaf conductance through the summer was investigated. The development of portable porometers (Turner *et al.* 1969; Turner and Parlange 1970; Beardsell *et al.* 1972) allowed for measurement of Douglas-fir leaf conductance directly in the field. During three field seasons, 31 days of data with the pressure chamber and porometer were obtained. Each point (Fig. 4) represents an average of several leaf conductance observations on current year's foliage of a single Douglas-fir sapling. The observations were taken over a 5- to 10-h period centered around midday

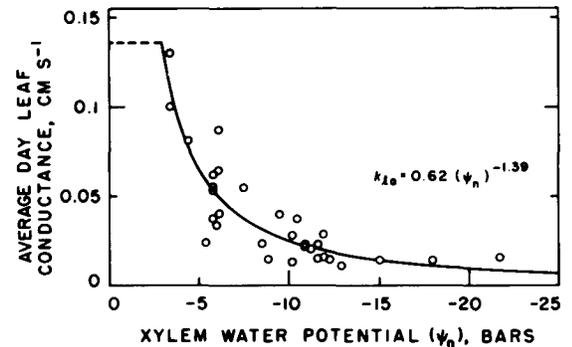


FIG. 4. The relation between average day leaf conductance (k_{1a}) of current year's foliage and xylem water potential at night (Ψ_n). Each point was the average of several leaf conductance measurements taken throughout the day. The parameters of the equation were arrived at by a least-squares-curve fit of the allometric function ($1 \text{ bar} = 10^5 \text{ Pa}$). Data from Running (1976) and Emmingham (1974).

on generally sunny days. Xylem water potential (Ψ_n) was measured on each tree before dawn, and ranged from -3.4 to -21.8 bars. Leaf conductance (k_1) varied from 0.33 to 0.0033 cm s^{-1} during the day (Running 1976). Average leaf conductance (k_{1a}) was within the range 0.014 to 0.13 cm s^{-1} .

The relation between k_{1a} and Ψ_n was fitted by a least-squares-curve fit routine to the allometric function (Eq. 3). The curve was truncated at -3 bars to give a maximum average daily conductance of 0.1347 cm s^{-1} , because xylem water potential was never observed above that level. The maximum k_{1a} was only about one-third of maximum observed k_1 because even during periods when trees were well watered, k_1 in the afternoon was much less than in the morning.

$$[3] \quad k_{1a} = \begin{cases} 0.62 (\Psi_n)^{-1.39}, & < -3 \text{ bars} \\ 0.13465, & \geq -3 \text{ bars} \end{cases}$$

Because a wide variety of day types were included in the data set, this approach accounts for variations observed in k_1 from a variety of environmental factors.

Frost

The effect of low air temperatures on leaf

conductance was included in two ways. When average day temperature was less than -2°C , photosynthesis was set at zero by truncating the temperature curve. This was based on laboratory studies by Reed (1968), who found stomata of Douglas-fir closed at or below -2°C . Drew *et al.* (1972) found a similar response in *Pinus ponderosa* Laws.

In addition, a delayed effect of low temperatures was included following a pattern demonstrated for *Olea europaea* by Larcher (1969), for *Picea sitchensis* by Neilson *et al.* (1972), and for *Pinus cembra* by Tranquillini and Machl-Ebner (1971). When night temperature fell below -2°C , a frost reduction factor was computed and used to lower the next day's leaf conductance. The frost reduction function had two elements. Days until recovery (D_r) depended upon severity of the frost (Eq. 4) and ranged from 1 to 10 days for night minimum temperatures (T_m) between -2 and -7°C .

$$[4] \quad D_r = 0, \quad T_m \geq -2^{\circ}\text{C} \\ = -2(T_m + 2), \quad -7^{\circ}\text{C} \leq T_m < -2^{\circ}\text{C} \\ = 10, \quad T_m < -7^{\circ}\text{C}$$

The frost reduction factor (F) (Eq. 5) reduced photosynthesis on the day after frost to less than 10% of the potential. On each succeeding day without frost, the frost reduction factor was increased until it returned to a value of one.

$$[5] \quad F = 1 - [(D_r - D_t)/D_r],$$

where D_t = days since frost. Chlorophyll breakdown and other biochemical reactions may also occur, but we subsume such effects into a reduction of leaf conductance.

Cold Soils

Soil temperature has been recognized as an important factor in plant growth and distribution (Richards *et al.* 1952; Billings and Mooney 1968). Both transpiration (Babalola *et al.* 1968) and photosynthesis (Havranek 1972) of various conifers have been shown to decrease at low soil temperatures. We chose a function that gave 100, 50, and 0% of maximum average leaf conductance (k_{1a}) at 5, 0, and -2°C soil temperature (T_s), respectively (Eq. 6), a response similar to that of a variety of plants from the North Temperate Zone (Anderson and McNaughton 1973).

$$[6] \quad k_{1a} = 0.1565 [1 - e^{-0.2811(T_s + 2)}]$$

This reduction in leaf conductance and, indirectly, photosynthesis may be overstated. Evaporative demand in the winter is particularly low during periods of cloudy weather, and water deficits necessary to close stomata would not develop. Also, Turner and Jarvis (1975) found that both hardened and unhardened Sitka spruce were able to carry on photosynthesis at pretreatment rates after the root system was frozen for 1 day.

More work on the photosynthetic response of Douglas-fir to environmental conditions during the dormant season would be helpful to determine if there is an adjustment to temperature such as that found by Mooney and Harrison (1969) for other plants.

Factors other than xylem water potential, cold air, and soil temperatures may also affect stomatal behavior (for example, CO_2 concentration, wind, and humidity). For our purposes, however, such factors are assumed to be of minor importance in comparing photosynthetic potentials of forests dominated by Douglas-fir.

Of the photosynthesis models reviewed (Botkin 1969; Wuensher and Kozlowski 1971; Idso and Baker 1968; Conner *et al.* 1971; and Sollins *et al.* 1973), none was developed with the same objectives as this study and only Conner *et al.* (1971) included both temperature and moisture stress effects in their models.

The Computer Simulations

To provide an index of photosynthesis for different forest environments the previously discussed relations were assembled in a computer program. The photosynthesis simulator was coded in FORTRAN IV for a general model processor called FLEX 1 developed by Overton *et al.* (1973). The program is available upon request from the authors.

The sequence of operations for estimation of each day's net photosynthesis was as follows. Potential day photosynthesis was computed on the basis of average air temperature, day length, and total shortwave incoming solar radiation, assuming a maximum average daily leaf conductance of $0.13465 \text{ cm s}^{-1}$ (Running 1976; Emmingham 1974).

Predicted day photosynthesis was the product of potential photosynthesis and estimated leaf conductance. The most restrictive leaf conductance computed from predawn xylem water potential, night minimum temperature, or soil

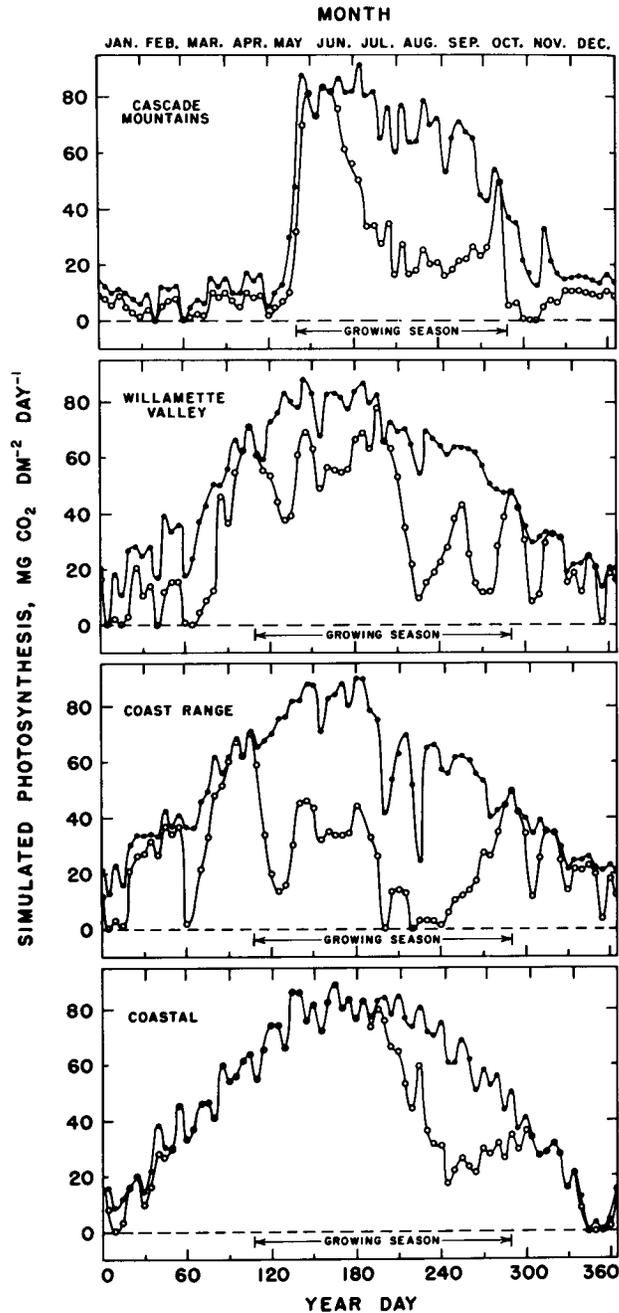


FIG. 5. The yearly pattern of photosynthesis at four sites in western Oregon. Potential values (●) assume no limitation by drought or by extremes in temperature; predicted values (○) include reductions from effects of drought and temperature.

temperature was used to compute predicted photosynthesis.

Respiration at night was computed from average night temperature (T_n). Net potential

and predicted photosynthesis were estimated by deducting night respiration from predicted and potential day photosynthesis.

TABLE 1. A summary of simulated potential (P) and predicted (A) photosynthesis for four forest sites in western Oregon

Location	Growing season, days	Simulated photosynthesis yearly total, mg CO ₂ dm ⁻²		% during dormant season		Annual reduction (P-A)/P
		P	A	P	A	
Cascade Mountains	138	13 457	7 211	29	30	46
Willamette Valley	183	18 715	11 709	32	33	37
Coast Range	183	18 895	9 352	37	55	51
Coastal	183	18 645	15 086	32	37	19

Results

Averages of simulated photosynthesis for 5-day periods are plotted in Fig. 5. Although the major environmental controls upon carbon assimilation were the same, the intensity and duration of their influence differed greatly among the sites. For example, only light and average temperature constrained carbon assimilation at the coastal site for most of the year. Two unusually cold periods (days 5–20 and 340–360) and a moderate summer drought (days 200–250) reduced the predicted below the potential by 19% (Table 1). At the interior Coast Range site, however, predicted carbon uptake was less than half the potential.

The Coast Range and Willamette Valley locations were influenced more by frost, particularly in early spring (days 60–90), as a result of cold air drainage and cloud-free night skies. A reduction in xylem water potential, probably associated with low root uptake in cold soils, occurred in late spring (days 100–140) and caused predicted photosynthesis to fall well below potential. During the latter part of summer (days 200–250), drought was severe, especially at the interior Coast Range site. During fall and winter, low light and temperature reduced the potential, but little further reduction was predicted from frost or cold soil. Reductions of 37 and 51% below yearly potential were predicted in the valley and interior Coast Range sites, respectively (Table 1).

At the mountain site, potential for winter photosynthesis was low because of cold air temperatures. In the fall, repeated frosts (days 285–320) reduced predicted photosynthesis far below potential. As cloud cover became more common during early winter (days 330–365), night frosts were less frequent and predicted photosynthesis more closely approached potential. Throughout the winter, snow covered the

site, and soil temperatures of about 1°C provided an additional constraint.

Average daily potentials were nearly equal on the four sites during the growing season, ranging from 98 to 103 mg CO₂ dm⁻² day⁻¹. Because the growing season was 45 days shorter at the Cascade Mountains location (Table 1), the accumulated potential for that season was about 50% of that at the coastal area.

The high summer potentials for photosynthesis were not fully realized because reductions from drought ranged from 25% at the Coast to 65% at the interior Coast Range site.

Dormant season contributions to annual predicted assimilation ranged from 30% at the mountain site to 55% at the interior Coast Range site (Table 1).

Because the same assumptions concerning the degree of control by temperature, light, and drought were applied to each area, differences in predicted annual carbon assimilation provide an index to forest productivity. Predicted photosynthesis was closely correlated ($r^2 = 0.99$) (Fig. 6) to a crude estimate of forest productivity (cubic volume of tree boles for Douglas-fir stands at 100 years (McArdle *et al.* 1961)).

Discussion

By combining the influence of light, temperature, and drought upon photosynthesis, we computed an index to seasonal and annual differences in carbon assimilation. This is a major step away from single factor analysis. The procedure permits, with some knowledge of climate and soil water supply, a means of identifying seasonal limitations upon carbon assimilation. The index is by no means a substitute for ecosystem analysis, which includes total carbon budgets (Sollins *et al.* 1973; Woodwell and Botkin 1970; Reichle 1975). It has the advantage,

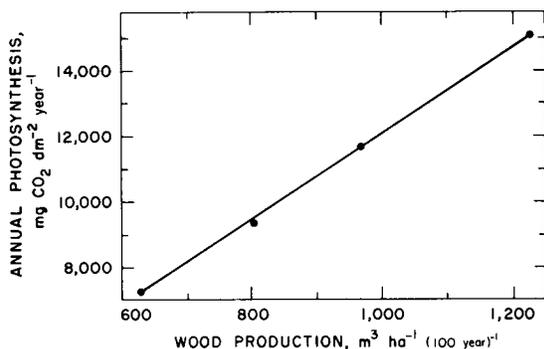


FIG. 6. A comparison of annual predicted photosynthesis and wood production for a 100-year period. Wood production was estimated from site index tables (McArdle *et al.* 1961).

however, of relative simplicity because the structure of the forest (that is, amount and distribution of foliage, twigs, stem, and roots) need not be known to make comparisons.

Evaluation of four forest microclimates with the physiologically based model of photosynthesis showed that significant assimilation occurred during the dormant season (even at midelevation) and that all sites were affected by drought. The most mesic location suffered a 19% loss of potential, mainly because of water deficits. This supports the hypothesis that high productivity of coniferous forest in the western United States results from mild winters (Franklin and Dyrness 1973). Summer drought combined with mild winter temperatures may explain why coniferous rather than deciduous species dominate western temperate forests. These factors also contribute to the massive accumulation of biomass in some coniferous forests.

The three low-elevation sites had similar yearly potentials, and all four sites had similar summer potentials (Table 1). Thus the general assumption that lower productivity at midelevations is associated with cool summer temperatures appears unfounded. Rather, low winter temperatures would significantly reduce yearly photosynthesis. Winter assimilation was highest during cloudy periods as a result of reduced frost. Clear days and nights were accompanied by low night minimum temperatures resulting in reduced carbon uptake.

The high correlation between the annual photosynthesis index and forest productivity was unexpected, because respiration in a large portion of the plant was ignored. We expected a

discrepancy where drought provided a major limitation in the Coast Range and low temperatures in the Cascades, because drought is usually associated with high temperatures, which would result in high respiration for the entire tree. Respiration would be less where low temperatures provide the predominant control of carbon assimilation. Accounting for leaf respiration may be adequate for comparing sites that are environmentally dissimilar, because foliage represents most respiring tissue on all sizes of trees (Yoda *et al.* 1965).

In further studies comparing productivity and the annual photosynthesis index for several forest sites in the central Cascade Mountains of Oregon, the correlation between these variables was much lower. Therefore, we are expanding the photosynthesis index to represent the carbon balance for a 2-m-tall sapling to accommodate different respiration rates of nonphotosynthetic tissue.

Estimates of dormant-season photosynthesis were not supported by extensive work on Douglas-fir although high rates of carbon fixation in dormant Douglas-fir were reported by Walker *et al.* (1972) and Salo (1974). *Abies alba* and other conifers as reviewed by Bauer *et al.* (1975) were less sensitive to cold than assumed in this study for Douglas-fir. Continued study of how cold air, cold soil, and dormancy affect photosynthesis in conifers of western North America is needed to clarify the importance of dormant season environment to forest productivity.

New studies may improve the photosynthetic model but are unlikely to change the general conclusions that summer drought and mild winters are extremely important in determining the productivity of western Oregon forests. Also, the ability to interpret climatic constraints upon production should aid the silviculturalist in selecting appropriate practices.

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- ANDERSON, J. E., and S. J. MCNAUGHTON. 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. *Ecology*, **54**: 1220-1234.
- BABALOLA, O., L. BOERSMA, and C. T. YOUNGBERG. 1968. Photosynthesis and transpiration of Monterey pine seedlings as a function of soil water suction and soil temperature. *Plant Physiol.* **43**: 515-521.
- BATES, E. M., and W. CALHOUN. 1969. Local climatological data for Oregon State University. Spec. Rep. 277. U.S. Dep. Commer., Natl. Oceanic Atmos. Adm., Natl. Weather Serv., Agric. Ext. Stn., Oregon State Univ.
- BAUER, H., W. LARCHER, and R. B. WALKER. 1975. Influence of temperature stress on CO₂-gas exchange. In *Photosynthesis and productivity in different environments*. International Biological Programme. Vol. 1. 3. Cambridge University Press, England. pp. 557-586.
- BEARDSSELL, M. F., P. G. JARVIS, and B. DAVIDSON. 1972. A null-balance diffusion porometer suitable for use with leaves of many shapes. *J. Appl. Ecol.* **9**: 677-690.
- BILLINGS, W. D., and H. A. MOONEY. 1968. The ecology of arctic and alpine plants. *Biol. Rev.* **43**: 481-529.
- BOTKIN, D. R. 1969. Prediction of net photosynthesis of trees from light intensity and temperature. *Ecology*, **50**: 854-858.
- BROWN, K. W. 1969. A model of the photosynthesizing leaf. *Physiol. Plant.* **22**: 620-637.
- CLEARY, B. D. 1971. The effect of plant moisture stress on physiology and establishment of planted Douglas-fir and ponderosa pine seedlings. Ph.D. Thesis, Oregon State University, Corvallis.
- CLEARY, B. D., and R. H. WARING. 1969. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. *Can. J. Bot.* **47**: 167-173.
- CONNOR, D. J., B. R. TUNSTALL, R. VAN DEN DRIESSCHE. 1971. An analysis of photosynthetic response in a brigalow forest. *Photosynthetica*, **5**: 218-225.
- DAUBENMIRE, R. 1968. *Plant communities: a textbook of plant synecology*. Harper and Row, New York.
- DREW, A. P., L. G. DREW, and H. C. FRITTS. 1972. Environmental control of stomatal activity in mature semiarid site ponderosa pine. *Ariz. Acad. Sci.* **7**: 68-93.
- DYRNESS, C. T., J. F. FRANKLIN, and W. H. MOIR. 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. *Coniferous For. Biome Bull.* **4**. Coniferous For. Biome, US/IBP, Univ. Wash. AR-10, Seattle, WA 98195.
- EMMINGHAM, W. H. 1974. Physiological responses of four Douglas-fir populations in three contrasting field environments. Ph.D. Thesis, Oregon State University, Corvallis, Oregon.
- . 1977. Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments. *Can. J. For. Res.* **7**. This issue.
- FRANKLIN, J. F., and C. T. DYRNESS. 1973. *Natural vegetation of Oregon and Washington*. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-8.
- HAVRANEK, W. 1972. Ueber die Bedeutung der Bodentemperatur fuer die Photosynthese und Transpiration junger Forstpflanzen und fuer die Stoffproduktion an der Waldgrenze. *Angew. Bot.* **46**: 101-116.
- IDSO, S. G., and D. G. BAKER. 1968. The naturally varying energy environment and its effects upon net photosynthesis. *Ecology*, **49**: 311-316.
- LARCHER, W. 1969. The effect of environmental and physiological variables on the carbon dioxide gas exchange of trees. *Photosynthetica*, **3**: 167-198.
- MCARDLE, R. E., W. H. MEYER, and D. BRUCE. 1961. The yield of Douglas-fir in the Pacific Northwest. *Tech. Bull.* 201. U.S. Dep. Agric., Washington, D.C.
- MOONEY, H. A., and A. T. HARRISON. 1969. The influence of conditioning temperature on subsequent temperature-related photosynthetic capacity in higher plants. In *Prediction and measurement of photosynthetic productivity*. Proc. IBP/PP Tech. Meet., Trebon, 14-21 Sept. 1969.
- NEILSON, R. E., M. M. LUDLOW, and P. G. JARVIS. 1972. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). II. Response to temperature. *J. Appl. Ecol.* **9**: 721-745.
- OVERTON, W. S., J. A. COLBY, J. GOURLEY, and C. WHITE. 1973. FLEX I user's manual. US/IBP. Coniferous For. Biome Int. Rep. 126.
- REED, K. L. 1968. The effects of sub-zero temperatures on the stomata of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). M.S. Thesis, University of Washington, Seattle, WA.
- REED, K. L., and R. H. WARING. 1974. Coupling of environment to plant response: a simulation model of transpiration. *Ecology*, **55**: 62-72.
- REED, K. L., and W. L. WEBB. 1972. Criteria for selecting an optimal model: terrestrial photosynthesis. In *Proceedings of Symposium on coniferous forest ecosystems*. Edited by J. R. Franklin, L. J. Dempster, and R. H. Waring. U.S. Dep. of Agric. For. Serv. Pac. NW For. Range Exp. Stn., Portland, Oregon. pp. 227-236.
- REICHLE, D. E. 1975. Advances in ecosystem analysis. *Bioscience*, **25**: 257-264.
- RICHARDS, S. J., R. M. HAGEN, and T. M. MCCALLA. 1952. Soil temperature and plant growth. In *Soil physical conditions in plant growth*. Edited by H. T. Shaw. Academic Press, New York. pp. 303-480.
- RUNNING, S. W. 1976. Environmental control of leaf water conductance in conifers. *Can. J. For. Res.* **6**: 104-112.
- SALO, D. J. 1974. Factors affecting photosynthesis in Douglas-fir. Ph.D. Thesis, University of Washington, Seattle, WA.
- SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, and E. A. HEMMINGSEN. 1965. Sap pressure in vascular plants. *Science*, **148**: 339-346.

- SOLLINS, P., D. E. REICHLER, and J. S. OLSON. 1973. Organic matter budget and model for a southern Appalachian *Liriodendron* forest. U.S.A.E.C. Rep. EDFB-IBP-73-2, Oak Ridge Natl. Lab., Oak Ridge, Tenn.
- TRANQUILLINI, W., and I. MACHL-EBNER. 1971. Ueber den Einfluss von warme auf das Photosynthesevermogen der Zirbe (*Pinus cembra* L.) und der Alpenrose (*Rhododendron ferrugineum* L.) im Winter. Rep. Kevo Subarct. Res. 8: 158-166.
- TROUGHTON, J. H. 1975. Photosynthetic mechanisms in higher plants. In Photosynthesis and productivity in different environments. Int. Biol. Program. Vol. 3. Cambridge University Press, England. pp. 357-391.
- TURNER, N. C., and P. G. JARVIS. 1975. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) IV. Response to soil temperature. J. Appl. Ecol. 12: 561-576.
- TURNER, N. C., and J. Y. PARLANGE. 1970. Analysis of operation and calibration of a ventilated diffusion porometer. Plant Physiol. 46: 175-177.
- TURNER, N. C., F. C. C. PEDERSEN, and W. H. WRIGHT. 1969. An aspirated diffusion porometer for field use. Spec. Bull. Soils XXIX/200. Conn. Agric. Exp. Stn., New Haven.
- WALKER, R. B., D. R. M. SCOTT, D. J. SALO, and K. L. REED. 1972. Terrestrial process studies in conifers—a review. In Proceedings of a symposium on coniferous forest ecosystems. Edited by J. R. Franklin, L. J. Dempster, and R. H. Waring. U.S. Dep. Agric. For. Serv. Pac. NW For. Range Exp. Stn., Portland, Oregon. pp. 211-227.
- WARING, R. H. 1969. Forest plants of the eastern Siskiyou: their environmental and vegetational distribution. Northwest Sci. 43: 1-17.
- WARING, R. H., and B. D. CLEARY. 1967. Plant moisture stress: evaluation by pressure bomb. Science, 155: 1248-1254.
- WARING, R. H., K. L. REED, and W. H. EMMINGHAM. 1972. An environmental grid for classifying coniferous forest ecosystems. In Proceedings of a symposium on coniferous forest ecosystems. Edited by J. R. Franklin, L. J. Dempster, and R. H. Waring. U.S. Dep. Agric. For. Serv. Pac. NW For. Range Exp. Stn., Portland, Oregon. pp. 79-91.
- WARING, R. H., and C. T. YOUNGBERG. 1972. Evaluating forest sites for potential growth response of trees to fertilizer. Northwest Sci. 46: 68-75.
- WEBB, W. L. 1972. A model of light and temperature controlled net photosynthetic rates for terrestrial plants. In Proceedings of a symposium on coniferous forest ecosystems. Edited by J. R. Franklin, L. J. Dempster, and R. H. Waring. U.S. Dep. Agric. For. Serv. Pac. NW For. Range Exp. Stn., Portland, Oregon. pp. 237-242.
- WOLTER, K. E. 1968. A new method for marking xylem growth. Forest Sci. 14: 102-104.
- WOODWELL, G. M., and D. B. BOTKIN. 1970. Metabolism of terrestrial ecosystems by gas exchange techniques: the Brookhaven approach. In Analysis of temperate forest ecosystems. Edited by D. E. Reichle. Springer-Verlag, New York. pp. 73-85.
- WORRALL, J. 1971. Absence of "rest" in the cambium of Douglas-fir. Can. J. For. Res. 1: 84-89.
- WUENSCHER, J. E., and T. T. KOZLOWSKI. 1971. Relationship of gas-exchange resistance to tree seedling ecology. Ecology, 52: 1015-1023.
- YODA, K., K. SHINOZAKI, H. OGAWA, K. HOZUMI, and T. KIRA. 1965. Estimation of the total amount of respiration in woody organs of trees and forest communities. J. Biol. Osaka City Univ. 16: 15-26.
- ZOBEL, D. B., W. A. MCKEE, and G. M. HAWK. 1976. Relationships of environment to composition, structure and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monogr. 46: 135-156.