Remote Sensing of Radiation Intercepted by Vegetation to Estimate Aboveground Net Primary Production Across Western Oregon

by

Beverly E. Law

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AN ABSTRACT OF THE THESIS OF

Beverly E. Law for the degree of Doctor of Philosophy in Forest Science presented on September 3, 1993.

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Remote sensing of variables necessary to estimate net primary production of vegetation over large temporal and spatial scales has been a goal of climate change research. This thesis consists of two studies that address the reliability of satellite and airborne sensors to quantify a basic component of all production models, the amount of light intercepted by vegetation canopies throughout the year.

The studies focus on an empirical model of net primary production: $NPP = [IPAR*f(T)*f(D)*f(V)]*\varepsilon_u$, where IPAR is the amount of incident photosynthetically active radiation intercepted by vegetation during the year, and environmental limits to production are freezing temperatures (T), drought (D), and high vapor pressure deficit (D). A relatively constant energy-use

efficiency coefficient (ε_u) would allow broad application of this model to a wide variety of natural vegetation types and climate conditions.

The first study showed that the normalized difference vegetation index (NDVI), calculated from field spectrometry, provided a good linear estimate of the fraction of incident PAR intercepted by constructed canopies of bitterbrush ($R^2 = 0.83$) and manzanita shrubs ($R^2 = 0.86$) at an open canopy ponderosa pine site. In the second study, Thematic Mapper Simulator NDVI explained 97% of the variation in %IPAR by shrub and forested sites across Oregon. These studies demonstrated the general ability to estimate %IPAR from remotely sensed observations.

The second study showed that the fraction of light intercepted by forest and shrub vegetation, coupled with meterological station measurements of total annual incident radiation, explained 70% of the variation in primary production. Additional limitations on the utilization of light should be considered to estimate production. Constraints on the ability of each species to use intercepted light, as defined by freezing temperatures, drought, and vapor pressure deficit, were quantified from hourly meteorological station measurements and physiological measurements in the field. The environmental limits to light capture by photosynthesis, however, did not improve the ability to explain variation in above-ground NPP across the forested and shrub sites. Differences in carbon allocation patterns among plant life forms appear to be important to fully test primary production models.

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This dissertation was written as two manuscripts for submission to professional journals. Several people provided support in the development of each study. In the first study, Dr. Samuel Goward, Dr. Warren Cohen, and Dr. William Ripple contributed many ideas and technical advise on remote sensing, and critiqued the manuscript. Dr. Richard Waring was co-author of the manuscript, and provided many helpful comments on preliminary drafts. John Runyon and Dr. Barbara Yoder also contributed constructive ideas. Thanks to Fred Huemmrich, Rich McCreight, and Dr. Chaur Fong Chen for advice on spectral measurements and analysis, and to Dr. Susan Stafford, Dr. Steve Knowe, and Dr. Tom Sabin for statistical advice.

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Last and foremost, special thanks to Steve Paulsen for his enduring love, encouragement, and support, and his willingness to discuss burning science issues at all hours of the day and night. His pragmatism and sense of humor helped to buoy me during moments when I felt like I was rearranging the deck chairs on the Titanic. The iceberg transformed into an ice cube and melted, and I am happily relaxing in the shade of a palm somewhere in Hawaii...at least until my (our) next fantastic adventure.

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INTRODUCTION

To address ecological changes that are occurring at regional to global scales, we must focus on questions at large temporal and spatial scales. Remotely sensed observations coupled with ecological modelling offer potential for meeting this challenge by providing a means to evaluate dynamic ecosystem characteristics, such as net primary production, with limited field measurements over extensive areas. The studies in this thesis were designed to evaluate the ability of remote sensing spectral indices to estimate structural vegetation properties such as light interception, and to determine if a modified empirical model of light interception and energy-use efficiency explained variation in above-ground production by forest and shrub sites across Oregon.

Net primary production has been repeatedly identified as the most important carbon cycle variable for quantifying biological activity in a comparable way across regions and biomes (Running 1990). Direct measurements of net primary production (NPP) are not feasible at large spatial scales, as reflected in the paucity of reliable measurements of this variable. Approaches to modelling NPP range from simple empirical models to physiological process models. The process models should yield relatively accurate predictions, but they often require detailed information not easily obtained at large spatial scales (Agren 1991). Alternatively, the simple empirical model may provide rough estimates of current production with a limited number of measurements.

The empirical model developed by Monteith (1977) and others is:

$$NPP = IPAR^{*}\varepsilon \tag{1}$$

where IPAR is the annual incident photosynthetically active radiation intercepted by vegetation, and ε is energy-conversion efficiency. The ε value can vary due to photosynthetic pathway (C_3 vs. C_4 plants), developmental stage, vegetation density, and environmental stresses, but it often varies much less than IPAR. For C_3 crop plants, ε is relatively constant at 1.4 g of dry matter produced per MJ of energy absorbed, provided they are not water, temperature, or nutrient limited (Field 1991). Photosynthesis by natural perennial vegetation, however, is frequently limited below its maximum potential by several environmental factors. Therefore, the model has been modified to account for the environmental limits to the ability of plants to utilize radiation intercepted throughout the year by isolating the climatic constraints from nutrition related biochemical constraints, both subsumed in ε:

$$NPP = [IPAR^{*}f(T)^{*}f(D)^{*}f(V)]^{*}\varepsilon_u \tag{2}$$

where freezing temperatures (T), drought (D), and high vapor pressure deficit (V) limit the ability to utilize intercepted light for production (Landsberg 1986). A constant energy-use efficiency coefficient (ε_u) would allow broad application of the model across diverse climatic conditions and vegetation types (Running 1990).

Application of the energy-use efficiency model to large spatial scales could be accomplished through remotely sensed estimates of IPAR, and meteorological measurements of incident radiation, air temperature, and humidity. Goward et al. (1993) have suggested that it may be possible to estimate some meteorological variables from remotely sensed observations, such as incident radiation from the Total Ozone Mapping Spectrometer (TOMS), and air temperature and humidity from the Advanced Very High Resolution Radiometer (AVHRR).

The percent of incident photosynthetically active radiation intercepted by vegetation (%IPAR) has been shown to be a linear or near-linear function of normalized difference vegetation index (NDVI) (Choudhury 1987, Sellers 1987, Goward 1993). The NDVI is a dimensionless index between -1.0 and 1.0, and is calculated from surface reflectance in the near-infrared (NIR) and red (R) portions of the electromagnetic spectrum (NDVI = NIR-R/NIR+R). The spectral band widths and spatial resolution vary by instrument and platform. The spectrometer instrument used in the field in Chapter I has 10 nm bandwidths, and spectral data used in Chapter II were acquired from the aircraft flown Thematic Mapper Simulator (TMS) sensor, which has 7 broad bands (NIR = 760-900 nm; R = 630-690 nm) and a spatial resolution of 25 m. It may be possible to combine the %IPAR estimated from NDVI with annual incident PAR from meteorological stations or the TOMS satellite sensor to calculate the amount of incident photosynthetically active radiation intercepted by vegetation through the year (MJ m^{-2} y^{-1}). The estimate of IPAR could then be applied in the energy-use efficiency model (equation 2) to estimate net primary production.

Each chapter of this thesis was written as a stand-alone document. The first chapter, accepted by Ecological Applications (Law and Waring 1993), evaluates the ability of several spectral vegetation indices to estimate IPAR and leaf area index of two shrub species at the OTTER Metolius site, an open ponderosa pine forest on the east side of the Cascade Mountains. Several studies have shown that spectral vegetation indices such as the simple ratio (SR = NIR/R) and NDVI are related to structural properties of canopies, such as leaf area index, total biomes, and IPAR. The specific purpose of my study was to determine if IPAR was a linear function of NDVI within a shrub species at a given site, as found in previous studies on other vegetation (Asrar et al. 1984, Choudhury 1987).

In Chapter II my objectives were to determine the relation between NDVI and IPAR across forest and neighboring shrub sites along an environmental gradient in western Oregon, and to evaluate the energy-use efficiency model across these life forms. As part of the Oregon Transect Ecosystem Research Project (OTTER), Runyon et al. (1993) showed that above-ground NPP by forest trees was linearly related to IPAR, once they had accounted for freezing temperatures, drought, and high vapor pressure deficit influences on the ability to utilize intercepted light. This resulted in a fairly consistent ε_u across sites, suggesting broad application of the model may be possible.

I chose to apply the energy-use efficiency model to several of the OTTER sites and nearby shrub sites, using the general thresholds to stomatal conductance that Runyon et al. (1993) obtained from the literature on several tree species. The rationale is that as stomata partially or completely close in response to these environmental factors, photosynthesis is severely limited or stops due to decreased CO_2 availability, and consequently limits production (Schulze and Hall 1982, Farquhar and Sharkey 1982). The general thresholds were applied by reducing hourly or daily IPAR from the annual total IPAR. If application of the general thresholds to obtain a modified IPAR came close to explaining differences in ANPP across sites, then I planned to determine if species-specific thresholds from field physiological measurements improved the relationship. The shrub sites, which were within existing remote sensing imagery and near the forested sites, provided a good opportunity to test the universality of the energy-use efficiency model.

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Chapter I

APPLYING SPECTRAL INDICES TO ESTIMATE LEAF AREA INDEX AND RADIATION INTERCEPTED BY UNDERSTORY VEGETATION

ABSTRACT

To estimate leaf area index (LAI), intercepted radiation, and other related characteristics of vegetation, ecologists often require separate consideration of the understory and overstory components of vegetation. In the open ponderosa pine (*Pinus ponderosa*) forests of east-central Oregon, bitterbrush (*Purshia tridentata*) and manzanita (*Arctostaphylos patula*) are major understory species. We constructed artificial canopies of these two species and determined whether remotely sensed properties of canopy reflectance might be used to estimate LAI, and the fraction of photosynthetically active radiation intercepted (f_{IPAR}). Although the two species differed in their canopy structures and leaf characteristics, they showed similar light extinction coefficients, varying only from 0.52 for bitterbrush to 0.46 for manzanita as derived from the Beer-Lambert Law. The relationship between f_{IPAR} and LAI was asymptotic at an LAI of 6 for both species. The normalized difference vegetation index (NDVI) provided a good linear estimate of f_{IPAR} (R^2 = 0.86 manzanita, and 0.83 bitterbrush), and the simple ratio of near infrared to red (SR) permitted a linear estimate of LAI (R^2 = 0.86 manzanita, and 0.74 bitterbrush) of this vegetation growing on soils with uniform reflectance properties. Aerial estimates of overstory and understory cover derived from aircraft or satellites provide a basis for assessing the proportional contribution of understory shrub cover to the total vegetation, given that basic relationships between spectral reflectance, LAI, and f_{IPAR} have been established, as in this study.

Key words: remote sensing; intercepted photosynthetically active radiation (IPAR); leaf area index (LAI); spectral vegetation indices.

INTRODUCTION

Ecologists recognize that understory plants contribute significantly to forest ecosystem primary and secondary productivity in moderately open forest canopies over extensive geographic areas. Yet remotely sensed estimates of leaf area index (LAI) and related variables rarely distinguish understory contributions to the total (Gholz et al. 1991, Spanner et al. 1990). The process model, FOREST-BGC, requires LAI as a key structural variable to calculate transpiration, photosynthesis, and related ecosystem processes (Running 1993). To interpret remotely sensed estimates of LAI adequately, we sought to distinguish the contributions of understory vegetation to the total signal and to confirm that relationships between LAI , light absorption, and widely accepted spectral vegetation indices apply equally well to all components of the canopy. We chose to evaluate structural reflectance properties of two species of shrubs, bitterbrush (*Purshia tridentata*) and greenleaf manzanita (*Arctostaphylos patula*), that play important roles in the functioning of open ponderosa pine (*Pinus ponderosa* Laws.) forests characteristic of one of the sites on the NASA-supported Oregon Transect Ecosystem Research (OTTER) project.

The response of plant canopies to radiation is a function of the intensity of radiation in various spectral regions, and the absorbing and transmitting properties of the vegetation (Gates et al. 1965). Leaves reflect little in the blue and red (R) wavelengths due to absorption by photosynthetic pigments, and reflect strongly in the near-infrared (near-IR) due to intra- and inter-leaf scattering (Curran 1983, Tucker 1979, Knipling 1970). At the canopy level, multiple scattering between layers of vegetation increases near-IR reflectance, and is related to canopy geometry and leaf optical properties (Colwell 1974, Knipling 1970). Vegetation indices which include near-IR and red spectral regions enhance the contrast between soil and vegetation reflectances. Based on these biophysical characteristics, the normalized difference vegetation index (NDVI = NIR-R/NIR+R), simple ratio (SR = NIR/R), and other vegetation indices have been used to estimate properties of the vegetation such as LAI (Gholz et al. 1991, Tucker et al. 1985, Curran 1983).

METHODS

Study Site

A total of six sites were selected over a range of forest types and climatic conditions to estimate net primary productivity (NPP) and other ecosystem characteristics from remote sensing and ground measurements (Runyon et al. 1993). This study was limited to Site 5 near the Metolius River on the dry, east side of the north-central Cascade mountains 15 km west of Sisters, Oregon .

The Metolius site supports an open ponderosa pine forest, which was thinned in 1989 (44° 22' N. Lat., 121° 41' W. Long., elevation 1030 m). It represents two forest communities: *Pinus ponderosa/Purshia tridentata/Festuca idahoensis* and *Pinus ponderosa/Purshia tridentata-Arctostaphylos patula* (Franklin and Dyrness 1973). The first community has an understory that consists of a bitterbrush- (*Purshia tridentata*) dominated shrub layer, over a perennial bunch grass layer of Idaho fescue (*Festuca idahoensis*). The other community has an understory of bitterbrush and greenleaf manzanita (*Arctostaphylos patula*). The characteristics of the two shrub species differ in that manzanita has relatively large (4.5 cm long and 2.5 cm wide), dark green, persistent leaves, which are held erect at the ends of long branches. Bitterbrush, a deciduous shrub, has very small, gray-green leaves, which are arranged in fascicles along the branches.

Digitized aerial photography showed that the understory covered approximately 18 percent of the total area, and represented 46 percent of the total vegetation cover, where scene components consisted of overstory, understory, shade, and soil or litter (Spanner et al. 1993). The pumice soils are considered to be minimally altered. Soils are classed as a dystric cryandept, a light colored andic (high in ash content) incepticol that is low in nutrients (P. Claycomb, Oregon State University, personal communications).

Sampling

Spectral reflectance and f_{IPAR} data were collected on 23 bitterbrush and 27 manzanita plots July 11-30, 1991 (solar zenith angle 34 to 44°), on clear days from 1000 to 1500 Pacific daylight time (PDT). Sampling was conducted near mid-day to minimize shadow effects.

To obtain a range of LAIs and f_{IPAR}, sample plots were created artificially by sticking shrub branches (approximately 35 cm in height) into bare soil. Fresh branches were cut just before data were collected to avoid alteration of spectral reflectance due to drying of leaves. New branches were selected for each plot, which was arranged to mimic the natural canopy architecture. A rectangular frame (16x20 cm in size) was positioned at the top of each canopy, 50 cm from the spectrometer. The frame size was smaller than the average unmanipulated bitterbrush shrub size (35x35 cm). The frame was painted flat black to minimize reflectance of light. It served as a guide for plot size while creating each canopy, and as a scaling factor for estimating LAI (cm^2 foliage/cm^2 ground area). Sampling was conducted in the following sequence: Spectral radiance from the reference panel followed by canopy radiance, measurement of f_{IPAR}, removal of plant material from the plot for transfer to the laboratory, and finally, radiance from the soil on each plot. Each sequence took approximately 10 minutes to complete, which was well within the suggested 20 minute interval for reference panel measurement (Goward, personal communications). The 8-scan average option on the spectrometer was used for all radiance measurements.

A spectrometer (Spectron Engineering SE-590) with a 15° field of view was used to obtain radiance measurements. The SE-590 was mounted on a boom that extended from a tripod, and was positioned at nadir viewing angle directly over the center of the sampling area. The instrument was positioned with a bore site, level, and plumb bob to ensure the field of view was within the sample frame.

When all plant material on each plot was harvested, it was sealed in plastic bags, and put on ice for measurement of LAI at the laboratory that evening. Measurements of LAI and f_{IPAR} were also taken on 14 randomly selected unmanipulated plots of each species to determine a realistic range of these variables.

Three 100 m transects were established to provide understory cover estimates, using the line-intercept method (Deuser and Shugart 1978). Understory species were recorded to the nearest cm as they intercepted the transects. The cover estimates by species were used in calculations of site-level LAI and f_{IPAR}.

PAR Interception

Canopy transmittance of PAR for each plot was measured with a sunfleck ceptometer (Decagon SF-80) in single sensor mode, immediately after SE-590 scans of the plot were taken. The ceptometer measures instantaneous fluxes of PAR (400-700 nm). Under-canopy PAR (Q_t) was sampled on a 4 x 5 grid (20 observations), spaced evenly under the 16 x 20 cm sample frame. Twenty instantaneous readings were averaged per observation. Ten observations of incident PAR (Q_o) were taken immediately afterwards above the canopy. Canopy transmittance was calculated as the ratio (Q_t/Q_o). Transmittance values were logarithm-transformed, then averaged, since transmitted PAR is log normally distributed due to spatial variability of canopies (Lang and Yueqin 1986). The fraction of PAR intercepted by the canopy (f_{IPAR}) was calculated as unity minus the mean transmitted PAR for each plot, assuming reflectance is negligible (Russell et al. 1989).

Leaf Area Index

The LAI for each plot was determined using procedures described by Waring et al. (1982). In the laboratory, fresh weight for the plant material from each plot was obtained (FW_{plot}), then a subsample was selected and weighed (FW_{s1}). Leaves were removed from the subsample and weighed ($FW\ LVS_{s1}$). A subsample of these leaves was taken for surface area determination (LA_{s2}) with a Li-Cor area meter (LI-3300). The leaf samples were oven dried at 70°C for 48 h, and dry weights then obtained ($DW\ LVS_{s1}$ and $DW\ LVS_{s2}$).

Plot LAI (one-sided leaf area projected over ground area) was calculated by:

$$LAI = \frac{FW_{plot}\left(\frac{FW\ LVS_{s1}}{FW_{s1}}\right)\left(\frac{DW\ LVS_{s1}}{FW\ LVS_{s1}}\right)\left(\frac{LA_{s2}}{DW\ LVS_{s2}}\right)}{320\ cm^2} \qquad (1)$$

Light extinction coefficients (k) were calculated from the empirical Beer-Lambert Law (Larcher 1983):

$$k = -\ln(Q_t/Q_o)/LAI \qquad (2)$$

Extinction coefficients indicate the attenuation of light within a canopy for a given LAI, with low *k* values occurring in summer due to maximum light penetration (Jarvis and Leverenz 1983, Larcher 1983, Gholz et al. 1991). They were calculated from nonlinear regressions by the Marquardt method of direct numerical search for least squares estimates (SAS Institute, Inc. 1987). The extinction coefficients were used in the estimation of site-level f_{IPAR} by the understory shrubs. The Beer-Lambert Law was used to calculate f_{IPAR} of understory obscured by trees, and f_{IPAR} of understory in the open (21% and 18% of air photo scene; Spanner et al. 1993). Other data used in the calculations include the site-averaged tree LAI and the assumed *k* for conifers (1.1, 0.50, respectively; Runyon et al. 1993), unmanipulated plot LAI, and the transect percent cover estimates of the shrub species.

Spectral Vegetation Indices

Spectral reflectance values were calculated by dividing the measured spectral radiance from a plot scene by the corresponding spectral radiance from the reference panel (Deering 1989). Several vegetation indices were calculated from spectral reflectance curves, using average blue (B = 469-489 nm), green (G = 550-568 nm), red (R = 660-680 nm), and near infrared (NIR = 780-820 nm) reflectances. The waveband ranges were selected by determining the minimum reflectances for B and R, and maximum reflectance for G and NIR from the first derivative of the canopy reflectance for all plots, +/- 10 nm in the visible bands and +/- 20 nm in the NIR. The NDVI, SR, the normalized difference green-red (NDGR = G-R/G+R), and normalized red index (NRI = R/B+G+R) were calculated to explore their relationships to LAI and f_{IPAR} over the range of these variables.

The color indices NDGR and NRI are not commonly used because they do not include the near infrared band, which provides information on vegetation structure. They were assessed as possible estimators of f_{IPAR} and LAI, to determine if instruments lacking near infrared bands (e.g. color video cameras) might prove useful in future research.

Statistical Analysis

Regression analysis was performed using the vegetation variables LAI and f_{IPAR} as the dependent variables and the spectral indices as the independent variables. This allowed for comparison of the potential ability of different spectral indices to estimate LAI and f_{IPAR}. Nonlinear regressions were perfomed when simple linear models were apparently inadequate or inappropriate. The decision on which spectral index was a better or more useful estimator of a vegetation variable was determined by the selection of the simplest model that explained the most variation in the dependent variable, and appeared to be sensitive over the range of the dependent variable. Slopes and intercepts of linear regressions were compared between species using the Giant Size Regression (GSR) technique, as described by Cunia et al. 1973 and Neter et al. 1990.

RESULTS

Leaf Area Index and Intercepted PAR

Plot LAIs ranged from 1.3 to 9 for manzanita and 0.5 to 10 for bitterbrush. Corresponding f_{IPAR} ranged from 0.38 to 0.94 for manzanita, and 0.20 to 0.95 for bitterbrush. In comparison, LAI's of 14 naturally growing shrubs of each species ranged from 3.1 to 9.5 for manzanita (mean = 5.4, SD = 1.66), and 0.9 to 6.2 for bitterbrush (mean = 3.8, SD = 1.18), and f_{IPAR} ranged from 0.58 to 0.96 for manzanita (mean = 0.83, SD = 0.06), and 0.74 to 0.91 for bitterbrush (mean = 0.84, SD = 0.10). The LAI values may seem higher than one would expect because projected leaf area was calculated for a given shrub over the small ground area of the sample frame (320 cm^2).

The f_{IPAR} increased with LAI, with a functional asymptote at an LAI of 6 for both species (Fig. I.1, $R^2 = 0.71$ for manzanita; $R^2 = 0.85$ for bitterbrush). The asymptote was determined as the point at which the change in predicted f_{IPAR} was less than three percent (Ripple 1985). The regression equations were very similar for the two species with different foliar displays. A comparison of the regression lines for the two species showed there was no evidence that the slopes and intercepts were significantly different from each other ($P = 0.05$). Light extinction coefficients (k) from the Beer-Lambert equation were 0.52 for bitterbrush and 0.46 for manzanita.

Percent cover estimates from the transects for bitterbrush and manzanita were 31% and 1%, respectively. Site-averaged LAIs were 1.2 for bitterbrush, and 0.1 for manzanita. Tree and understory data from this study, Runyon et al., and Spanner et al. (both in this issue) yielded a site-level f_{IPAR} by the understory of 0.16. The combined f_{IPAR} by overstory trees (0.29; Runyon et al.

1993) and understory shrubs suggests that about 45% of the incident radiation was intercepted by vegetation on the site. We estimated understory aboveground net primary production (ANPP) using the Monteith (1977) model of light-use efficiency, further modified to take into account that only about 30% of the total PAR intercepted by the vegetation could be utilized at Site 5 due to constraints on photosynthesis associated with frost, drought, and extreme humidity deficits (Runyon et al. 1993). With an annual incident PAR of 2385 MJ m^{-2} recorded at a meteorological station, the overstory trees intercepted 690 MJ m^{-2} while the understory vegetation intercepted about 380 MJ m^{-2}, and utilized about 115 MJ m^{-2} of intercepted radiation annually. The light-use efficiency values of ANPP under environmental constraints across the Oregon transect averaged about 1.0 g of dry matter production per MJ (Runyon et al. 1993). Our estimate of understory ANPP, assuming the same conversion factor, averaged 115 g m^{-2} yr^{-1}.

Spectral Vegetation Indices and Vegetation Variables

There appeared to be no real differences in soil spectra across the site. The coefficient of variation in the red and near infrared reflectances ranged from 5 to 7 percent for all of the soil reflectance scans, and 2 to 4 percent for NDVI calculated from these reflectances. Regressions of LAI and f_{IPAR} on the spectral indices were performed with and without the plot soil data point, which was calculated from the average soil spectra. Results from regressions with the soil data point are reported. The R^2 values for regressions without the soil data point were typically 0.01 to 0.16 lower than for regressions with the soil data point. One exception was the relationship of f_{IPAR} to NRI, where the R^2 was 0.28 lower than the regression with the soil data point.

The f_{IPAR} was linearly related to NDVI (Fig. I.2, $R^2 = 0.86$, and 0.83 for manzanita and bitterbrush), and curvilinearly related to SR (Table I.1, $R^2 = 0.84$ manzanita, and 0.77 bitterbrush). The f_{IPAR} was linearly related to the color indices NDGR ($R^2 = 0.76$ manzanita, and 0.67 bitterbrush), and NRI ($R^2 = 0.77$ manzanita, and 0.53 bitterbrush) (Table I.1). For the relationship between f_{IPAR} and NDVI, there was no evidence that the slopes and intercepts of the regression lines of the two species were sufficiently different from each other ($P = 0.05$).

Linear regressions showed that SR was a better estimator of LAI (Fig. I.3, $R^2 = 0.86$ manzanita, and 0.74 bitterbrush) than NDVI ($R^2 = 0.61$, and 0.55), NDGR ($R^2 = 0.74$, and 0.55), and NRI ($R^2 = 0.72$ and 0.41). Nonlinear regressions of LAI on NDVI, NDGR, and NRI showed improvement of model fit to the data for NDVI ($R^2 = 0.87$ manzanita, and 0.76 bitterbrush), slight improvement for NDGR ($R^2 = 0.74$ manzanita, and 0.61 bitterbrush), and no real improvement for NRI ($R^2 = 0.74$ manzanita, and 0.42 bitterbrush) over the linear regressions (Table I.2). Comparison of regression lines of the two species for the relationship between LAI and SR showed that the slopes were not significantly different, but there was evidence that the lines did not have a common intercept ($P = 0.05$).

DISCUSSION

The relationship between f_{IPAR} and LAI has been shown to be asymptotic at an LAI of 4 to 6 in previous studies on other vegetation types, such as agricultural crops and conifers (Choudhury 1987, Norman and Jarvis 1975, Pierce and Running 1988). For example, Asrar et al. (1984) found that PAR absorption by winter wheat increased rapidly with an increase in LAI and leveled off above LAI 6.0. Results of this study, where f_{IPAR} was asymptotic at an LAI of 6 for both shrub species, appear to support these previous findings in spite of differences in canopy architectures.

The highly reflective soils in this study did not contribute much to variability in spectral vegetation indices (c.v. of soil spectra were 5 and 7% in red and near-IR). Minimally altered soils, like the pumice-derived soils in this study, have higher reflectances in the red (650 - 690 nm) and near-infrared bands (above 740 nm), and less variation than other soils with substantial organic content. However, a fair amount of statistical variability in vegetation indices such as the SR and NDVI can be expected as a result of variation where background soil reflectances change across landscapes (Huete et al. 1985, Hall et al. 1990). Asrar et al. (1984) found a good, linear relationship between NDVI and f_{IPAR} for spring wheat grown in a loamy, calcareous soil. They indicated that some of the scatter in data points could have been be due to soil moisture variation. Choudhury (1987) suggested that curvilinearity in the relationship between NDVI and f_{IPAR} decreases, and the curvilinearity between SR and f_{IPAR} increases as the magnitude of soil reflectance increases. The soil background did not alter the linearity of the relationship between NDVI and f_{IPAR} at our site, however, this may not be the case at other locations where reflectance properties of background material are more variable (Huete 1989, Huete et al. 1985).

Our relationship between the SR and LAI was linear, in contrast to the asymptotic relationships reported at higher LAI with several airborne sensors flown across the OTTER sites (Spanner et al. 1993), and by previously studies (Peterson et al. 1987, Spanner et al. 1990, Herwitz et al. 1989). When our instrument was flown on an ultralight aircraft at 100 m AGL, however, a similar linear relationship was reported by R. McCreight (Spanner et al. 1993). As the distance between sensor and target increases, the effect of the atmosphere on scattering visible light could certainly contribute to some loss in sensitivity (Spanner et al. 1993). In any case, those situations where understory vegetation plays a major role are not likely to exhibit extremely high values of LAI.

Asrar et al. (1984) examined the relationship between vegetation indices and f_{IPAR}, and found SR to be sensitive to canopy geometry and solar zenith angle, particularly at solar zenith angles between 40° and 60°. On the other hand, NDVI is relatively insensitive to solar zenith angle up to 60° (Asrar et al. 1984, Shibayama et al. 1986). Other bi-directional reflectance studies suggest that only when the solar zenith angle is greater than 55°-60°, will a large bi-directional reflectance (BRDF) effect on canopy reflectance be observed (Kimes et al. 1980). All of our data were collected when solar zenith angles were between 34° to 44°, so the relationships with SR, and certainly with NDVI, are not likely to need corrections.

The OTTER project made use of our ground surveys to account for the contribution of understory vegetation to satellite estimates of LAI and f_{IPAR} (Goward et al., in review). The linear relationship derived between the AVHRR sensor NDVI and f_{IPAR} measured beneath tree canopies across the Oregon

Transect did not apply well to site 5. Our estimate of total f_{IPAR} at this site, including understory and overstory, was 0.45. This value comes much closer to the predicted value derived from the other sites where understory vegetation plays a lesser role.

Our estimate of understory ANPP (115 g m^{-2} y^{-1}) combined with measured overstory ponderosa pine ANPP at Site 5 (150 g m^{-2} y^{-1}; Runyon et al. 1993) yields a total of 265 g m^{-2} y^{-1}. The understory vegetation thus contributed more than 40% of the total ANPP at the site. The total estimated ANPP of 265 g m^{-2} y^{-1} compares closely with the 220 g m^{-2} y^{-1} of ANPP reported by Gholz (1982) for a nearby closed-canopy stand of ponderosa pine, which had a less developed understory not accounted for in the ANPP estimate.

The examination of spectral vegetation indices and various properties of specific kinds of vegetation improve our understanding of basic relationships, and increases the reliability of remotely sensed interpretation of vegetation types and broad landscape patterns. We recognize that soil background conditions, both the color and wetness, affect interpretation of NDVI as well (Huete and Jackson 1988). In this study we minimized the influence of atmosphere, solar zenith angle, and soil variation to characterize relationships with the vegetation alone. In a companion paper, Goward et al. (in review) provide a full range of reflectance spectra for all of the major components of overstory and understory vegetation, soils, litter, and bark found at each of the six OTTER study sites. Such full-site analyses are required to interpret remotely sensed data across a broad range of vegetation and environmental conditions like the Oregon Transect.

As more advanced sensors become available, data with high-spectral and spatial resolution can provide the ecological community more insights into area occupied by specific kinds of vegetation and other site features. For example, the two imaging spectrometers, CASI and AVIRIS, described in Spanner et al. (1993), are capable of discerning much more detail than any present satellite sensor. For many purposes, computer analysis of video coverage from a light aircraft will serve ecologists interested in estimating the contribution of various components in selected scenes. To translate cover estimates into LAI or f_{IPAR}, however, requires knowledge of relationships such as those specified on the two shrub species reported in this study.

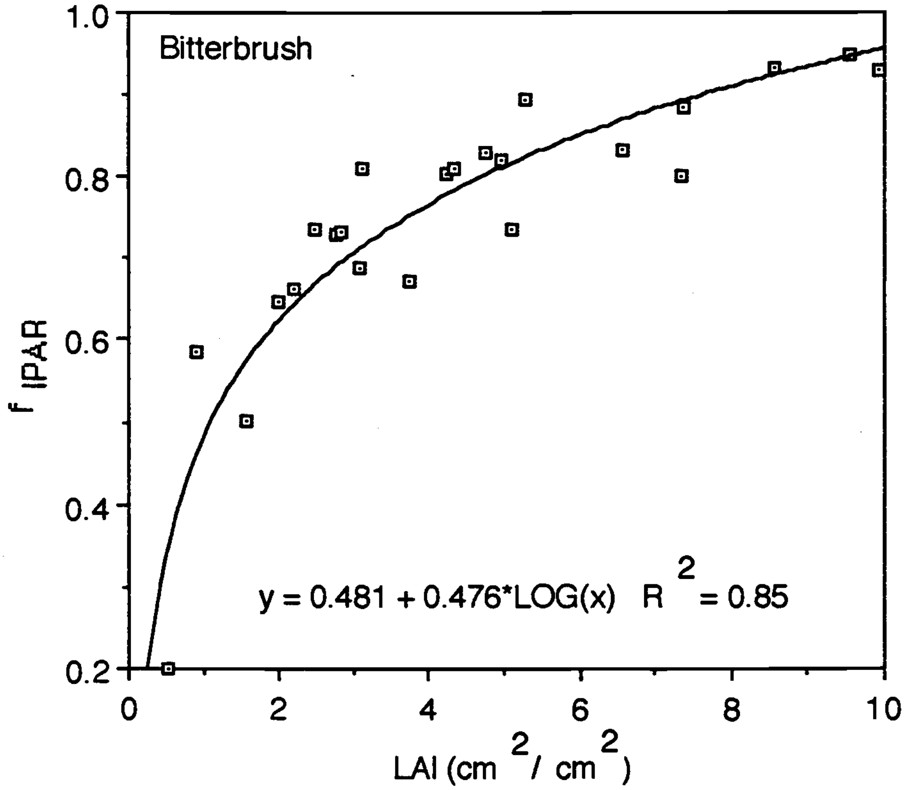

Fig. I.1. Relationship between leaf area index and fraction of photosynthetically active radiation intercepted by constructed canopies of bitterbrush and manzanita.

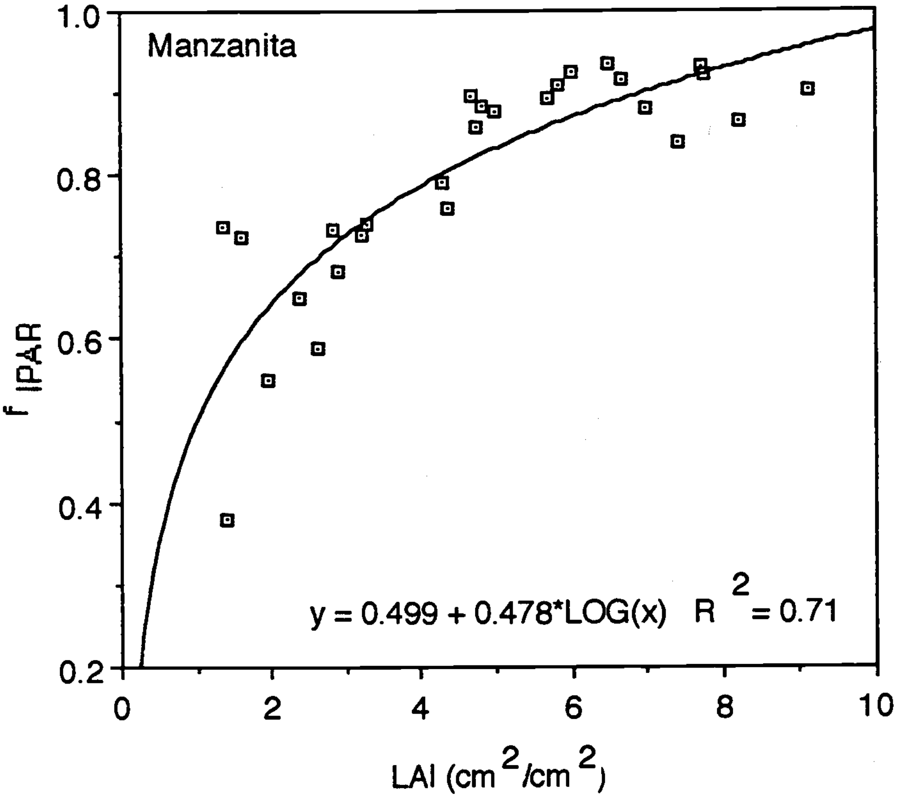

Fig. I.1, Continued.

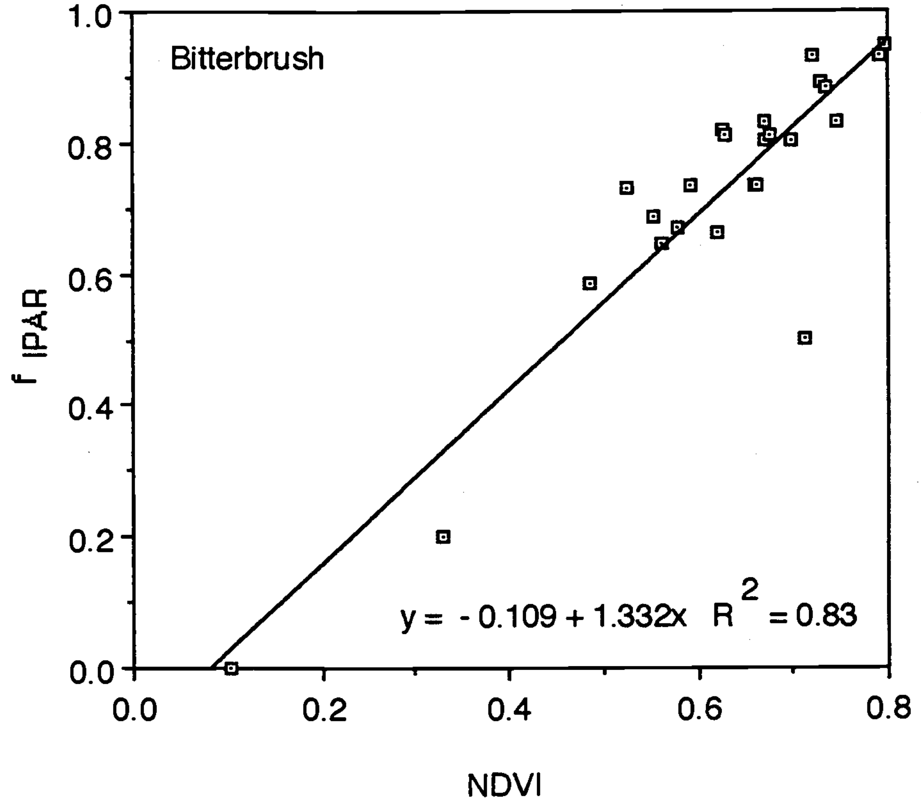

Fig. I.2. Relationship between normalized difference vegetation index and fractio of photosynthetically active radiation intercepted by constructed canopies of bitterbrush and manzanita. The normalized difference vegetation index (NDVI) was recorded by a spectrometer in the field.

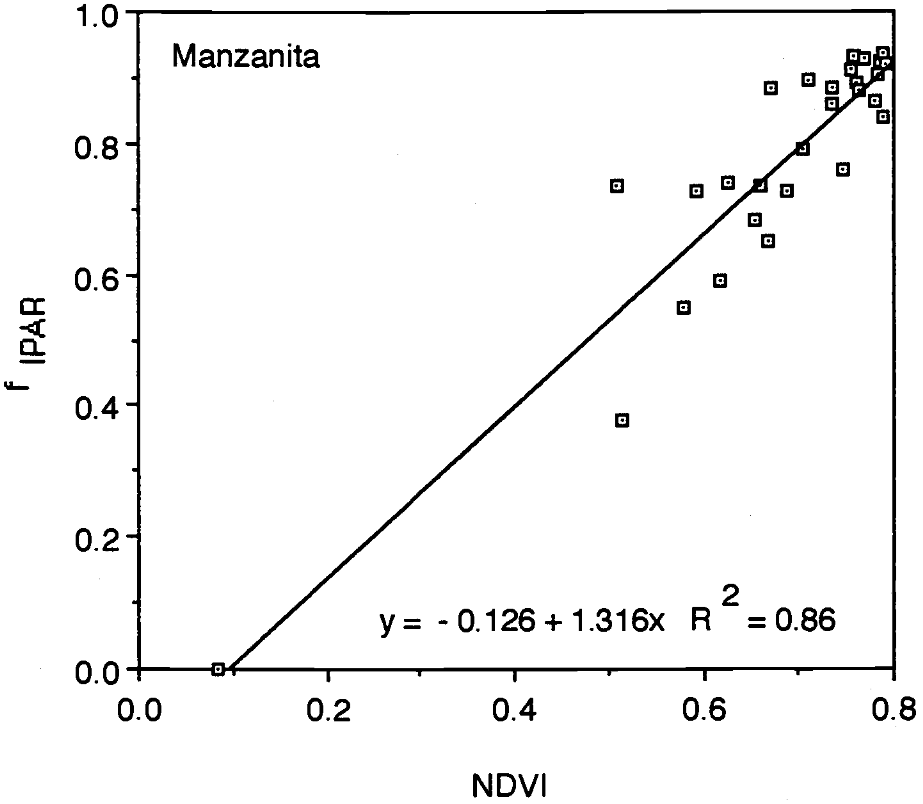

Fig. I.2, Continued.

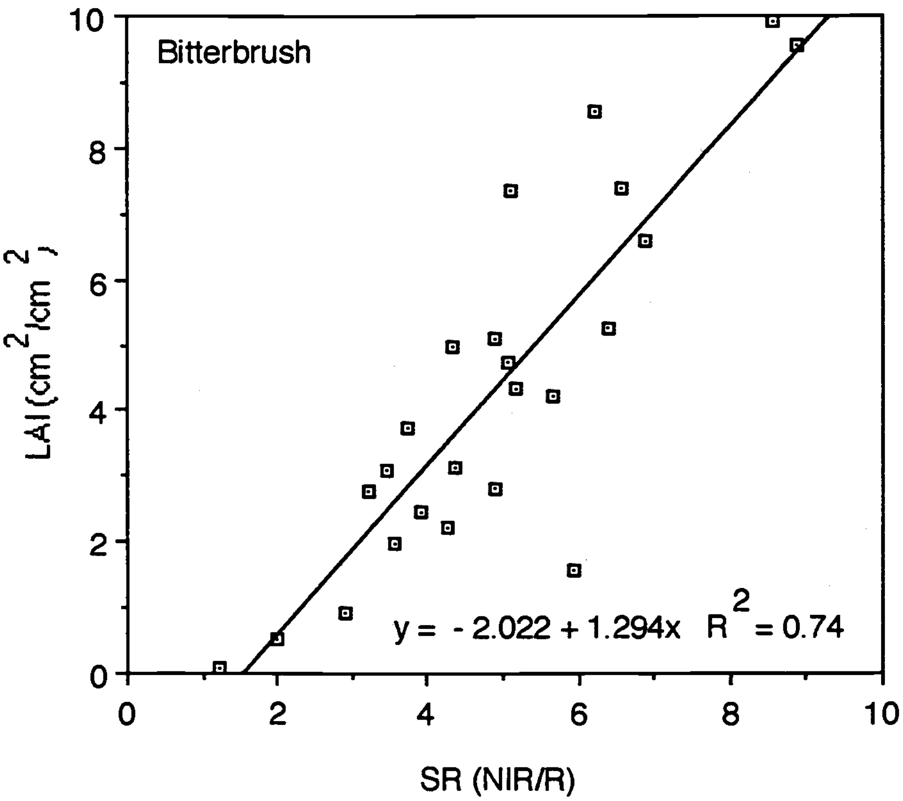

Fig. I.3. Relationship between the simple ratio vegetation index and leaf area index of bitterbrush and manzanita.

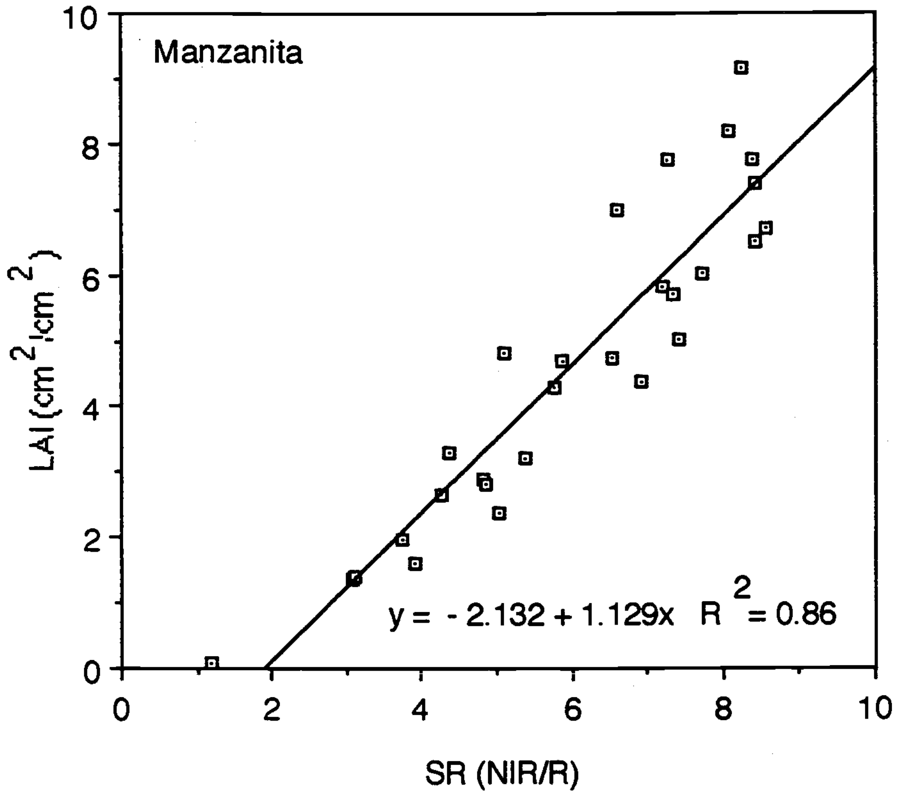

Fig. I.3, Continued.

Table I.1. Regression equations for fraction intercepted photosynthetically active radiation in relation to spectral vegetation indices.

Dependent variable: f_{IPAR}

	Model	MSE	R^2
Independent variable:			
Normalized Difference Vegetation Index (NIR-R/NIR+R):			
manzanita	$y = -0.126 + 1.316x$	0.006	0.86
bitterbrush	$y = -0.109 + 1.332x$	0.009	0.83
Simple Ratio (NIR/R):			
manzanita	$y = 3.229e-2 + 0.987LOG(x)$	0.007	0.84
bitterbrush	$y = 5.037e-2 + 1.018LOG(x)$	0.012	0.77
Normalized Difference Green-Red (G-R/G+R):			
manzanita	$y = 0.479 + 1.715x$	0.010	0.76
bitterbrush	$y = 0.508 + 2.055x$	0.018	0.67
Normalized Red Index (R/(B+G+R)):			
manzanita	$y = 2.199 - 4.387x$	0.010	0.77
bitterbrush	$y = 2.258 - 4.432x$	0.024	0.53

Table I.2. Regression equations for leaf area index in relation to spectral vegetation indices. Nonlinear regressions are of the form: $y = e^{(a+bx)}+e$.

Dependent variable: LAI

	Model	MSE	R^2
Independent variable:			
Simple Ratio (NIR/R):			
manzanita	$y = -2.132 + 1.129x$	0.006	0.86
bitterbrush	$y = -2.022 + 1.294x$	2.039	0.74
Normalized Difference Vegetation Index (NIR-R/NIR+R):			
manzanita	$y = e^{(-3.153 + 6.553x)}$	0.804	0.87
bitterbrush	$y = e^{(-2.397 + 5.825x)}$	2.055	0.76
Normalized Difference Green-Red (G-R/G+R):			
manzanita	$y = e^{(0.592 + 5.000x)}$	1.544	0.74
bitterbrush	$y = e^{(0.617 + 6.885x)}$	3.078	0.61
Normalized Red Index (R/(B+G+R)):			
manzanita	$y = e^{(5.676 - 13.015x)}$	1.583	0.74
bitterbrush	$y = e^{(5.741 - 12.536x)}$	4.650	0.42

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Chapter II

COMBINING REMOTE SENSING AND CLIMATIC DATA TO ESTIMATE NET PRIMARY PRODUCTION ACROSS WESTERN OREGON

ABSTRACT

A range in productivity and climate exists along a west-east transect in Oregon. Remote sensing and climatic data acquired during the Oregon Transect Ecosystem Research Project (OTTER) were combined with data from additional field studies at several of the OTTER forested sites and neighboring shrub sites to evaluate the degree to which climate constrains the ability of vegetation to utilize intercepted photosynthetically active radiation (IPAR). Study objectives were to determine the relationship between remotely sensed NDVI and %IPAR, and to evaluate the relationship between above-ground net primary production (ANPP) and IPAR through a simple empirical energy-use efficiency model. The %IPAR was linearly related to Thematic Mapper Simulator (TMS) normalized difference vegetation index (NDVI) ($R^2 = 0.97$). Vegetation intercepted from 24.8% to 99.9% of incident PAR, and ANPP ranged from 53 g m^{-2} y^{-1} to 1310 g m^{-2} y^{-1}. Constraints on the ability of each species to use intercepted light, as defined by differential responses to freezing temperatures, drought, and vapor pressure deficit, were quantified from hourly meteorological station measurements near the sites, and field physiological measurements. Vegetation could utilize from 30% of intercepted radiation at the eastside semi-arid juniper woodland and shrub sites to 97% at the maritime coastal sites. The environmental limits to light capture by photosynthesis, however, did not explain the full variation observed in ANPP, and suggested that shrubs allocate a greater proportion of photosynthate below-ground than trees.

INTRODUCTION

Ecological changes are occurring at regional to global scales, and consequently, we need to address ecological questions at these scales. A number of researchers are developing models to estimate rates of important ecosystem functions, but some of the models require specific measurements not easily attainable over extensive regions (Agren et al. 1991). Alternatively, other models are being designed to evaluate regional to global scale patterns of key ecosystem characteristics, such as production, through the use of remotely sensed information (Running 1993).

Net primary production (NPP) is the basic energy source for growth and maintenance processes upon which higher plants depend. Net primary production has been linked to climatic patterns by approaches ranging from simple correlations to sophisticated simulation models (Holdridge 1947, Agren et al. 1991, Raich et al. 1991). An approach that has been pursued by some investigators on the Oregon Transect Ecosystem Research Project (OTTER) involves the combination of remotely sensed observations of vegetation and climatic variables, and a constrained energy-conversion efficiency model (Goward et al. 1993, Runyon et al. 1993). The study reported here focused on that approach by applying it to forest overstory and understory shrub and herb vegetation, and treeless areas occupied by shrub vegetation near some of the OTTER sites.

There is experimental evidence and theoretical support that the percent of incident photosynthetically active radiation intercepted by vegetation (%IPAR), and potentially used for photosynthesis, is a monotonic and near-linear function of normalized difference vegetation index (NDVI) calculated from reflectance in the near infrared (NIR) and red portion of the electromagnetic spectrum (Choudhury 1987, Asrar et al. 1993). Although NDVI relates well to %IPAR, it often does not capture dynamic physiological processes which occur on fine temporal scales. Many species under seasonal stress (e.g. drought, vapor pressure deficit) are subject to midday photosynthetic depressions, which may not be accompanied by changes in canopy architecture, and thus NDVI (Tenhunen et al. 1987, Gamon et al. 1992). However, NDVI could be used to estimate %IPAR. Incident PAR can be estimated from meteorological stations, or from long-wave ultraviolet measurements by the Total Ozone Mapping Spectrometer (TOMS) sensor (Eck and Dye 1991, Goward et al. 1993). The %IPAR and incident PAR can be combined to estimate annual intercepted photosynthetically active radiation (IPAR).

The amount of light intercepted by vegetation is a major determinant of production (Monteith 1981). Studies have shown that net primary production is linearly related to annual IPAR (MJ m^{-2} y^{-1}) under ideal conditions. An empirical model developed by Monteith (1977) and others is:

$$NPP = IPAR^{*}\varepsilon \qquad (1)$$

where ε is energy-conversion efficiency of 1 to 2 g of above- plus below-ground dry matter produced per MJ of energy absorbed (Monteith 1977). However, ε may vary when environmental conditions are less than favorable for growth. A more explicit formulation has been proposed (Runyon et al. 1993, Landsberg 1986) which separates environmental from biochemical components subsumed in the ε coefficient in equation (1):

$$NPP = [IPAR^{*}f(T)^{*}f(D)^{*}f(V)]^{*}\varepsilon_u \qquad (2)$$

where the environmental limits to production are freezing temperatures (T), drought (D), and vapor pressure deficit (V). This may result in a constant coefficient, defined as energy-use efficiency (ε_u), for natural perennial vegetation (although C_4 plants would likely have a different ε_u) and allow a broad application of the model to a wide variety of conditions and vegetation types (Landsberg 1986).

In a study that was part of the OTTER project, Runyon et al. (1993) showed that ε for above-ground NPP (ANPP) by trees varied from 0.18 to 0.92 g MJ^{-1}, with no general relationship between ANPP and IPAR across a range of forest types and climatic conditions. They assumed that some sites were subject to substantial environmental constraints on photosynthesis, and applied the environmental limitations in equation (2) to estimate the extent to which trees utilized IPAR. This approach was based on the assumption that when stomata partially or completely close in response to freezing temperatures, soil drought, and high vapor pressure deficits, photosynthesis is greatly limited or stops (Downton et al. 1988, Schulze and Hall 1982). They applied general stomatal conductance thresholds determined from previous studies on several conifer species. This improved (linearized) the relationship between ANPP and IPAR, and resulted in a generally consistent energy-use efficiency (ε_u), averaging 0.8 g MJ^{-1} for ANPP, and 1.3 g MJ^{-1} for total NPP. The ability to estimate ANPP or NPP from IPAR has the potential to be applied to large spatial scales through remote sensing estimates of IPAR.

The objectives of the study reported here were to (1) evaluate whether remotely sensed observations of canopy reflectance at these sites might be used to estimate the percent of incident PAR intercepted by both tree and shrub forms of vegetation, (2) evaluate the relationship between ANPP and IPAR for 3 of the 6 OTTER sites, and 3 neighboring shrub sites, (3) determine if the general environmental thresholds applied by Runyon et al. in equation (2) improve the relationship between ANPP and IPAR, and if not, (4) determine if species-specific environmental thresholds derived from field measurements of stomatal conductance, vapor pressure deficit, and predawn xylem water potential improve the relationship. A linear relationship between ANPP and IPAR would indicate a generally consistent energy-use efficiency coefficient across vegetation types. If so, estimates of the environmental constraints on production could be combined with remotely sensed estimates of annual IPAR in equation (2) to estimate above-ground net primary production.

METHODS

Study Sites

This study was conducted at three of the Oregon Transect Ecosystem Research (OTTER) project sites (Fig. II.1). The Oregon transect consists of six sites in a range of forest types and climatic conditions from coastal alder (*Alnus rubra* Bong.) and interior-valley Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), to ponderosa pine (*Pinus ponderosa* Laws.) and juniper woodlands (*Juniperus occidentalis* Hook.) on the east side of the north-central Cascade mountains. The sites are located along a 250 km west to east transect at approximately 44° north latitude. The OTTER project was designed to develop approaches to extrapolate point measurements and estimates of ecosystem structure and function to large geographic areas (Peterson and Waring 1993). The present study is one of several continuation studies conducted at the OTTER sites.

Some of the OTTER sites have open areas of shrub vegetation within or near the sites. To test the model in equation (2) on other vegetation types in addition to forests, I selected three shrub areas at least 50 by 50 m in size, near each of the three forested OTTER sites. The Cascade Head forested site (site 1) consists of alder (*Alnus rubra*), a deciduous tree, salmonberry (*Rubus spectabilis* Pursh), a deciduous clonal shrub, and swordfern (*Polystichum munitum* (Kaulf.) Presl), an evergreen perennial herb. In an adjacent area (site 1-O), clearcut 15 years ago, 2 to 2.5 m tall salmonberry (*R. spectabilis*) now dominate. The *A. rubra/R. spectabilis* community is consistently associated with *P. munitum*, and often pioneers on logged or burned lands in the Sitka spruce (*Picea sitchensis*) Zone in the Coast Ranges of Oregon (Franklin and Dyrness 1973).

The Corvallis forested site (site 2) contains Douglas-fir (*Pseudotsuga menziesii*), Himalaya blackberry (*Rubus procerus* Muell.), and swordfern. The accompanying shrub site (site 2-O) has dense, 2 to 2.5 m tall Himalaya blackberry (*R. procerus*). Coniferous stands in the Willamette valley are composed primarily of Douglas-fir (*P. menziesii*). Site 2 is similar to the *Pseudotsuga menziesii /Corylus cornuta californica/Bromus vulgaris* community type identified in the Willamette valley, though *C. cornuta* is less than 5% cover, *B. vulgaris* is absent, and *R. procerus* dominates the forest floor (92% cover) (Franklin and Dyrness 1973). Himalaya blackberry is an introduced clonal shrub species, now well established in western Oregon (Gilkey and Dennis 1980).

The Sisters site (site 6) is a juniper woodland (*Juniperus occidentalis*), with sagebrush (*Artemisia tridentata* Nutt.) and green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.). The companion shrub site (site 6-O) has sagebrush (*A. tridentata*) and green rabbitbrush (*C. viscidiflorus*). The shrub *A. tridentata* is semi-deciduous, maintaining 30-50% of its foliage through the winter, and *C. viscidiflorus* is a deciduous shrub. Both of the Sisters sites have relatively dispersed vegetation cover.

The OTTER Metolius site (site 5), included in limited analyses, was divided into ponderosa pine forest (*Pinus ponderosa*), with bitterbrush (*Purshia tridentata* (Pursh) DC.), a deciduous shrub, and an adjacent open area of bitterbrush (site 5-O). The *P. ponderosa* forest is very open, with 31% cover of *P. tridentata* (Law and Waring 1993).

The Cascade Head site is characterized by a cool, moist maritime climate most of the year. The Corvallis site is in the interior valley between two mountain ranges, and is subject to dry summers, and relatively cooler winters. The Metolius and Sisters sites are on the east side of the Cascade mountains, more continental, and subject to hot, dry summers and cold winters. Table II.1 summarizes the study sites and species sampled at each site.

Remote Sensing Measurements

Remotely sensed data were acquired from a Daedalus Thematic Mapper Simulator flown on a NASA ER-2 aircraft in support of the OTTER project in 1990. The sensor was flown at an altitude of approximately 20 km mean-sea-level on June 25, 1990 between 1100 and 1400 local solar time. The TMS data were converted to radiance in Thematic Mapper equivalent channels, then atmospherically corrected to surface radiance by NASA Ames Research Center (Spanner et al. 1993, NASA Ames 1990, Wrigley et al. 1992). Sunphotometer measurements of aerosol optical depth were made at the site within two hours of overflight, and used for the atmospheric correction. Surface reflectance was calculated from the atmospherically corrected radiances divided by incident solar irradiance for each band.

Sites were located on the imagery from air photos and intimate knowledge of ground features. Sites on the imagery ranged in size from a minimum of 2 by 2 pixels (50 by 50 m) for the Corvallis shrub site of *R. procerus*, 3 by 3 pixels (75 by 75 m) for shrub sites 1-O and 6-O, 5 by 5 pixels (125 by 125 m) for forested sites 1 and 2, to 10 by 10 pixels (250 by 250 m) for the juniper woodland (site 6). Imagery for the OTTER Metolius site (site 5) was included in this portion of the study. The site 5 forested and shrub areas selected were approximately 3 by 3 pixels (75 by 75 m) in size. The normalized difference vegetation index (NDVI = (NIR-R)/(NIR+R)) was calculated from

TMS NIR (760-900 nm) and red (630-690 nm) channels for each pixel at a site, then averaged. The relationship between site-averaged July NDVI and percent photosynthetically active radiation intercepted by vegetation was evaluated.

Climatic Measurements

Meteorological stations (Campbell Scientific Instruments, Inc., Logan Utah) were placed in open areas near each site during the NASA funded OTTER project in 1990 (Runyon et al. 1993). The Cascade Head and Corvallis stations were within 5 km of the sites. The OTTER Metolius site (site 5) station provided climate data for the Sisters site (site 6), approximately 20 km distant, and was supplemented with precipitation data from a weather station at Redmond, Oregon (Runyon et al. 1993). Each meteorological station measured incident solar radiation (400-1200 nm), air temperature, precipitation, and relative humidity by minute and integrated hourly values that were recorded on an internal data logger.

Though field data on vegetation were collected in 1992, the meteorological stations were operational from only July to December 1992, so I chose to use the complete data set from 1990 with the assumption (later tested) that the climate for the two years was similar. Relative humidity and air temperature data allowed calculation of hourly vapor pressure deficit (Monteith and Unsworth 1990, Murray 1967). Incident PAR was estimated as 50% of incident solar radiation (Monteith and Unsworth 1990, Rao 1984). Hourly, daily, and annual sums of incident PAR were calculated to determine intercepted PAR and to quantify the environmental limits to production in equation (2).

Intercepted Photosynthetically Active Radiation (IPAR)

Percent intercepted PAR (%IPAR) was estimated at each site by measuring canopy transmittance of photosynthetically active radiation (PAR = 400 to 700 nm) with a sunfleck ceptometer (SF-80, Decagon Devices, Inc., Pullman, WA). Measurements were made on cloudless days during July 1992 between 1200 and 1400 local solar time. Sampling was conducted on a systematic grid, with 50 to 200 sampling grid points at a site, depending on homogeneity of canopy cover. Canopy transmittance (Q_t/Q_o) was calculated by dividing the below-canopy PAR (Q_t) by average incident PAR (Q_o). Transmittance values were logarithm-transformed to adjust for log normal distribution due to spatial variability of canopies (Lang and Yueqin 1986). The %IPAR was calculated from:

$$\%IPAR = (1 - Q_t/Q_o)*100 \qquad (3)$$

This calculation provides a reasonable estimate of radiation absorbed by the canopy, although it assumes PAR reflectance is negligible (Asrar et al. 1989, Russell et al. 1989).

The %IPAR by understory at the forested sites was estimated by applying the %IPAR from above and below understory canopy measurements to the percent of incident PAR transmitted by the overstory canopy. The amount of radiation intercepted by vegetation through the year was calculated from %IPAR and annual integrated incident PAR measured hourly at the meteorological stations near each site (Table II.2).

I assumed that %IPAR was constant through the year. It is important to note that this approach probably underestimates understory IPAR at the forested sites, because of the complex light regime of gaps and sunflecks as sun angle changes through the day and season (Smith et al. 1989). For coniferous species, reduced LAI (approximately 30%) during the dormant season will have minimal effect on annual IPAR (Runyon et al. 1993, Spanner et al. 1993). For deciduous species, the leaf-off and transition periods were noted in the field. I assumed that no PAR was intercepted during leaf-off, and 50% of the maximum IPAR estimate was intercepted during leaf transition periods. Some species maintained 30 to 50% of their foliage through the winter (*Artemisia tridentata, Rubus procerus, Polystichum munitum*), so I adjusted the percent of maximum IPAR for each species accordingly.

The relationship between above-ground net primary production and annual leaf-on IPAR across sites was evaluated.

Physiological Measurements

Stomata respond to radiation, air temperature, vapor pressure deficit (VPD), and soil water supply (Jarvis and Leverenz 1983, Jones 1983, Cowan 1977). When stomatal closure is complete, no photosynthesis is possible. Response to freezing temperatures is well documented, so I chose not to measure this variable. In higher plants, CO_2 uptake is blocked as soon as the CO_2 assimilation organs begin to freeze (Berry and Bjorkman 1980). In most vascular plants, this occurs at temperatures between -1 to -3°C, though leaves of evergreen conifers don't freeze until temperatures of -3 to -5°C, and sclerophyllous trees and shrubs of dry regions have a -1 to -5°C low temperature limit for CO2 uptake (Larcher 1983). Photosynthesis may be at or near zero for several hours after temperature rises above freezing levels (Larcher 1983, Jones 1983, Kaufmann 1982). In applying freezing temperature constraints to the ability to use intercepted light, I assumed that stomata close at -2°C for all species for the following 24 h, and subtracted IPAR for that period from the total annual IPAR.

Physiological measurements were made in May through early October 1992. To evaluate plant response to drought, I measured predawn xylem water potential, followed by stomatal conductance later that morning. Predawn xylem water potential ($\Psi_{predawn}$) indicates the availability of soil water (Kramer 1983). Plant species may differ in the ability to continue to extract soil water by extending root growth and by maintaining slightly open stomata (Schulze 1986, DeLucia and Schlesinger 1991), so I compared $\Psi_{predawn}$ and stomatal conductance on a selection of major tree, shrub, and herb species present at the study sites.

Xylem water potential was measured with a pressure chamber before sun-rise (0400 to 0530 PDT) on twigs from 5 to 10 plants of each species listed in Table 11.1 (Scholander et al. 1965). The number of samples was adjusted to maintain a standard error of approximately 0.05 MPa. Measurements were made at monthly intervals (bi-weekly in July) at the same locations, but not on the same individual plants within sites. Mean $\Psi_{predawn}$ was calculated for each species on a sampling day, and plotted against maximum stomatal conductance observed that day.

Stomatal conductance was measured with a steady state porometer (Li-Cor, model LI-1600). The porometer measures the rate of diffusive water loss from plant leaves. Ten to 15 plants of each species were sampled in the same area and on the same day as the $\Psi_{predawn}$ measurements, and on additional dates for the evaluation of VPD influence on conductance. Stomatal conductance was measured between 0800 and 1200 Pacific Standard Time (PDT) when maximum diurnal stomatal conductance typically occurs (Running

1980, DeLucia and Schlesinger 1991). Sun-lit intact foliage was sampled at ambient environmental conditions on clear days.

To minimize error from porometry, sampling was conducted when leaf temperature was at least 10°C, and dew had evaporated. Measurements were completed within 60 s to avoid altering leaf surface humidity (McDermitt 1990). For species with more than one leaf cohort (*Pseudotsuga menziesii, Juniperus occidentalis*), measurements were made on foliage that had emerged the previous summer, then on current year foliage once it had fully expanded, because maximum conductance is affected by leaf age and does not reach a peak value until some time after leaf emergence (Jones 1983).

Stomatal conductance was calculated on a projected leaf area basis (Farquhar and von Caemmerer 1982). Projected leaf area (one-sided) was determined with a surface area meter (Li-Cor, model LI-1300, Lincoln, Nebraska) on the day of sampling.

Humidity was measured near the plant canopies that stomatal conductance was measured on, at least every 30 minutes, to estimate stomatal response to vapor pressure deficit. A wet- and dry-bulb Assman psychrometer was used to acquire temperatures for calculation of humidity and VPD (Monteith and Unsworth 1990, Murray 1967, USDC Weather Bureau 1953).

I plotted stomatal conductance against VPD, and against mean Ψ_{predawn} for each species. Boundary-line analysis was used to determine maximum stomatal conductance for a given VPD or Ψ_{predawn}. Boundary-line analysis allows pooling of data from many measurement periods and environmental conditions to identify general patterns of response (Jones 1983, Pezeshki and Hinckley 1982). It approximates the response to VPD or Ψ_{predawn} when other factors are not limiting. Limiting values of VPD and Ψ_{predawn} for 50% reduced stomatal aperture and complete stomatal closure were determined from the boundary-line analysis. Complete stomatal closure was approximated as the point where the boundary line reached a minimum stomatal conductance. The conductance observed beyond stomatal closure is assumed to be cuticular diffusion, which can vary among species (Running 1973).

The monthly $\Psi_{predawn}$ values for a species were interpolated to estimate daily $\Psi_{predawn}$. For periods when $\Psi_{predawn}$ values were below the closure threshold, I assumed that stomata remain closed for 24 h, and subtracted IPAR for that period from the total annual IPAR. For periods when $\Psi_{predawn}$ was at intermediate values corresponding to approximately half stomatal closure, IPAR was reduced by 50%.

After sequentially accounting for leaf off, freezing temperatures, and drought, I applied constraints on stomatal conductance associated with VPD thresholds at hourly intervals, and reduced IPAR by 50% or 100% for partial or complete stomatal closure. This allowed for interaction between intermediate levels of stomatal closure due to drought, and intermediate levels due to VPD.

The calculation of annual IPAR and sequential reductions in IPAR over the year were accomplished with a SAS program I wrote for application to hourly meteorological station data (SAS Institute, Inc. 1987). I repeated the program run, changing only the $\Psi_{predawn}$ and VPD constraints from the general thresholds applied by Runyon et al. (1993) in their study to the species-specific thresholds (Table II.3). The general thresholds to temperature, $\Psi_{predawn}$, and VPD were based on previous studies on several tree species.

For the forested sites, understory and overstory modified IPAR estimates were summed, with the assumption that microclimate of the understory was similar to surrounding open areas. This was a fair assumption since site 1 is bound by the ocean and a road, site 2 is on a slope adjacent to an urban area, measurements were made within 100m from an edge, and both sites are small enough for the understory environments to be coupled to the atmosphere due to strong edge influences (Franklin et al. 1993, Black and Kelliher 1989). The Metolius and Sisters forested sites have very dispersed canopies, thus the understory environments at these sites are probably closely coupled with the atmosphere.

The modified IPAR estimates using species-specific thresholds were compared to estimates from general thresholds by evaluating the relationship between site-level above-ground NPP and the modified IPAR that resulted from each method.

To determine if there was a relatively constant ε_u for most of the sites or separate relationships for forested versus shrub sites, I included sites 5 and 5-O in the analysis of the relationship between ANPP and species-specific modified IPAR. The IPAR and ANPP values for *P. ponderosa* were obtained from the Runyon et al. (1993) study, and the values for *P. tridentata* were calculated from Law and Waring data (1993). The threshold values from *C. viscidflorus* were used for *P. tridentata*, since they are both deciduous shrubs growing in a similar habitat. The general thresholds from Runyon et al. (1993) were applied to their $\Psi_{predawn}$ seasonal data, because *P. ponderosa* was one of the tree species their general thresholds were based on. Separate regression lines for shrub versus forested sites were calculated in the relationship between ANPP and modified IPAR. The slopes and intercepts were compared using the Giant Size Regression (GSR) technique (Cunia et al. 1973, Neter et al. 1990).

Above-ground Net Primary Production (ANPP)

Annual above-ground net primary production (g m^{-2} y^{-1}) includes new foliage, stem and branch production. No mortality was noted, so current production losses to morality, herbivore grazing, and nonfoliar litterfall was assumed zero. Random samples of 10-30 plants of the shrub and herb species were selected for harvest at the six sites. The Himalaya blackberry (*R. procerus*) was harvested in 1 m^{-2} plots because of its trailing habit (M. Newton pers. comm.). Sample size for shrub and herb species was based on variability in biomass dry weight from a pre-season harvest (Eckblad 1991).

Shrubs and herbs were harvested at the end of growing season, before litterfall loss, and current year's aboveground growth was separated from the remaining biomass. Old and new biomass were oven dried at 70°C until dry weight had stabilized (approximately 2 weeks), then weighed. Production per unit area (g m^{-2} y^{-1}) of each sample was calculated from measurements of the canopy area. Average growth of a species was scaled to the site area by percent cover. Growth of *R. spectabilis* was calculated based on dry weight per shrub and number of shrubs per m^{-2}, because the canopies are tightly interwoven. The area estimate of ANPP for site 2-O *R. procerus* was the mean of the 1 m^{-2} plots because cover was very uniform across the site. At the forested sites and the Sisters shrub site, which has dispersed shrub cover, four 100 m transects were established to provide cover estimates for each species, using the line-intercept method (Deuser and Shugart 1978). Plant species were recorded to the nearest cm as they intercepted the transects. Above-ground NPP estimates for major tree species at the forested sites were obtained from Runyon et al. (1993).

Tree and understory data from the forested sites were summed to get total ANPP for vegetation at the site, and used with overstory plus understory IPAR in the across-site relationships between ANPP and IPAR, and ANPP and modified IPAR (general and species-specific modified IPAR).

RESULTS

Thematic Mapper Simulator NDVI Observations and %IPAR

Climate conditions across sites are reflected in the percent of incident light intercepted by vegetation. The climate from west to east across Oregon is progressively drier, and summer and winter temperatures are more extreme. Vegetation intercepted from 99.9% and 99.0% at the Cascade Head alder and salmonberry sites (sites 1 and 1-O), to 26.7% and 24.8% of incident PAR at the Sisters juniper and shrub sites (sites 6 and 6-O) east of the Cascade mountains (Table II.2). Understory %IPAR was very low at the two forested sites west of the Cascade mountains (2.9% at site 1, and 6.5% at site 2), but accounted for more of the total %IPAR in the relatively open forest canopies east of the Cascades. At Sisters site 6, the understory intercepted 10.2% of incident PAR, and the overstory juniper intercepted 16.5%. After leaf-off duration was accounted for, annual intercepted PAR ranged from 497 MJ m^{-2} at site 6-O to 2233 MJ m^{-2} at site 2.

The TMS NDVI observations indicated the gradient of vegetation conditions across sites (Fig. II.2). The NDVI values were higher on the west side of the Cascade mountains (sites 1,1-O, 2, 2-O), where vegetation cover is more dense and lush. The relatively open Metolius sites (5 and 5-O) had intermediate NDVI values, and the two Sisters sites (6 and 6-O) had the lowest values. Between forested and shrub areas at each location (e.g. sites 1 and 1-O), NDVI values were generally higher for the shrub vegetation, except site 5 (ponderosa pine and gray-green bitterbrush understory) had a higher NDVI than the primary cover of bitterbrush at site 5-O (0.50 and 0.36, respectively).

There was a strong linear relationship between the ground-measured %IPAR and the June TMS NDVI measurements (Fig.II.2, %IPAR = -3.1 + 125.05*NDVI, $R^2 = 0.97$).

Above-ground Net Primary Production (ANPP)

Above-ground net primary production varied from 53 g m^{-2} y^{-1} at site 6-O to 1310 g m^{-2} y^{-1} at site 2 (overstory + understory) (Table II.4). Of the shrub sites, the salmonberry site (site 1-O) had the highest ANPP at 769 g m^{-2} y^{-1}. The understory at the Metolius ponderosa pine site contributed 46% of the total ANPP, the highest proportion of shrub ANPP recorded at any of the forested sites. Understory contributions to total site ANPP were 7.5% at Cascade Head site 1, 11.5% at Corvallis site 2, and 22.6% at the Sisters juniper woodland.

Energy-conversion and Energy-use Efficiency

The annual leaf-on IPAR explained 70% of the variation in ANPP across sites (Fig. II.3). Energy-conversion efficiency (ε = ANPP/IPAR) increased from east to west from 0.11 at site 6-O to 0.88 at site 1 (Fig. II.4). When the general environmental thresholds were applied to annual intercepted light (equation 2), they did not improve the R^2 of the relationship between ANPP and IPAR ($R^2 = 0.68$; Fig. II.5), but the intercept did approach zero. This lead to the question of whether the application of species-specific environmental constraints would improve the relationship between ANPP and IPAR, and result in a consistent ε_u.

Stomatal Response to Drought and Vapor Pressure Deficit (VPD)

Boundary lines show that the maximum stomatal response of all species to VPD was generally curvilinear, with conductance often decreasing rapidly at first, and then leveling off as VPD increased (Figs. II.6 through II.8). There was much variation in conductance for a given VPD, because of sampling under different conditions at different times of the year.

Stomatal closure in response to high VPDs appeared to have occurred between 1.5 and 2.0 KPa for most species (Fig. II.6 to II.8, and Table II.3). This is close to the general thresholds reported by Runyon et al. (1993) (1.5 KPa for partial closure, and 2.5 for complete stomatal closure; Table II.3). Stomata were not observed to close during measurement of *A. rubra* and *R. spectabilis* at Cascade Head, and VPDs reached only 1.2 and 1.5 KPa, respectively. Cascade Head is on the coast and generally humid for most of the year.

Seasonal variation in predawn water potential of each species are shown in Figure II.9. None of the species at Cascade Head had Ψpredawn values below -1.0 MPa. The greatest differences in Ψpredawn among species occurred at Corvallis. The swordfern *P. munitum* reached the lowest Ψpredawn value at -4.0 MPa in August. Minimum Ψpredawn values at all sites were reached in August and September, the typical timing of extreme drought in Oregon.

Boundary-line analysis of stomatal response to Ψ_{predawn} proved difficult, due to the limited data set (Figs. II.10 through II.12). Corvallis was the only site where Ψ_{predawn} thresholds could be determined from the data. Complete stomatal closure apparently occurred at -2.0 MPa for *P. menziesii*, the same value obtained by Running (1976) in Oregon, and partial closure was at -1.5 MPa. The shrub *R. procerus* appeared to be more sensitive to

$\Psi_{predawn}$, with closure at -0.7 MPa. Swordfern (*P. munitum*) stomata closed at approximately -4.0 MPa.

For purposes of applying specific thresholds to conductance to modify IPAR, thresholds from other sources were obtained when they were not apparent from this study (Table II.3).

To evaluate potential error in the use of 1990 meteorological station radiation data for dates in 1992 when predawn water potential limited stomatal conductance, I compared 1992 incident radiation integrated over those dates to 1990 radiation integrated over the same dates for each species. There was at most a 2% difference in the integrated radiation between the two years for all species. Radiation integrated from July through September, when most drought stress occurred (if at all), was 4% lower in 1992 at Cascade Head, and 2% and 3% higher in 1992 at Corvallis and Sisters, respectively. Because diurnal variation in VPD is greatest in June through September, and meteorological data were not collected January through June, 1992, it still appeared to be better to use the complete meteorological data set for 1990.

Energy-use Efficiency Revisited

Because of the lack of improvement in the relationship between ANPP and IPAR modified by the general limits to photosynthesis, I applied species-specific limits. This only slightly improved the relationship between ANPP and modified IPAR (R^2 = 0.73 compared with 0.68 using general limits; Fig. II.5). The ε_u values varied from 0.34 at site 6-O to 1.02 at site 2. Therefore, calculation of modified IPAR from species-specific and general thresholds provided little improvement in the model's ability to explain variation in ANPP.

The ponderosa pine site (5) is intermediate in canopy structure between the juniper woodland and Douglas-fir sites. Enough data were available from sites 5 and 5-O to apply the general constraints to ponderosa pine, and the rabbitbrush constraints to bitterbrush. The linear relationship between ANPP and modified IPAR improved when sites 5 and 5-O were added to the analysis ($R^2 = 0.78$; Fig. II.13). The inclusion of site 5 and 5-O data, however, reinforce the suggestion of separate energy-use efficiencies for above-ground production by forested and shrub sites. To evaluate the possibility of different energy-use efficiencies between life forms, I applied separate linear regressions for shrub versus forested sites (Fig. II.14). A comparison of the regression lines showed that the slopes (predicted ε_u) were significantly different from each other, and there was no evidence that the intercepts were significantly different ($P = 0.05$; regression slope for forested sites = 1.03, shrub sites = 0.52). The ε_u for the shrub sites varied from 0.34 at site 6-O to 0.64 at site 1-O, with a mean of 0.49 (Fig. II.4, Table II.4). For the forested sites, ε_u ranged from 0.74 at site 6 to 1.02 at site 2, with a mean of 0.89. This is close to the mean ε_u of 0.80 Runyon et al. (1993) obtained across 8 OTTER forest sites (included 2 fertilized subsites), when only trees were included in the relationship. The mean ε_u across all 8 sites (shrub and forest) in the present study is 0.69 (range 0.34 to 1.02).

The relative contribution of the environmental factors for determination of ε_u are shown in Table II.5. Among sites, the reductions in IPAR ranged from 6.6% for alder at Cascade Head to 70.3% for rabbitbrush at Sisters. The largest reductions were for the three species at Sisters, where freezing temperatures, drought, and VPD all strongly affect production. The mild, moist climate at Cascade Head was reflected in the smallest reductions in IPAR; very little reduction in IPAR was due to freezing temperatures (0 to 0.6%), and no reduction from drought for all three species. Swordfern at Cascade Head and

Corvallis had the largest reductions in IPAR among species at the two sites. The total reductions in IPAR were very similar among juniper, sagebrush, and rabbitbrush at Sisters. For juniper, reductions due to drought, VPD, and temperature were approximately equal, but for the two shrub species, reductions from VPD were the largest of the three environmental variables. At Corvallis, blackberry had the lowest reduction, with drought responsible for two-thirds of the reduction.

DISCUSSION

The July NDVI calculated from remotely sensed observations appears to provide a good estimate of maximum %IPAR (Fig. II.2). This agrees with previous studies at the OTTER sites with various sensors, such as the AVHRR NDVI across the six forested sites, and field spectrometry of understory species at the ponderosa pine site (Goward et al. 1993, Law and Waring 1993). Results from the present study compare closely with Goward et al. (1993) when they used the July satellite AVHRR NDVI, and tree %IPAR across 5 original OTTER sites (%IPAR = -4.0 + 121*NDVI, $R^2 = 0.99$). In their analysis, they excluded the ponderosa pine site (site 5) because the large amount of understory may have contributed to the NDVI, and understory was excluded from their %IPAR estimates.

The reduction in light interception and amount of vegetation from west to east is captured in the decrease in NDVI. The influence of soil background conditions on the spectral signal, however, must be taken into account. From field spectra, Goward et al. (1993) found that as canopy NDVI decreased from west to east across the Oregon transect, so did the background NDVI. They suggested that this spatial correlation may indicate general regional environmental characteristics, and therefore NDVI may still be diagnostic of regional ecosystem activity. To better explain landscape properties, techniques including mixture models of scene components, and second order derivatives of hyperspectral measurements are being developed, and have promise for application with the new high resolution sensors (Goward et al. 1993, Strahler et al. 1986).

The amount of incident radiation intercepted by plants and used for photosynthesis depends on a combination of environmental factors and plant biochemistry. Physiological responses to environmental factors vary in time and space. Plants respond to radiation and VPD diurnally, and to soil moisture over days to weeks. At longer time scales, soil moisture and nutrient availability tend to limit leaf area development and IPAR (Schulze 1982, Pielke et al. 1993, Running and Nemani 1989). On an annual basis, however, growth would appear to be linearly related to IPAR if drought, vapor pressure deficit, and temperatures were not limiting stomatal conductance and photosynthetic rates. The linear relationship between ANPP and IPAR observed in this study (Fig. II.3), before modification by these factors, may be due to the large effect of leaf duration on IPAR estimates for deciduous canopies which exist at many of the sites. Seasonally inactive evergreen vegetation, however, is known to depart from such a simple relationship (Running and Nemani 1988, Field 1991). Thus, although there was a linear relationship between ANPP and IPAR across the sites in this study, I attempted to determine if the relationship improved when the three environmental limits were taken into account.

The energy-use efficiency model focuses on environmental limits to the ability of plants to use intercepted PAR for production (Landsberg 1986). Through the course of a year, incident radiation is strongest in the summer when drought and VPD restrict production the most. Therefore, these two environmental factors can critically influence the ability of plants to use available light during the growing season. Light levels are lowest in winter, when freezing temperatures can restrict photosynthesis by foliated plants. Environmental constraints in the energy-use efficiency model, when applied to hourly and daily radiation data, capture the interactions with variation in light intensity as defined in equation (2).

The application of general environmental thresholds to modify IPAR (Fig. II.5) was a preliminary test of whether these general thresholds improved the ability to explain differences in ANPP across sites. Although they did not improve the R^2, the intercept approached zero as would be expected, once environmental constraints on the harsher sites were taken into account (Fig. II.3 vs. II.5). The next step was to determine if more refined species-specific thresholds improved the relationship. Only minor changes resulted (Fig. II.5), suggesting that when different life forms are included in the relationship, other factors may also be important.

Figure II.14 suggests that perhaps a separate ε_u exists for above-ground production by shrubs and trees. Although the data are limited in this study, previous authors have indicated reasons for why this may be the case. Field (1991) mentioned that ε in equation (1) may vary due to photosynthetic pathway, canopy architecture, developmental stage, respiration costs, carbon allocation patterns, and vegetation density (i.e. competition for resources), though ε often varies less than IPAR and may be nearly constant across a range of chronic stresses. Running (1990) suggested that once meteorological components had been separated from biochemical components of ε (equation 2), variation in the resulting ε_u should represent nutrition related biochemical factors, and fundamentally different physiology, such as C_3 and C_4 plants. A strong, possible reason for variation in ε_u is species or life form differences in carbon allocation patterns, which may be reflected in total NPP (above- and below-ground) (Field 1991).

Environmental constraints throughout the year influence the plant life form best adapted to a given location. Shade-grown perennial herbaceous plants, such as *P. munitum* at sites 1 and 2, allocate the greatest portion of carbohydrates to growing leaves (Schulze 1982). Swordfern has rhizomes, where a large amount of carbohydrate reserves are probably stored and mobilized for rapid spring growth. Underground rhizomes of perennial herbs may contain as much as 35% to 60% stored carbohydrate at the end of a growing season (Mooney 1972).

Colonizers, such as *R. spectabilis* at sites 1 and 1-O, have large rhizomes and are adapted to rapidly colonize open areas, and to resprout after fire or browsing. The rhizomes of *R. spectabilis* fill unoccupied areas of stands, replacing dead or non-producing ramets. These rhizomes account for as much as 40% of the harvested plant biomass, excluding roots (Tappeiner et al. 1991).

The trailing stems of *R. procerus* (sites 2 and 2-O) layer over older stems, and allocate a large portion of their carbohydrates to the new roots initiated from the layering stems (Bell and Tomlinson 1980, Schulze et al. 1986). The apparently low above-ground production by *R. procerus* could be partly due to its vine-like architecture, which may incur a large cost of annual partial replacement compared to permanent wood production by trees (Mooney 1972, Schulze et al. 1986).

Shrubs generally have higher root:shoot ratios than do trees. A larger fraction of shrub production is in root growth, which has persistence value for access of soil water, and survival of fire, browsing, and drought which may damage or destroy shoots (Whittaker and Woodwell 1968). Large storage reserves in roots provide a competitive advantage for shrubs by supplying resources for early spring growth, before full leaf-out of the overstory. Kuppers (1984) observed that hydraulic conductance per sapwood area was higher in shrub species (including *Rubus*, *Prunus*) than in tree species (e.g. *Acer*), indicating that trees must put more carbon into wood per unit leaf biomass to sustain comparable plant water relations. In arid and semi-arid environments like the Sisters and Metolius sites, trees and shrubs have extensive root systems, and root:shoot ratios increase with increasing drought (Schulze 1982). Finally, plants on relatively disturbed habitats, such as *Rubus* spp., allocate more resources to reproduction than do plants at more mature sites (Mooney 1972). Thus, carbon allocation patterns differ among life forms, and, with variation in the harshness of environment, influence the relationship between ANPP and IPAR.

To better assess environmental limits on production across life forms, estimates of below-ground production for total NPP could be obtained through a method developed by Raich and Nadelhoffer (1989). They have estimated below-ground production of forest trees from a correlation between measured annual litterfall and CO_2 efflux from the soil. The present study suggests the necessity of developing this relationship for other life forms. The simplest approach would be to select areas with homogeneous shrub cover, where other vegetation does not confound litterfall and CO_2 efflux estimates.

The data presented here are for above-ground production. Runyon et al. (1993) estimated an average ε_u of 1.32 g MJ^{-1} for total NPP by trees at the OTTER sites. If the shrub sites had a similar ε_u, total NPP would be 1584 g m^{-2} y^{-1} (51% below-ground NPP) at the Cascade Head *R. spectabilis* site, 1705 g m^{-2} y^{-1} (69% below-ground NPP) at the Corvallis *R. procerus* site, and 204 g m^{-2} y^{-1} (74% below-ground NPP) at the Sisters shrub site. The trend in below-ground NPP would agree with the observation of Whittaker and Woodwell (1968) that a large portion of total shrub production is below-ground, and the general observation that as environment becomes harsher, more production goes underground for capture of scarce resources of nutrients and water. The total NPP estimate for *R. spectabilis* is 3% less than the estimate for *A. rubra*, *R. procerus* is 11% more than *P. menziesii*, and *A. tridentata/C. viscidflorus* is 32% less than the *J. occidentalis* estimate.

Accurate estimates of IPAR by forest understory vegetation require measurement of diurnal and seasonal IPAR, and perhaps knowledge of diffuse and direct radiation interception. These measurements are possible, but not entirely practical for large scale studies. In this study, IPAR by understory at the forested sites may have been underestimated, because the influence of changing sun angle is not accounted for. As solar zenith angle becomes larger, more direct light may reach the forest floor than when %IPAR measurements were taken in mid-summer with the sun directly overhead (Smith et al. 1989). At the *R. procerus* site, annual IPAR may have been overestimated, because %IPAR was also measured when the sun was directly overhead, and there was minimal shading from trees along the edge. Large solar zenith angles in the winter, however, may result in more shading of the open site. This could partly explain the deviation of this site from the regression line in Figure II.13.

Some shade-adapted species, such as swordfern, may more efficiently absorb diffuse and spectrally altered radiation from passage through multiple leaf layers than sun-adapted plants. Measurements in the 400-700 nm wavelengths may underestimate productivity of these plants if they use a greater percentage of light at 700-750 nm than sun-adapted plants (Lee 1986).

Remote sensing instruments may not detect more than the top one-half to one-third of closed-canopy forests (Goward, pers. comm.). Furthermore, understory in these forests contribute very little to total IPAR and NPP. It is in more open-canopy forests, such as the juniper woodland, that shrub cover contributes most to reflectance characteristics.

The practical application of the energy-use efficiency model to coarse-scale ecological studies relies on our ability to improve it while still maintaining its simplicity. It requires a combination of good environmental measurements, improved knowledge of carbon allocation patterns, and advances in remote sensing data analysis to estimate IPAR by dispersed canopies. Broad application of the model for above-ground production estimates may be possible through stratification by vegetation type (e.g. grasslands, shrublands, forests), and development of relationships between ANPP and IPAR to obtain constant energy-use efficiency coefficients for each type.

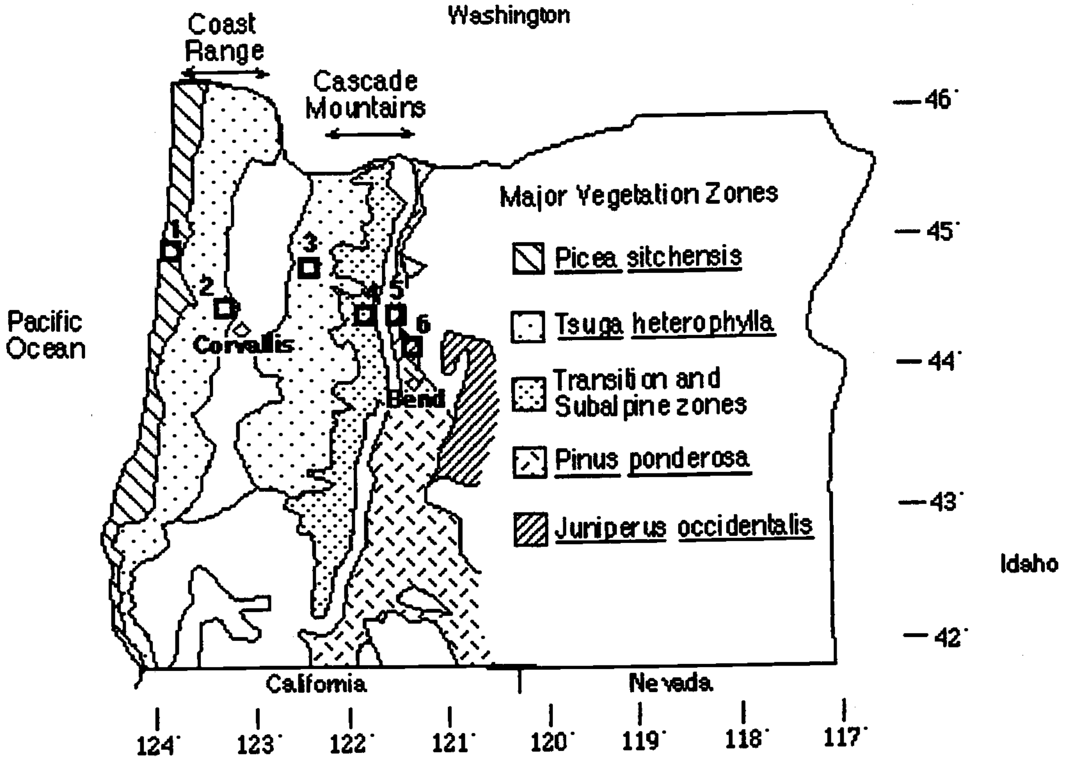


Fig. II.1. Location map of study sites. The Oregon Transect Ecosystem Research Project (OTTER) sites which were used in the present study are site 1 (Cascade Head alder), site 2 (Corvallis Douglas-fir), site 5 (Metolius ponderosa pine), and site 6 (Sisters juniper woodland). (After Franklin and Dyrness 1973, and Runyon et al. 1993).

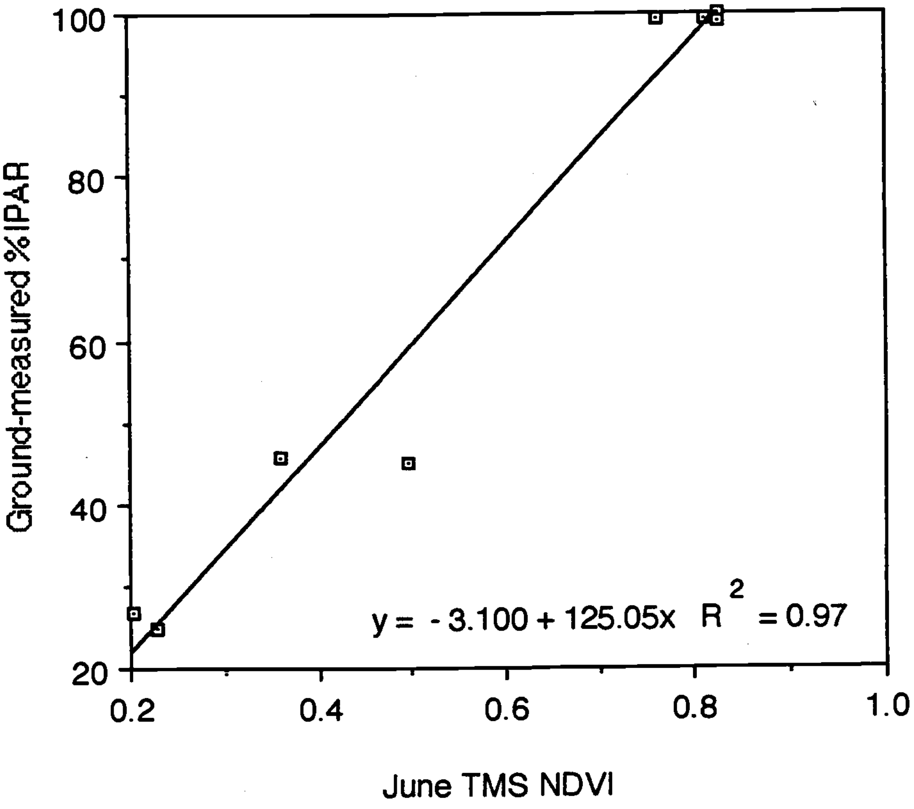


Fig. II.2. Relationship between percent of incident photosynthetically active radiation intercepted by vegetation and June Thematic Mapper Simulator normalized difference vegetation index. The regression relation compares closely with previous results across five Oregon Transect forested sites with the Advanced Very High Resolution Radiometer (AVHRR) NDVI (%IPAR = -4.0 + 121*NDVI, $R^2 = 0.99$; Goward et al. 1993).

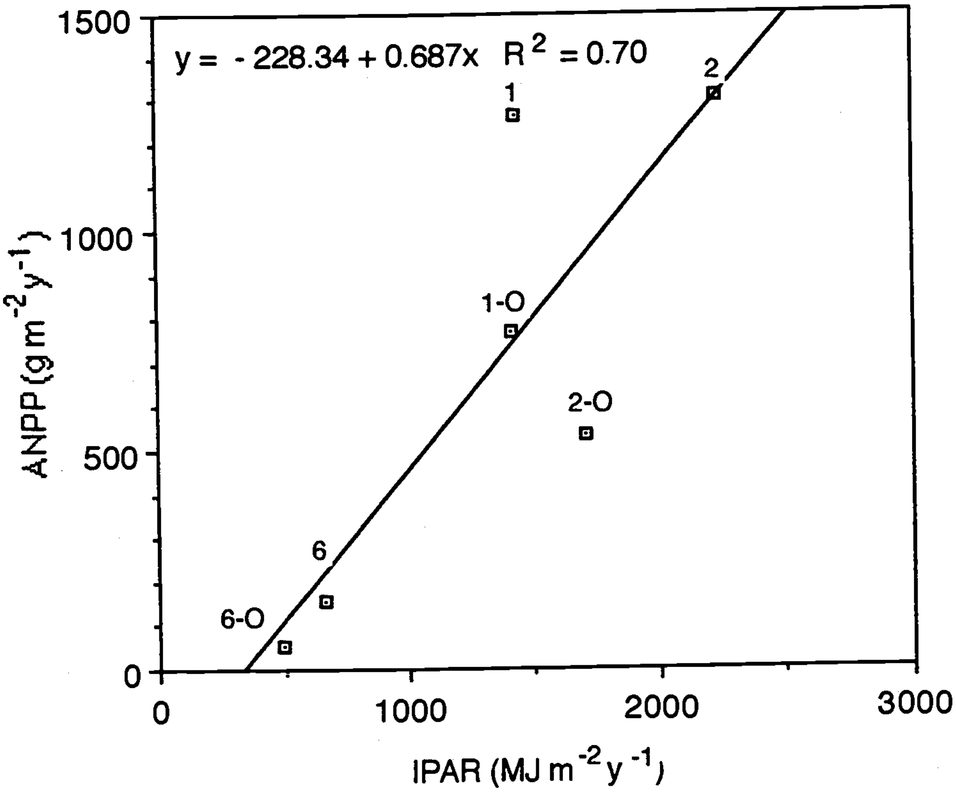


Fig. II.3. Above-ground net primary production in relation to intercepted photosynthetically active radiation. Interception of photosynthetically active radiation (IPAR) by the vegetation explained 70% of the variation in above-ground net primary production (ANPP) across sites. Site 1 = Cascade Head alder; site 1-O = Cascade Head salmonberry; site 2 = Corvallis Douglas-fir; site 2-O = Corvallis Himalaya blackberry; site 6 = Sisters juniper woodland; site 6-O = Sisters sagebrush and rabbitbrush.

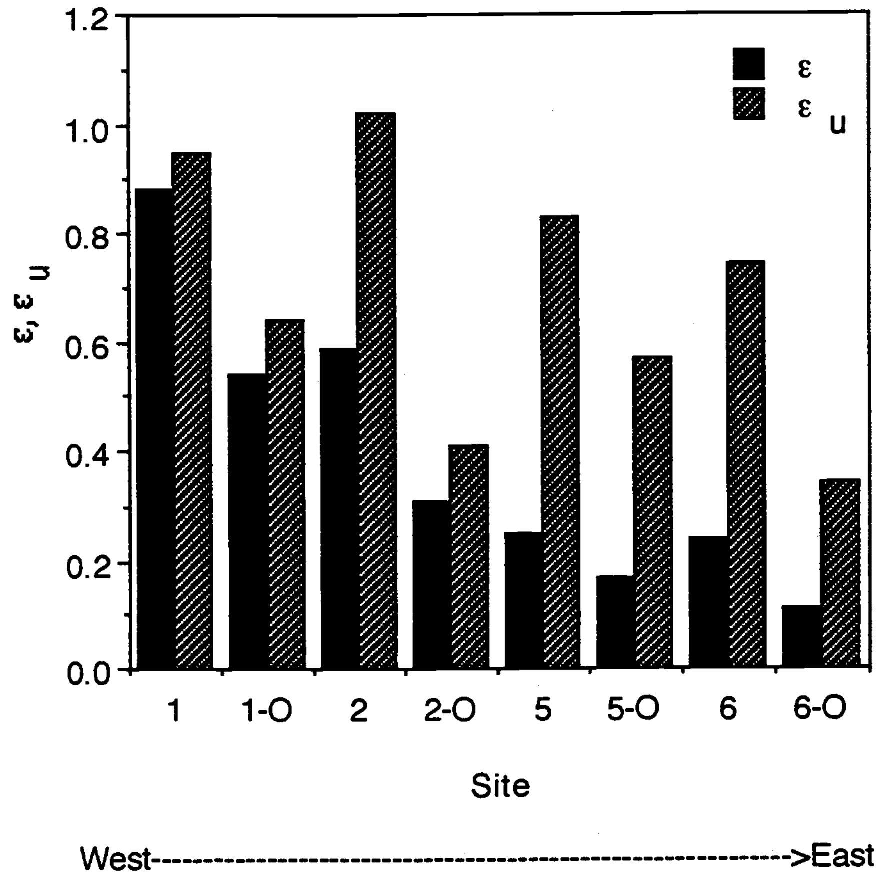


Fig. II.4. Energy-conversion and energy-use efficiency of above-ground production across sites. Energy-conversion efficiency (ε = ANPP/IPAR) generally decreases from west to east, and energy-use efficiency (ε_u = ANPP/modified IPAR) is relatively constant among forested sites, and among shrub sites. The ε and ε_u values are lower at the shrub sites than the neighboring forested sites. Sites 1, 2, 5, and 6 are the forested sites, and -O are the shrub sites at the same geographic location.

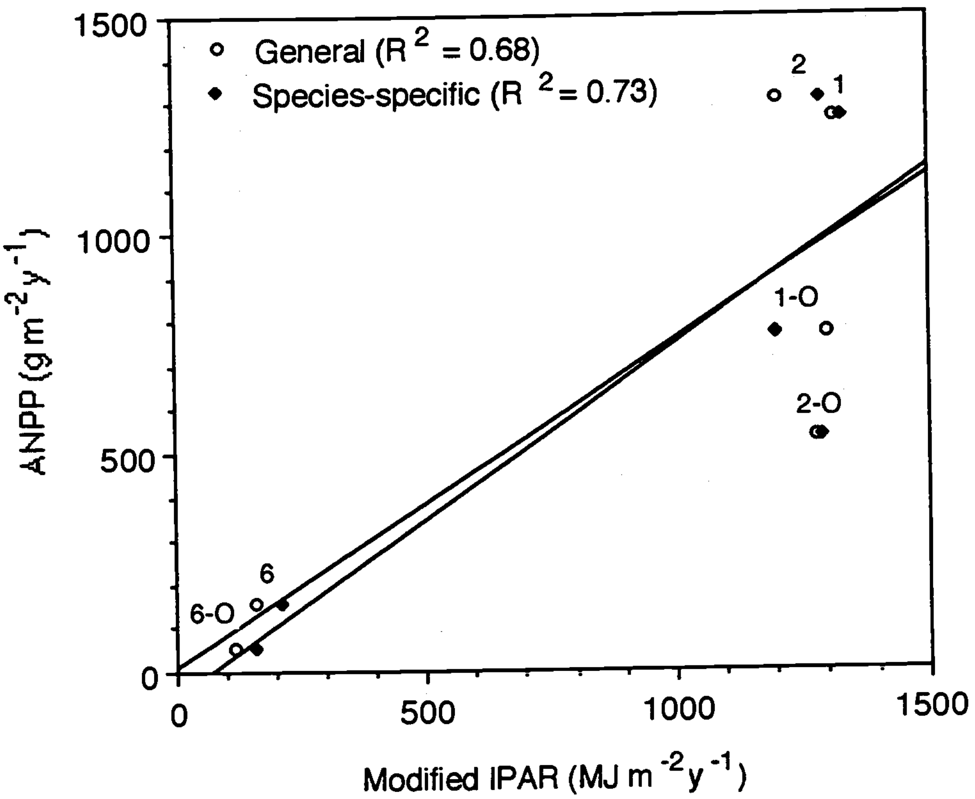


Fig. II.5. Relationship between above-ground net primary production and modified intercepted photosynthetically active radiation. Environmental constraints were applied as modifiers of IPAR. The general and species-specific environmental limits to production did not markedly improve the relationship between IPAR and above-ground net primary production (ANPP). The regression equation for general limits to production was (y = 13.165 + 0.746x), and for species-specific limits was (y = -53.408 + 0.805x). Site 1 = Cascade Head alder, site 1-O = Cascade Head salmonberry, site 2 = Corvallis Douglas-fir, site 2-O = Corvallis Himalaya blackberry, site 6 = Sisters juniper woodland, site 6-O = Sisters sagebrush and rabbitbrush.

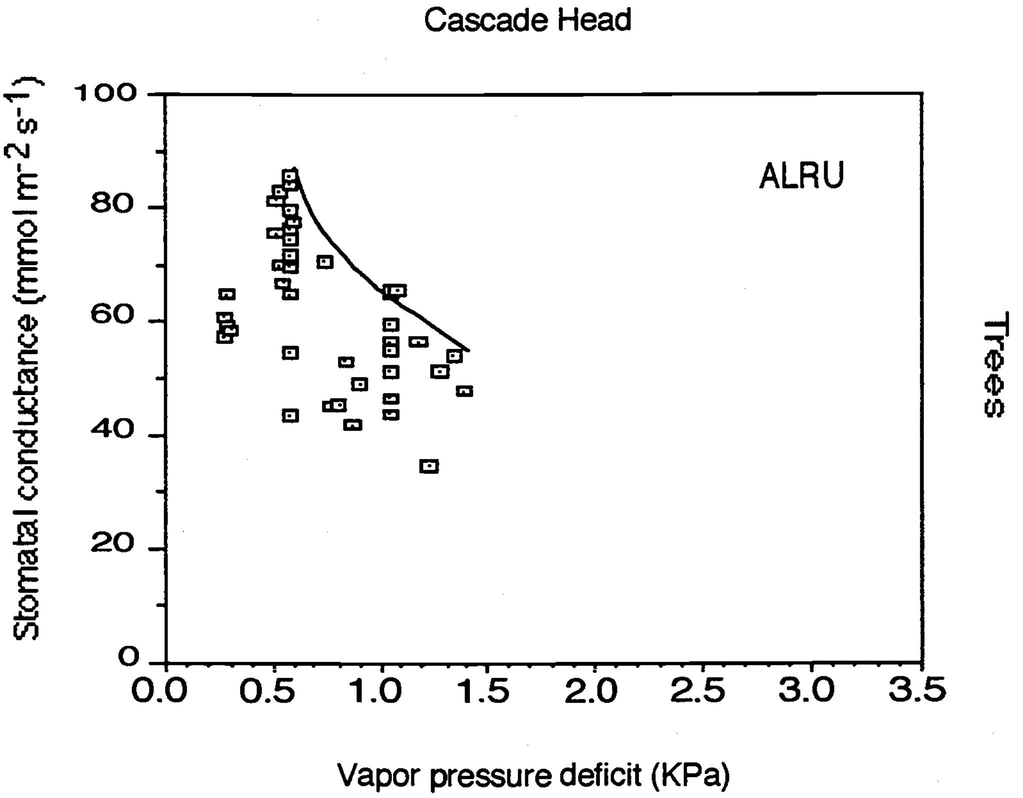


Fig. II.6 through 8. Stomatal conductance versus vapor presssure deficit (VPD) at Cascade Head, Corvallis, and Sisters. Boundary lines were drawn through the highest conductances for a given VPD. I assume that for points below the line, stomatal conductance was limited by factors other than VPD. Solid arrows (⬇) indicate approximate VPD thresholds when stomata closed, and open arrows (⇩) indicate approximate VPD thresholds when stomata were half way closed.

Fig. II.6. Stomatal conductance versus vapor pressure deficit at Cascade Head. No apparent stomatal closure threshold for *Alnus rubra* (ALRU) was reached during the time measurements were made.

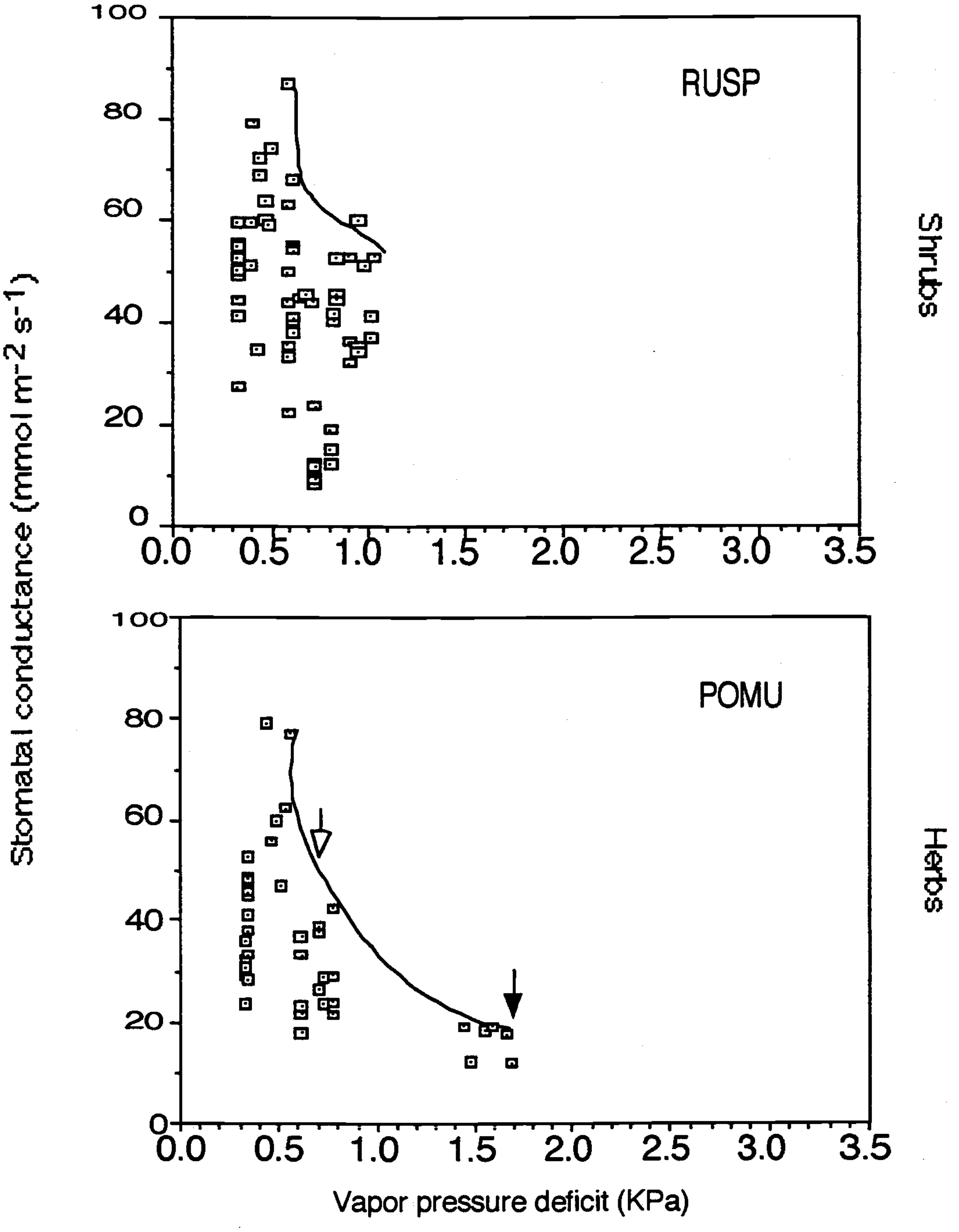
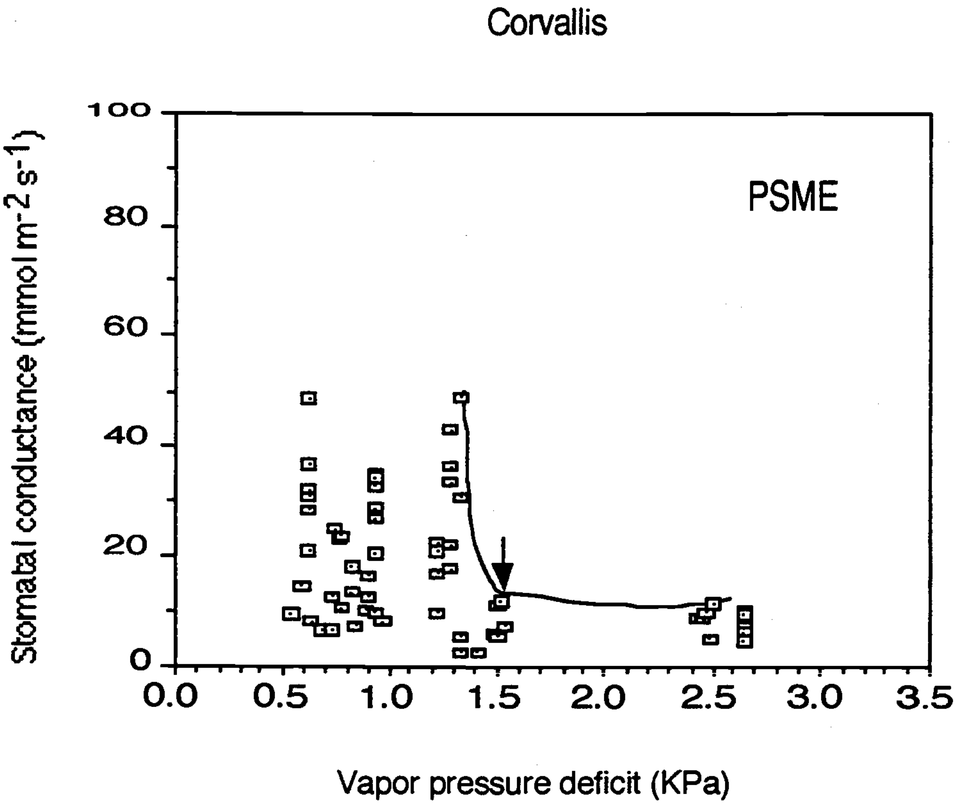


Fig. II.6, Continued. Stomatal conductance versus ambient vapor pressure deficit for *Rubus spectabilis* (RUSP) and *Polystichum munitum* (POMU) at Cascade Head. No apparent stomatal closure was reached during measurements on RUSP. Stomatal closure by POMU appears to have occurred at approximately 1.7 KPa, and partial closure at 0.7 KPa.



Trees

Fig. II.7. Stomatal conductance versus vapor pressure deficit at Corvallis. Stomatal closure by *Pseudotsuga menziesii* (PSME) appears to have occurred at approximately 1.5 KPa. A threshold for partial closure may not be appropriate due to steepness of the slope.

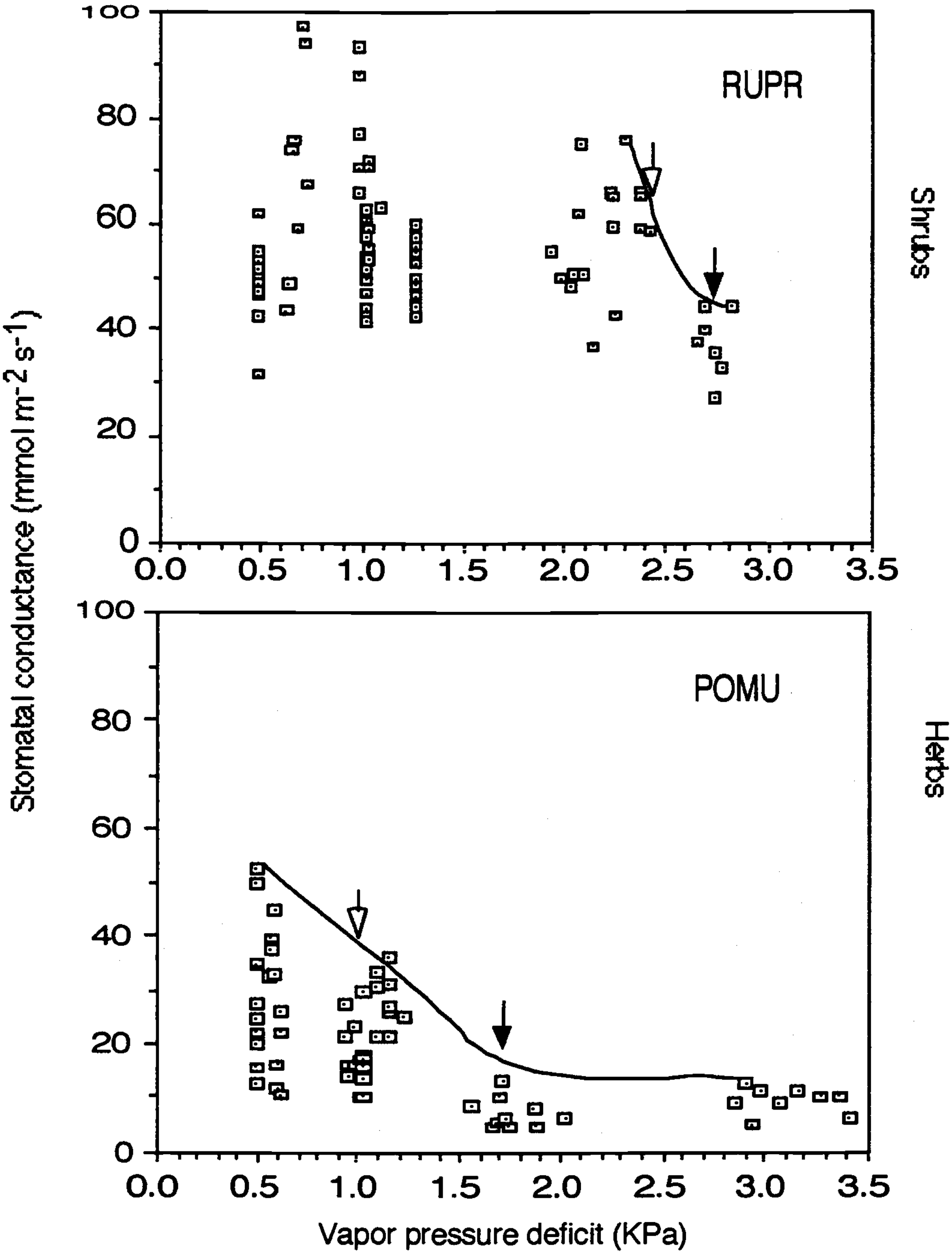
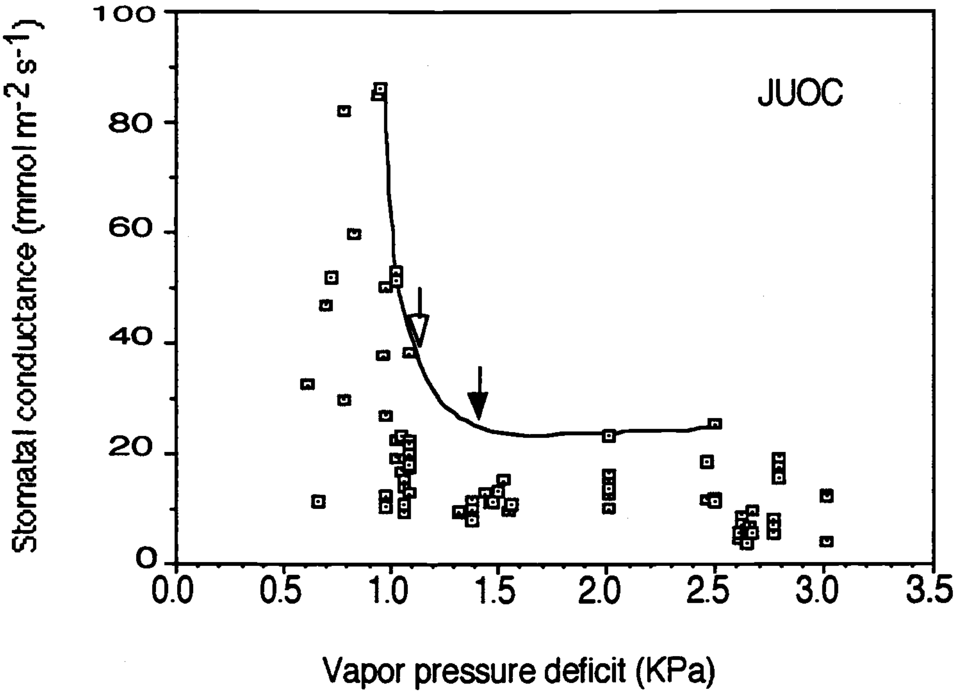


Fig. II.7, Continued. Stomatal conductance versus vapor pressure deficit for *Rubus procerus* (RUPR) and *Polystichum munitum* (POMU) at Corvallis. Stomatal closure for RUPR appears to have occurred at 2.7 KPa and partial closure at 2.4 KPa. Stomatal closure for POMU appears to have occurred at 1.7 KPa and partial closure at 1.0 KPa.

Sisters



Trees

Fig. II.8. Stomatal conductance versus vapor pressure deficit at Sisters. Threshold for full stomatal closure by *Juniperus occidentalis* (JUOC) was approximately 1.4 KPa, and partial closure 1.1 KPa.

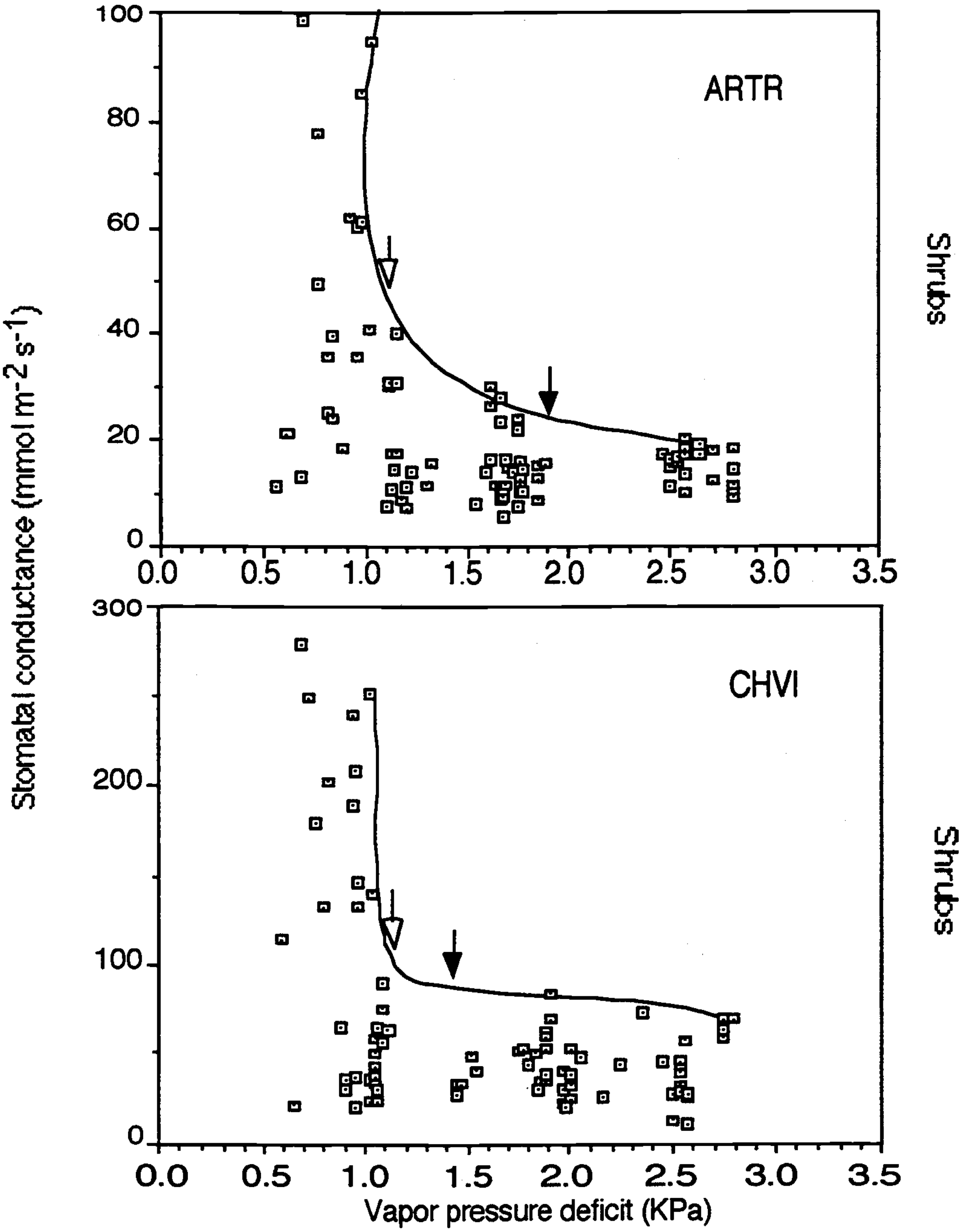


Fig. II.8, Continued. Stomatal conductance versus vapor pressure deficit for *Artemisia tridentata* (ARTR) and *Chrysothamnus viscidiflorus* (CHVI) at Sisters. Vapor pressure deficit thresholds for ARTR were approximately 1.9 KPa for full stomatal closure, and 1.0 KPa for partial closure. Thresholds for CHVI were approximately 1.4 KPa for full closure, and 1.1 KPa for partial stomatal closure.

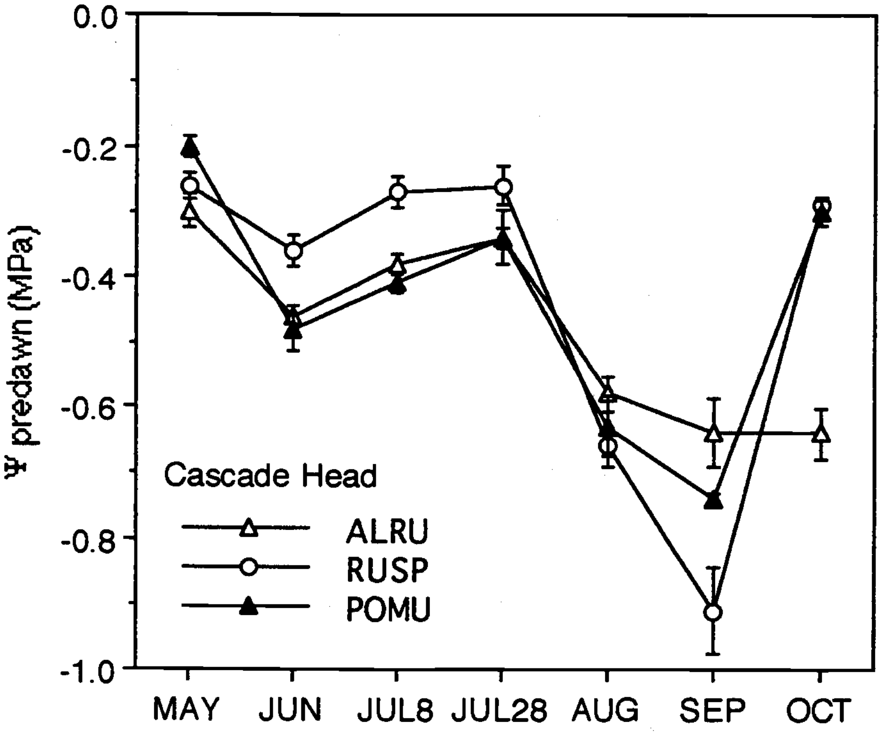


Fig. II.9. Seasonal variation in predawn xylem water potential. Mean and standard errors of predawn xylem water potential (Ψpredawn) are given for each site visit at Cascade Head, Corvallis, and Sisters. Daily Ψpredawn were interpolated from these data and used as a modifier to IPAR.

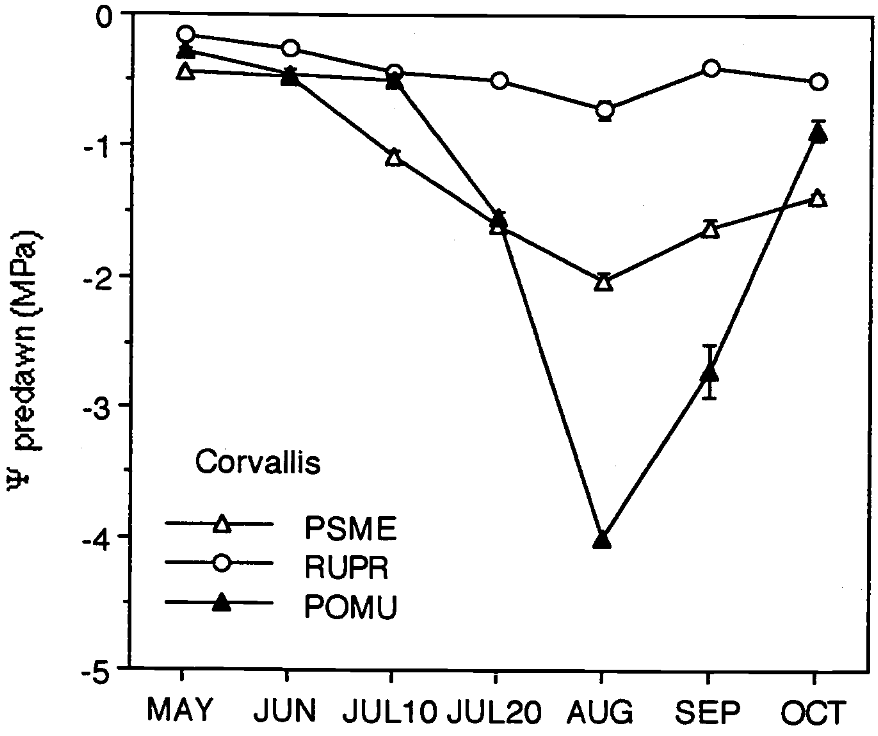


Fig. II.9, Continued.

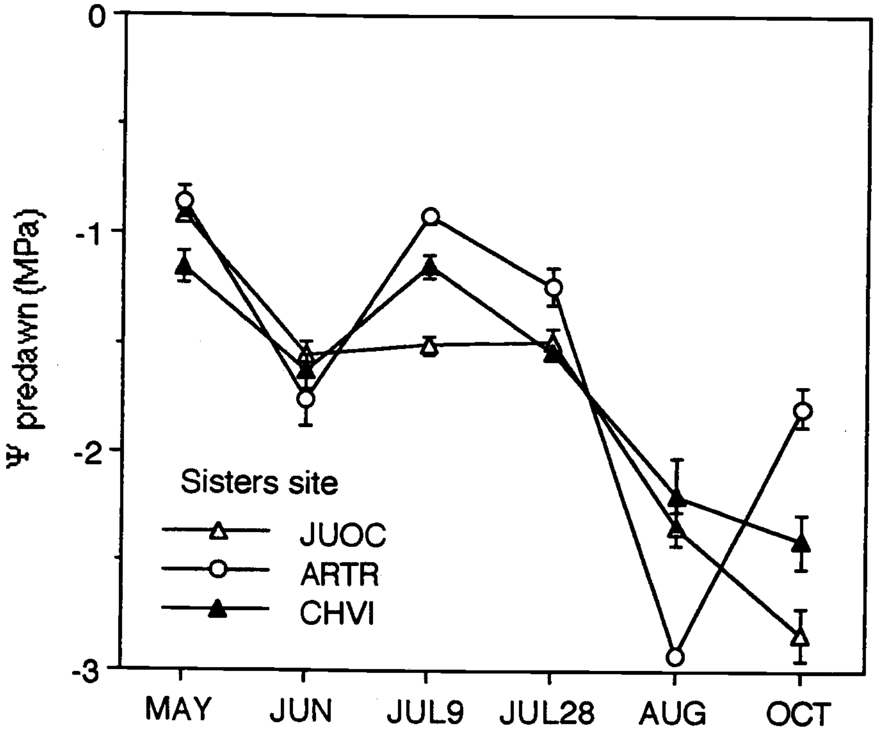


Fig. II.9, Continued.

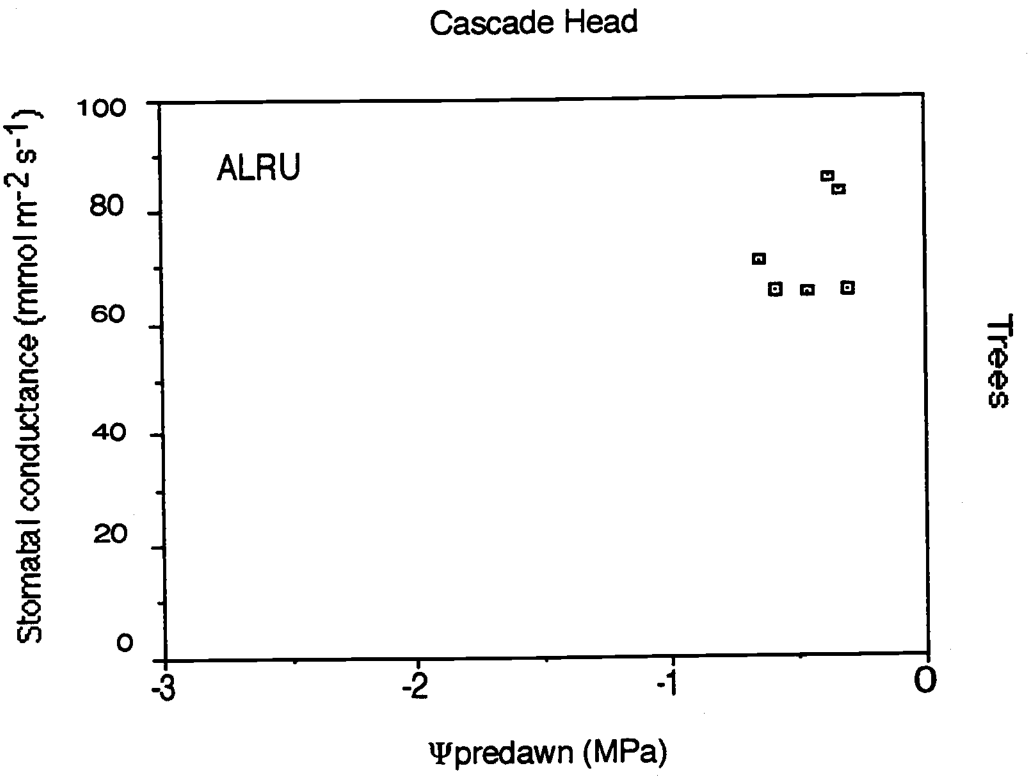


Fig. II.10. through 12. Stomatal conductance versus predawn water potential at Cascade Head, Corvallis, and Sisters. Maximum morning stomatal conductance and average predawn water potential (Ψpredawn) (n = 5 to 15 plants) were measured on the same day to determine threshold values of predawn water potential when there was full or partial stomatal closure. Solid arrows (↓) indicate approximate Ψpredawn when stomata closed, and open arrows (⇩) indicate approximate one-half closure.

Fig. II.10. Stomatal conductance versus predawn water potential at Cascade Head. No apparent stomatal closure threshold was reached for *Alnus rubra* (ALRU).

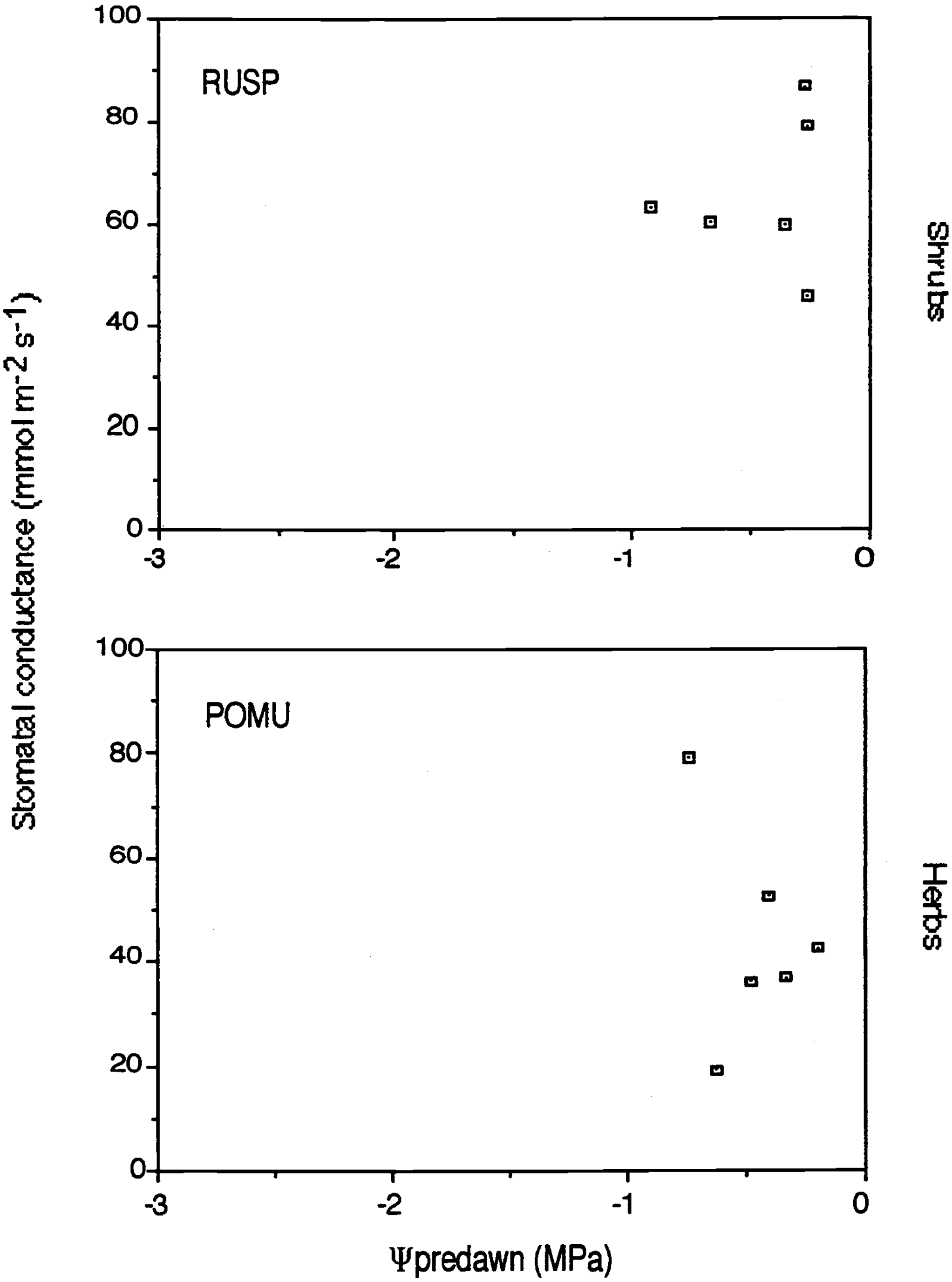


Fig. II.10, Continued. Maximum stomatal conductance and predawn xylem water potential of *Rubus spectabilis* (RUSP) and *Polystichum munitum* (POMU) at Cascade Head. No apparent stomatal closure threshold was reached for both species.

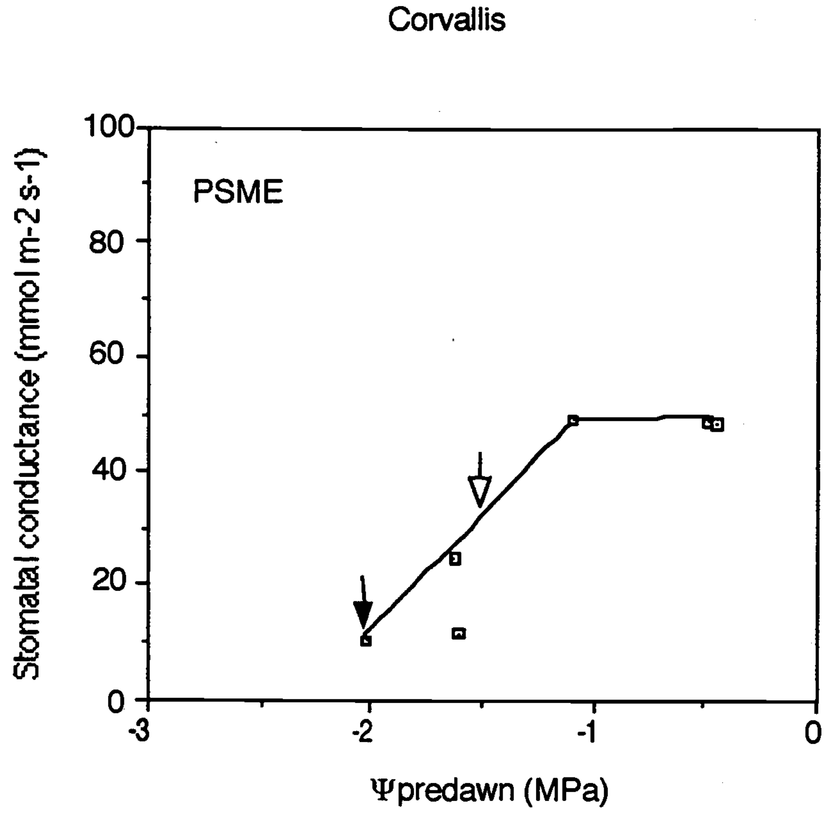


Fig. II.11. Stomatal conductance versus predawn water potential at Corvallis. Stomatal conductance thresholds for *Pseudotsuga menziesii* (PSME) appear to be -2.0 MPa full stomatal closure, and -1.5 MPa partial closure.

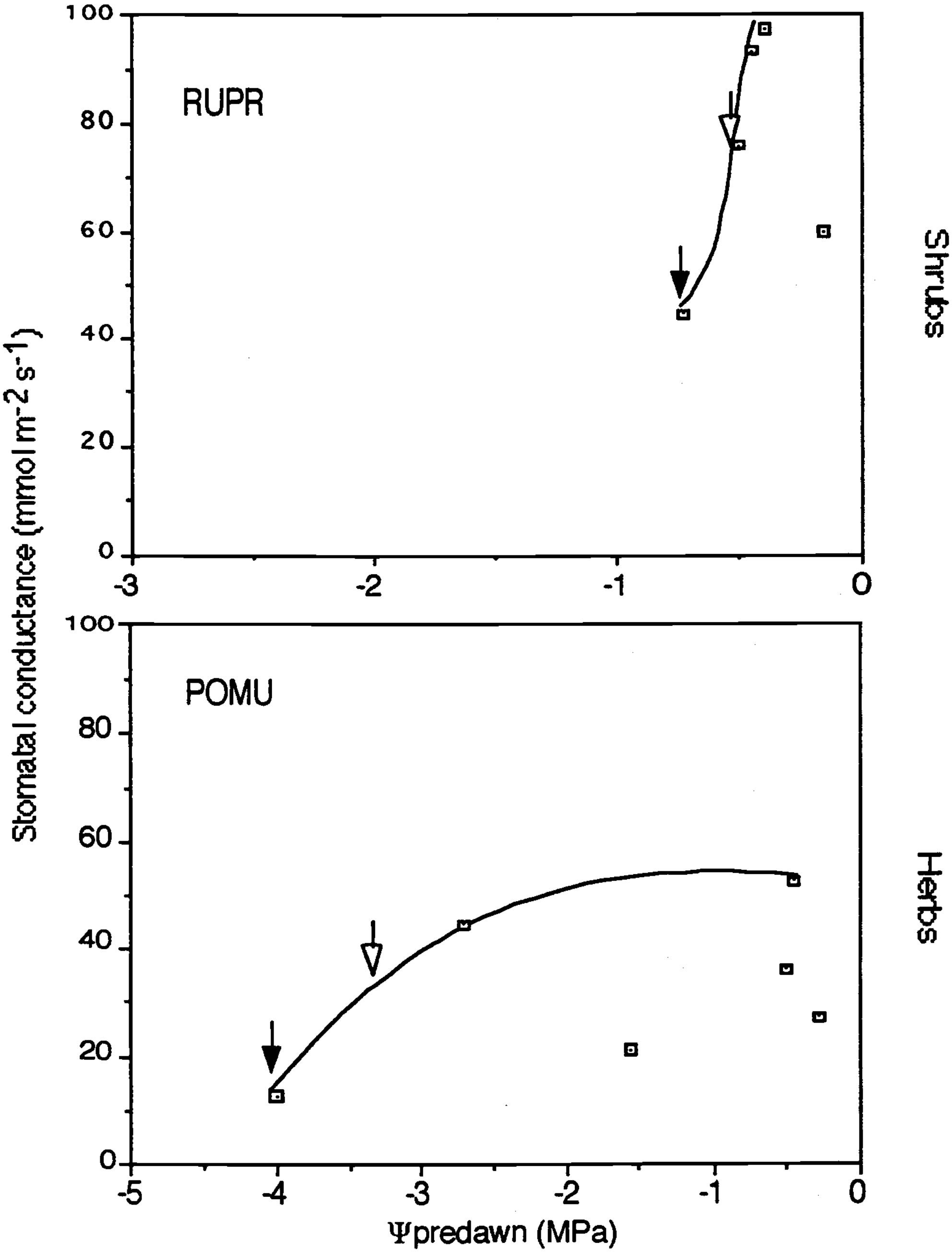


Fig. II.11, Continued. Stomatal conductance and predawn xylem water potential of *Rubus procerus* (RUPR) and *Polystichum munitum* (POMU) at Corvallis. Stomatal conductance thresholds appear to be -0.7 MPa full stomatal closure and -0.5 MPa partial closure for RUPR, and -4.0 MPa full closure and -3.3 MPa partial closure for POMU.

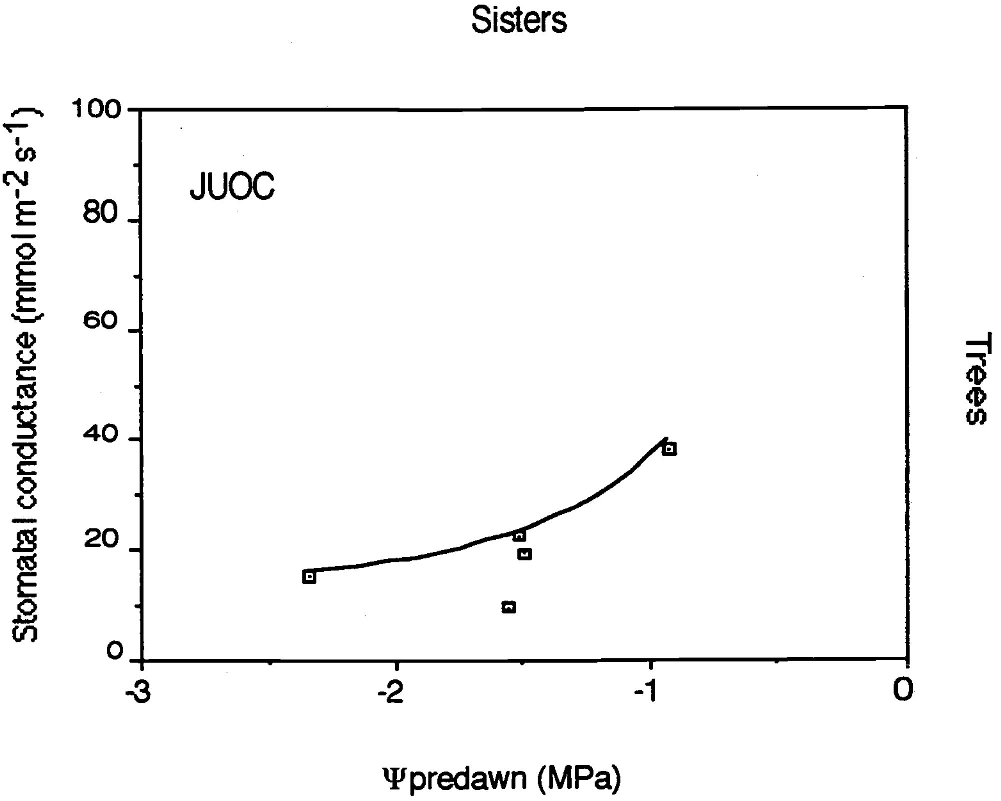


Fig. II.12. Stomatal conductance versus predawn water potential at Sisters. Stomatal closure thresholds in response to low predawn xylem water potential for *Juniperus occidentalis* (JUOC) are difficult to determine from the data.

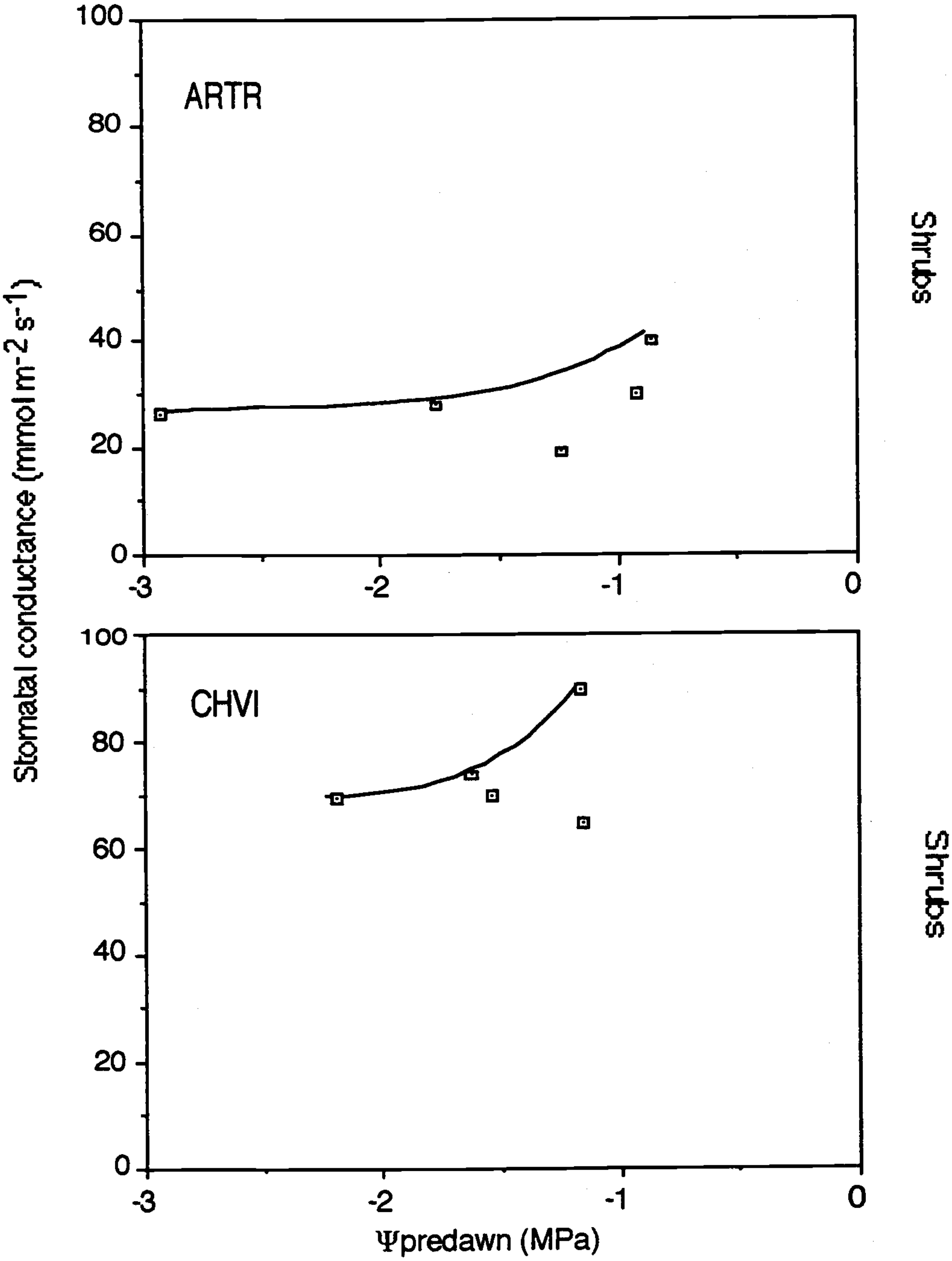


Fig. II.12, Continued. Maximum stomatal conductance and predawn xylem water potential of *Artemisia tridentata* (ARTR) and *Chrysothamnus viscidiflorus* (CHVI) at Sisters. Thresholds of stomatal closure are difficult to determine from the data for the two species.

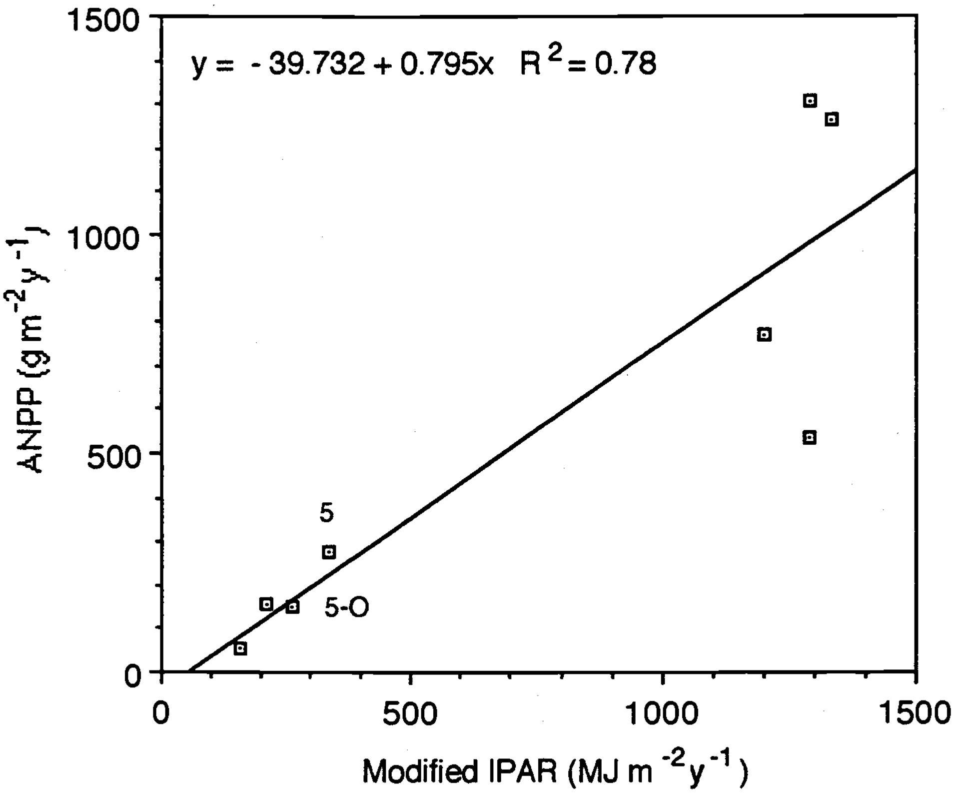


Fig. II.13. Relationship between above-ground net primary production and modified intercepted photosynthetically active radiation, including two additional sites. The environmental limits to production were applied to two additional sites, the Oregon transect ponderosa pine site 5 (*Pinus ponderosa*) and an adjacent shrub site which consists of bitterbrush (*Purshia tridentata*, site 5-O). The additional sites improved the relationship between above-ground net primary production (ANPP) and modified intercepted photosynthetically active radiation. The mean ε_u for above-ground production across all sites was 0.69.

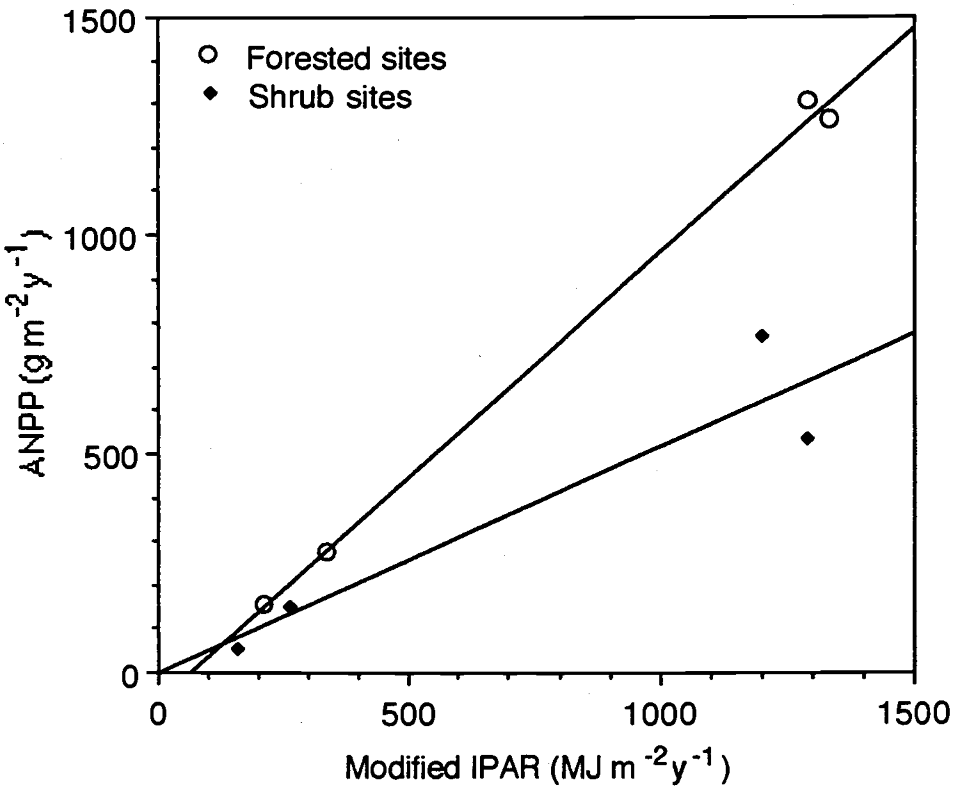


Fig. II.14. Relationship between above-ground net primary production and modified intercepted photosynthetically active radiation by forested versus shrub sites. Forested and shrub sites in Fig. II.13 were distinguished by separate linear regressions. The linear regression for forested sites is ($y = -63.787 + 1.03x$, $R^2 = 0.99$), with mean ε_u of 0.89, and for shrub sites is ($y = -2.706 + 0.521x$, $R^2 = 0.88$), with mean ε_u of 0.49. The slopes were significantly different from each other, and there was no evidence that the intercepts were significantly different ($P = 0.05$).

Table II.1. Characteristics of study sites.

	Site							
Feature	Cascade Head		Corvallis		Metolius		Sisters	
Site Number	forested (1)	shrub (1-O)	forested (2)	shrub (2-O)	forested (5)	shrub (5-O)	forested (6)	shrub (6-O)
Physiographic Province[1]	Western coast range		Interior valley		Eastern high Cascades		High lava plain	
Dominant Species (% cover)								
Tree	Alnus rubra (ALRU) (>90)		Pseudotsuga menziesii (PSME) (>90)		Pinus ponderosa (PIPO) (21)		Juniperus occidentalis (JUOC) (6.7)	
Shrub	Rubus spectabilis (RUSP) (32.4)	Rubus spectabilis (RUSP) (100)	Rubus procerus (RUPR) (91.7)	Rubus procerus (RUPR) (100)	Purshia tridentata (PUTR) (30.9)	Purshia tridentata (PUTR) (35.8)	Artemisia tridentata (ARTR) (9.0)	Artemisia tridentata (ARTR) (11.8)
							Chrysothamnus viscidiflorus (CHVI) (3.6)	Chrysothamnus viscidiflorus (CHVI) (8.2)
Herb	Polystichum munitum (POMU) (35.2)		Polystichum munitum (POMU) (4.9)					
Stand density (trees ha^{-1}>5 cm)[2]	1793		226		600		141	
Elevation (m)	240	240	170	170	1030	1030	930	930

1 Provinces from Franklin and Dyrness (1973).

2 From Runyon et al. 1993.

Table II.2. Climate data and intercepted photosynthetically active radiation at study sites.

	Site							
	Cascade Head		Corvallis		Metolius		Sisters	
	1	1-O	2	2-O	5	5-O	6	6-O
1990 Precip. (cm)	251	251	98	98	54	54	22	22
1990 Mean Annual Temperature (°C)	10.1	10.1	11.2	11.2	7.4	7.4	9.1	9.1
Annual Incident PAR (MJ m^{-2})	1935	1935	2267	2267	2735	2735	2735	2735
Percent IPAR								
Trees	97.0		92.9		28.6		16.5	
Shrubs	2.08	99.0	5.5	87.7	16.4	45.7	5.7 (ARTR) 4.5 (CHVI)	13.8 (ARTR) 11.0 (CHVI)
Herbs	0.82		1.0					
Total	99.9 ± 0.21	99.0 ± 0.11	99.4 ± 1.14	87.7 ± 0.18	45.0 ± 3.20	45.7 ± 2.98	26.7 ± 1.20	24.8 ± 1.39
Annual IPAR (MJ m^{-2})[1]	1433	1419	2233	1706	1102	891	656	497

[1] Annual IPAR is the sum intercepted PAR for the year, when leaves were on the vegetation. Leaf-off and leaf transition periods varied by species. RUPR and POMU held 50% of their foliage through the winter, and ARTR held 67% of its foliage. Leaf-off and transition dates were noted in the field, and incident radiation on those dates was deducted from the annual sum accordingly.

Table II.3. Thresholds of stomatal conductance. Thresholds to vapor pressure deficit (VPD) and predawn xylem water potential ($\psi_{predawn}$) from other sources were used when they were not apparent in this study. A freezing temperature threshold of -2 °C (no radiation utilized for 24 h period) was used for all species (Larcher 1983). The $\psi_{predawn}$ thresholds apply for 24 h, and VPD thresholds apply for 1 h.

Thresholds	Full closure VPD (KPa)	Partial closure VPD (KPa)	Full closure $\psi_{predawn}$ (MPa)	Partial closure $\psi_{predawn}$ (MPa)
General[1]	2.5	1.5	-1.5	-1.0
Cascade Head				
ALRU[2]	1.8	1.3	-1.5	-1.4
RUSP	2.6[3]	1.2	NA[4]	NA
POMU	1.7	0.7	-4.0[5]	-3.3[5]
Corvallis				
PSME	1.5	–	-2.0	-1.5
RUPR	2.7	2.4	-0.7	-0.5
POMU	1.7	1.0	-4.0	-3.3
Sisters				
JUOC	1.4	1.1	-3.0[6]	-1.5[6]
ARTR	1.9	1.0	-4.5[7]	-1.5[7]
CHVI	1.4	1.1	-4.5[7]	-1.5[7]

[1] Source is Runyon et al. (1993), for major tree species in Oregon.

[2] Source is Shengjun Lu (1989) on *Alnus rubra* (ALRU) at Cascade Head.

[3] Thresholds for *Rubus spectabilis* (RUSP) if project boundary line out to maximum conductance at stomatal closure (10 mmol m^{-2} s^{-1}; Jones 1983).

[4] A threshold did not appear to be reached, and other sources were not available.

[5] Threshold from *Polystichum munitum* (POMU) at Corvallis. A threshold did not appear to be reached at Cascade Head.

[6] Sources are Miller et al. (1991), and DeLucia and Schlesinger (1991).

[7] Sources are Miller (1988) and DeLucia and Schlesinger (1991).

Table II.4. Production and energy-conversion/energy-use efficiency. Above-ground biomass (± SE) and above-ground net primary production (ANPP) for the study sites, and energy-conversion efficiency (ε = ANPP/IPAR) and energy-use efficiency (ε_u = ANPP/IPAR$_u$).

Site	Total biomass (g m^{-2} y^{-1})	ANPP (g m^{-2} y^{-1})	ε	ε_u
Cascade Head (1)				
ALRU[1]	12030 ± 900	1170 ± 90	0.84	0.90
RUSP	242 ± 73	54 ± 7.2	1.82	2.16
POMU	85 ± 13	41 ± 6.4	2.99	4.54
Total	12357	1265	0.88	0.95
Cascade Head (1-O)				
RUSP	3468 ± 182	769 ± 49	0.54	0.64
Corvallis (2)				
PSME[1]	47120 ± 10300	1160 ± 250	0.55	0.97
RUPR	236 ± 43	144 ± 31	1.34	1.76
POMU	12 ± 2	6 ± 0.2	0.30	0.57
Total	47368	1310	0.59	1.02
Corvallis (2-O)				
RUPR	1017 ± 73	535 ± 19	0.31	0.41
Metolius (5)				
PIPO[1]	1490 ± 300	150 ± 30	0.19	0.62
PUTR	494 ± 42	129 ± 12	0.40	1.36
Total	1984	279	0.25	0.83
Metolius (5-O)				
PUTR	572 ± 48	150 ± 14	0.17	0.57
Sisters (6)				
JUOC[1]	1080 ± 280	120 ± 40	0.27	0.82
ARTR	86 ± 16	29 ± 6	0.25	0.78
CHVI	27 ± 5	6 ± 0.5	0.07	0.23
Total	1157	155	0.24	0.74
Sisters (6-O)				
ARTR	144 ± 9	39 ± 4	0.14	0.43
CHVI	59 ± 6	14 ± 1	0.06	0.22
Total	160	53	0.11	0.34

[1] After Runyon et al. 1993.

Table II.5. Reductions in intercepted photosynthetically active radiation due to environmental factors. The percent annual intercepted PAR (IPAR) that could not be utilized due to freezing temperature, drought, and vapor pressure deficit (VPD).

Site	Freezing Temperature (%)	Drought (%)	VPD (%)	Total (%)
Cascade Head				
ALRU	0	0	6.6	6.6
RUSP	0	0	15.4	15.4
POMU	0.6	0	33.4	34.0
Corvallis				
PSME	2.8	20.2	20.1	43.1
RUPR	1.7	14.5	7.7	23.9
POMU	1.6	6.4	39.9	47.9
Metolius				
PIPO[1]	36.0	13.0	20.0	69.0
PUTR[2]	12.5	23.2	34.6	70.3
Sisters				
JUOC	25.2	22.6	19.7	67.5
ARTR	16.6	19.6	31.6	67.8
CHVI	12.5	23.2	34.6	70.3

[1] After Runyon et al. 1993.

[2] CHVI thresholds applied to bitterbrush (PUTR).

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