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REMOTE SENSING OF LEAF AREA INDEX AND RADIATION INTERCEPTED BY UNDERSTORY VEGETATION¹

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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} ($R^2 = 0.86$ for manzanita and 0.83 for bitterbrush), and the simple ratio of near infrared to red (SR) permitted a linear estimate of LAI ($R^2 = 0.86$ for manzanita and 0.74 for 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: *Arctostaphylos patula*; east-central Oregon; intercepted photosynthetically active radiation (IPAR); leaf area index (LAI); Oregon transect; OTTER project; *Purshia tridentata*; remote sensing; 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 (Spanner et al. 1990, Gholz et al. 1991). The process model, FOREST-BGC, requires LAI as a key structural variable to calculate transpiration, photosynthesis, and related ecosystem processes (Running 1994 [this issue]). 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 National Aeronautics and Space Administration (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 (NIR) due to intra- and inter-leaf scattering (Knipling 1970, Tucker 1979, Curran 1983). At the canopy level, multiple scattering between layers of vegetation increases NIR reflectance and is related to canopy geometry and leaf optical properties (Knipling 1970, Colwell 1974). Vegetation indices that include NIR 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 (Curran 1983, Tucker et al. 1985, Gholz et al. 1991).

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

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from remote sensing and ground measurements (Runyon et al. 1994 [this issue]). 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, 121°41' W, 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 $\approx 18\%$ of the total area, and represented 46% of the total vegetation, where scene components consisted of overstory, understory, shade, and soil or litter (Spanner et al. 1994 [this issue]). The pumice soils are considered to be minimally altered. Soils are classed as a dystric cryandept, a light-colored andic (high in ash content) inceptisol that is low in nutrients (P. Claycomb [Oregon State University], *personal communication*).

Sampling

Spectral reflectance data and data on the fraction of photosynthetically active radiation intercepted, f_{IPAR} , were collected on 23 bitterbrush and 27 manzanita plots 11–30 July 1991 (solar zenith angle 34° to 44°), on clear days from 1000 to 1500 Pacific daylight time (PDT). Sampling was conducted near midday to minimize shadow effects.

To obtain a range of leaf area indexes (LAIs) and f_{IPAR} , sample plots were created artificially by sticking shrub branches (≈ 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. Each plot was arranged to mimic the natural canopy architecture. A rectangular frame (16 \times 20 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 (35 \times 35 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 (foliage area/ground area, both in square centimetres). 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 ≈ 10 min to complete, which was well within the suggested 20-min interval for reference panel measurement (S. N. Goward, *personal communication*). The eight-scan average option on the spectrometer was used for all radiance measurements.

A spectrometer (SE-590, Spectron Engineering, Denver, Colorado, USA) 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 sight, 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 centimetre 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 sunflecks 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_i) was sampled on a 4 \times 5 grid (20 observations), spaced evenly under the 16 \times 20 cm sample frame. Twenty instantaneous readings were averaged per observation. Ten observations of incident PAR (Q_0) were taken immediately afterwards above the canopy. Canopy transmittance was calculated as the ratio (Q_i/Q_0). 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 mass for the plant material from each plot was obtained (FM_{plot}), then a subsample was selected and weighed (FM_{s1}). Leaves were removed from the subsample and weighed ($FM_{LVS_{s1}}$). 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 masses then obtained ($DM\ LVS_{s1}$ and $DM\ LVS_{s2}$).

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

$$LAI = \frac{FM_{plot} \left(\frac{FMLVS_{s1}}{FM_{s1}} \right) \left(\frac{DMLVS_{s1}}{FMLVS_{s1}} \right) \left(\frac{LA_{s2}}{DMLVS_{s2}} \right)}{320\text{ cm}^2}$$

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

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

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 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. 1994 [this issue]). Other data used in the calculations include the site-averaged tree LAI and the assumed k for conifers (1.1 and 0.50, respectively; Runyon et al. 1994 [this issue]), unmanipulated plot LAI, and the transect percentage 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 ($B = 469\text{--}489\text{ nm}$), green ($G = 550\text{--}568\text{ nm}$), red ($R = 660\text{--}680\text{ nm}$), and near-infrared ($NIR = 780\text{--}820\text{ nm}$) 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, $\pm 10\text{ nm}$ in the visible bands and $\pm 20\text{ nm}$ in the NIR . The normalized-difference vegetation index (NDVI), the simple ratio ($SR = NIR/R$), the normalized-difference green-red index [$NDGR = (G - R)/(G + R)$], and the 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 performed 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 leaf area indexes (LAIs) ranged from 1.3 to 9 for manzanita and 0.5 to 10 for bitterbrush. Corresponding f_{IPAR} (the fraction of photosynthetically active radiation intercepted) ranged from 0.38 to 0.94 for manzanita and 0.20 to 0.95 for bitterbrush. In comparison, LAIs of 14 naturally growing shrubs of each species ranged from 3.1 to 9.5 for manzanita (mean $\pm 1\text{ SD} = 5.4 \pm 1.7$), and 0.9 to 6.2 for bitterbrush (3.8 ± 1.2), and f_{IPAR} ranged from 0.58 to 0.96 for manzanita (mean = 0.83 ± 0.06), and 0.74 to 0.91 for bitterbrush (0.84 ± 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. 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 $< 3\%$ (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 ($P = .05$). Light extinction coefficients (k) from the Beer-Lambert equation were 0.52 for bitterbrush and 0.46 for manzanita.

Percentage 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. (1994) and Spanner et al. (1994) yielded a site-level f_{IPAR} by the understory of 0.16. The combined f_{IPAR} by overstory trees (0.29; Runyon et al. 1994) and understory shrubs suggests that $\approx 45\%$ 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 $\approx 30\%$ 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. 1994). 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 $\approx 380 \text{ MJ/m}^2$, and utilized $\approx 115 \text{ MJ/m}^2$ annually. The light-use efficiency values of ANPP under environmental constraining conditions across the Oregon transect averaged $\approx 1.0 \text{ g}$ of dry matter production per megajoule (Runyon et al. 1994). Our estimate of understory ANPP, assuming the same conversion factor, averaged $115 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

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% for all of the soil reflectance scans, and 2% to 4% 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 (normalized red index), 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. 2, $R^2 = 0.86$ and 0.83 for manzanita and bitterbrush, respectively), and curvilinearly related to the simple ratio (SR) (Table 1, $R^2 = 0.84$ for manzanita, and 0.77 for bitterbrush). The f_{IPAR} was linearly related to the color indices NDGR (normalized-difference green-red) ($R^2 = 0.76$ for manzanita, and 0.67 for bitterbrush), and NRI (normalized red index) ($R^2 = 0.77$ for manzanita, and 0.53 for bitterbrush) (Table 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 ($P = .05$).

Linear regressions showed that SR was a better estimator of LAI (Fig. 3, $R^2 = 0.86$ for manzanita and 0.74 for 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 ($R^2 = 0.87$ for manzanita and 0.76 for bitterbrush), slight improvement for NDGR ($R^2 = 0.74$

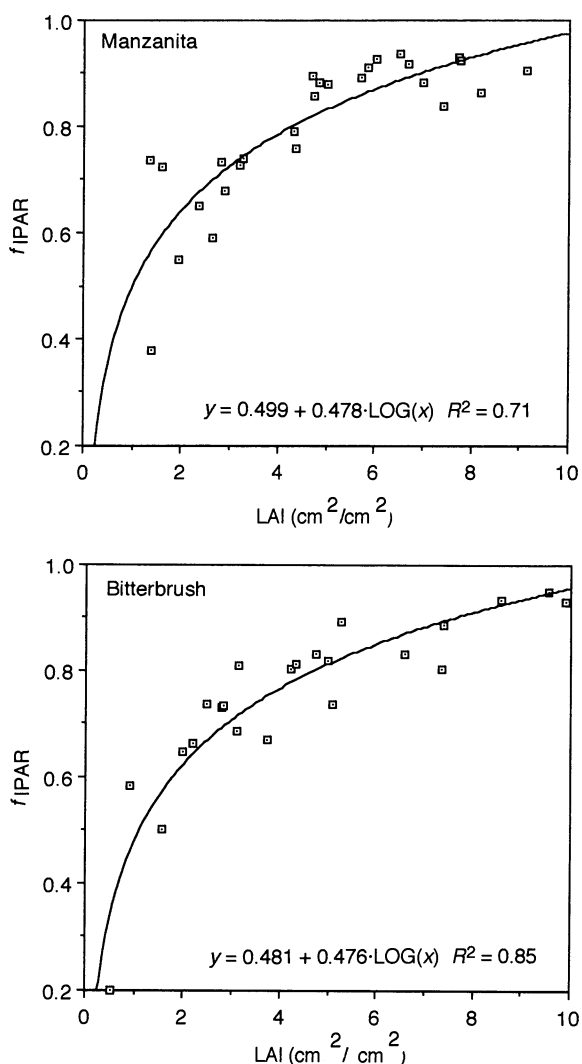


FIG. 1. The relationship between leaf area index (LAI) and fraction of photosynthetically active radiation intercepted by the constructed canopies (f_{IPAR}) at site 5 near the Metolius River in Oregon ($n = 23$ bitterbrush plots, $n = 27$ manzanita plots).

for manzanita and 0.61 for bitterbrush), and no real improvement for NRI ($R^2 = 0.74$ for manzanita and 0.42 for bitterbrush) over the linear regressions (Table 2). Comparison of the 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 ($P = .05$).

DISCUSSION

The relationship between f_{IPAR} (the fraction of photosynthetically active radiation intercepted) and LAI (leaf area index) has been shown to be asymptotic at an LAI of 4 to 6 in previous studies on other vegetation

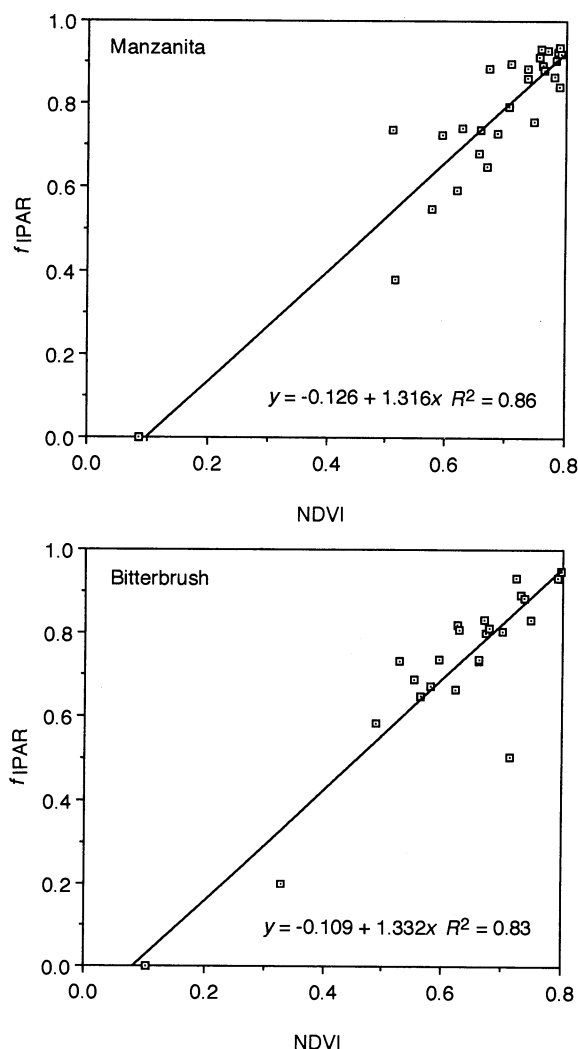


FIG. 2. The relationship between the normalized difference vegetation index [$\text{NDVI} = (\text{NIR} - \text{R})/(\text{NIR} + \text{R})$] recorded by a spectrometer in the field and the fraction of photosynthetically active radiation intercepted by the canopy (f_{IPAR}) ($n = 23$ bitterbrush plots, $n = 27$ manzanita plots). See Table 1 for explanation of symbols.

types, such as agricultural crops and conifers (Norman and Jarvis 1975, Choudhury 1987, 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 the present 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 (coefficients of variation of soil spectra were 5% and 7% in red and near-infrared). 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 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 et al. 1985, Huete 1989).

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. 1994 [this issue]), and by previous studies (Peterson et al. 1987, Herwitz et al. 1990, Spanner et al. 1990). When our instrument was flown on an ultralight aircraft at 100 m above ground level, however, a similar linear relationship was reported by R. McCreight (Spanner et al. 1994 [this issue]). 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. 1994 [this issue]). In any case, those situations where understory vegetation plays a

TABLE 1. Regression equations for the dependent variable fraction of photosynthetically active radiation intercepted by the canopy (f_{IPAR}) and spectral vegetation indices for 23 bitterbrush and 27 manzanita plots.

Dependent variable: f_{IPAR}		MSE	R^2
Model			
Independent variable*			
Normalized-difference vegetation index; NDVI = [(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; SR = (NIR/R)			
Manzanita	$y = 3.229e^{-2} + 0.987 \log(x)$	0.007	0.84
Bitterbrush	$y = 5.037e^{-2} + 1.018 \log(x)$	0.012	0.77
Normalized-difference green-red index; NDGR = [(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; NRI = [R/(B + G + R)]			
Manzanita	$y = 2.199 - 4.387x$	0.010	0.77
Bitterbrush	$y = 2.258 - 4.432x$	0.024	0.53

* NIR = near-infrared band (780–820 nm); R = red band (660–680 nm); G = green band (550–568 nm); B = blue band (469–489 nm).

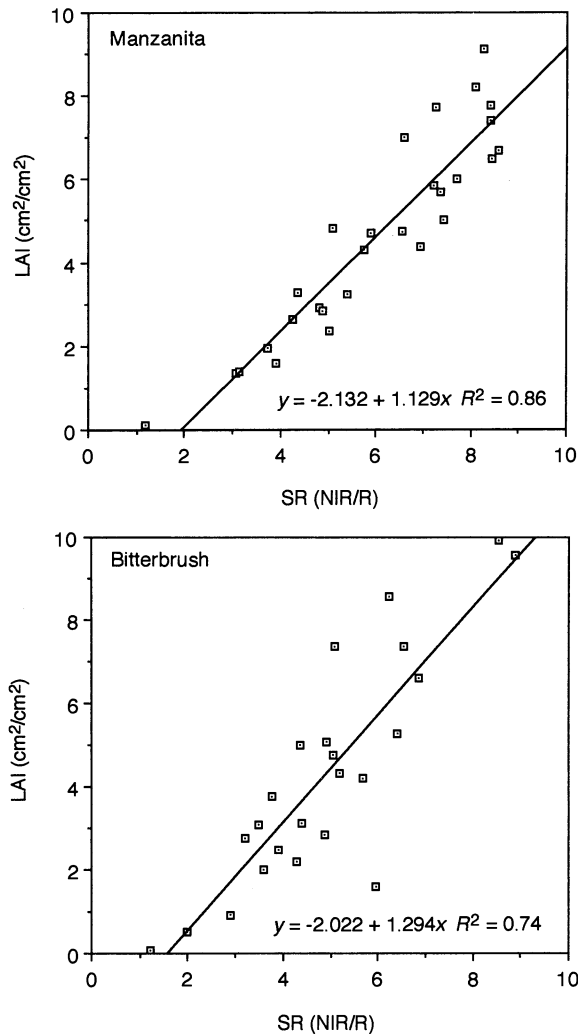


FIG. 3. The relationship between the simple ratio vegetation index ($SR = NIR/R$) and the leaf area index (LAI) ($n = 23$ bitterbrush plots, $n = 27$ manzanita plots). See Table 1 for explanation of symbols.

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 $>55^\circ$ – 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° and 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. 1994b [this issue]). The linear relationship derived between the Advanced Very High Resolution Radiometer (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 aboveground net primary productivity, ANPP ($115 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) combined with measured overstory ponderosa pine ANPP at site 5 ($150 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; Runyon et al. 1994 [this issue]) yields a total of $265 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. The understory vegetation thus contributed $>40\%$ of the total ANPP at the site. The total estimated ANPP of $265 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ compares closely with the $220 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ 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 improves 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 color and wetness—affect interpretation of NDVI as well (Huete and Jackson 1988). In the present 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. (1994a) provide a full range of reflectance spectra for all of the major components of overstory

TABLE 2. Regression equations for the dependent variable leaf area index (LAI) and spectral vegetation indices for 23 bitterbrush and 27 manzanita plots. Nonlinear regressions are of the form: $y = e^{(a+bx)} + \epsilon$. See Table 1 for explanation of symbols.

Dependent variable: LAI			
Model		MSE	R ²
Independent variable			
Simple ratio, $SR = (NIR/R)$			
Manzanita	$y = -2.132 + 1.129x$	0.006	0.86
Bitterbrush	$y = -2.022 + 1.294x$	2.039	0.74
Normalized difference vegetation index; $NDVI = [(NIR - R)/(NIR + R)]$			
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 index; $NDGR = [(G - R)/(G + R)]$			
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; $NRI = [R/(B + G + R)]$			
Manzanita	$y = e^{(5.676 - 13.015x)}$	1.583	0.74
Bitterbrush	$y = e^{(5.741 - 12.536x)}$	4.650	0.42

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 the 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. (1994 [this issue]), 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 for the two shrub species reported in this study.

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