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William E. Winner

An extreme range in forest productivity occurs along a 250 km west-east transect at 44° N latitude in western Oregon, USA. Associated with this transect is a wide array of climates. Measurements made across the transect were used to provide forest stand-level data for a remote sensing project and to test principles on how climate constrains tree above-ground net primary production (ANPP) by limiting the quantity of intercepted photosynthetically active radiation (IPAR) utilized by the different forest canopies.

Forest stand tree growth was assessed by gauging annual biomass increments and tree density. Meteorological stations at each of the sites provided information on climate and incident radiation. Intercepted PAR for the various forest canopies was

assessed with an integrating radiometer. Percent IPAR along the transect ranged from 99.5%, at a dense western hemlock-Douglas-fir forest, to 22% at an open juniper woodland. Leaf area index (LAI) was measured by three different methods: (1) light interception; (2) an instrument that measured the gap fraction of the canopies; and (3) sapwood/LAI ratios. There was relatively close correspondence between the measured LAIs for the three methods. LAI estimates varied across the transect by more than a factor of ten: from 0.5 to over 10. ANPP followed similar trends, ranging from a high of 17 Mg ha^{-1} yr^{-1} to a low of 1.4 Mg ha^{-1} yr^{-1} at the east end of the transect. Production rates (g of dry matter accumulated per MJ of intercepted PAR) varied by a factor of four across the transect.

Previous work has shown that environmental stress can reduce production rates. Accordingly, I developed a simple model based on tree-level physiological principles that would limit the utilization of IPAR when photosynthesis was restricted. Three climatic variables were assessed from field and meteorological measurements at each site: (1) freezing temperatures; (2) drought; and (3) vapor pressure deficits. When these factors were determined to constrain photosynthesis, IPAR was reduced. With information on the seasonal occurrence of these factors we could assess the relative importance of each factor and their integrated effect upon productivity. The reduction of annual IPAR reflected regional climate patterns. Total reduction in annual IPAR ranged from 8% for a moist sitka spruce forest to

77% for a dry juniper woodland. This approach provides a simple method for estimating climatic constraints on forest above-ground net primary production.

Environmental Limits on Above-Ground Production: Observations from the Oregon Transect

by

John R. Runyon

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Redacted for Privacy

Head of department of General Science

Redacted for Privacy

Dean of Graduate School

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Typed by John Runyon

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TABLE OF CONTENTS

INTRODUCTION 1

CLIMATIC CONSTRAINTS ON ABOVE-GROUND FOREST PRODUCTION: A MODEL OF UTILIZED INTERCEPTED PHOTOSYNTHETICALLY ACTIVE RADIATION 4

Introduction 5

Study Sites 6

Field Methods and Observations 8

Production Rate Assessment and Specification of Environmental Constraints 21

Results 28

Discussion 30

Conclusions 32

BIBLIOGRAPHY 45

LIST OF FIGURES

FIGURE PAGE

1 Map of the study area in Oregon showing the location of the study sites and the major vegetation zones. 34

2 Estimates of annual intercepted PAR compared to above-ground net primary production. 35

3 Seasonal trends (1990-1991) in predawn water potentials for the three sites experiencing significant drought stress. 36

4 Estimates of utilized intercepted PAR explain much of the varience in net primary production for the range of forest stands across the study transect. 37

5 The fraction of annual intercepted PAR that could not be used by the various forest stands because of freezing temperatures, drought, or vapor pressure deficits. 38

LIST OF TABLES

TABLE		PAGE
1	Characteristics of the study sites across the transect.	39
2	Climate data, percent intercepted PAR, and total annual IPAR for the study sites.	40
3	Total stand tree above-ground biomass and net primary production for the study sites.	41
4	Comparison of the different methods for estimating leaf area index (LAI ± S.E.) for the variety of different stands across the Oregon transect: 1) LI-COR LAI-2000; 2) Decagon ceptometer with K = 0.5; and 3) derived from the relationship between sapwood area at the base of the live crown and LAI for the various tree species.	42
5	Criteria for reducing intercepted PAR based on physiological thresholds applicable to all major tree species in Oregon.	43
6	The production rate and utilized production rate values for the sites along the transect.	44

ENVIRONMENTAL LIMITS ON ABOVE-GROUND PRODUCTION: OBSERVATIONS FROM THE OREGON TRANSECT

INTRODUCTION

Forecasts of possible near-term changes in the Earth's climate have created a demand 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 which link scales of observation between detailed site-specific knowledge and regional assessments. For example, assessment of the role of forest ecosystems in the planetary carbon cycle requires concepts which incorporate detailed understanding of the mechanisms which control primary productivity but are, at the same time, sufficiently generalized to permit extrapolation across landscapes.

Previous research has demonstrated a relationship between patterns of ecosystem production and climate. For example, terrestrial net primary production has been correlated with climate variables such as precipitation and temperature (Holdridge 1947, Rosenzweig 1968, Lieth 1975). These models, however, do not provide mechanistic links between the climate and ecosystem activity. Alternatively, there are now a number of researchers who are attempting to develop ecosystem process models which, through links to remotely sensed observations, permit assessment of regional to global-scale patterns in ecosystem production (e.g., Dickinson 1983, Sellers 1985, Running et al. 1989). Currently, ecosystem process models require detailed specification of ecosystem structure and function to operate.

There may be an intermediate ground between the simple correlation models (e.g., Holdridge 1947, Rosenzweig 1968, Lieth 1975) and the detailed process models (e.g., Running and Coughlan 1988) of ecological systems which will effectively describe environmental limits on primary production. For example, all net primary production depends upon interception of light. Several studies have shown that, under ideal conditions, the rate of primary production is linearly related to light interception (Monteith 1977, Linder 1985, Landsberg 1986). Estimation of canopy light interception from remotely sensed observations appears possible (Kumar and Monteith 1982, Asrar et al. 1985, Sellers 1985, Goward and Huemmrich 1992). However, this ideal production rate appears to vary in the presence of variable environmental conditions (Russel et al. 1989). The possibility of using additional remotely sensed observations to identify these environmental constraints exists but the utility of doing so is uncertain (Waring et al. 1992, manuscript submitted).

In Oregon a west to east transect between at 44°-45° north latitude crosses a wide range of climates and vegetation types. Gholz (1982), who conducted a comprehensive study of the relationship between climate and forest processes in this region, found net primary production varied more than tenfold along the transect. Due to the diversity of climates and production across Oregon, I felt that transect provided an ideal setting to examine the patterns of the conversion of intercepted photosynthetically active radiation (IPAR) into the production of dry matter.

I found that the production rate (grams of biomass produced per unit of radiation intercepted) varied more than fourfold across the transect. I hypothesized that much of the variability in production per unit IPAR is a function of climate. This thesis outlines the development and application of a simple model that incorporates physiological constraints as a limitation on the utilization of IPAR. Based on generalized tree-level physiological mechanisms controlling carbon uptake, I applied a simple set of rules to define when radiation is not utilized by the variety of forest canopies for production. As expected, much of the variability in production rates could be accounted for by including the climatic constraints. When applied along a regional gradient of production, this approach provides a tool for gauging the relative contributions of each climatic factor in reducing the utilization of radiation by forest systems.

CLIMATIC CONSTRAINTS ON ABOVE-GROUND FOREST PRODUCTION: A MODEL OF UTILIZED INTERCEPTED PHOTOSYNTHETICALLY ACTIVE RADIATION

by

J. R. Runyon

INTRODUCTION

A group of scientists, sponsored by the NASA Oregon Transect Ecosystem Research (OTTER) project, have undertaken an intensive effort to evaluate the use of remote sensing to characterize a gradient of primary production observed in the coniferous forests of the northwestern United States. The goal of this project is to investigate the use of both a detailed process model and the more general model of light interception as a means to study regional patterns in primary production for forest systems. To support this work an intensive series of ground measurements have been collected to describe and evaluate both primary production and environmental conditions in forest stands located along a transect encompassing a range of climates.

The objectives of this paper are to: 1) Report the basic forest stand-level and meteorological information collected for the OTTER project which has been used and reported by the other investigators, and 2) to examine the patterns of the conversion of intercepted photosynthetically active radiation (IPAR) into the production of dry matter for a variety of forest stands and climatic conditions.

Field observations have been used to test the ability of remote sensing to estimate ecosystem structure and function. They will also be used as inputs and validation for an ecosystem process model, FOREST-BGC (Running and Coughlan 1988, Running and Gower 1991). In addition, knowledge of production in this region will serve as a test of the production rate concept: grams of biomass produced per unit of radiation intercepted by the different forest canopies (Monteith 1972, 1977). The diversity of forest ecosystems and environments across the OTTER transect provides an ideal setting to examine the variability in production per unit IPAR as a function of climate. In addition, the observations from this study permit investigation of some of the tree-level physiological mechanisms controlling the variation in forest production rates.

STUDY SITES

Six primary study areas were selected (Fig. 1); they fall along a west to east transect about 250 km long lying between at 44^0-45^0 north latitude. The transect crosses a wide range of climates and vegetation types. 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 low winter temperatures. Most of the precipitation for the region falls between October and June. Summers are generally dry with 2-3 months of low precipitation, which results in significant drought stress for much of the region's forests (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 forests across the transect display almost the complete range of net primary production found in North America (Gholz 1982, Jarvis and Leverenz 1983).

The primary criteria I used for the selection of a particular forest stand was year-around accessibility to a nearby site for a meteorological station. Near three of the six primary stands, I selected an additional stand with enhanced nitrogen status. At site 1, named Cascade Head, I collected data from a deciduous nitrogen-fixing alder (*Alnus rubra*) stand (site 1A). At site 3, named Scio, I selected a mixed stand of 30 yr old western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) that had been fertilized previously (1988) with an aerial application of urea. On this site (site 3F) fertilization was continued through 1990, 1991 and 1992 with manual application of N twice a year -- spring and fall -- for a total of 300 kg N ha^{-1} yr^{-1}. Finally, at site 5, named Metolius, I selected a stand of ponderosa pine (*Pinus ponderosa* Laws.) that was undergoing application of sewage sludge. Table 1 contains a description of the study sites.

FIELD METHODS AND OBSERVATIONS

Climate Measurements

Beginning in the summer of 1989, a meteorological station was established at five sites. The station used for site 5, Metolius, also served for site 6, named Juniper for the analysis presented here. In addition, to provide a summary of the climate for the Juniper site, 20-year climate averages from a nearby weather station in Redmond, Oregon are also reported. The meteorological stations (Campbell Scientific Instruments, Inc., Logan, UT) were located no more than 15 km from the forest stand. Air temperature, precipitation, relative humidity and total incident shortwave solar radiation (400-1200 nm) were collected every minute and then integrated or averaged hourly and recorded on an internal data logger. At approximately one month intervals, the data logger files were transferred to the memory on a portable computer.

Through the course of the study, I detected some instrument problems. Beginning in approximately June 1990, the relative humidity data from four of the stations (excluding site 4) began to decline from expected values. Readings decreased randomly in discrete steps due to a decrease in the sensor sensitivity resulting from the moist climate of Oregon. The data were corrected using the logic developed by Running and others (1987) in which minimum temperature serves as an approximation of dew-point temperature, with relative humidity then varying by a known function with daytime temperature. When this was tested against earlier calibrated data, the procedure provided a good agreement with the observed relative humidities at sites 2 and 3 ($R^2 = 0.84$ and 0.79, respectively). Separately, at site 4, named Santiam Pass, heavy snow pack conditions necessitated the removal of the meteorological station for a 5 month period. Comparable data were obtained from a nearby meteorological station operated by the Oregon Department of Transportation which reports in the NOAA monthly climate data summaries.

In general, the climate followed normal patterns for the transect (Gholz 1986): cool and moist at the coastal site, becoming increasingly warm and dry moving from west to east across the transect (Table 2). Site 3, Scio, has higher precipitation levels due to the orthographic influence of the Cascade mountain range. The patterns of total incident solar radiation also follows a trend determined by the number of cloudy days. The maximum solar radiation is achieved at station 5, which occurs in the rain shadow of the Cascades. Because total short-wave solar radiation was recorded I reduced measurements by 50% to estimate only the photosynthetically active portion of the spectrum (Monteith and Unsworth 1990). The average annual total PAR across the transect, 2,100 MJ m^{-2} yr^{-1}, is close to the estimated incident PAR for temperate regions (Jarvis and Leverenz 1983).

Intercepted Photosynthetically Active Radiation (IPAR)

I estimated IPAR by measuring the tree canopy transmitted radiance at each site, assuming the remainder is either absorbed or reflected. IPAR for only the trees was measured, with no attempt to estimate the influence of the understory vegetation on radiation interception. To determine tree canopy transmittance of photosynthetically active radiation I used a sunfleck ceptometer (Decagon Devices, Inc., Pullman, WA). The instrument measures instantaneous fluxes of solar radiation in the photosynthetically active region (PAR 400-700 nm). Measurements at all sites were made on cloudless days during July-August 1991. To minimize shadow effects, measurements were taken between 1200 and 1400 local solar time. Depending on the variability of the overstory, below canopy PAR was sampled at least 200 to 60 points along north-south and east-west transects. At each sample point the instrument was held level and turned in a circle to collect 20 measurements of PAR at 15^0 increments. These 20 measurements were then averaged and stored in the instrument's memory. Total incident PAR was measured in a nearby clearing or road at the beginning and end of the sample period and at intervals of approximately every 10 minutes during the sample transects.

Canopy transmittance (Qi/Qo) was calculated by dividing the average below-canopy PAR (Qi) by the average incident PAR (Qo). Percent intercepted PAR (IPAR) was calculated from the formula:

$$\mathbf{IPAR = (1 - Qi/Qo) \cdot 100} \qquad (1)$$

This calculation of IPAR overestimates the fraction of PAR actually absorbed by the forest canopy since it does not account for the fraction reflected skyward. Because the reflectance off the canopy is relatively small this calculation of IPAR is a reasonable approximation of the radiation absorbed by the canopy (Asrar et al. 1984).

Percent IPAR values varied more than fourfold across the transect (Table 2). These values reflected relative tree canopy closure and stocking densities for the various forest stands. In general, tree canopy IPAR decreased moving west to east across the transect, although the maximum, 99.5%, was observed at site 3 (Scio), in the western foothills of the Cascades. There was no significant difference between the fertilized and control IPAR values for the stands at sites 3 and 5. The minimum canopy IPAR, 22%, was observed at the open juniper (*Juniperus occidentalis* Hook.) woodland (site 6) east of the Cascades.

Above-Ground Tree Biomass and Leaf Area

For this analysis, only tree above-ground biomass and leaf area index (LAI: $m^2\,m^{-2}$, projected) was assessed for all sites.

Understory vegetation, however, can contribute a significant amount to stand leaf area and biomass. For example, in old-growth forest communities in the western Oregon Cascades, shrub and herb leaf area contributed from 3% to 14% of the total (Gholz et al. 1976). The proportion of understory LAI varied across the transect, with the greatest contributions in the open stands east of the Cascade mountains (Law, personal communication). In order to emphasize only the patterns of tree processes across the transect, for this analysis no attempt was made to estimate understory vegetation LAI or biomass.

Woody biomass

To establish patterns of above-ground biomass and productivity I sampled trees at study stands at all sites, 1-6. I selected at least 20 circular plots, of 50 m^2 each, randomly in each stand. I measured the diameter at breast height (dbh; diameter at 1.37 m) of every tree >5 cm in diameter in each plot. I used tree counts and basal area measurements for the plots to compute average numbers of trees ha^{-1}, 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 in the sites using allometric relations developed for that species from destructive samples in the Pacific Northwest ((Bormann 1990 (sitka spruce), Gholz et al. 1979 (all other species)). I derived an estimate of total above-ground standing woody biomass by multiplying the measure of average weighted basal area per ha for each species by the biomass regression equations.

Above-ground standing biomass of the trees generally decreased from west to east across the transect (Table 3). Biomass estimates ranged from less than 12 Mg ha^{-1} at the east-side juniper woodland (site 6) to almost 710 Mg ha^{-1} at the old-growth sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock conifer stand (site 1) at Cascade Head.

Leaf area index (LAI)

The leaf area index for each site was estimated using three independent methods. First, LAI was estimated from previously observed ratios between the area of sapwood at the base of the live tree crown and leaf area. Because sapwood conducts water from the roots to the leaves, there is a close relationship between sapwood area and LAI (Waring et al. 1982). Sapwood area was measured from increment cores collected from a random selection of trees on each plot. I measured sapwood radius at breast height to the nearest mm and then used these values to calculate sapwood cross sectional area. I divided the the total basal area by the sapwood area to calculate the fraction of sapwood relative to heartwood for each species. To provide accurate estimates of LAI per sapwood area, I compensated for taper from the measurement height to the live crown using a relationship developed by Ryan (1989) between relative tree height and sapwood area. 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 (Strahler, personal communication). For each tree species, relative height (height to the base of the live crown/total height) was computed and relative sapwood area was estimated from the a plot of the relationship between the two variables. Percent tapers of sapwood area ranged from 47% of breast height for Douglas-fir to no taper for juniper. These estimates were consistent with previous observations of sapwood taper. For example, Maguire and Hann (1987) reported tapers for Douglas-fir of 39% to 74% from breast height to the base of the live crown. Published species-specific LAI/sapwood ratios ($m^2\,cm^{-2}$) were used to calculate stand leaf areas. The relationship between LAI and sapwood area is reasonably constant for a given species within a broad geographic region.

Secondly, I estimated LAI with the LI-COR LAI-2000 (LI-COR Inc, Lincoln, NE). 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

$$f(\theta) = -\exp(-g(\theta)\ \mathrm{FAI}/\cos\theta) \qquad (2)$$

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:

$$\mathbf{LAI = FAI \cdot R} \qquad (3)$$

Gower and Norman (1991) found R to vary between 1.49 and 1.67 for four species of conifer. I 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 one week 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 close by, readings were made in these clearings before and after each transect, and interpolated values were used to calculate sky brightness for the periods in between reference readings. Second, when large clearings in the stands were not available, a second LAI-2000 unit was set up in the nearest clearing to monitor sky conditions while the measurements were being made. As a check on the interpolation method, both methods were used at sites 1 and 3. I found no significant difference between the methods. In general, however, interpolation must be used judiciously.

Direct sunlight on the canopy causes errors in the LAI-2000 measurements of 10 to 50% (Welles and Norman 1991). As a result, measurements were made on cloudy days, or close enough to sunset so that no direct beam radiation was present. The one exception was at site 5, where the large number of transects and lack of clouds prohibited working in ideal conditions. At this site, the 10 transects were measured during the day, and one transect (chosen as "typical") was remeasured after sunset. This provided a correction factor for adjusting the rest of the transects for the effect of direct sunlight, which was large (1.5) in this case.

Third, LAI was estimated after the method of Pierce and Running (1988), which used the relation:

$$\mathbf{LAI} = \mathbf{-\ln(Qi/Qo)/k} \qquad (4)$$

where k is the empirically determined extinction coefficient that for conifers has been found to range between 0.4 and 0.65 (Jarvis and Leverenz 1983). The method for obtaining Qi and Qo has been discussed already. Note that equations 2 and 4 can be written in similar forms, but should not be confused: transmitted light Qi/Qo is not gap fraction, $f(\theta)$, since in this case transmitted light includes direct beam and diffuse sky radiation, and also the effects of scattering in the canopy; zenith angle θ is not included in equation 4, but likely affects the value of the empirical constant K. In this study, K was assumed to be 0.5, which is a good approximation for conifers (Pierce and Running 1988). For the alder stand (1A) a K value of 0.6 was used as an average for deciduous canopies (Jarvis and Leverenz 1983). Values of K were also computed based on the ceptometer measurements of transmitted light and independent determinations of LAI by the sapwood method and the LAI-2000.

There was relatively close correspondence between the measured LAIs for the three methods (Table 4). The ratio of leaf area to sapwood area varied more than sixfold across the transect. Species such as juniper and ponderosa pine that are adapted to arid environments maintain fewer leaves to a comparable amount of conducting tissue than do maritime species. Leaf area indices varied more than tenfold across the transect, with higher values west of the Cascades. Based on the ceptometer measurements ($k = 0.5$), LAI values ranged from a low of 0.5 at site 6 to a high of 10.6 at the dense western hemlock-Douglas-fir stand at site 3. No significant difference was observed between the LAIs for the fertilized and control stands for sites 3 and 5. At the Santiam Pass stand (site 4), an infestation of western spruce budworm (*Choristoneura occidentalis* Freedman) defoliated the new growth on many of the trees. In addition, shortly after the study began, the Metolius site (site 5) was altered by mechanical harvesting, which left only patches of small trees. As a result, for both stands, leaf areas were reduced by these disturbances. Therefore, leaf area estimates based on the light interception measurements do not represent the undisturbed state of subalpine mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) or dry site ponderosa pine forests in this region.

Foliage biomass

To convert from area to foliage biomass, I applied specific leaf areas ($cm^2\ gm^{-1}$ dry weight) measured on foliage samples collected at the sites. In July five branches were shot from mid-canopy from dominant representatives of all of the major tree species at the six sites. Representative samples of needles from each branch were analyzed for fresh needle area (one-sided) with the LI-COR leaf area meter (LAI-3100; LI-COR inc., Lincoln NE), and then dryed at 70°C to a constant weight and weighed. The average specific leaf area of the five branches was then estimated and these values were pooled with the averages for the other tress to provide a site average. These values were then applied to the LAI estimates from light transmittance (ceptometer, $K = 0.5$) to yield total foliage biomass ($Mg\ ha^{-1}$).

Tree Above-Ground Net Primary Production

Woody biomass production

Growth was determined by annual tree dbh changes estimated from measurements of growth rings. Increment cores were taken from a random selection of trees in each sample plot beginning with an initial random choice and then every fifth tree in sequence. Measurements were made of the current-year's growth (1990) and of the previous five years. No significant difference was found between the current year-growth increment and the average of the previous five years for any of the sites. As a result, the five-year average growth increments were used to compute the average annual increment for each site. These values were then applied to the species regression relationships (Gholz et al. 1979) and average trees per ha to estimate woody biomass production (Mg ha^{-1} yr^{-1}).

Foliage production

In order to gauge patterns of foliage biomass production across the transect I measured the fraction of new growth in the summer during maximum canopy development. Five branches were collected from each of the species on the sites and specific leaf areas (cm^2 gm^{-1} dry weight) were measured on subsamples of current year age-class and on subsamples of all other age-classes. These values were then pooled for each site and used to provide an estimate of percent new production. The estimate of percent new foliage production was applied to the estimate of total foliage biomass to provide yearly foliage production (Mg ha^{-1} yr^{-1}). No measurements from Santiam Pass stand (site 4) were collected as a result of extensive spruce budworm damage. Instead, Gholz's (1982) estimate of new foliage growth fraction for a similar subalpine stand was used to compute total foliage production for site 4.

Total above-ground net primary production

Total annual above-ground net primary production (ANPP) of the trees was calculated by adding the woody biomass increment and foliage production estimates. Forest ANPP ranged from nearly 17 Mg ha^{-1} yr^{-1} at the Scio site on the west slope of the Cascades to less than 2 Mg ha^{-1} yr^{-1} at the Metolius and Juniper sites east of the Cascade crest (Table 3). The ANPP trends observed along the transect were similar to those observed by Gholz (1982). Most Douglas-fir stands reach peak growth rates at approximately 30 years, which was near the the age of the Scio stand (Turner and Long 1975). The similar production values for both the ponderosa pine stand (site 5) and the juniper stand (site 6) were probably an artifact of stand management. Site 5 had most of the large trees removed in 1989. As a result, most of the remaining ponderosa pine trees were former understory components still exhibiting suppressed growth. Juniper ranks among the least productive evergreen tree communities (Gholz 1980).

PRODUCTION RATE ASSESSMENT AND SPECIFICATION OF ENVIRONMENTAL CONSTRAINTS

Monteith (1972, 1977) has demonstrated that above-ground dry matter accumulation rates are linearly related to IPAR in well-watered agricultural crops. This may be stated as a simple expression:

$$PR = ANPP/IPAR \tag{5}$$

where

PR = production rate (g MJ^{-1})

$ANPP$ = above ground net primary production (g m^{-2} yr^{-1})

$IPAR$ = annual intercepted PAR (MJ m^{-2} yr^{-1})

Values for agricultural crops generally range between 1 and 2 g/MJ. Values reported for forests generally vary between 0.5 and 1.0 g MJ^{-1} (Linder, 1985).

The Utilized IPAR Production Rate Assessment

Previous work has shown that environmental limitations, such as drought stress, reduce the biomass accumulation rates per unit intercepted radiation (Jarvis and Leverenz 1983, Byrne et al. 1986, Linder 1987, Monteith 1988, Russell et al. 1989). This suggests that calculations of production rate which include consideration of environmental control over tree-level physiological processes might produce a more robust description of the primary production rates observed in Oregon. In order to predict yearly ANPP rates in relation to IPAR for the variety of forest stands and climates represented along the transect, I chose to assess general environmental controls that are independent of ecosystem type and do not change from season to season. Biomass accumulation is the result of the integration of a number of complex processes. Nevertheless, to develop a simple model, I selected factors that I could generalize to all forest settings. Leaf stomatal control of the uptake of carbon dioxide and transpiration is the primary limitation on photosynthesis, and thus is a generic principle that can be applied to all vegetation (Wong et al. 1979, Running 1984).

I hypothesized that production is constrained primarily by climatic control over stomatal conductance and transpiration. Other constraints on production that limit radiation intercepted by the canopy are also incorporated into this approach through the accounting of IPAR. Environmental stresses will tend to reduce canopy growth and development. Nutrient limitations, for example, constrain production, and through a restriction of leaf area, reduce IPAR.

Three universal controls over stomatal conductance are: 1) freezing temperatures; 2) soil drought; and 3) air vapor pressure deficits. All of these factors limit photosynthesis rates and, over the course of the growing season, production. Essentially, when these climatic factors are constraining, stomatal restriction limits carbon dioxide uptake and the IPAR is therefore not fully utilized for production. This concept of "utilized IPAR" may be stated in the form:

$$\mathbf{IPAR_u = f(T) \cdot f(D) \cdot f(V)\ IPAR} \qquad (6)$$

where

f(T) = temperature factor (0 or 1)

f(D) = drought factor (0, 0.5, 1)

f(V) = vapor pressure deficit factor (0, 0.5, 1)

IPAR = total intercepted PAR for the hour assessed (MJ m^{-2})

Hourly assessments of the constraining factors and IPAR are made and then summed to provide yearly estimates. This total yearly $IPAR_u$ value is then substituted into eq. 3 to determine the utilized IPAR production rate. The temperature factor is either 0 when low temperatures are constraining photosynthesis or 1 when this factor is not limiting. The other factors -- drought and vapor pressure deficits -- can take on values of 0 when stomata are assumed to be closed, 0.5 for partial limitations on stomatal conductance, or 1.0 when no climatic constraints are present, depending upon the severity of the conditions. Since drought and vapor pressure deficits can simultaneously limit stomatal conductance, I assumed these factors can interact (both equal to 0.5) to yield a total utilized IPAR of 25% of the total IPAR.

Explicit definition of the functional form of each factor would require detailed consideration of species-level physiological response to these environmental constraints. In this analysis I wished to empirically explore the validity of this concept across the transect by applying a set of simple rules to determine the magnitude of each factor in limiting carbon uptake. Based on general tree physiological principles, each constraining factor was defined *a priori* and then applied to reduce IPAR (Table 5). This model, expressed as discrete thresholds, does not possess the degree of mechanistic detail incorporated into a process-level model with continuous functions. The approach, however, does use many of the same physiological principles explicitly defined in FOREST-BGC. For example, the FOREST-BGC model, which emphasizes leaf area index a a key structural attribute, constrains leaf growth, and thus carbon gain, at predawn water stress levels around -1.8 and -2.0 MPa (Running and Gower 1991). This level is very close to the threshold (-1.5 MPa) defined in the utilized IPAR model for complete stomatal closure.

Calculation of the Utilized IPAR Production Rate

Hourly-integrated incident radiation for the sites was collected by the meteorological stations. I assumed that percent interception, as estimated from the summer ceptometer measurements, was constant through the year. There is evidence, however, that LAI, and thus energy interception, varies through the course of the year (Jarvis and Leverenz 1983, Russel et al. 1989, Gholz et al. 1991). Minimum LAI occurs in the winter when radiation intensity is reduced from short days and clouds, and thus seasonal changes in LAI have a negligible effect on radiation interception estimates (Running, personal communication). The one deciduous stand on the transect, site 1A, was assumed to have no IPAR during periods of leaf-off (November to May) and one-half IPAR during the leaf transition periods (October and April).

Specification of the threshold limits was defined on general principles of tree physiology that are applicable to all forest types rather than species-specific relationships. The environmental thresholds for constraining the utilization of IPAR was based on data for a variety of tree species in the Pacific Northwest. For example, the criteria for limiting stomatal conductance at different evaporative demands (vapor pressure deficits) was generalized from data from eight different (N = 2231) coniferous and deciduous species (Waring and Franklin 1979). Data from the meteorological stations and simple field measurements were used to assess the periods when the thresholds were applied. When conditions were found to limit carbon uptake the hourly radiation (IPAR) was subtracted from the annual total IPAR.

Freezing temperatures: Cold temperatures can reduce photosynthetic rates in trees for a number of hours even after the temperature returns to more optimal conditions (Pharis et al. 1972, Kaufmann 1982, Jones 1983). At -2^0C, net photosynthesis, in a variety of tree species, is at or near zero (Larcher 1983).

For all sites, I used hourly mean meteorological data to define temperatures. I assumed that for a period of 24 hours after a temperature recording of -2°C or less no there was net carbon uptake. For the hours when temperatures achieved these thresholds, all IPAR was subtracted from the annual total.

Drought: When soil water is reduced, predawn water potentials in trees fall in concert with restrictions in stomatal conductance (Running 1976). At predawn levels between -1.0 and -1.5 MPa, moderate reductions in conductance have been observed (Waring and Schlesinger 1985). Complete stomatal closure is attained for most conifer tree species when predawn xylem pressure potentials are less than -1.5 MPa (Lassore and Salo 1981).

I used predawn water potentials to assess water stress levels at each site. To determine average water stress for each of the sites, I measured predawn water potentials on five trees at least once a month during the dry season. To define the beginning of the periods when the site exhibited moderate or extreme soil drought conditions predawn water potentials were measured with the pressure bomb method (Scholander et al. 1965, Waring and Cleary 1967) During periods when drought conditions were moderate (-1.0 to -1.5 MPa), I assumed that there were some limitations on stomatal diffusion of carbon dioxide, and thus subtracted half the incident IPAR. When drought conditions were severe (<-1.5 MPa) I assumed complete closure of stomata, and all IPAR for the period was subtracted from the yearly total.

Vapor pressure deficits (VPD): High evaporative demands at the leaf will reduce stomatal conductance. During periods of low relative humidity, the supply of water from the root system may not be able to sustain the evaporative demand. For a variety of trees, conductance is effectively stopped by vapor pressure deficits that exceed 25 mb, regardless of the water status of the tree (Waring and Franklin 1979, Losch and Tenhunen 1981). At vapor pressure deficit levels between 15 to 25 mb, stomatal conductance is reduced in a variety of tree species (Waring and Franklin 1979).

Vapor pressure deficits were calculated from the hourly average relative humidity and air temperature data collected by the meteorological stations (Monteith and Unsworth 1990). I assumed that during periods of extreme vapor pressure deficits (> 25 mb) the stomata were effectively closed, reducing all hourly IPAR from the annual total. When vapor pressure deficits were moderate (15-25 mb), some conductance was assumed to occur. During these periods half the IPAR load was subtracted from the annual total.

RESULTS

A comparison of total forest above-ground production versus total annual IPAR for the Oregon Transect reveals that the production rate varies considerably, between 0.24 g MJ^{-1} at the Metolius site and 0.92 g MJ^{-1} at the coastal alder site (Fig. 2, Table 6). This factor of four variation indicates that the production rate per unit IPAR does not provide a general description of forest primary production processes in this region. Given the diversity of climatic conditions encountered, this is to be expected. While all sites experienced periods when freezing temperatures and extreme vapor pressure deficits limited carbon uptake, only sites 2, 5 and 6 experienced soil drought conditions (< -1.0 MPa) sufficient to limit the utilization of annual IPAR (Fig. 3).

Constraining IPAR when climatic factors are limiting stomatal conductance appears to have accounted for most of the variation observed in the production rate. The utilized IPAR production model effectively normalizes the relation between production and intercepted radiation (Fig. 4). For most of the sites the utilized IPAR production rate is approximately 1 g MJ^{-1} (Table 6). This suggests that the climatic constraints on photosynthesis is the primary determinant of variation in production across the Oregon Transect. At least in Oregon, the utilized IPAR concept appears valid.

The large deviation in the utilized IPAR production rate observed at Site 1 appears to be related to stand age. This is an old-growth stand, with some Douglas-fir trees over 300 years old, considerably older than the other stands across the transect. Evidence suggests that larger trees and mature stands have reduced rates of photosynthesis and higher ratios of maintenance respiration to photosynthesis (Waring and Schlesinger 1985, Ryan 1989, Yoder personal communication). As a result, for the older stand at site 1, higher maintenance costs and other constraints on photosynthesis would be expected to further reduce the utilization of IPAR. In addition, the reduced production rate at site 4 may be related to additional physiological stress from the insect defoliation.

Below-ground production was not considered in the analysis for two reasons. First, below-ground production is difficult to measure, and there are, as a result, considerable inaccuracies inherent in the estimates (Long and Hutchin 1991). Second, regional trends in below-ground production were expected to be nearly proportional to the relative magnitude of above-ground foliage production (Nadelhoffer et al. 1985, Raich and Nadelhoffer 1989). With this assumption, the general relationship between utilized IPAR and ANPP should not change if the below-ground components of production were included in the analysis.

DISCUSSION

The vegetation ecosystem structure and processes in this region generally follow the pattern of climate, with highly productive, closed canopy forests on the coast and western slope of the Cascades, degrading to quite low production, open forests in the rain shadow of the mountains. Leaf area index and annual IPAR and both follow similar trends. Annual IPAR, which effectively describes the capture of solar radiation by the variety of forest stands along the transect, sets the maximum available energy for the transformation of carbon dioxide into biomass.

Environmental constraints influence the conversion of solar energy into dry matter through two mechanisms. First, climate limits forest canopy development and thus the amount of radiation a stand can intercept. For example, there is a correlation between site water balance (Grier and Running 1977) and low night temperatures (Waring et al. 1978) with canopy development. This effect is characterized by an assessment of percent IPAR, which describes canopy development. Second, environmental factors constrain the utilization of IPAR by limiting photosynthesis even after light has been intercepted by the forest canopy. Stomatal closure from freezing temperatures, drought or high evaporative demand reduce photosynthesis rates and, when integrated over the year, constrain annual growth increments. This process of environmental controls limiting production is captured by the utilized IPAR production model.

The contribution of the climatic components in determining the utilized IPAR production rate across the transect illustrates the variations in environmental constraints on production encountered in western Oregon. When all of the environmental constraints were accounted for, reductions in annual IPAR ranged from 8% to 77% across the transect (Fig. 5). The largest reductions in annual IPAR were experienced at the dry east-side sites. Conversely, the cool, moist Cascade Head sites showed little reduction in annual IPAR.

The relative contributions of each climatic factor reflects the patterns of regional climate. The Cascade Head sites (1 and 1A) experienced almost no constraints from freezing temperatures and drought. At the other end of the transect, the Juniper site (6) displayed extreme constraints on the utilization of PAR from both freezing temperatures and summer drought. Site 2 experienced significant decreases in annual IPAR from both drought and vapor pressure deficits, 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.

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 regional patterns of climatic stress on the annual carbon budget (Cannel 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 can continue through the winter months (Emmingham and Waring 1977, Waring and Franklin 1979).

CONCLUSIONS

The value of the utilized IPAR production rate model is that it 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 relatively simple but realistic model of forest ecosystem dynamics based on the principles of IPAR production rate, modulated by climatic factors. 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 forest ecosystem dynamics.

Figure 1. Map of the study area in Oregon showing the location of the sites and the major vegetation zones (After Gholz 1982, Franklin and Dyrness 1973).

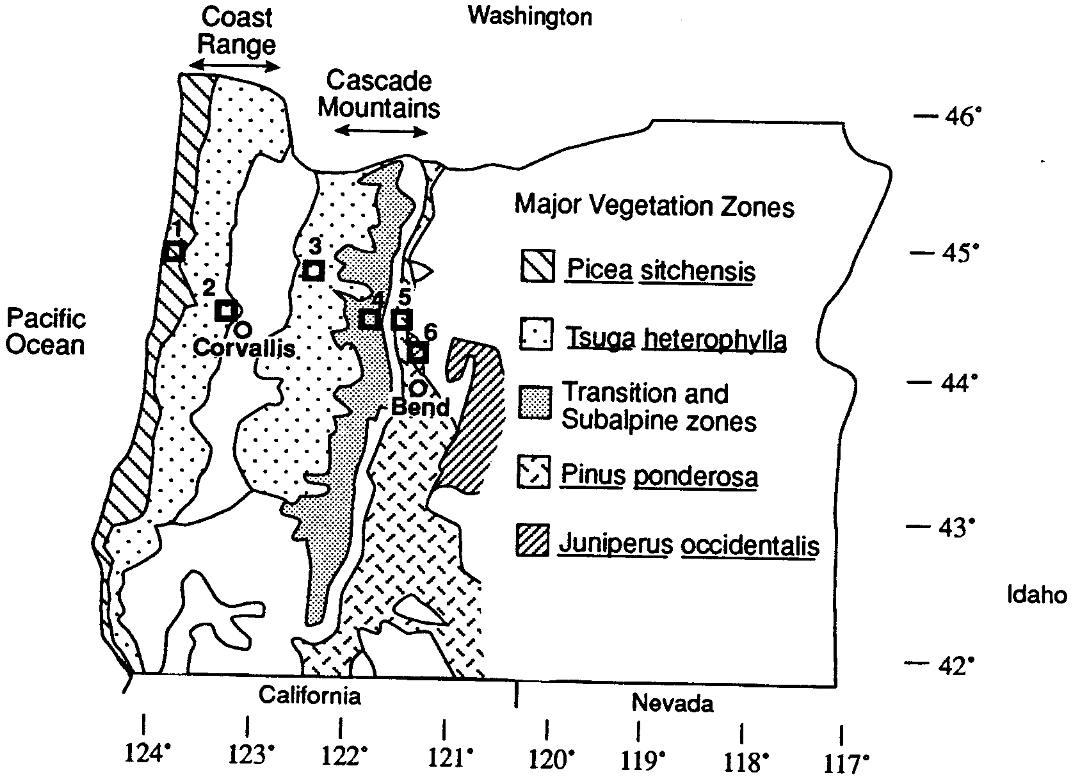

Figure 2. Estimates of annual intercepted PAR compared to above-ground net primary production. Dashed lines express production rate rate values (grams of dry matter accumulated per MJ of PAR intercepted). Linear $R^2 = 0.82$.

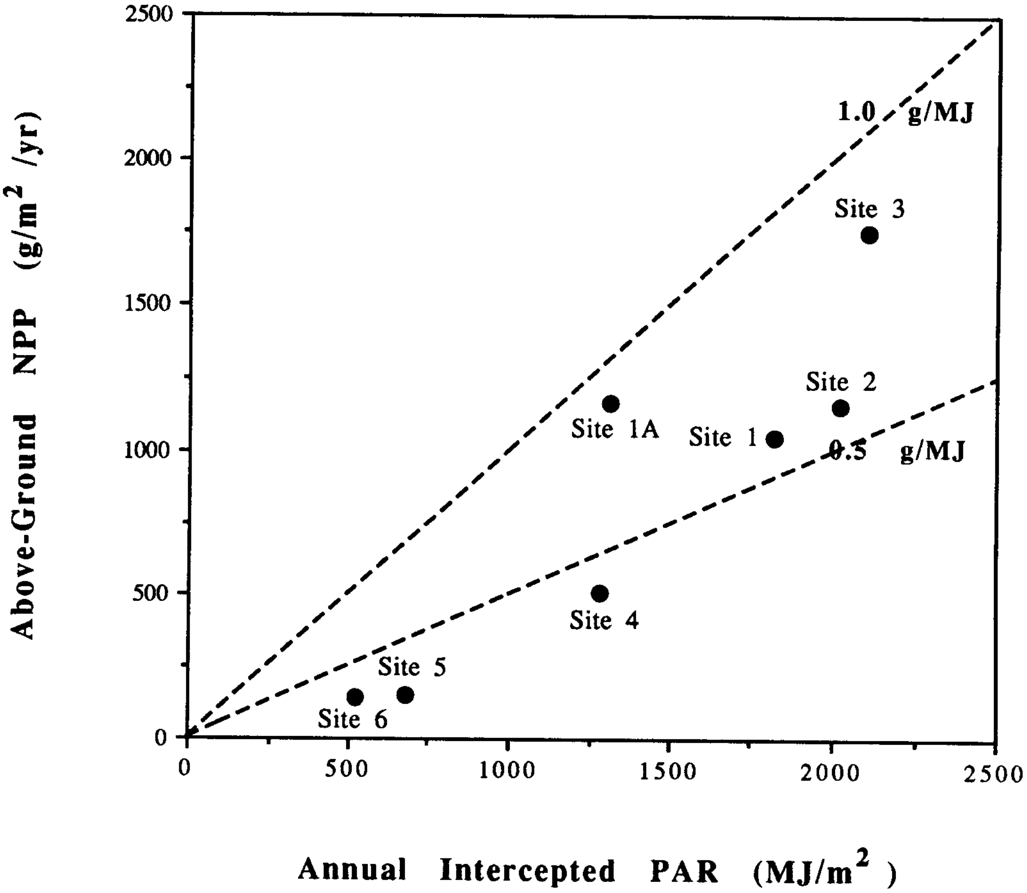

Figure 3. Seasonal trends (1990-1991) in predawn xylem water potental for the three sites experiencing significant drought stress (< -1.0 MPa).

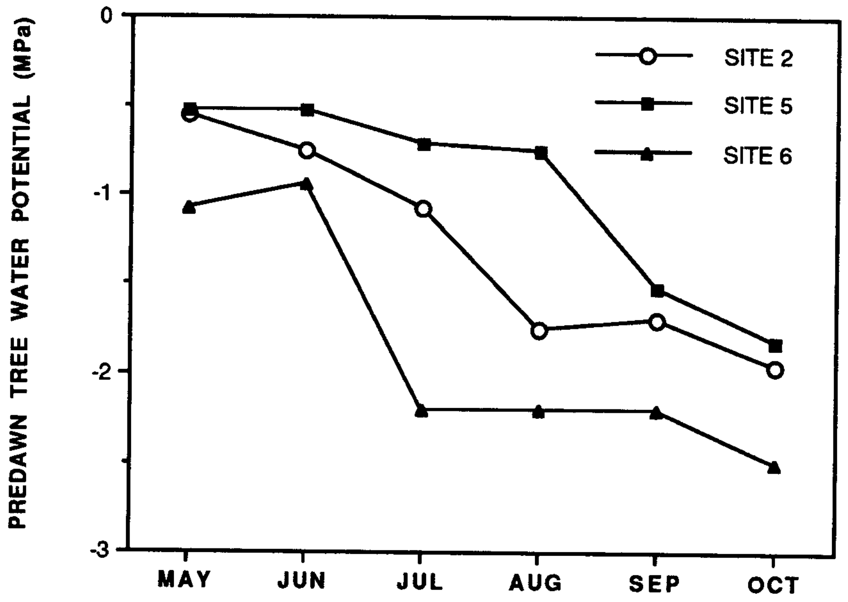

Figure 4. Estimates of utilized intercepted PAR explain much of the variance in net primary production for the range of forest stands across the study transect. Linear R^2 0.98, excluding the old-growth stand from the regression.

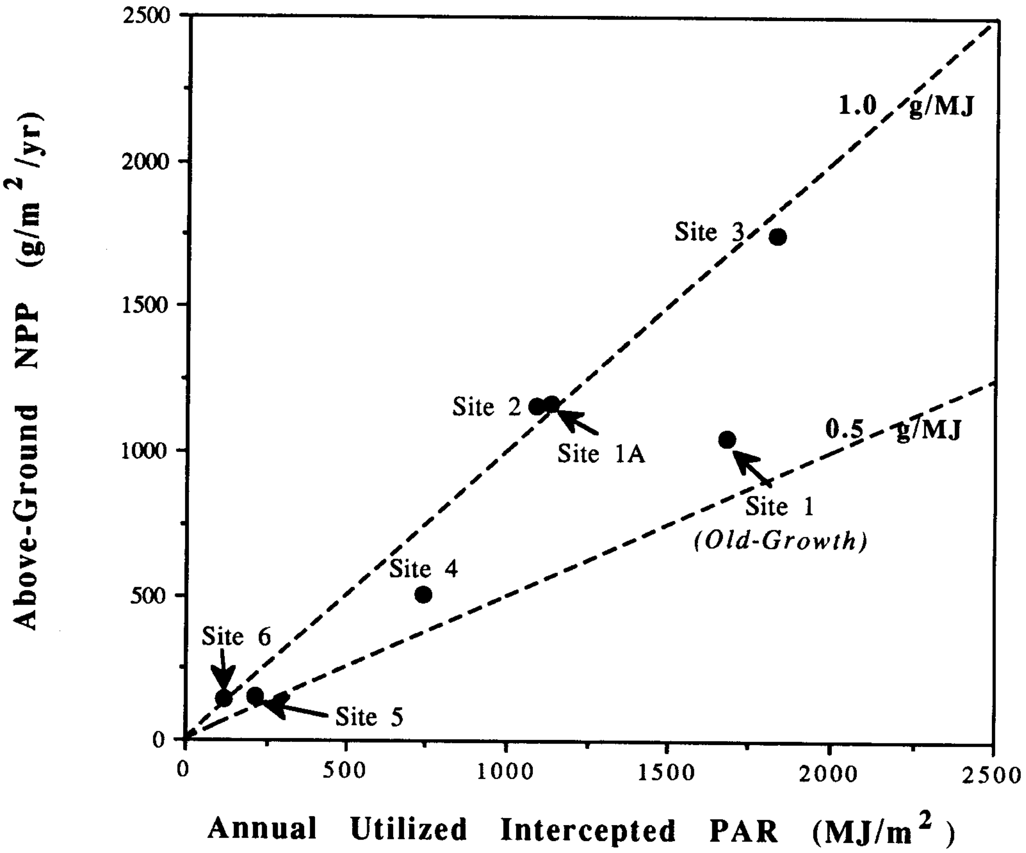

Figure 5. The fraction of annual intercepted PAR that could not be used by the various forest stands because of freezing temperatures, drought, or vapor pressure deficits (VPD). Values ranged from less than 10% at the cool, moist coastal forest stand (site 1) to a much as 77% at the cold, dry juniper woodland.

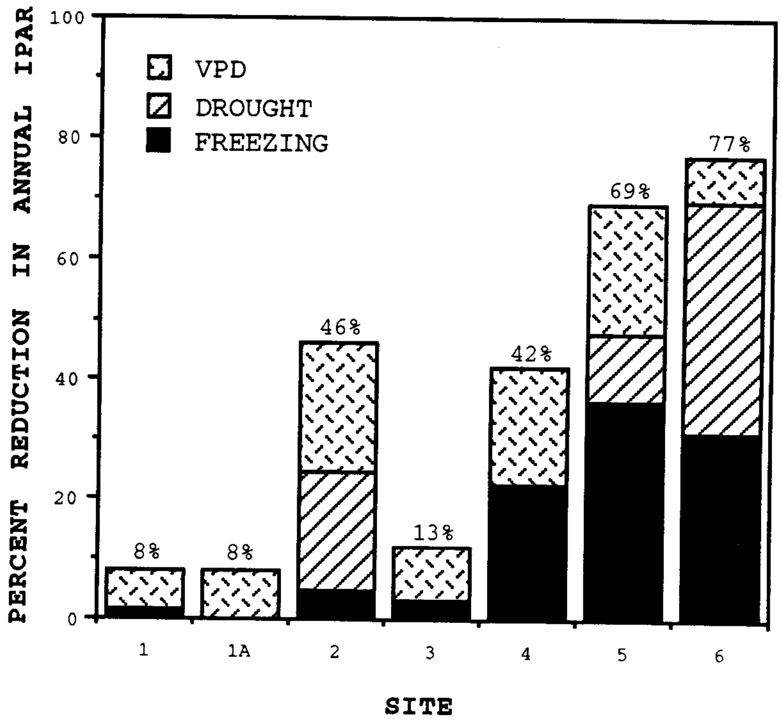

Table 1. Characteristics of the study sites across the transect.

	Site						
Feature	1	1A	2	3*	4	5*	6
Site Name	Cascade Head (Old-Growth)	Cascade Head (Alder)	Warings Woods	Scio	Santiam Pass	Metolius	Juniper
Physiographic Province[1]	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	130°	--	160°	325° (--)	--	--	--
Stem Density (no.ha^{-1})>5 cm	385	1793	226	870 (980)	1740	600 (1051)	141
Basal Area (m^2 ha^{-1})	98.2	35	51.3	67 (63)	83.3	6.8 (11.3)	9.3
Ave. Max. Canopy Ht (m)	50	13	40	30	20	7	10

* Fertilized stand data in parentheses when different from control stand.

[1] Physiographic provinces from Franklin and Dyrness (1973).

Table 2. Climate data, percent intercepted photosynthetically active radiation (IPAR ± S.E.), and total annual IPAR for the study sites.

	Site						
Feature	1	1A	2	3	4	5	6
1990 Precip. (cm)	251	251	98	118	181	54	22[1]
1990 Mean Annual Temperature (°C)	10.1	10.1	11.2	10.6	6.0	7.4	9.1[1]
Total Annual Incident PAR (MJ m^{-2})	1887	1887	2146	2113	2087	2385	2385
Percent IPAR	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 m^{-2})	1839	1310	2020	2103	2103	1282	682

[1] Site 6 rainfall and temperature data from from 20 year NOAA averages for Redmond, OR.

Table 3. Stand tree above-ground biomass (± S.E.) and net primary production (ANPP ± S.E.) for the study sites.

	Site								
Feature	1	1A	2	3	3F	4	5	5F	6
Tree Biomass (Mg ha^{-1})									
Wood	702	116	461	393	377	364	13	18	8
Foliage	8.3	4.3	10.2	15.3	15.3	6.3	1.9	1.9	2.8
Total Biomass	710.8 ± 114	120.3 ± 9	471.2 ± 103	408.3 ± 31	392.3 ± 66	370.3 ± 63	14.9 ± 3	19.9 ± 4.7	10.8 ± 2.8
Tree Biomass Production (Mg ha^{-1} yr^{-1})									
Woody	8.3	7.4	8.7	12.9	16.0	3.5	1.1	1.0	0.6
Foliage	2.2	4.3	2.9	4.6	4.6	1.6[1]	0.4	0.4	0.8[2]
Total Production	10.5 ± 1.6	11.7 ± 0.9	11.6 ± 2.5	17.5 ± 1.3	20.6 ± 3.5	5.1 ± 0.7	1.5 ± 0.3	1.4 ± 0.4	1.4 ± 0.4

1 No data due to spruce budworm damage. Estimate of percent foliage production from Gholz (1982).

2 No data. Estimate of percent foliage production from Gholz (1982).

Table 4 Comparison of the different methods for estimating leaf area index (LAI ± S.E.) for the variety of different stands across the Oregon transect: 1) LI-COR LAI-2000; 2) Decagon ceptometer with K = 0.5; and 3) derived from the relationship between sapwood area at the base of the live crown and LAI for the various tree species. K values based on LAI-2000 and sapwood are indicated.

	Site						
Method	1	1A	2	3	4	5	6
LAI-2000							
Site LAI	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
Ave k values[1]	0.46	0.71	0.45	0.62	0.32	0.44	0.63
Ceptometer							
Site LAI (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[2]							
Site LAI	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
Ave K values[1]	0.62	ND	0.71	0.61	0.34	0.32	0.63

* K = 0.6 for the alder stand at site 1A.

[1] Average K values were computed based on ceptometer measurements of transmitted light and independent determinations of LAI by the sapwood method and the LAI-2000.

[2] LAI/sapwood ratios ($m^2\ cm^{-2}$) for the following tree species (Waring et al. 1982): Site 1, western hemlock (0.46); site 2, Douglas-fir (0.54); site 3, the value is an average assuming one-half the basal area is Douglas-fir and one-half western hemlock (0.50); site 4, mountain hemlock (0.16); site 5, ponderosa pine (0.25). Site 6 juniper LAI/sapwood ratio (0.07) from Waring (1980).

Table 5. Criteria for reducing intercepted PAR 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-hr period*

SOIL DROUGHT

- *If predawn water potential less than -1.5 MPa, assume no radiation utilized*
- *If predawn water potential is between -1.0 to -1.5 MPa, assume half radiation utilized*

VAPOR PRESSURE DEFICITS (VPD)

- *IF VPD exceeds 25 mb, assume no radiation utilized*
- *If VPD is between 15 to 25 mb, assume half radiation utilized*

Table 6. The production rate and utilized production rate ($IPAR_u$) values for the sites along the transect.

	Site						
	1	1A	2	3	4	5	6
Production Rate ($g\ MJ^{-1}$)	0.57	0.89	0.57	0.83	0.40	0.22	0.27
$IPAR_u$ Production Rate ($g\ MJ^{-1}$)	0.63	1.03	1.06	0.96	0.69	0.70	1.15

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