Combining Remote Sensing and Climatic Data to Estimate Net Primary Production Across Oregon

Beverly E. Law; Richard H. Waring

COMBINING REMOTE SENSING AND CLIMATIC DATA TO ESTIMATE NET PRIMARY PRODUCTION ACROSS OREGON[1]

BEVERLY E. LAW AND RICHARD H. WARING
Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. A range in productivity and climate exists along an east–west transect in Oregon. Remote sensing and climatic data for several of the Oregon Transect Ecosystem Research Project (OTTER) forested sites and neighboring shrub sites were combined to determine whether percentage intercepted photosynthetically active radiation (%IPAR) can be estimated from remotely sensed observations and to evaluate climatic constraints on the ability of vegetation to utilize intercepted radiation for production. The Thematic Mapper Simulator (TMS) normalized difference vegetation index (NDVI) provided a good linear estimate of %IPAR ($R^2 = 0.97$). Vegetation intercepted from 24.8% to 99.9% of incident photosynthetically active radiation (PAR), and aboveground net primary production (ANPP) ranged from 53 to 1310 $g \cdot m^{-2} \cdot yr^{-1}$. The ANPP was linearly related to annual IPAR across sites ($R^2 = 0.70$). Constraints on the ability of each species to utilize 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 semiarid juniper woodland and shrub sites to 97% at the maritime coastal sites. Energy-use efficiency (ε_u), calculated from aboveground production and IPAR modified by the environmental limits, averaged 0.5 g/MJ for the shrub sites and 0.9 g/MJ for the forested sites.

Key words: Alnus rubra; climate; intercepted photosynthetically active radiation; modelling; net primary production; Pinus ponderosa; Pseudotsuga menziesii; shrubs; understory; western Oregon.

INTRODUCTION

Ecological changes are occurring on 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 models require specific measurements not easily attainable over extensive regions (Ågren et al. 1991). Remote sensing does not suffer from this constraint, so models are being designed to evaluate regional to global patterns of key ecosystem characteristics, such as primary production, through the use of remotely sensed data (Running 1994).

Net primary production (NPP) has been linked to climatic patterns by approaches ranging from simple correlations to sophisticated simulation models. An approach that has been proposed by investigators on the Oregon Transect Ecosystem Research (OTTER) project involves the use of remotely sensed estimates of canopy light interception (Goward et al. 1994*b*) and an energy-use efficiency model (Runyon et al. 1994) to estimate NPP. The study reported here applied this approach to several OTTER sites, including forest understory shrubs and herbs in the estimates, and to nearby sites occupied primarily by shrubs. The purpose was to evaluate effectiveness of the approach across plant life forms.

The percentage of incident photosynthetically active radiation intercepted by vegetation (%IPAR), and potentially used for photosynthesis, is a near-linear to linear function of the normalized difference vegetation index (NDVI) calculated from reflectance in the near infrared (NIR) and red (R) portion of the electromagnetic spectrum (Asrar et al. 1994). Incident PAR can be estimated from meteorological stations, or from satellite sensors such as the geostationary satellite (GOES), and the Total Ozone Mapping Spectrometer (TOMS; Gautier et al. 1980, Eck and Dye 1991). 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. Studies have shown that net primary production is linearly related to annual IPAR (megajoules per square metre per year) under ideal conditions. An empirical model developed by Monteith (1977) and others is:

$$NPP = IPAR \cdot \varepsilon, \qquad (1)$$

where ε is energy-conversion efficiency of 1–5 g of dry matter produced per megajoule of energy absorbed. The ε value may vary when environmental conditions are less than favorable for growth. Landsberg (1983) and Prince (1991) have suggested that environmental modifiers that act on an optimal ε should be added to the model to account for environmental effects on the efficiency with which absorbed radiation is utilized. For operational purposes, an explicit formulation has

TABLE 1. Characteristics of study sites, including percentage cover and aboveground net primary production of dominant species (ANPP).

		Site					
		Cascade Head		Corvallis		Metolius	
Site number: Physiographic province:		Forested (1)	Shrub (1-O)	Forested (2)	Shrub (2-O)	Forested (5)	Shrub (5-O)
		Western coast range		Interior valley		Eastern high Cascades	
Feature							
	Tree:	*Alnus rubra*		*Pseudotsuga menziesii*		*Pinus ponderosa*	
% cover		>90		>90		21	
ANPP (g·m^{-2}·yr^{-1})*		1170 ± 90		1160 ± 250		150 ± 30	
	Shrub:	*Rubus spectabilis*	*Rubus spectabilis*	*Rubus procerus*	*Rubus procerus*	*Purshia tridentata*	*Purshia tridentata*
% cover		32.4	100	91.7	100	30.9	35.8
ANPP (g·m^{-2}·yr^{-1})*		54 ± 7.2	769 ± 49	144 ± 31	535 ± 19	129 ± 12	150 ± 14
	Herb:	*Polystichum munitum*		*Polystichum munitum*			
% cover		35.2		4.9			
ANPP (g·m^{-2}·yr^{-1})*		41 ± 6.4		6 ± 0.2			
Total ANPP (g·m^{-2}·yr^{-1})		1265	769	1310	535	279	150
Total biomass (g·m^{-2}·yr^{-1})		12357	3468	47368	1017	1984	572

* Mean ± 1 SE.

been proposed (Runyon et al. 1994) which applies environmental modifiers to IPAR estimates:

$$\text{NPP} = [\text{IPAR} \cdot f(T) \cdot f(D) \cdot f(\text{VPD})] \cdot \varepsilon_u, \qquad (2)$$

where the environmental limits to production are freezing temperatures (T), drought (D), and high vapor pressure deficit (VPD). The environmental modifiers are determined from the fraction of annual IPAR that is intercepted when these environmental conditions occur. This may result in a constant energy-use efficiency coefficient (ε_u) for natural perennial C_3 vegetation (C_4 plants can have a higher ε_u [Prince 1991]), and allow broad application of the model to diverse climatic conditions and vegetation types.

Runyon et al. (1994) showed that ε for aboveground NPP (ANPP) by trees varied from 0.18 to 0.92 g/MJ, with no linear relationship between ANPP and IPAR across a range of forest types and climatic conditions. They applied environmental limitations in the form shown in Eq. 2 to estimate the extent to which trees utilized IPAR. The generalized environmental thresholds were derived from previous studies on conifers. The approach was based on the premise 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, and annual growth is reduced (Downton et al. 1988). This method linearized the relationship between ANPP and IPAR, and resulted in a generally constant ε_u averaging 0.8 g/MJ for ANPP. The ability to estimate ANPP or NPP from IPAR has the potential to be ap-

plied to extensive areas through remote sensing estimates of IPAR (Prince 1991).

The objectives of the study reported here were to: (1) evaluate whether remotely sensed observations of canopy reflectance might be used to estimate the percentage of incident PAR intercepted by forested sites (overstory trees and understory shrubs and herbs) and nearby shrub sites, (2) evaluate the relationship between ANPP and IPAR across these sites, (3) determine if the application of general environmental thresholds in Eq. 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.

METHODS

Study sites

This study was conducted at four of the Oregon Transect Ecosystem Research project sites. The Oregon transect consists of nine sites, two of which are fertilized subsites, in a range of climatic conditions and primarily coniferous forest types. The sites are located along a 250-km west to east transect at ≈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 1994). The present study is one of several continuation studies

TABLE 1. Continued.

Site	
Sisters	
Forested (6)	Shrub (6-O)
High lava plain	
Juniperus occidentalis 6.7 120 ± 40	
Artemisia tridentata 9.0 29 ± 6	Artemisia tridentata 11.8 39 ± 4
Chrysothamnus viscidiflorus 3.6 6 ± 0.5	Chrysothamnus viscidiflorus 8.2 14 ± 1
155 1157	53 160

conducted at the OTTER sites (Law 1993). Table 1 summarizes the study sites used here and species sampled at each site.

In order to apply the model in Eq. 2 to other vegetation types in addition to forests, the sites used in this study included four forested OTTER sites and four nearby shrub sites with areas ≥50 × 50 m. 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 yr ago, 2–2.5 m tall *R. spectabilis* now dominate. The Corvallis forested site (site 2) has Douglas-fir (*Pseudotsuga menziesii*), Himalaya blackberry (*Rubus procerus* Muell.), and swordfern. The neighboring shrub site (site 2-O) has dense, 2–2.5 m tall *R. procerus,* which is an introduced clonal shrub species now well established in western Oregon. The OTTER Metolius site (site 5) is ponderosa pine forest (*Pinus ponderosa*), with bitterbrush (*Purshia tridentata* [Pursh] DC.), a deciduous shrub, and the adjacent shrub area is primarily *P. tridentata* (site 5-O). The *P. ponderosa* forest is very open, with 31% cover of *P. tridentata* (Law and Waring 1994). The Sisters site (site 6) is a juniper woodland (*Juniperus occidentalis*) with sagebrush (*Artemisia tridentata* Nutt.), a semi-deciduous shrub, and green rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), a deciduous shrub. The adjacent shrub site (site 6-O) has *A. tridentata* and *C. viscidiflorus*. The Sisters sites have relatively dispersed canopy cover.

Cascade Head is characterized by a cool, moist mar-

itime climate most of the year. Corvallis 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, where climate is more continental; summers are hot and dry, and winters are more severe.

Remote sensing measurements

Remotely sensed data were acquired from a Daedalus Thematic Mapper Simulator (TMS) flown on a NASA ER-2 aircraft in support of the OTTER project. The sensor was flown at an altitude of ≈20 km mean sea level on 25 June 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. 1994). Sunphotometer measurements of aerosol optical depth were made at the site within 2 h 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. The normalized difference vegetation index (NDVI = [NIR − R]/[NIR + R]) was calculated from TMS NIR (wavelength: 760–900 nm) and R (wavelength: 630–690 nm) channels for each 25-m pixel (minimum of four pixels per site), then averaged. The relationship between June site-averaged NDVI and %IPAR by vegetation was evaluated.

Climatic measurements

Meteorological stations (Campbell Scientific Instruments, Logan, Utah, USA) were placed in open areas near each site during the NASA-funded OTTER project in 1990 (Runyon et al. 1994). The stations measured incident solar radiation (wavelength: 400–1200 nm), air temperature, precipitation, and relative humidity, and recorded integrated hourly values. Though field data on vegetation were collected in 1992, the meteorological stations were operational from only August to December 1992, so the complete data set from January to December 1990 was used with the assumption (later tested) that the climate for the 2 yr was similar. Relative humidity and air temperature data allowed calculation of hourly vapor pressure deficit. Incident PAR was estimated as 50% of incident solar radiation (Monteith and Unsworth 1990).

Intercepted photosynthetically active radiation

The %IPAR was estimated at each site by measuring incident PAR (wavelength: 400–700 nm; Q_0) and below-canopy PAR (Q_t) with a sunfleck ceptometer (SF-80, Decagon Devices, Pullman, Washington, USA). Measurements were made on cloudless days in July 1992, between 1200 and 1400 local solar time. Sam-

TABLE 2. Climate data, percentage intercepted photosynthetically active radiation (IPAR), and total annual IPAR for the study sites.

	Site					
	Cascade Head		Corvallis		Metolius	
	1	1-O	2	2-O	5	5-O
1990 precip. (cm)	251	251	98	98	54	54
1990 mean annual temperature (°C)	10.1	10.1	11.2	11.2	7.4	7.4
Annual incident PAR (MJ/m²)	1935	1935	2267	2267	2735	2735
Percentage IPAR						
Trees	97.0		92.9		28.6	
Shrubs	2.08	99.0	5.5	87.7	16.4	45.7
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
Annual IPAR (MJ/m²)*	1433	1419	2233	1706	1102	891

* Annual IPAR is the sum of intercepted PAR for the portion of the year when leaves were attached.
† ARTR = *Artemisia tridentata*; CHVI = *Chrysothamnus viscidiflorus*.
‡ Mean ± 1 SE.

pling was conducted on a systematic grid, with 50–200 grid points at a site, depending on homogeneity of canopy cover. The %IPAR was calculated as in Runyon et al. (1994; %IPAR = $[1 - Q_t/Q_0] \cdot 100$) with the exception that canopy transmittance (Q_t/Q_0) values were logarithm-transformed in the present study prior to calculation of site median transmittance. This method adjusts for lognormal distribution due to spatial variability of canopies (Lang and Yueqin 1986).

The %IPAR was assumed to be constant through the year. This may underestimate 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 leaf area index (LAI) during the dormant season when incident radiation is lowest will have minimal effect on annual IPAR estimates (Runyon et al. 1994, Spanner et al. 1994). Daily %IPAR was adjusted for each deciduous and semi-deciduous species according to leaf duration recorded in the field (Law 1993).

The %IPAR by understory at the forested sites was estimated by applying the %IPAR calculated from above and below understory canopy measurements to the percentage 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 (Table 2).

Physiological measurements

Stomata respond to radiation, air temperature, vapor pressure deficit (VPD), and soil water supply (Jones 1992). Response to freezing temperatures is well documented (Larcher 1983), so this variable was not measured. In applying freezing temperature constraints to the ability to use intercepted light, stomata were as-

sumed to close at −2°C for all species for the following 24 h, as in Runyon et al. (1994), and IPAR for those periods was subtracted from the total annual IPAR.

Physiological measurements were made May–early October 1992. Stomatal conductance had not been measured in the Runyon et al. (1994) study, so physiological measurements were made in the present study on major tree species at the study sites, in addition to shrubs and herbs. To evaluate plant response to drought, predawn xylem water potential ($\Psi_{predawn}$) was measured; stomatal conductance was measured later that morning. 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), so the relationship between stomatal conductance and $\Psi_{predawn}$ was compared across tree, shrub, and herb species at the sites.

Xylem water potential was measured with a pressure chamber before sunrise (0400–0530) on twigs from 5 to 10 plants of each species listed in Table 1 (Scholander et al. 1965). Measurements were made at monthly intervals (biweekly in July) at the same locations, but not on the same individual plants within sites. Maximum stomatal conductance was plotted against mean $\Psi_{predawn}$ observed that day for each species.

Stomatal conductance was measured with a steady-state porometer (LI-COR, Model LI-1600, Lincoln, Nebraska, USA). Ten to 15 plants of each species were sampled in the same area and on the same days as $\Psi_{predawn}$ measurements and on additional dates for evaluation of VPD influence on conductance. Stomatal conductance was measured between 0800 and 1200 Pacific Daylight Time when maximum diurnal stomatal conductance typically occurs (DeLucia and Schlesinger 1991). Sunlit intact foliage was sampled at ambient environmental conditions on clear days. Stomatal conductance was calculated on a projected leaf

TABLE 2. Continued.

Site	
Sisters	
6	6-O
22	22
9.1	9.1
2735	2735
16.5	
5.7 (ARTR)†	13.8 (ARTR)
4.5 (CHVI)†	11.0 (CHVI)
26.7 ± 1.20	24.8 ± 1.39
656	497

area basis (LI-COR, Model LI-1300; Farquhar and von Caemmerer 1982).

Humidity was measured near the plant canopies for which stomatal conductance was measured, at least every 30 min, to estimate stomatal response to vapor pressure deficit. A wet- and dry-bulb Assmann psychrometer was used to acquire temperatures for calculation of humidity and VPD (Monteith and Unsworth 1990).

Stomatal conductance was plotted against VPD and against mean $\Psi_{predawn}$ for each tree, shrub, and herb species in order to define species-specific thresholds.

Boundary-line analysis was used to determine maximum stomatal conductance for a given VPD or $\Psi_{predawn}$. Boundary-line analysis allows pooling of data from many measurement periods and environmental conditions to identify general patterns of response to VPD or $\Psi_{predawn}$ when other factors are not limiting (DeLucia and Schlesinger 1991). Limiting values of VPD and $\Psi_{predawn}$ for 50% 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. Conductance observed when stomata were completely closed is assumed to be cuticular diffusion, which can vary among species (Jones 1992).

Monthly $\Psi_{predawn}$ values for a species were interpolated to estimate daily $\Psi_{predawn}$. When daily $\Psi_{predawn}$ reached half or complete stomatal closure thresholds, 50 or 100% IPAR was summed for the next 24 h and reduced from the annual total IPAR as in Runyon et al. (1994). After sequentially accounting for leaf duration, freezing temperatures, then drought, VPD thresholds were applied at hourly intervals. This hierarchical approach allowed for interaction between intermediate levels of stomatal closure from drought and VPD. An SAS program was written for application to hourly meteorological station data and calculation of annual IPAR with sequential reductions in IPAR over the year to get modified IPAR (SAS Institute 1987). The program was run twice for species at each site, changing only the $\Psi_{predawn}$ and VPD constraints from the general environmental thresholds to species-spe-

TABLE 3. Threshold values of vapor pressure deficit (VPD) and predawn water potential ($\Psi_{predawn}$) on stomatal conductance. Thresholds 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).

Thresholds	Full closure VPD (kPa)	Partial closure VPD (kPa)	Full closure $\Psi_{predawn}$ (MPa)	Partial closure $\Psi_{predawn}$ (MPa)
General*	2.5	1.5	−1.5	−1.0
Cascade Head				
Alnus rubra†	1.8	1.3	−1.5	−1.4
Rubus spectabilis	2.6‡	1.2	NA§	NA
Polystichum munitum	1.7	0.7	−4.0‖	−3.3‖
Corvallis				
Pseudotsuga menziesii	1.5	⋯	−2.0	−1.5
Rubus procerus	2.7	2.4	−0.7	−0.5
Polystichum munitum	1.7	1.0	−4.0	−3.3
Sisters				
Juniperus occidentalis	1.4	1.1	−3.0¶	−1.5¶
Artemisia tridentata	1.9	1.0	−4.5#	−1.5#
Chrysothamnus viscidiflorus	1.4	1.1	−4.5#	−1.5#

* General thresholds from Runyon et al. (1994) for major tree species in Oregon.
† Source is Lu (1989) on *Alnus rubra* (ALRU) at Cascade Head.
‡ Threshold for *Rubus spectabilis* (RUSP) if project boundary line out to maximum conductance at stomatal closure (10 mmol·m⁻²·s⁻¹; Jones 1992).
§ Threshold did not appear to be reached; other sources were not available.
‖ Threshold from *Polystichum munitum* (POMU) at Corvallis.
¶ Sources are DeLucia and Schlesinger (1991) and Miller et al. (1991).
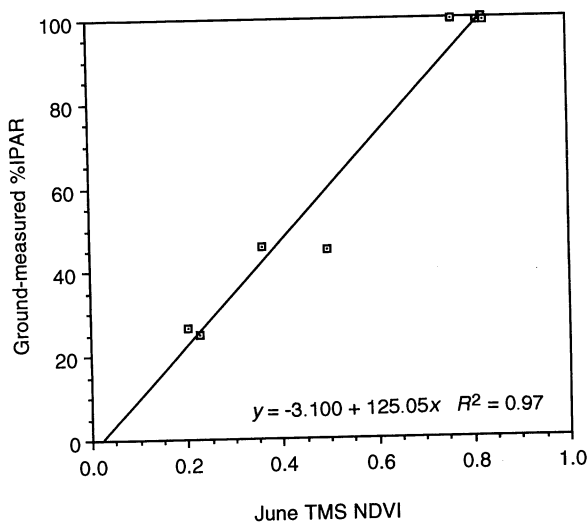# Sources are Miller (1988) and DeLucia and Schlesinger (1991).

FIG. 1. The relationship between the percentage of incident photosynthetically active radiation intercepted (%IPAR) at eight sites and normalized difference vegetation index (NDVI) recorded by the Thematic Mapper Simulator.

cific thresholds for trees, shrubs, and herbs (Table 3). Runyon et al. (1994) applied the general thresholds to trees only.

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 bounded by the ocean and a road, site 2 is on a slope adjacent to an urban area, and both sites are small enough for the understory environments to be coupled to the atmosphere due to strong edge influences (Black and Kelliher 1989, Franklin et al. 1993). The Metolius and Sisters forested sites have very dispersed canopies; thus the understory environments at these sites are probably closely coupled to the atmosphere.

Annual IPAR modified by species-specific environmental thresholds were compared to IPAR modified by general thresholds by evaluating the relationship between site-level aboveground NPP (overstory plus understory) and the modified IPAR that resulted from each method. To determine if there were separate relationships between ANPP and species-specific modified IPAR for shrub vs. forested sites, separate regression lines were calculated. The slopes and intercepts were compared using the Giant Size Regression (GSR) technique (Cunia 1973).

Aboveground net primary production

Annual aboveground net primary production (grams per square metre per year) includes new foliage, stem, and branch production. No current production losses to morality were noted. Ten to 30 plants of each shrub and herb species were randomly selected for harvest at the sites. Himalaya blackberry (*Rubus procerus*) was harvested in 1-m² plots due to its trailing habit (M. Newton, Oregon State University, *personal communication*). Sample sizes were based on variability in dry biomass from pre-season harvests (Eckblad 1991).

Shrubs and herbs were harvested at the end of the growing season, before litterfall loss. This method may result in underestimating ANPP when there is an overlap of production and senescence (Jones et al. 1992). Current year's aboveground growth and the remaining biomass were oven-dried at 70° until mass had stabilized. Annual production per unit area (grams per square metre per year) was calculated from number of shrubs per square metre and cover estimates using the line-intercept method (Deuser and Shugart 1978). For the forested sites, ANPP by trees (Runyon et al. 1994) was summed with understory ANPP.

RESULTS

Thematic Mapper Simulator NDVI observations and %IPAR

The Oregon climate from west to east is progressively drier, and summer and winter temperatures are progressively more extreme. Vegetation intercepted from 99.9% of incident PAR at the Cascade Head alder site to 26.7% and 24.8% at the Sisters juniper and shrub sites east of the Cascade mountains (Table 2). Understory %IPAR was lowest at the two forested sites west of the Cascades (2.9% at site 1 and 6.5% at site 2) and accounted for more of the total %IPAR in the open forest canopies east of the Cascades. At Sisters site 6, understory intercepted 10.2% of incident PAR, and the overstory juniper intercepted 16.5%. Annual IPAR ranged from 497 MJ·m^{-2}·yr^{-1} at site 6-O to 2233 MJ·m^{-2}·yr^{-1} at site 2.

The TMS NDVI observations (Fig. 1) 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 higher for the shrub vegetation at the Corvallis and Sisters sites, the Cascade Head alder and salmonberry sites had the same NDVI (0.83), and the Metolius ponderosa pine site 5 had a higher NDVI than bitterbrush at site 5-O (NDVI = 0.50 and 0.36, respectively).

There was a strong linear relationship between ground-measured %IPAR across sites and June TMS NDVI measurements (Fig. 1; %IPAR = −3.1 + [125.05·NDVI], R^2 = 0.97). The %IPAR at forested sites included overstory and understory contributions. Results compare closely with a similar analysis performed by Goward et al. (1994b) when they used July satellite Advanced Very High Resolution Radiometer (AVHRR) NDVI, and %IPAR by trees across five OTTER sites (%IPAR = −4.0 + [121·NDVI], R^2 = 0.99).

In their analysis, the ponderosa pine site was excluded because the large amount of understory probably contributed to NDVI, and understory light interception was not included in the site %IPAR estimates.

Aboveground net primary production

Aboveground net primary production varied from 53 $g \cdot m^{-2} \cdot yr^{-1}$ at site 6-O to 1310 $g \cdot m^{-2} \cdot yr^{-1}$ at site 2 (overstory plus understory; Table 1). Of the shrub sites, the salmonberry site (site 1-O) had the highest ANPP at 769 $g \cdot m^{-2} \cdot yr^{-1}$. The bitterbrush 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.

Stomatal response to drought and vapor pressure deficit

The relationship between maximum stomatal conductance of all species and VPD was generally curvilinear, with conductance often decreasing rapidly at first, and then leveling off as VPD increased (Fig. 2). Stomatal closure in response to high VPDs appeared to occur between 1.5 and 2.0 kPa for most species (Table 3). This is close to the general thresholds Runyon et al. (1994) selected from the literature (1.5 kPa for partial closure and 2.5 kPa for complete stomatal closure; Table 3). Stomatal closure did not occur during measurement of *Alnus rubra* and *Rubus spectabilis* at Cascade Head, and VPDs reached only 1.2 and 1.5 kPa, respectively. Cascade Head is on the coast and is humid for most of the year.

Seasonal variation in predawn water potential of each species at the forested sites is shown in Fig. 3. None of the species at Cascade Head had $\Psi_{predawn}$ values more negative than -1.0 MPa. The greatest differences in $\Psi_{predawn}$ among species occurred at Corvallis. The lowest $\Psi_{predawn}$ values for the year were in August and September at all sites, the typical timing of extreme drought in Oregon.

Boundary-line analysis of stomatal response to $\Psi_{predawn}$ proved difficult, due to the limited data set. Corvallis was the only site where $\Psi_{predawn}$ thresholds could be determined from the data (Table 3). Complete stomatal closure apparently occurred at -2.0 MPa for *Pseudotsuga menziesii,* the same value obtained by Running (1976) in Oregon, and partial closure was at -1.5 MPa. The stomata of the shrub *Rubus procerus* appeared to be more sensitive to $\Psi_{predawn}$, with closure at -0.7 MPa. Swordfern (*Polystichum munitum*) stomata closed at ≈ -4.0 MPa. For purposes of applying species-specific thresholds to conductance to modify IPAR, thresholds from other sources were obtained when they were not apparent from this study (Table 3).

To evaluate potential error in the use of 1990 meteorological station radiation data, 1992 incident ra-
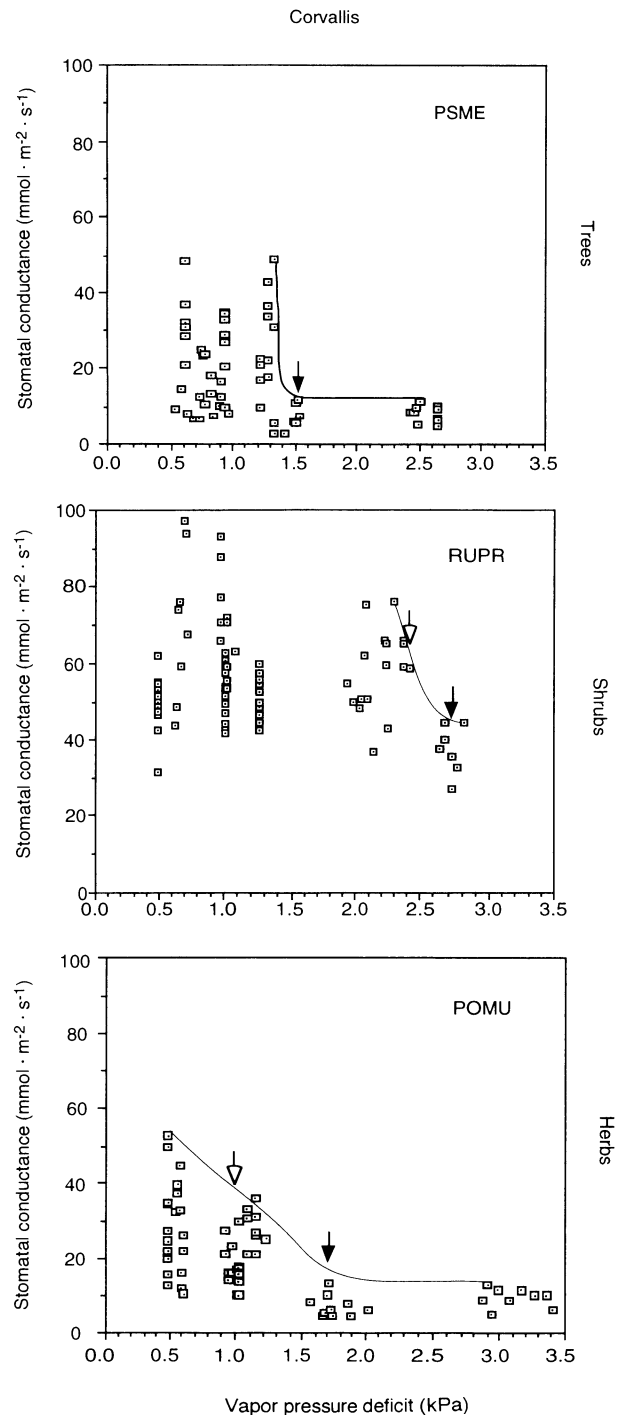

FIG. 2. Stomatal conductance vs. vapor pressure deficit (VPD) for trees (PSME = *Pseudotsuga menziesii*), shrubs (RUPR = *Rubus procerus*), and herbs (POMU = *Polystichum munitum*) at the Corvallis site. Boundary lines were drawn through the maximum stomatal conductance for a given VPD. Points below the line are assumed to be limited by factors other than VPD. Complete (closed arrows) and partial (open arrows) stomatal closure in response to VPD and predawn water potential were determined from boundary line analysis of field data from each site to obtain species-specific modifiers to IPAR.
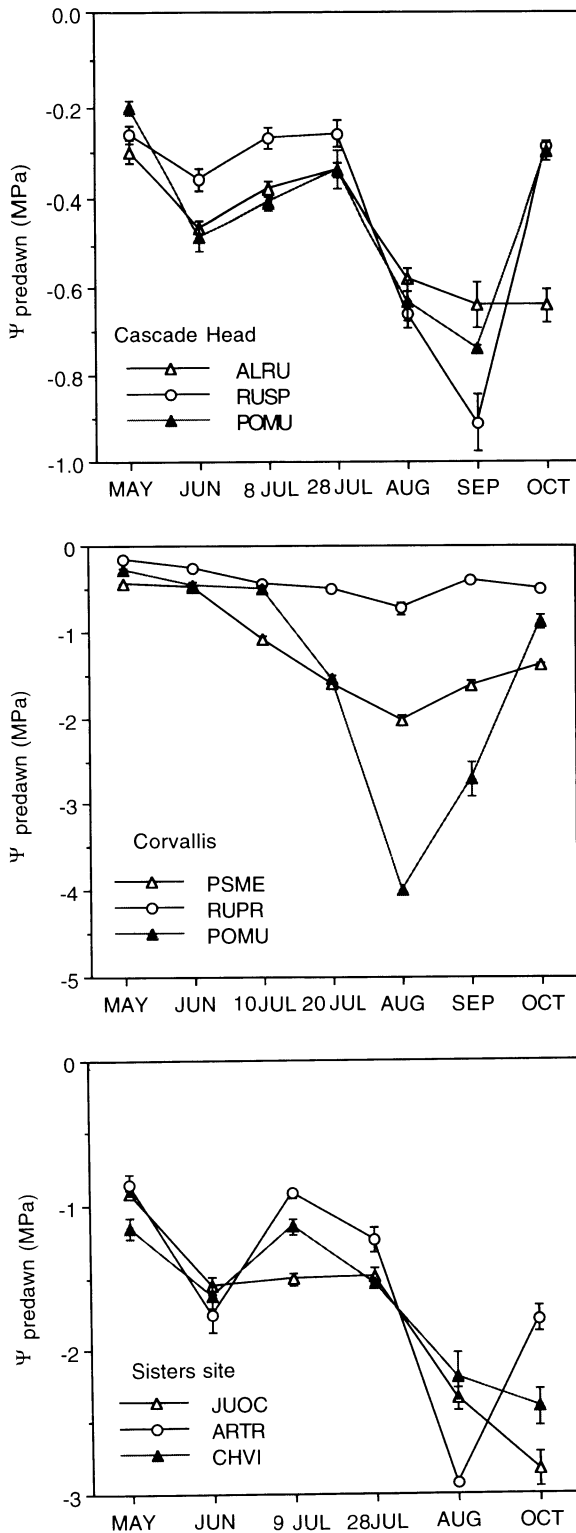
diation integrated over the dates when $\Psi_{predawn}$ limited stomatal conductance for each species was compared to 1990 radiation. There was at most a 2% difference in the integrated radiation between the 2 yr for all species. Because diurnal variation in VPD is greatest in June–September, and meteorological data were not available for January–July 1992, it was more reasonable to use the complete meteorological data set for 1990.

Energy-conversion and energy-use efficiency

The annual IPAR accounted for 70% of the variation in ANPP across sites (Fig. 4). Energy-conversion efficiency (ε = ANPP/IPAR) increased from east to west (0.11 at site 6-O to 0.88 at site 1; Fig. 5). When the general environmental thresholds were applied to IPAR (Eq. 2) as suggested by Runyon et al. (1994), they did not improve the R^2 of the relationship between ANPP and IPAR (R^2 = 0.68; Fig. 6), but the intercept approached 0. The IPAR modified by species-specific thresholds only slightly improved the relationship between ANPP and IPAR (R^2 = 0.73; Fig. 6). The ε_u values varied from 0.34 at site 6-O to 1.02 at site 2.

To evaluate the possibility of different energy-use efficiencies between life forms, separate linear regressions were applied for shrub vs. forested sites in the relationship between ANPP and modified IPAR (Fig. 7). Enough data were available from sites 5 and 5-O to include them in the relationship by applying the general constraints to ponderosa pine, and the rabbitbrush constraints to bitterbrush. Comparison of the regression lines showed that the slopes (predicted ε_u) of shrub vs. forested sites 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. 5). 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. (1994) obtained for trees at nine OTTER sites (seven were coniferous, including two fertilized subsites). There may be a fairly consistent ε_u for aboveground production by the shrub sites that is less than ε_u for the forested sites.

The relative contribution of the environmental factors for determination of ε_u are shown in Table 4. Among sites, the reductions in IPAR due to the species-specific environmental limits ranged from 6.6% for alder at Cascade Head to 70.3% for rabbitbrush at Sisters. The

FIG. 3. Seasonal variation in predawn xylem water potential ($\Psi_{predawn}$) at three sites (mean ± 1 SE). Daily $\Psi_{predawn}$ values were interpolated from these data and used as modifiers to IPAR when $\Psi_{predawn}$ dropped below specified thresholds. Measurements were made on at least 5–10 plants per species

on each sampling date to assure a standard error of ≈0.05 MPa. ALRU = *Alnus rubra*, RUSP = *Rubus spectabilis*, POMU = *Polystichum munitum*, PSME = *Pseudotsuga menziesii*, RUPR = *Rubus procerus*, JUOC = *Juniperus occidentalis*, ARTR = *Artemisia tridentata*, and CHVI = *Chrysothamnus viscidiflorus*.

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, and no reduction from drought for all three species. Runyon et al. (1994) found similar reductions in IPAR (8% total, mostly due to VPD) at the OTTER Cascade Head Sitka spruce–hemlock forest. Swordfern at Cascade Head and Corvallis had the largest reductions in IPAR among species at the two sites. At Corvallis, blackberry had the lowest reduction in IPAR, primarily from drought.

DISCUSSION

The June NDVI calculated from remotely sensed observations appears to provide a good estimate of maximum %IPAR (Fig. 1). This agrees with previous studies at the OTTER sites with various sensors, such as the AVHRR NDVI across forested sites, and field spectrometry of understory species at the ponderosa pine site (Goward et al. 1994b, Law and Waring 1994). 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, should not be ignored. From field spectra of scene components, Goward et al. (1994a) found that, as canopy NDVI decreased from west (Cascade Head) to east (Sisters) across the Oregon transect, so did the background soil/litter NDVI. They suggested that this spatial correlation of canopy and background NDVI may indicate general regional en-

FIG. 5. The range in energy-conversion efficiency (ε = ANPP/IPAR) and energy-use efficiency (ε_u = ANPP/modified IPAR) across sites, from west (sites 1 and 1-O) to east (sites 6 and 6-O). Modified IPAR is defined in the Fig. 6 legend. Sites 1, 2, 5, and 6 are the forested sites, and -O are the shrub sites at the same geographic location.

vironmental conditions, and therefore scene NDVI may still be diagnostic of vegetation light interception.

On an annual basis, growth would appear to be linearly related to IPAR if drought, vapor pressure deficit, and temperatures are not limiting to stomatal conductance and photosynthetic rates. The linear relationship between ANPP and IPAR observed in this study (Fig. 4), before modifying IPAR by these factors, may be due to the large effect of leaf duration on IPAR by deciduous canopies that 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). The large improvement in the relationship between tree ANPP and IPAR observed by Runyon et al. (1994) when the environmental limits had been used to modify IPAR, may have been largely due to the dominance of evergreen trees at eight of the nine sites used in their study.

The application of general environmental thresholds to modify IPAR (Fig. 6) did not account for the variation in ANPP across sites, but the intercept approached 0, as would be expected once environmental constraints on the harsher sites were taken into account (Fig. 4 vs. Fig. 6). Thus, the approach of constraining IPAR by environmental limits makes more biological sense when both evergreen and deciduous vegetation are included in estimates of production. Only minor improvements resulted in the relationship between ANPP and IPAR when species-specific modifiers were applied to IPAR, suggesting that when different life forms are combined in area estimates of production, additional factors may be important.
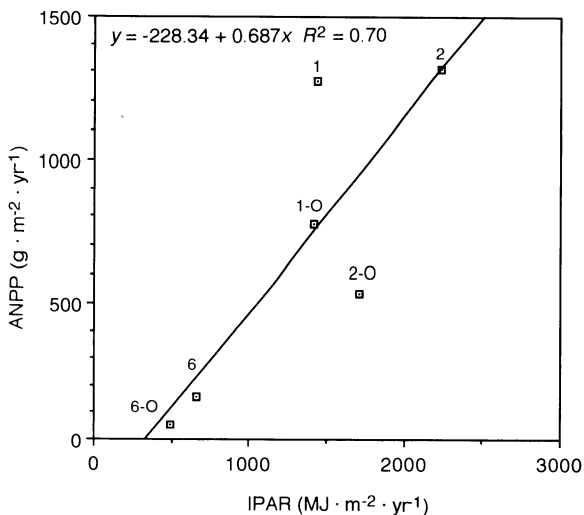
FIG. 4. The relationship between annual aboveground net primary production (ANPP) and annual intercepted photosynthetically active radiation (IPAR) at three shrub and three forested sites (overstory plus understory). Site 1 = Cascade Head alder; site 1-O = Cascade Head salmonberry; site 2 = Corvallis Douglas-fir; site 2-O = Corvallis Himalaya blackberry; site 6 = Sisters juniper woodland; site 6-O = sagebrush and rabbitbrush shrub.
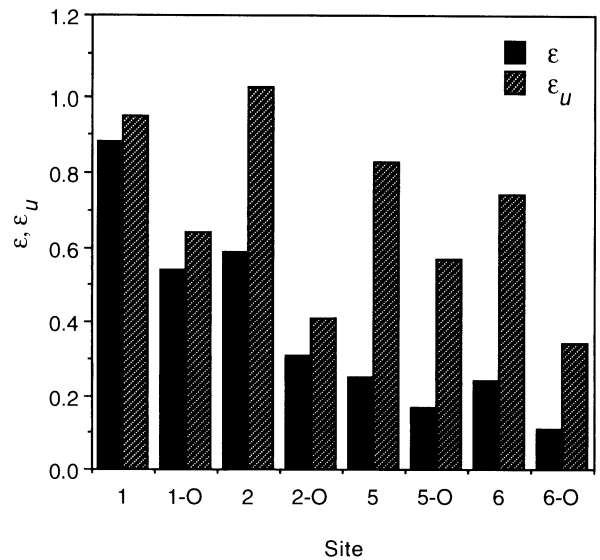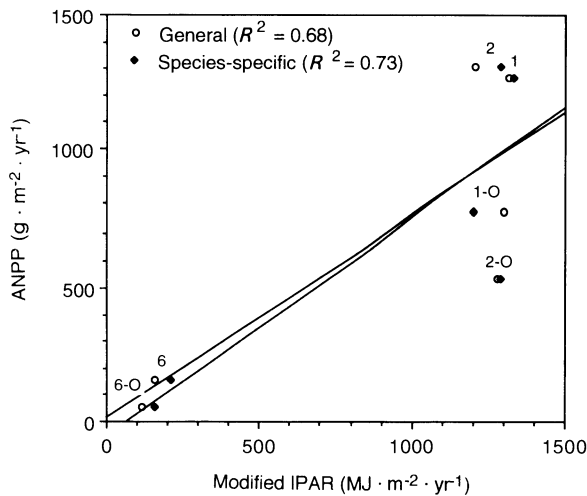
FIG. 6. The relationship between aboveground net primary production (ANPP) and modified annual intercepted photosynthetically active radiation at six sites (Modified IPAR, values resulting when environmental constraints were applied as modifiers of intercepted photosynthetically active radiation). The general modifiers to IPAR were obtained from Runyon et al. (1994), and species-specific modifiers were from this study or other sources. The regression equation for the general modifiers was ($y = 13.165 + 0.746x$), and for species-specific modifiers was ($y = -53.408 + 0.805x$).

annual partial replacement compared to permanent wood production by trees (Schulze et al. 1986).

Shrubs generally have higher root : shoot ratios than trees. A larger fraction of shrub production is in root growth, which has persistence value for access of soil water, and for survival from fire, browsing, and drought, all of which may damage or destroy shoots (Whittaker and Woodwell 1968). Küppers (1984) observed that hydraulic conductance per sapwood unit area was higher in shrub species (e.g., *Rubus* and *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 semiarid 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 may result in a more negative slope of the relationship between ANPP and IPAR for shrubs than for trees.

The practical application of the energy-use efficiency model to estimate production in coarse-scale ecological studies relies on our ability to improve it while still maintaining its simplicity. It requires a combination

Fig. 7 indicates that perhaps a lower energy-use efficiency exists for aboveground production by shrub areas than forested areas. Although the data are limited in this study, previous authors have indicated reasons why this may be the case. Field (1991) mentioned that ε in Eq. 1 may vary due to photosynthetic pathway, canopy architecture, developmental stage, and vegetation density (i.e., competition for resources). Running (1990) suggested that once environmental components had been separated from biochemical components of ε (Eq. 2), variation in the resulting ε_u should represent nutrition-related biochemical factors and fundamentally different physiology (e.g., C_3 and C_4 plants). A highly possible reason for variation in ε_u of aboveground production is life form differences in carbon allocation patterns, which may be reflected in total NPP (Field 1991).

Colonizers, such as *Rubus spectabilis,* have large rhizomes and are adapted to resprout after fire or cutting. The rhizomes of *R. spectabilis* fill unoccupied areas of stands, replacing dead or unproductive ramets. These rhizomes account for as much as 40% of the harvested plant biomass, excluding roots (Tappeiner et al. 1991). The trailing stems of *Rubus procerus* layer over older stems and allocate a large portion of their carbohydrates to new roots initiated from the layering stems (Schulze et al. 1986). The apparently low aboveground production by *R. procerus* could be partly due to its vine-like architecture, which may incur a large cost of
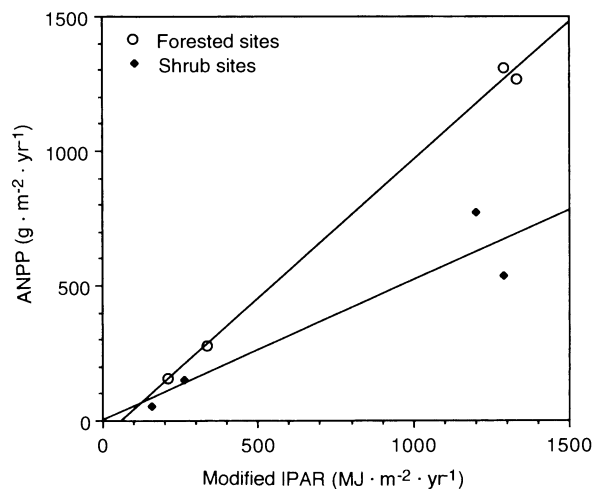

FIG. 7. The Oregon transect ponderosa pine site 5 (*Pinus ponderosa*) and an adjacent bitterbrush shrub site (*Purshia tridentata*; site 5-O) were added to the relationship between aboveground net primary production (ANPP) and modified intercepted photosynthetically active radiation (Modified IPAR [defined in Fig. 6 legend]). Forested and shrub sites were distinguished by separate regressions. The linear regression for forested sites is ($y = -63.787 + 1.03x$, $R^2 = 0.99$), with mean energy-use efficiency (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 4. The percentage annual intercepted PAR (IPAR) that could not be utilized due to freezing temperature, drought, and vapor pressure deficit (VPD).

Site	Temperature (%)	Drought (%)	VPD (%)	Total (%)
Cascade Head				
Alnus rubra	0	0	6.6	6.6
Rubus spectabilis	0	0	15.4	15.4
Polystichum munitum	0.6	0	33.4	34.0
Corvallis				
Pseudotsuga menziesii	2.8	20.2	20.1	43.1
Rubus procerus	1.7	14.5	7.7	23.9
Polystichum munitum	1.6	6.4	39.9	47.9
Metolius				
Pinus ponderosa*	36.0	13.0	20.0	69.0
Purshia tridentata†	12.5	23.2	34.6	70.3
Sisters				
Juniperus occidentalis	25.2	22.6	19.7	67.5
Artemisia tridentata	16.6	19.6	31.6	67.8
Chrysothamnus viscidiflorus	12.5	23.2	34.6	70.3

* After Runyon et al. (1994).
† CHVI thresholds applied to bitterbrush (PUTR).

of good environmental measurements, improved knowledge of carbon allocation patterns across life forms, and advances in remote sensing data analysis to estimate IPAR by dispersed canopies. For aboveground production estimates, stratification by vegetation type (e.g., grasslands, shrublands, and forests), and determination of a separate energy-use efficiency coefficient for each type may allow broad application of the model.

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