Environmental Limits on Net Primary Production and Light-Use Efficiency Across the Oregon Transect

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ENVIRONMENTAL LIMITS ON NET PRIMARY PRODUCTION AND LIGHT-USE EFFICIENCY ACROSS THE OREGON TRANSECT[1]

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Abstract. Due to climate differences, an extreme range in productivity occurs along a 250-km, west-east transect at ≈44° north latitude in western Oregon, USA, where coniferous evergreen forests dominate. As part of the Oregon Transect Ecosystem Research (OTTER) project, our objective was to evaluate how climate constrains net primary production (NPP) by limiting the utilization of intercepted photosynthetically active radiation (IPAR). The forests measured along the transect intercepted from 22% to 99.5% of the incident PAR. With data collected from recording meteorological stations installed near each site, we defined the hourly conditions when photosynthesis was partly or completely limited by drought, extreme humidity deficits, or frost. From this analysis we calculated that the fraction of incident PAR that could be utilized throughout the year ranged from 92% in the coastal rainforests to <25% in the juniper woodland. NPP varied from 3 to 26 $Mg \cdot ha^{-1} \cdot yr^{-1}$ with the fraction of belowground NPP, estimated from litterfall, increasing from 20% to 60% of the total as the environment becomes harsher. Light-use efficiency (ε_u), calculated under conditions when the environment did not constrain photosynthesis, averaged 0.8 g/MJ for aboveground NPP and 1.3 g/MJ for total NPP.

Key words: biomass; climate; intercepted photosynthetically active radiation (IPAR); leaf area index; light-use efficiency; modelling; net primary production; Oregon transect; OTTER project; western Oregon.

Introduction

Forecasts of possible near-term changes in the Earth's climate have created a need for concepts and methods to monitor and model global-scale ecosystem dynamics. Characterization of large area patterns in ecosystem structure and function requires new perspectives to interpolate from detailed site-specific knowledge. In the Oregon Transect Ecosystem Research (OTTER) project we had the opportunity to compare a variety of ecosystem models across a range in vegetation (Peterson and Waring 1994 [this issue]).

Previous research has demonstrated a relationship between patterns of ecosystem production and climate. For example, biospheric production has been correlated with climate variables such as precipitation and temperature (Holdridge 1947, Rosenzweig 1968, Lieth 1975). These correlative models, however, do not provide mechanistic links between climate and biospheric activity. Alternatively, a number of researchers have begun to develop ecosystem process models that, when linked to remotely sensed observations, show some

potential for assessing regional- to global-scale patterns in ecosystem production (e.g., Dickinson 1983, Sellers 1985, Running et al. 1989). Most ecosystem models require initial specification of structure such as leaf area index and standing biomass, some knowledge of soil properties, and daily climatic data (see Running 1994 [this issue]).

There may be an intermediate ground between the simple correlation models and the detailed process models that will effectively describe environmental limits on primary production. For example, all net primary production depends upon interception of light by vegetation. Several studies have shown that the rate of primary production is linearly related to light interception under ideal conditions with a light-conversion efficiency (ε) of 1–2 g of dry matter produced per megajoule of absorbed photosynthetically active radiation (Monteith 1977, Linder 1985, Landsberg 1986). Estimation of canopy light interception from remotely sensed observations appears possible (Kumar and Monteith 1982, Sellers 1985, Asrar et al. 1986, Goward and Huemmrich 1992). At times, ε varies when environmental conditions are unfavorable (Russel et al. 1989). The possibility of using additional remotely sensed observations to identify these environmental
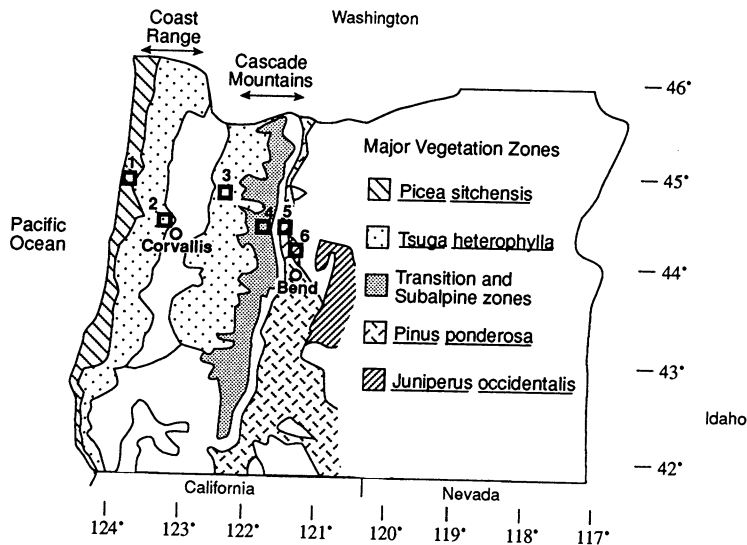
Fig. 1. Map of the study area in Oregon showing the location of the sites and the major vegetation zones (after Franklin and Dyrness 1973, Gholz 1982). Site 1 = old-growth Sitka spruce/western hemlock; site 1A (contained within site 1) = alder; site 2 = Douglas-fir/Oregon white oak; site 3 = Douglas-fir/western hemlock; site 4 = subalpine forest; site 5 = ponderosa pine; site 6 = juniper woodland.

conditions is discussed by Goward et al. (1994 [this issue]).

Our main objectives in this paper are (1) to test the generality of the light-conversion efficiency model over a range of representative forest stands in western Oregon and, if necessary, (2) to modify the model to account for conditions when factors other than light limit photosynthesis and growth. In addition, we summarize information on stand structure, soils, and climate necessary for other investigators to relate their remotely sensed observations, calculate fluxes, and validate detailed ecosystem models.

STUDY SITES

Six study areas were chosen along a 250-km, west-to-east transect, at ≈44° north latitude. The transect encompasses a wide range of climates and vegetation types (Fig. 1). Two mountain ranges—the Coast Range and the Cascades—influence regional weather patterns. On the west end of the transect the climate is primarily maritime, characterized by cool temperatures and low evaporative demand for most of the year. At the east end of the transect, in the rain shadow of the Cascades, the climate is more continental, with hot, dry summers and cold winters. Most of the precipitation for the region falls between October and June. Summers are generally dry with 2–3 mo lacking effective precipitation except along the Pacific Coast (Waring and Franklin 1979). This range in climate influences regional vegetation patterns (Franklin and Dyrness 1973). Stands were selected in the same forest community types reported by Gholz (1982), encompassing six different vegetation zones, ranging from lush, coastal forests to dry juniper woodlands. The forest stands along the transect display almost the complete range of net primary production found in North America (Gholz 1982, Jarvis and Leverenz 1983).

The primary criteria for selecting each of the forest stands were year-round accessibility and a secure site nearby for installing a meteorological station. Throughout the Pacific Northwest region, soil nitrogen is known to limit growth (Gessel and Walker 1956, Waring and Franklin 1979, Waring et al. 1992). Therefore, subsidiary stands were selected along the transect where nitrogen fertilizer was applied or nitrogen-fixing plants were abundant. At site 1, Cascade Head, we collected data from a red alder (*Alnus rubra* Bong.) stand (site 1A). At site 3, Scio, we selected a 55 × 55 m mixed stand of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) that had been previously fertilized in 1988 with an aerial application of 300 kg/ha of urea. On site 3F fertilization was continued through 1990 and 1991 with manual application of N twice a year—spring and fall—for a total of 460 kg·ha^{-1}·yr^{-1}. Finally, at site 5, Metolius, we selected a stand of ponderosa pine (*Pinus ponderosa* Laws.) that had undergone application of sewage sludge for 5 yr previous to 1989. Table 1 contains a brief description of all the study sites.

METHODS

Climatic measurements

Meteorological stations (Campbell Scientific Instruments, Inc., Logan, Utah, USA) were installed in secure, open areas <1 km to a maximum of 15 km from all but the juniper woodland (site 6) at the eastern

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TABLE 1. Characteristics of the study sites across the transect.

	Site						
Feature	1	1A	2	3*	4	5*	6
Site name	Cascade Head (old-growth)	Cascade Head (alder)	Waring's Woods	Scio	Santiam Pass	Metolius	Juniper
Physiographic province†	Western coast range	Western coast range	Interior valley	Low-elevation west Cascades	High Cascades summit	Eastern high Cascades	High lava plain
Dominant species	Picea sitchensis, Tsuga heterophylla	Alnus rubra	Pseudotsuga menziesii	Tsuga heterophylla, Pseudotsuga menziesii	Tsuga mertensiana	Pinus ponderosa	Juniperus occidentalis
Elevation (m)	240	200	170	800 (640)	1460	1030 (1030)	930
Slope (%)	12	0	13	12 (0)	0	0	0
Aspect (degrees)	130	...	160	325 (···)	...	...	...
Stem density (no./ha) >5 cm	385	1793	226	870 (980)	1740	600 (1051)	141
Basal area (m²/ha)	98.2	35	51.3	67 (63)	83.3	6.8 (11.3)	9.3
Av. max. canopy height (m)	50	13	40	30	20	7	10

* Fertilized stand data in parentheses when different from control stand.
† Physiographic provinces from Franklin and Dyrness (1973).

extent of the transect (Fig. 1). The station at site 5 served to provide radiation, humidity, and temperature data for site 6, supplemented with precipitation data from a weather station at Redmond, Oregon. Each meteorological station collected air temperature, relative humidity, precipitation, and incident solar radiation (400–1200 nm) every minute and was programmed to integrate hourly values into an internal data logger. At monthly intervals we transferred the accumulated data to a portable computer, and analyzed them upon return to Oregon State University in Corvallis.

We noted a loss of sensitivity by some humidity sensors in June 1990. Data from those sensors that did not show near 100% humidity values at night were adjusted henceforth by assuming that the minimum temperature was an approximation of dew point (Riha and Campbell 1985). Although this is by no means a perfect assumption when weather conditions are changing (see discussion by Goward et al. 1994 [this issue]), it provided a fair estimate ($R^2 = 0.84$ and 0.79) of observed relative humidities when compared with calibrated data collected the previous year at sites 2 and 3. This approach to estimating relative humidity is also the one used by Running et al. (1987) to construct meteorological data sets from minimum/maximum temperature records to drive the ecosystem model, FOREST-BGC (Running and Gower 1991).

As a result of heavy snow pack, the meteorological station at site 4 (Santiam Pass) was removed for a 5-mo winter period. Data were substituted from a nearby meteorological station operated by the Oregon Department of Transportation and reported in the National Oceanic and Atmospheric Administration (NOAA) monthly climate data summaries.

Soil water status

Water storage capacity of soils for each site was derived from the previous work of Gholz (1982) in which a number of intact cores were collected from soil profiles down to a maximum depth of 1 m. Pressure volume curves defined the upper (-0.03 MPa) and lower (-1.5 MPa) limits of extractable water. Gholz's calculations of available water took into account variation in bulk density and rock content as described by Waring and Major (1964).

We were concerned that soil water storage estimates could grossly underestimate available water (Running 1994 [this issue]), particularly where soils were rocky and root penetrated through a friable bedrock such as at site 2 (Corvallis). In addition, where seepage water from upslope positions supplemented local precipitation, as at site 3 (Scio), we needed an independent means of assessing the availability of water to the vegetation. We chose as an alternative to monitoring changes in soil water content to measure pre-dawn xylem water potentials with a pressure bomb between 2200 and 2400 local solar time on five trees at each site (Scholander et al. 1965, Waring and Cleary 1967). Measurements were initiated in May or June on all sites and continued at generally monthly intervals through October, after which heavy rains commenced. Sample size was increased at times above five trees to maintain a standard error of estimate around the mean of <0.05 MPa.

Intercepted photosynthetically active radiation (IPAR)

We estimated IPAR with a sunflect ceptometer (Decagon Devices, Inc., Pullman, Washington, USA) by measuring the radiance (400–700 nm) transmitted through the tree canopy at each site, and assuming that the remainder was either absorbed or reflected. Measurements at all sites were made on cloudless days during July–August 1991 between 1200 and 1400 local solar time. From 60 to 200 sampling-grid points were required to provide good estimates at each site following procedures described by Pierce and Running (1988). Canopy transmittance (Q_t/Q_0) was calculated by dividing the average below-canopy PAR (Q_t) by the average incident PAR (Q_0). The fraction of PAR intercepted (f_{IPAR}) was calculated from the formula:

$$f_{IPAR} = (1 - Q_t/Q_0). \qquad (1)$$

This calculation of f_{IPAR} is a reasonable calculation of the radiation absorbed by the canopy (Asrar et al. 1984) although it ignores the small fraction of reflected light essential for analysis by remote sensing.

Aboveground biomass

The aboveground biomass of trees was one of the important variables that various remote-sensing techniques sought to predict in the OTTER project (Wu and Strahler 1994 [this issue]). To provide good estimates of this variable, we established at least 20 circular plots of 50 m², randomly, in each stand. We measured the diameter at breast height (dbh) of every tree >5 cm in diameter in each plot. We used tree counts and basal area measurements for the plots to compute the average number of trees per hectare and to estimate the relative contribution of each tree species to the total basal area.

Stem, bark, and branch biomass was computed for each species using appropriate regression equations developed from destructive analyses in the Pacific Northwest (Bormann 1990 [Sitka spruce], Gholz et al. 1979 [all other species]). We derived an estimate of aboveground standing woody biomass by multiplying the measure of average weighted basal area per hectare for each species by the biomass regression equations.

Leaf area index (LAI)

Leaf area index (projected surface) is an important structural variable that integrates environmental constraints, including nutrient limitations (Waring 1983). Because LAI is a critical initializing variable for the FOREST-BGC model, we estimated it with three independent methods. First, LAI was determined from previously defined ratios between leaf area and the area of sapwood at the base of the live tree crown (Waring et al. 1982). Sapwood area was calculated from measuring the radius of sapwood to the nearest millimetre on increment cores collected at breast height (1.4 m)

from a random selection of all tree species present on each plot. We divided the total stand basal area by the sapwood area to estimate sapwood basal area per hectare.

We compensated for taper from breast height to the live crown using a relationship developed by Ryan (1989). Total tree heights, height to the base of the live crown, and crown diameter measurements were taken on a random selection of at least 20 trees by triangulation by another team of scientists working on the project (A. H. Strahler, *personal communication*). For each tree species the ratio of distance to live crown/total height was calculated and the decrease in sapwood area from dbh to the live crown thereby estimated. The calculated decrease in sapwood area ranged from zero in juniper to 47% in tall Douglas-fir. These latter estimates were consistent with those reported by Maguire and Hann (1987) on large Douglas-fir. Finally, species-specific estimates of leaf area/sapwood ratios were used to calculate LAI for each stand (Waring 1980, Waring et al. 1982).

Second, we estimated LAI with the LI-COR LAI-2000 (LI-COR, Inc., Lincoln, Nebraska, USA). This instrument measures the gap fraction, $f(\theta)$, of the canopy based on diffuse blue light attenuation at five zenith angles (θ) simultaneously (Welles and Norman 1991). LAI and leaf angle information is obtained by inverting the relationship:

$$f(\theta) = -\exp[-g(\theta) \cdot FAI/\cos \theta], \qquad (2)$$

where FAI is the foliage area index, and $g(\theta)$ is the fraction of foliage projected toward angle θ. Gower and Norman (1991) have shown that in conifers the projected FAI is essentially a shoot area index, and the estimation of a needle-based leaf area index can be made by multiplying FAI by R, the measured projected needle area per projected shoot area:

$$LAI = FAI \cdot R. \qquad (3)$$

Gower and Norman (1991) found R to vary between 1.49 and 1.67 for four species of conifer. We assumed a value of 1.5 for this study for sites 1, 2, 3, and 5. At site 1A (alder) and 6 (juniper) no correction for needles was necessary. Due to defoliation of new growth by the spruce budworm (*Choristoneura occidentalis* Freedman) and a significant amount of lichen in the canopy, a value of 1.3 for R was used as a reasonable estimate for site 4.

LAI determinations with the LAI-2000 were made during a 1-wk period in June 1991 by walking along transects through the sites, and recording sky brightness as viewed through the canopy at the five angles of view. Measurement points were established by using intervals approximately equal to the canopy height. Reference readings of sky brightness were obtained by two methods. First, in cases where there was a sufficiently large clearing nearby, comparative measurements of sky brightness could be obtained quickly.

Where such comparisons were not readily available, a second LAI-2000 unit was set up in the nearest clearing while measurements were made simultaneously beneath the forest canopy. Both procedures gave similar results when tested at sites 1 and 3.

Because direct sunlight on the canopy causes errors of 10%–50% in the LAI-2000 measurements (Welles and Norman 1991), we collected data on cloudy days, or close to sunset so that possible interference from direct beam radiation was minimum. The one exception was at site 5, where a large number of transects was required and cloud cover was often lacking. At this site 10 transects were measured during the day, and 1 transect (chosen as "typical") was remeasured at sunset. In this way we derived a correction factor (1.5) for measurements made along the other transects for periods under direct sunlight.

Third, LAI was estimated from measurements of transmitted PAR recorded on cloudless days following procedures described by Pierce and Running (1988), which used the relation:

$$LAI = -\ln(Q_t/Q_0)/k, \qquad (4)$$

where k is the empirically determined extinction coefficient that for conifers ranges throughout most of the day between 0.4 and 0.65 (Jarvis and Leverenz 1983). We assumed a k of 0.5 as a good average. The method for obtaining Q_t and Q_0 was discussed previously (see *Intercepted photosynthetically active radiation*). Note that Eqs. 2 and 4 can be written in similar forms, but should not be confused. Transmitted light Q_t/Q_0 is not gap fraction, $f(\theta)$, because it includes direct beam and diffuse sky radiation, and also the effects of scattering in the canopy; zenith angle θ is not included in Eq. 4, but likely affects the value of the empirical constant k. For the alder stand (1A) a k value of 0.6 was assumed as representative of deciduous canopies (Jarvis and Leverenz 1983). Values of k were also computed independently on the basis of leaf area determinations from sapwood area estimates and the fraction of blue light transmitted through the canopy measured with the LAI-2000.

Foliage biomass

Foliage biomass estimates are required to calculate nutrient and carbon cycling through forest ecosystems. We converted from leaf area estimates by measuring specific leaf masses (SLM) on five branches collected from the mid-canopy of trees representing the major species at each site during July 1990. Matson et al. (1994 [this issue]) describes variation in SLM throughout the year. On fresh samples of needles, the projected area was determined with the LI-COR leaf area meter (LAI-3100; LI-COR, Inc., Lincoln, Nebraska, USA), and then dried at 70°C for 24 h and weighed. The average specific leaf area (in square metres per kilogram) of each of the five branches was thus determined, these values were averaged, and the averages were ap-

plied to convert LAI estimates obtained with the sunflect ceptometer to foliar biomass for the tree canopy.

Net primary production

Net primary production (NPP) includes new foliage production and branch, stem, and root growth. Tree mortality would contribute to a reduction in estimates of NPP, but none was noted in 1990, although a wind storm in 1989 uprooted large ponderosa pine trees on sites 5 and 5F, which resulted in subsequent logging of the remaining large trees just previous to our measurements.

Our measurements of new foliage production and annual litterfall served as reference for remotely sensed estimates of seasonal change in canopy LAI and foliar biomass (Matson et al. 1994 [this issue], Spanner et al. 1994 [this issue]). To gauge patterns of foliage biomass production across the transect we measured the fraction of new growth observed in July during maximum canopy development. In most cases we used the same five branches collected for determining specific leaf area. The values were pooled for each site, weighted by the LAI of each species, and used to estimate new production from previous calculations of foliar biomass (in megagrams per hectare per year). A good estimate of new growth was not possible at site 4 (Santiam Pass) because of active defoliation by spruce budworm. We derived estimate of new foliage production from those published by Gholz for the same site (1982). At site 6 (juniper), where new foliage was not distinguishable from older foliage in July, we relied on a separate study to obtain estimates of the new foliage fraction of total leaf biomass Gholz (1980).

All litterfall estimates were derived because resources were lacking to make collections on all sites or to separate branches from other materials on those sites (1A, 1, 3, 3F) where collections were made (D. Myrold [Oregon State University], *personal communication*). Assuming that each stand was at steady-state LAI, we set the upper limit on litterfall from the seasonal difference in foliar biomass values presented in the paper by Matson et al. (1994 [this issue]). Because a certain loss of carbohydrates and minerals occurs at leaf abscission, an additional mass reduction was made of 15% for needles and 20% for broadleaf deciduous species (Sedell et al. 1974).

Belowground production was estimated from a correlation between measured annual CO_2 efflux from the soil and litterfall derived from a wide range of forests in different climatic zones (Raich and Nadelhoffer 1989). In applying the model, microbial activity is assumed in balance with litterfall, so that annual belowground carbon allocation (B_a, in grams per square metre per year), representing root production and associated respiration, can be derived from the equation:

$$B_a = 130 + 1.92(\text{leaf litterfall}). \qquad (5)$$

Respiration associated with construction and main-

tenance of roots has been assessed at roughly 50% of B_a (Ryan 1991a). If we assume that total mass of organic matter is twice that of its carbon content and that respiration involves half the total belowground allocation of carbon (B_a), then these two terms cancel and the values predicted for B_a in units of grams per square metre per year are equivalent to megagrams of dry matter per hectare per year when multiplied by 10^{-2}.

Growth in woody biomass of tree stems and branches, including bark, was determined from changes in tree diameter estimated from growth-ring measurements. Increment cores were taken from the first and fifth tree of each species on which diameters were measured to calculate standing biomass. Measurements were made of the current-year's ring width (1990) and of the previous 5 yr. No significant difference in annual increment was noted so the average from the previous 5 yr served as the basis for computing the annual increment for each site. These values were then applied to the species regression relationships and multiplied by the number of trees per hectare to obtain aboveground woody biomass production (in megagrams per hectare per year).
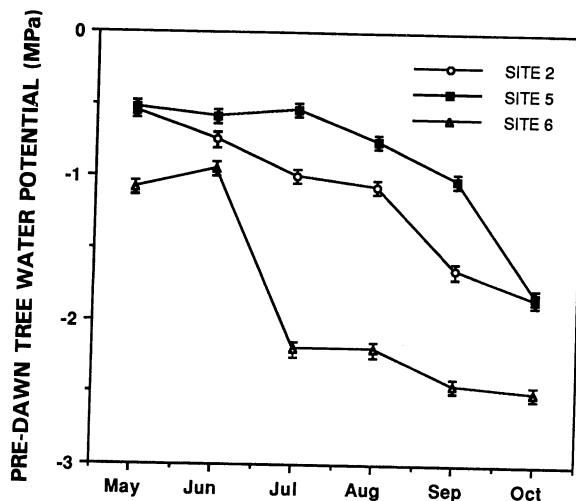

FIG. 2. Seasonal variation in pre-dawn water potentials occurred on only three of the sites across the Oregon transect. From this physiological measure of drought we reduced intercepted PAR most in the juniper woodland (site 6), intermediately in the Douglas-fir/oak community (site 2), and least in ponderosa pine (site 5). Measurements were made on at least five trees at each sampling date to assure a standard error of <0.05 MPa.

Calculation of intercepted PAR

Hourly incident radiation data for each site were available from the meteorological stations. For each forest canopy, the fraction of PAR intercepted (f_{IPAR}) was estimated from ceptometer measurements made in midsummer. We assumed, in most cases, that f_{IPAR} was constant through the year. Of course, LAI varies somewhat through the course of the year even in coniferous forests (Jarvis and Leverenz 1983, Russel et al. 1989, Gholz et al. 1991, Spanner et al. 1994 [this issue]). We reasoned, however, that changes in LAI of <30% (Spanner et al. 1994 [this issue]) have little influence on the total annual IPAR, in part because f_{IPAR} changes more slowly than LAI (Eq. 4) and also because the reduced LAI is displayed during the dormant season when radiation is lowest. The deciduous alder stand, site 1A, was assumed to intercept no PAR during periods of leaf-off (November to March) and to intercept one half the maximum f_{IPAR} during the transition between zero and full leaf display that occurs during the months of April through October. With these data, we calculated light-conversion efficiency (ε) as the ratio of NPP (in grams per square metre per year) to IPAR (in megajoules).

Because of our interest in quantifying the constraints of various climatic factors on NPP, we sought a way of linking climatic constraints on photosynthesis to IPAR. To do this we defined a light-use efficiency (ε_u) that quantifies constraints on production due to unfavorable temperature (T), drought (D), and vapor pressure deficits (VPD):

$$\varepsilon_u = f(T) \cdot f(D) \cdot f(\text{VPD}) \cdot \text{IPAR}. \qquad (6)$$

Freezing temperatures. — Freezing temperatures stop photosynthesis in trees for a number of hours even after temperature returns to more optimal levels (Pharis et al. 1972, Kaufmann 1982, Jones 1983). At $-2°C$ net photosynthesis in a variety of tree species is at or near zero (Larcher 1983). For all sites we first determined from the meteorological records if temperatures fell below $-2°C$ during a day. If sub-freezing temperatures occurred, we assumed no net photosynthesis for the following day and subtracted all recorded IPAR from the annual total.

Drought. — When soil water in the rooting zone is reduced to below some critical level, the maximum stomatal conductance becomes progressively reduced as well (Running 1976). When nearly all available water has been exhausted, stomatal closure is complete and no photosynthesis is possible. For most coniferous species, pre-dawn xylem pressure potentials of less than -1.5 MPa are associated with nearly complete stomatal closure (Lassoie and Salo 1981). At pre-dawn levels between -1.0 and -1.5 MPa, substantial limits on conductance also occur (Waring and Schlesinger 1985). Only at sites 3, 5, and 6 along the Oregon transect did pre-dawn water potentials reach critical levels that constrained stomatal conductance and photosynthesis (Fig. 2). At these sites we interpolated monthly data taken during the dry season to estimate daily pre-dawn water potentials (Ψ). At intermediate values of pre-dawn Ψ, IPAR was reduced by 50%; below -1.5 MPa we reduced IPAR by 100% for that day from the annual total.

Vapor pressure deficits (VPD). — High humidity deficits at the leaf surface place limits on stomatal con-

TABLE 2. Criteria for reducing the amount of PAR that is intercepted, based on physiological thresholds applicable to all major tree species in Oregon.

Freezing temperatures
  If less than $-2°C$, assume no radiation utilized for 24-h period
Soil drought
  If pre-dawn water potential < -1.5 MPa, assume no radiation utilized for 24-h period
  If pre-dawn water potential is between -1.0 and -1.5 MPa, assume half radiation utilized
Vapor pressure deficits (VPD)
  IF VPD exceeds 2.5 kPa, assume no radiation utilized for 1-h period
  If VPD is between 1.5 and 2.5 kPa, assume half radiation utilized for 1-h period
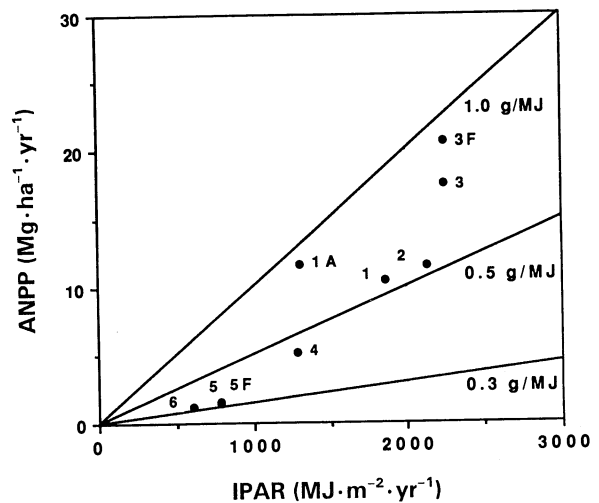

FIG. 3. Variation of aboveground net primary production (ANPP) with increasing interception of photosynthetically active radiation (IPAR) on sites across the Oregon transect. No constant light-conversion efficiency (ϵ) is indicated.

ductance, even under conditions when soil water is readily available (Schulze 1986). For a variety of trees, stomata close at vapor pressure deficits that exceed 2.5 kPa, and are substantially reduced in aperture at VPDs between 1.5 and 2.0 kPa (Waring and Franklin 1979). After accounting for sub-freezing conditions and extreme drought, we applied constraints on stomata associated with these VPD thresholds at hourly intervals, reducing IPAR by 50% or 100%. An interaction between intermediate levels of drought (pre-dawn $\Psi -1.0$ to -1.5 MPa) and intermediate VPD values resulted in a 75% reduction in IPAR. A summary of the threshold values and our reduction in IPAR is provided in Table 2.

RESULTS

Leaf area index (LAI)

The three methods of estimating LAI were generally in close agreement (Table 3). Leaf area indices, derived from ceptometer estimates, ranged from a low of 0.5 in the juniper woodland (site 6) to a high of 10.6 for the Douglas-fir/western hemlock forests at sites 3 and

3F. Fertilization with nitrogen did not induce an increase in LAI. Insect defoliation in the subalpine forest (site 4) was expected to reduce LAI values estimated from light interception compared to those derived from sapwood, but differences were only significant with the ceptometer. In the recently logged ponderosa pine stands (sites 3 and 3F), LAI values were about one third of the original (Gholz 1982).

Climatic differences and intercepted PAR

The climate along the Oregon transect becomes progressively less maritime moving inland. Annual precipitation declines by 10-fold from 251 cm at Cascade Head to 22 cm in the juniper woodland (Table 4). The coastal sites also record the most cloud cover, which reduces the incident PAR, assumed to be 50% of total

TABLE 3. Comparison of the different methods for estimating leaf area index (LAI) for the variety of different stands across the Oregon transect. LAI values are means ± 1 SE. k = the empirically determined light-extinction coefficient.

Method	Site						
	1	1A	2	3	4	5	6
LAI-2000							
Site LAI (m²/m²)	7.2 ± 0.4	3.9 ± 0.1	6.3 ± 0.2	8.5 ± 0.5	3.0 ± 0.2	0.8 ± 0.1	0.4 ± 0.3
Av. k values*	0.46	0.71	0.45	0.62	0.32	0.44	0.63
Decagon ceptometer							
Site LAI (in m²/m², with k = 0.5†)	6.6 ± 0.3	4.6 ± 0.2	5.7 ± 0.4	10.6 ± 0.4	1.9 ± 0.1	0.7 ± 0.1	0.5 ± 0.1
Sapwood‡							
Site LAI (m²/m²)	5.3 ± 1.0	ND	4.0 ± 1.0	8.7 ± 0.8	2.8 ± 0.6	1.1 ± 0.2	0.4 ± 0.1
Av. k values*	0.62	ND	0.71	0.61	0.34	0.32	0.63

* Average k values were computed based on ceptometer measurements of transmitted light and independent determinations of LAI by the sapwood method and the LI-COR LAI-2000.
† k = 0.6 for the alder stand at site 1A.
‡ LAI is derived from the relationship between sapwood area at the base of the live crown and LAI for the various tree species.

Table 4. Climate data, percentage of intercepted photosynthetically active radiation (IPAR), and total annual IPAR for the study sites.

Feature	Site						
	1	1A	2	3	4	5	6
1990 precipitation (cm)	251	251	98	118	181	54	22*
1990 mean annual temperature (°C)	10.1	10.1	11.2	10.6	6.0	7.4	9.1*
Total annual incident PAR (MJ/m²)	1934	1934	2267	2259	2088	2735	2735
Percentage IPAR (mean ± 1 SE)	96.4 ± 0.57	93.7 ± 0.85	94.1 ± 1.00	99.5 ± 0.10	61.4 ± 2.5	28.6 ± 3.2	22.0 ± 1.5
Annual IPAR (MJ/m²)	1864	1310†	2133	2248	1282	782	602

* Site 6 rainfall and temperature data are from 20-yr NOAA averages for Redmond, Oregon.
† The deciduous alder stand was assumed to have no IPAR during periods of leaf-off (November to March) and one half IPAR during the leaf transition periods (October and April).

incident short-wave radiation (Monteith and Unsworth 1990), to 1934 MJ/m² at site 1.

Foliage intercepted from 22% to 99.5% of incident PAR, with the low value recorded at site 6 and the high value at sites 3 and 3F (Table 4). The annual PAR intercepted by foliage varied from ≈2250 MJ/m² at site 3 to 600 MJ/m² at site 6.

Biomass and forest production

Total tree biomass across the transect ranged from >700 Mg/ha in the old-growth Sitka spruce and western hemlock forest (site 1) to ≈10 Mg/ha at site 6, the juniper woodland (Table 5). The foliage represented from 15.3 Mg/ha (site 3) to <2 Mg/ha (site 5). Litterfall followed the trends in foliar biomass, with the exception of the deciduous alder stand (site 1A), which sheds all of its foliage annually.

Net primary production varied from 3 $Mg \cdot ha^{-1} \cdot yr^{-1}$ at sites 5 and 6 to >25 $Mg \cdot ha^{-1} \cdot yr^{-1}$ at site 3F (Table 5). Belowground production represented from 20% to 32% of total NPP on sites on the western side of the Cascade Mountains and from 53% to 60% of total NPP for the east-side stands (sites 5, 5F, and 6).

Light-conversion and light-use efficiency

Across the transect, light-conversion efficiency, ε, for aboveground NNP varied from 0.18 to 0.92 g/MJ, indicating no general relationship between NPP and IPAR (Fig. 3). We inferred from this analysis that some forests along the Oregon transect experience severe constraints on photosynthesis, and perhaps on other processes that prevent the predominantly evergreen species from fully utilizing intercepted PAR.

Reducing annual IPAR with the environmental thresholds specified in Table 2 improved the general relation between production and intercepted radiation (Fig. 4a and b). Light-use efficiency, ε_u, averaged 0.8 g/MJ for aboveground NPP and 1.3 g/MJ for total NPP (Table 6). The general consistency of ε_u across the Oregon transect suggests that climatic constraints on photosynthesis are primary determinants of variations in light-conversion efficiency (ε).
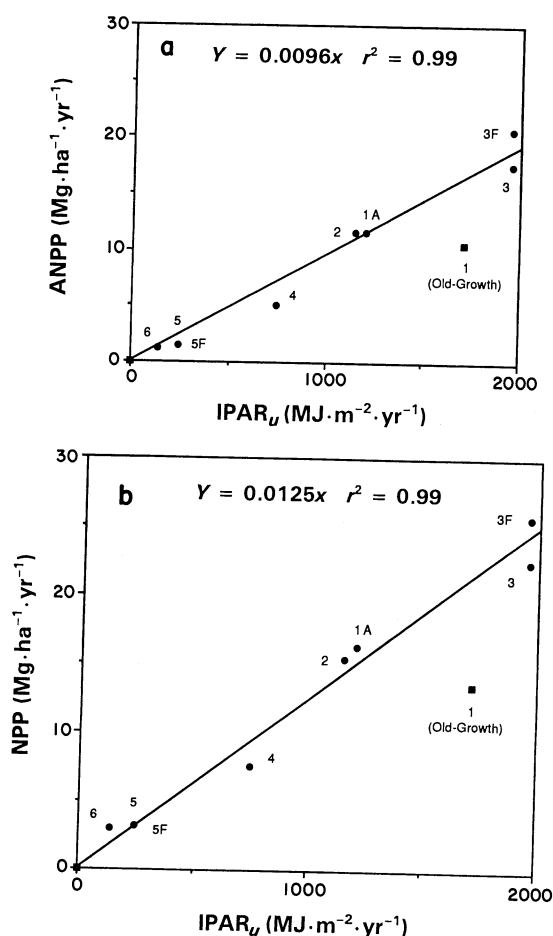

FIG. 4. (a) When constraints on intercepted photosynthetically active radiation (IPAR) were applied as defined in Table 2, the amount utilized ($IPAR_u$) correlated well with measured aboveground net primary production, ANPP. (b) Total net primary production (NPP) correlated well with estimates of annual $IPAR_u$. The Raich and Nadelhoffer (1989) model provided estimates of belowground allocation (Table 5), 50% of which was assumed as primary production (B_p). These B_p values were added to ANPP to obtain total NPP. The old-growth forest (site 1) was excluded from both regressions; when included, the r^2 were 0.89 and 0.88, respectively.

TABLE 5. Stand tree aboveground biomass and components of net primary production for the study sites (means $\pm$ 1 SE).

Feature	Site				
	1	1A	2	3	3F
Tree biomass (Mg/ha)					
Wood	702	116	461	393	377
Foliage	8.3	4.3	10.2	15.3	15.3
Total biomass (Mg/ha)	710.8 ± 114	120.3 ± 9	471.2 ± 103	408.3 ± 31	392.3 ± 66
Tree biomass production (Mg·ha⁻¹·yr⁻¹)					
Wood	8.3	7.4	8.7	12.9	16.0
Foliage	2.2	4.3	2.9	4.6	4.6
Aboveground NPP	10.5 ± 1.6	11.7 ± 0.9	11.6 ± 2.5	17.5 ± 1.3	20.6 ± 3.5
Leaf litterfall‡	1.9	3.4	2.6	3.8	4.0
Belowground NPP§	3.1	4.6	3.8	5.0	5.1
Total NPP	13.6	16.3	15.4	22.5	25.7

* No data due to spruce budworm damage. Value given is estimate of percentage foliage production from Gholz (1982).

† No data. Estimate of percentage foliage production from Gholz (1980).

‡ Leaf litterfall estimates were derived by assuming that foliage production equals turnover minus 15% mass loss for coniferous species and 20% mass loss for deciduous species.

§ Belowground production determined from Raich and Nadelhoffer's (1989) correlation with litterfall and total belowground carbon allocation.

When estimates of belowground production were added to ANPP, the resulting ε_u values were more comparable on all but sites 1 and 6. At site 6, small overestimates in estimating foliage production or litterfall could contribute to the unrealistically high light-use efficiency of 2.17 g/MJ. At site 1 the old-growth forest contains trees older than 300 yr. Such large old trees have greater maintenance respiration and lower photosynthetic activity than younger, smaller specimens of the same species (Sandford and Jarvis 1986, Ryan 1991b, Waring et al. 1993, Yoder et al. 1994).

Climatic constraints on production in western Oregon

The contribution of the climatic components in determining ε_u at the various sites illustrates how different environmental constraints play a role in limiting production across western Oregon (Fig. 5). When all of the environmental constraints were accounted for, annual reductions in IPAR ranged from 8% to 77% across the transect. The largest reductions in annual IPAR were observed on the dry east-side sites. Conversely, the cool, moist alder and Sitka spruce/hemlock forests at Cascade Head (sites 1A and 1) were least affected.

The importance of each climatic factor varied across the transect. Near the coast, sites 1 and 1A experienced almost no limitations from freezing temperatures or drought. Nutritional limitations could, however, affect canopy development and reduce light interception. Nitrogen, however, was readily available due to fixation by alder root nodules and through rapid decomposition (Johnson et al. 1982). At the other extreme, the juniper site displayed constraints on the utilization of PAR from freezing temperatures, summer drought, and high vapor pressure deficits (VPDs). In this analysis only sites 2, 5, and 6 experienced soil drought conditions ($\Psi < -1.0$ MPa) sufficient to limit the utilization of annual IPAR (Fig. 2). Site 2 experienced significant decreases in annual IPAR from both drought and VPDs, which is a characteristic of the regional climate (Waring and Franklin 1979).

Because incident radiation reaching the forest canopy varies through the year, the seasonal timing of environmental stress will influence the relationship between radiation interception and production. The influence of freezing temperatures is tempered by the decrease in incident PAR in the winter months. Conversely, drought and/or vapor pressure deficits, which occur during the summer months when incident radiation is high, can impose severe limitations on the conversion of solar energy into dry matter.

Although the relationships between utilized IPAR appear linear for both aboveground and total NPP (Fig. 4a and b), this is partly a result of the largest changes

TABLE 6. Light-conversion efficiency (ϵ) and light-use efficiency (ϵ_u) for aboveground net primary production (ANPP) and total NPP.

Efficiency (g/MJ)	Site								
	1	1A	2	3	3F	4	5	5F	6
ϵ ANPP	0.56	0.89	0.54	0.78	0.92	0.40	0.19	0.18	0.20
ϵ NPP	0.73	1.24	0.72	1.00	1.14	0.59	0.41	0.41	0.50
ϵ_u ANPP	0.61	1.03	1.01	0.89	1.05	0.69	0.62	0.58	0.87
ϵ_u NPP	0.79	1.35	1.34	1.15	1.31	1.01	1.32	1.32	2.17

TABLE 5. Continued.

	Site		
4	5	5F	6
364	13	18	8
6.3	1.9	1.9	2.8
370.3 ± 63	14.9 ± 3	19.9 ± 4.7	10.8 ± 2.8
3.5	1.1	1.0	0.6
1.6*	0.4	0.4	0.6†
5.1 ± 0.7	1.5 ± 0.3	1.4 ± 0.4	1.2 ± 0.4
1.1	0.4	0.5	0.5
2.4	1.7	1.8	1.8
7.5	3.2	3.2	3.0

$$Y = 73.2 \times 10^{-0.0058} \quad r^2 = 0.80$$

FIG. 6. The fraction of NPP allocated belowground decreased from 60% to near 20% as the fraction of intercepted PAR utilized ($IPAR_u$) increased from 23% to 92% across the transect.

in allocation being restricted to the least productive sites (5 and 6). As environmental constraints increased, as designated in Fig. 5, the fraction of NPP allocated belowground increased exponentially from ≈20% to near 60% over the range of the data (Fig. 6).

DISCUSSION

This study of vegetation patterns in western Oregon reaffirms and advances understanding of ecosystem processes under variable environmental conditions. Environmental constraints influence the conversion of solar energy into dry matter through two mechanisms. First, environmental constraints, including nutrient deficiencies, limit forest canopy development and thus the amount of radiation that vegetation can intercept. For this reason there is a correlation between site water balance (Grier and Running 1977) and low night temperatures (Waring et al. 1978) with canopy development. Any limitation on the extent of canopy development is characterized by an assessment of intercepted photosynthetically active radiation. Second, stomatal closure from freezing temperatures, drought, or high vapor pressure deficits (VPDs) reduce photosynthesis rates and, indirectly, annual growth. Refinements in the approach could take into account differences among species in rooting depth, sensitivity to humidity deficits, and allocation patterns associated with different life form, e.g., shrubs and trees. In the Pacific Northwest region the most sensitive tree species are restricted to the the coastal region and to riparian areas where the thresholds established for drought and for VPDs are rarely exceeded.

This assessment of the climatic constraints on productivity yields insights into controls for the annual carbon budgets in a variety of forest systems. There have been few other studies of the effects of stress on the annual carbon budget (Cannell 1989). In one example, Emmingham and Waring (1977) incorporated environmental stress into a model of photosynthesis at the leaf level that correlated well with annual production. The amount of carbon assimilated annually was reduced below the potential by low temperatures and summer drought. In addition, in the cool maritime climate of the Pacific Northwest, photosynthesis has been recognized as continuing throughout the winter months (Emmingham and Waring 1977, Waring and Franklin 1979). High rates of productivity in the coastal forests are also well established and come close to the maximum values at site 3 (Long 1982).
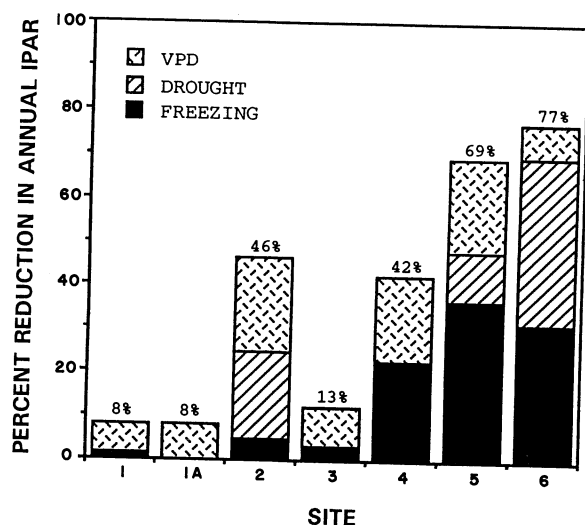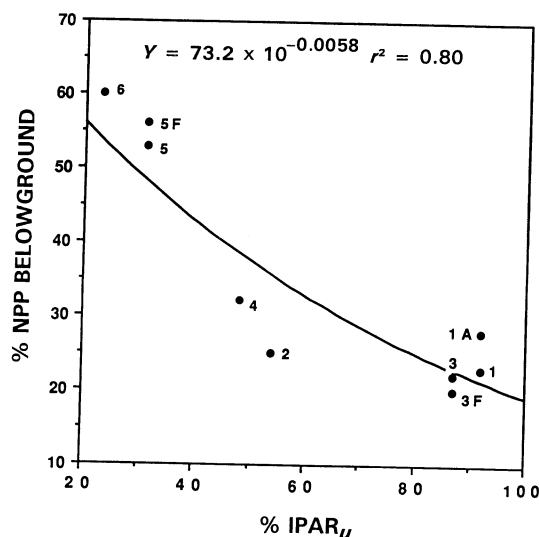

FIG. 5. The fraction of annual intercepted PAR that could not be utilized by the various forest stands because of freezing temperatures, drought, or vapor pressure deficits (VPD) ranged from 8% at the cool, moist coastal sites (1 and 1A) to as much as 77% at the cold, dry juniper woodland (site 6).

The intriguing relationship between the fraction of NPP allocated belowground and the amount of intercepted photosynthetically active radiation utilized (IPAR$_u$) displayed in Fig. 6 deserves further investigation. A study at site 3 has just been completed that monitored CO_2 flux from the soil throughout the year (K. Mattson [Oregon State University], *personal communication*). One of the important questions is how much time is required for the canopy to reach equilibrium following fertilization or other disturbance. The Raich and Nadelhoffer model looks robust, but we expect various species to differ in their allocation patterns on the same site, particularly shrub species that sprout from well-developed root systems (B. Law, *unpublished data*).

The current analysis reveals that the effects of environmental constraints on ecosystem productivity may be effectively expressed with relatively simple, empirical calculations. These results suggest that it may be possible to form a simple but realistic model of biospheric dynamics based on the principles of IPAR production rate, modulated by climatic factors that reduce light-conversion efficiency. This type of a model will be most suitable in global-scale analyses where either the detailed structural and physiological measurements are not available or when remotely sensed observations are employed to monitor contemporary global biospheric dynamics.

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