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RELATIONSHIPS BETWEEN NDVI, CANOPY STRUCTURE, AND PHOTOSYNTHESIS IN THREE CALIFORNIAN VEGETATION TYPES¹

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Abstract. In a range of plant species from three Californian vegetation types, we examined the widely used “normalized difference vegetation index” (NDVI) and “simple ratio” (SR) as indicators of canopy structure, light absorption, and photosynthetic activity. These indices, which are derived from canopy reflectance in the red and near-infrared wavebands, highlighted phenological differences between evergreen and deciduous canopies. They were poor indicators of total canopy biomass due to the varying abundance of non-green standing biomass in these vegetation types. However, in sparse canopies (leaf area index [LAI] $\approx 0-2$), NDVI was a sensitive indicator of canopy structure and chemical content (green biomass, green leaf area index, chlorophyll content, and foliar nitrogen content). At higher canopy green LAI values (>2 ; typical of dense shrubs and trees), NDVI was relatively insensitive to changes in canopy structure. Compared to SR, NDVI was better correlated with indicators of canopy structure and chemical content, but was equivalent to the logarithm of SR. In agreement with theoretical expectations, both NDVI and SR exhibited near-linear correlations with fractional PAR intercepted by green leaves over a wide range of canopy densities. Maximum daily photosynthetic rates were positively correlated with NDVI and SR in annual grassland and semideciduous shrubs where canopy development and photosynthetic activity were in synchrony. The indices were also correlated with peak springtime canopy photosynthetic rates in evergreens. However, over most of the year, these indices were poor predictors of photosynthetic performance in evergreen species due to seasonal reductions in photosynthetic radiation-use efficiency that occurred without substantial declines in canopy greenness. Our results support the use of these vegetation indices as remote indicators of PAR absorption, and thus *potential* photosynthetic activity, even in heterogeneous landscapes. To provide accurate estimates of vegetation-atmosphere gas fluxes, remote NDVI and SR measurements need to be coupled with careful estimates of canopy photosynthetic radiation-use efficiency.

Key words: *absorbed photosynthetically active radiation; biomass; chlorophyll content; dry matter yield; leaf area index; net primary production; normalized difference vegetation index; nitrogen content; photosynthesis; photosynthetic radiation-use efficiency; simple ratio; spectral vegetation indices.*

INTRODUCTION

Spectral vegetation indices based on contrasting canopy reflectance in the red and near-infrared wavebands are frequently applied to studies of vegetation from the canopy to the global scale. Two widely used indices

are the normalized difference vegetation index (NDVI) and the simple ratio (SR):

$$\text{NDVI} = (R_{\text{NIR}} - R_{\text{RED}})/(R_{\text{NIR}} + R_{\text{RED}}), \quad (1)$$

and

$$\text{SR} = R_{\text{NIR}}/R_{\text{RED}}, \quad (2)$$

where R_{NIR} and R_{RED} indicate reflectance in the near-infrared and red wavebands, respectively. These two indices are readily convertible:

$$\text{SR} = (1 + \text{NDVI})/(1 - \text{NDVI}). \quad (3)$$

The validity of these vegetation indices as quantitative indicators of canopy structure or NPP (net primary production) is largely based on empirical results with horizontally uniform canopies (e.g., Kumar and Monteith 1981, Hatfield et al. 1984, Bartlett et al. 1990) and model predictions (Asrar et al. 1984, Sellers 1985,

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1987) that indicate that NDVI (or SR) scales with fractional intercepted or absorbed photosynthetically active radiation (F_{IPAR} or F_{APAR}), and thus with net CO_2 uptake under non-stressed conditions. Originally based on the work of Monteith (1977), these relationships are often expressed as

$$\begin{aligned} NPP &= \epsilon \times \Sigma (APAR) \\ &= \epsilon \times \Sigma (F_{APAR} \times PAR) \\ &= \epsilon \times \Sigma (NDVI \times PAR) \end{aligned} \quad (4)$$

where ϵ is the "dry matter yield," a radiation-use efficiency term relating absorbed PAR to biomass accumulation (NPP; e.g., Sellers 1987, Hunt and Running 1992, Sellers et al. 1992). Typically, APAR is summed over a growing season and NPP represents the seasonal or annual accumulation of biomass.

In uniform annual vegetation under non-stressed conditions (Sellers 1987) or in natural vegetation at the continental or global scales (Goward et al. 1985, Tucker et al. 1986, Fung et al. 1987, Running and Nemani 1988), the relationships between NDVI, canopy structure, photosynthetic fluxes, and NPP appear to be remarkably consistent. These observations support the view that stress reduces the canopy's capacity to absorb PAR, and thus reduces NDVI or SR, while leaving ϵ (and presumably photosynthetic radiation-use efficiency) relatively constant (Kumar and Monteith 1981). However, relatively few studies have directly compared NDVI to measured photosynthetic fluxes, canopy structure, and PAR absorption in natural landscapes with vegetation of differing habits and phenologies exposed to seasonal or chronic stresses. A growing body of evidence indicates that the photosynthetic performance or NPP of stressed vegetation cannot always be predicted from NDVI alone, due to variation in ϵ (Running and Nemani 1988, Bartlett et al. 1990, Steinmetz et al. 1990, Demetriades-Shah et al. 1992a, Hunt and Running 1992, Running and Hunt 1993). The reliability of NDVI as a direct indicator of photosynthetic productivity is particularly suspect in evergreen vegetation, where the seasonal patterns of canopy greenness and photosynthetic activity often diverge (Gamon et al. 1993a). The large areal extent of evergreen vegetation (Lieth and Whittaker 1975), combined with deviations in ϵ , could lead to significant errors in NDVI-derived estimates of global carbon flux. Current uncertainties over the magnitude of vegetation-atmosphere gas fluxes and the role of terrestrial vegetation in global atmospheric and climatic regulation (D'Arrigo et al. 1987, Houghton 1987a, b, Mooney et al. 1987, Shukla et al. 1990, Tans et al. 1990) and the increased reliance on satellite-derived vegetation indices to estimate the production of terrestrial ecosystems (Waring et al. 1986, Hobbs and Mooney 1990) require a critical evaluation of NDVI and SR as universal indicators of vegetation structure and production, particularly in non-

uniform, evergreen vegetation subject to seasonal stresses.

As part of a larger, ongoing study of remote sensing and production at the Jasper Ridge Biological Preserve near Stanford, California, we evaluated NDVI and SR as indicators of canopy structure, PAR absorption, and photosynthetic activity in a large number of species from three vegetation types: grassland, chaparral ("shrubs"), and oak woodland ("trees"). To test the utility of these indices in interpreting remotely sensed data of mixed landscapes, we deliberately chose species with a wide range of canopy structure and phenology. By comparing near-simultaneous measurements of photosynthesis, canopy structure, and biochemical content with canopy reflectance on individual canopies of known identity, we were able to probe more directly the mechanistic relationships between vegetation indices, canopy composition, and photosynthesis than would be possible at coarser (e.g., satellite) scales where each pixel represents a mix of species and canopy types and where ground sampling and remote imagery cannot be coregistered readily. We focused mostly on NDVI because it is probably the more commonly used index for analyzing vegetation on a continental and global scale (e.g., Goward et al. 1985, Tucker et al. 1986, Fung et al. 1987, Running and Nemani 1988, Tucker et al. 1991). Some SR values are also presented to allow comparison of the two indices.

We evaluated the relationships between vegetation indices, canopy structure, and physiology at three levels. At one level, we examined correlations between NDVI and four measures of canopy structure and biochemical content: biomass, leaf area index, chlorophyll concentration, and foliar nitrogen concentration. Although these structural and chemical indicators are not direct measures of productivity, physiological activity, or energy transfer, they represent important determinants of physiological capacity and productivity and serve as useful measures of canopy "greenness." At a second level, we examined the relationships between vegetation indices and fractional intercepted PAR (F_{IPAR}), a measure of fractional absorbed PAR (F_{APAR}), and an indicator of potential CO_2 fixation (i.e., the maximum photosynthetic rates under non-stressed conditions). Finally, we compared NDVI and SR measured at different seasons with maximum daily rates of CO_2 exchange as indicators of seasonal photosynthetic activity and radiation-use efficiency. By comparing NDVI and SR with these measurements of canopy structure and photosynthetic activity, we evaluated the hypotheses that the indices' ability to predict photosynthetic CO_2 fluxes varies with the degree of synchrony between green canopy display and photosynthetic activity, and that NDVI and SR scale with canopy photosynthetic potential but not necessarily with actual photosynthetic rates.

TABLE 1. Vegetation types and species considered in this study, described by habit. Grassland list includes only the more common species (>10% of total cover or frequency, according to McNaughton 1968, and confirmed by field observations).

	Habit
Grassland species	
<i>Avena fatua</i>	annual
<i>Bromus rigidus</i>	annual
<i>Bromus mollis</i>	annual
<i>Centaurea solstitialis</i>	annual
<i>Cirsium vulgare</i>	annual
<i>Erodium cicutarium</i>	annual
<i>Eschscholzia californica</i>	annual/perennial
<i>Hemizonia luzulaefolia</i>	annual
<i>Lactuca serriola</i>	annual
<i>Lolium multiflorum</i>	annual
<i>Lotus subpinnatus</i>	annual
<i>Orthocarpus densiflorus</i>	annual
<i>Melica californica</i>	perennial
<i>Plantago erecta</i>	annual
<i>Stipa pulchra</i>	perennial
<i>Vulpia</i> spp.	annual
Chaparral shrubs	
<i>Diplacus aurantiacus</i>	drought-deciduous
<i>Heteromeles arbutifolia</i>	evergreen
<i>Artemisia californica</i>	drought-deciduous
<i>Adenostema fasciculatum</i>	evergreen
<i>Baccharis pilularis</i>	slightly drought-deciduous
<i>Rhamnus californica</i>	evergreen
<i>Quercus durata</i>	evergreen
Woodland tree species	
<i>Quercus agrifolia</i>	evergreen
<i>Quercus douglasii</i>	winter-deciduous
<i>Quercus lobata</i>	winter-deciduous

METHODS

The study site

All field measurements were made within a 20 ha area of Stanford University's Jasper Ridge Biological Preserve, San Mateo County, California, USA (37°24' N, 122°13'30" W), which has a Mediterranean-type climate with warm, dry summers and cool, wet winters. Measurements were conducted in three vegetation types: "grassland" (mixed forbs and grasses), chaparral "shrubs," and oak woodland "trees;" these types comprised most of the vegetation of the preserve. Part of the site's heterogeneity results from the presence of two soil types derived from serpentine and Franciscan greenstone (Page and Tabor 1967). Table 1 describes the study species by vegetation type and phenology.

Canopy reflectance

Measurements of canopy radiance were made with a portable spectroradiometer with a 15-degree field-of-view fore-optic (model SE590 with detector model CE390WB-R, Spectron Engineering, Incorporated, Denver, Colorado, USA). This instrument detects radiance in 252 bands, approximately uniformly distributed between 368.4 and 1113.7 nm, with a 10-nm bandwidth at half maximum response. All radiance measurements were made with the spectroradiometer

in a nadir orientation, positioned 1–4 m above the target, by mounting the instrument on a boom attached to a tall tripod. This enabled measurements to be made of tree and shrub canopies ≤ 3 m in height. Spectral scans of 10 chaparral and woodland species were taken on monospecific canopies, while scans of the grassland contained a mixture of species (Table 1). Soil reflectance was derived from 10 soil scans taken from a 1 m height at 10 locations at the field site. The NDVI of soils derived from both serpentine and greenstone were not significantly different (Student's *t* test), so measurements from both soil types were pooled to illustrate the mean soil value at the study site.

To facilitate comparison with satellite Advanced Very High Resolution Radiometer (AVHRR) data, we simulated United States National Oceanographic and Atmospheric Administration (NOAA) AVHRR bands 1 and 2 (as reported in Sellers 1987) from narrow-bandwidth spectra. The spectroradiometer signal at each narrow band coincident with AVHRR bands 1 and 2 was multiplied by the relative sensitivity of the AVHRR detector at that waveband, and the products were then integrated to yield raw signals for AVHRR bands 1 and 2. Vegetation indices were then calculated from reflectance (rather than radiance) in these bands to avoid problems arising from possible instrument drift and changes in solar irradiance. To calculate reflectance, canopy scans were bracketed by reference panel scans (taken within 15 min of canopy scans) which were then interpolated to match the times of the canopy scans. Canopy reflectance was calculated by dividing the canopy scans by the interpolated panel scans. The reference panel was either a halon standard, prepared according to Weidner and Hsia (1981), or a white wooden panel referenced to the halon standard. Calculations of NDVI and SR, from reflectance in these simulated bands, were done as follows:

$$\text{NDVI} = (R_2 - R_1)/(R_2 + R_1) \quad (5)$$

$$\text{SR} = R_1/R_2 \quad (6)$$

where *R* indicates reflectance and subscripts 1 and 2 indicate AVHRR bands 1 and 2 in the red and near-infrared wavebands, respectively.

Our spectroradiometer, manufactured in 1988, did not include the second-order blocking filter built into newer instruments, resulting in errors in the absolute values of NDVI and SR. Empirical tests with blocking filters indicated that this error ranged from $\approx 13\%$ (absolute NDVI ≈ 0.03) for bare soil to $\approx 5\%$ (absolute NDVI ≈ 0.03) for a fully closed, green canopy. The estimated errors for SR were $\approx 6\%$ (absolute SR ≈ 0.10) for bare soil and $\approx 10\%$ (absolute SR ≈ 0.42) for a fully closed, green canopy. Although these errors slightly affected absolute values of NDVI and SR, they did not alter the conclusions of this study, which were based primarily on relative values of NDVI and SR across species and canopy types.

Fractional IPAR

Estimates of fractional intercepted PAR (F_{IPAR}) were made with a 0.8-m "sunflecks ceptometer" (Decagon Devices, Pullman, Washington). F_{IPAR} , a unitless measure of light interception, was calculated as

$$F_{IPAR} = 1 - T/S \quad (7)$$

where T is the downwelling PAR reading below the canopy and S is the downwelling PAR reading above the canopy. For the shrubs and trees, each T and S value represented the mean of five readings made within a 1 m² area, while in the more horizontally uniform grassland canopies a single reading was used for each T and S value.

Phenology and leaf CO₂ flux

Seasonal canopy greenness and leaf photosynthetic activity were assessed by periodically measuring mid-day canopy spectral reflectance and leaf photosynthetic rates between August 1989 and November 1990. Canopy images from a video camcorder, mounted on the tripod boom adjacent to the spectroradiometer and connected to a remote television monitor, allowed us to visualize the canopy from the vantage point of the spectroradiometer to ensure that identical canopy regions were monitored each season.

Leaf-level photosynthetic rates at different times of the year were measured with a portable gas exchange system (LI-6200, LI-COR, Incorporated, Lincoln, Nebraska, USA). All gas exchange measurements were made on top-canopy leaves exposed to full sun between mid-morning and solar noon. During these measurements, the mean (± 1 SE) incident photosynthetic photon flux density (PPFD) was $1597 \pm 30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, ranging from a seasonal low of $1436 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (December 1989) to a seasonal high of $1736 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (May 1990). The selection of similar lighting conditions during measurements ensured that large seasonal changes in photosynthetic rates reflected variation in realized photosynthetic capacity associated with seasonal changes in instantaneous radiation-use efficiency (instantaneous net CO₂ assimilation divided by PPFD incident on the leaf during measurement). Preliminary plots of instantaneous radiation-use efficiency yielded figures that were virtually identical to net CO₂ assimilation (*data not shown*). Consequently, all leaf gas exchange results are presented as net CO₂ uptake only.

Canopy CO₂ flux

In concurrent studies at this site, canopy-level fluxes of CO₂ and water vapor for grassland using eddy covariance (Valentini et al., *in press*) and for evergreen oaks using a combination of ventilated chambers and sap-flow sensors (Goulden 1991, Goulden and Field 1994) were examined. In this study, we relate highlights of these canopy-level CO₂ flux results to the canopy-level vegetation indices.

Canopy structure and chemical content

The relationships between vegetation indices and indicators of canopy structure and chemical content (aboveground standing biomass, leaf area index, and chlorophyll and nitrogen concentrations) were determined in November 1990 and May–June 1991. Due to delayed winter rains, the appearance of most plants in November was characteristic of late-summer drought conditions. In contrast, the May–June measurements were made near the growing season peak for many species, following a period of abundant rain. Thus, the measurements made on these two dates highlighted seasonal differences in canopy development and physiological activity.

Leaf area index (LAI, one-sided leaf area divided by subtending ground area) and biomass were estimated from destructive harvests. Cylindrical sections of tree and shrub canopies were harvested by mounting a 30 cm diameter ring on a vertical rod. The ring was gradually lowered along the rod, and all plant material within the ring was removed and placed in a plastic bag for transport to the lab. Grassland harvesting methods were similar except that a 50 cm diameter ring was laid directly on the ground. To facilitate comparison with NDVI, all harvests were conducted on canopy portions previously measured with the spectroradiometer.

Canopy material was manually separated into live and dead portions and green and non-green portions prior to leaf area and biomass determinations. Correction factors for percentage of green canopy area and green canopy biomass were then estimated from the area and mass of each portion. Area, biomass, chlorophyll, and nitrogen were assayed from subsamples. These subsamples were then scaled to the canopy level with empirical factors that were the ratios of total harvest fresh mass to subsample fresh mass. Leaf area was measured in the laboratory with a leaf area meter (AMS, Delta T Devices, Cambridge, England). "Total LAI" (sometimes called "plant area index") was calculated from the projected, one-sided area of all aboveground canopy components (leaves, stems, and standing dead canopy material). "Green LAI" included green leaves only. All biomass was estimated on oven-dried canopy material. Chlorophyll was estimated spectrophotometrically in 80:20 (v:v) acetone:water extracts (Porra et al. 1989). Total nitrogen was estimated from green leaves using a micro-Kjeldahl technique (Isaac and Johnson 1976).

All estimates of canopy structure and chemical content (biomass, leaf area, chlorophyll, and nitrogen) were expressed on a ground area basis for comparison with reflectance- and transmittance-based measurements. To clarify data presentation, canopies were classified by habit and vegetation type into "grassland" (mixed grasses and forbs), chaparral "shrubs" (including evergreen and semideciduous species) and

woodland "trees" (both evergreen and deciduous; see Table 1).

Statistics

Statistical tests employed the Pearson Correlation and Multivariate General Linear Hypothesis (MGLH) routines in Systat Version 5.1 for the MacIntosh computer (Systat, Incorporated, Evanston, Illinois). General tests of linear association used the Pearson Correlation Matrix and Bonferroni probabilities. Comparisons between specific pairs employed the Student's *t* distribution or *F* distribution. In all cases, $P \leq 0.05$ was considered significant.

RESULTS

Phenology

Evergreen trees and shrubs showed little seasonality in NDVI (Fig. 1A). The study site also included a large number of "drought-deciduous" chaparral shrubs which lose many leaves following the onset of summer drought. NDVI readily detected the seasonal patterns of canopy greenness in these semideciduous species (Fig. 1B). Two examples were *Artemisia californica* and *Diplacus aurantiacus*, which varied from lush, green canopies during rainy periods in winter and spring to predominantly brown canopies during the summer and fall dry seasons. Between late summer and the onset of winter rains, these canopies retained only a few small green leaves and were primarily composed of dead leaves and branches (Table 2). Another species, *Baccharis pilularis* var. *consanguinea*, exhibited a degree of seasonality in NDVI and canopy greenness intermediate between most deciduous and evergreen species (Fig. 1B).

At the other extreme from the evergreens were the grassland canopies largely composed of mixed annual forbs and grasses (Table 1). At Jasper Ridge, the contrasting seasonality of the two dominant grassland types, serpentine and greenstone, were readily distinguishable with NDVI. The NDVI of the serpentine grassland peaked in the winter, while the NDVI of the greenstone grassland peaked in the spring. The higher peak in the greenstone grassland reflected the higher production and greater standing biomass of the greenstone species (*data not shown*). The delayed greenness on greenstone was partly due to the long time required for the new winter's growth to emerge through the previous season's dead standing biomass. Both canopies, which were dominated by "winter" annuals (Table 1), were largely composed of dead material by midsummer.

Canopy structure and chemical content

When identical sample sizes were compared, the correlations between NDVI and the natural logarithms of green LAI, green biomass, and chlorophyll yielded the highest correlation coefficients (Table 3). However,

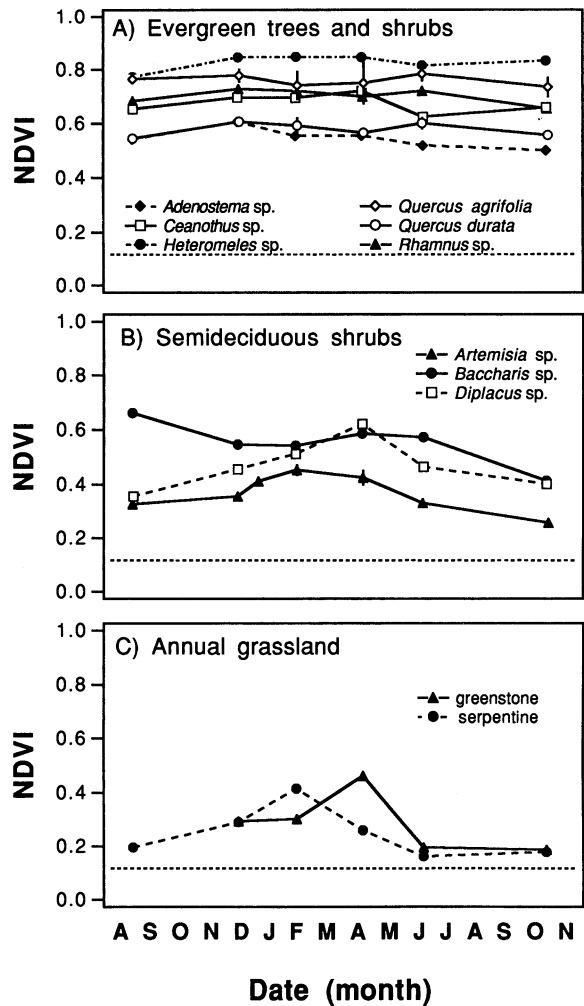


FIG. 1. Seasonal trends of the normalized difference vegetation index (NDVI), beginning in August 1989, and ending in November 1990, for (A) evergreen trees and shrubs, (B) semideciduous shrubs, and (C) two types of annual grassland. The predominant grassland species are indicated in Table 1. The dashed baseline illustrates the mean NDVI for bare soil. Data represent mean values; error bars represent ± 1 SE when it exceeds the width of the symbol.

these were not significantly different from those between NDVI and the logarithm of total LAI or nitrogen. Because of the widely varying percentage of green biomass in these canopies (Table 2), correction of biomass for percent greenness on a dry mass basis yielded a significantly higher correlation with NDVI. (Fig. 2A, B, Table 3). Similarly, NDVI was slightly (but not significantly) better correlated with green LAI than with total LAI (Fig. 2C, D, Table 3). Compared to SR, NDVI was better correlated with all indicators of canopy structure and chemical content, and in some cases (green LAI, N, Chl, and green biomass) these differences were significant. However, NDVI and the natural log of SR did not differ significantly in their correlations with structural and chemical indicators (Table 3),

TABLE 2. Percentage greenness of plant species from three Californian vegetation types, during two seasons. Percentage green leaf area is reported per total aboveground plant area and percentage green biomass is reported per total aboveground biomass on a dry mass basis. * Non-green area and biomass included dead and structural canopy material (data not shown). Sample sizes are indicated in parentheses.

	Green leaf area (%)		Green leaf biomass (%)	
	Nov 1990	May–Jun 1991	Nov 1990	May–Jun 1991
Grassland species				
Greenstone grassland spp.	0 (1)	51 (5)	0 (1)	48 (19)
Serpentine grassland spp.	0 (1)	25 (3)	0 (1)	15 (7)
Chaparral shrubs				
<i>Adenostema fasciculatum</i>	24 (2)	43 (2)	4 (2)	6 (2)
<i>Artemisia californica</i>	5 (2)	33 (2)	1 (2)	7 (2)
<i>Baccharis pilularis</i>	24 (2)	59 (2)	3 (2)	8 (2)
<i>Ceanothus cuneatus</i>	72 (1)	80 (1)	27 (1)	28 (1)
<i>Diplacus aurantiacus</i>	5 (1)	...	3 (1)	...
<i>Heteromeles arbutifolia</i>	87 (1)	...	27 (1)	...
<i>Quercus durata</i>	65 (1)	60 (2)	22 (1)	11 (2)
<i>Rhamnus californica</i>	66 (1)	82 (1)	12 (1)	26 (1)
Woodland trees				
<i>Quercus agrifolia</i>	73 (1)	84 (2)	32 (1)	31 (2)
<i>Quercus douglasii</i>	...	77 (1)	...	24 (1)
<i>Quercus lobata</i>	...	94 (2)	...	41 (2)

* Due to delayed winter rains, the November 1990 values were characteristic of late summer canopies. The May–June values were typical of the growing season peak for many species.

indicating the functional similarity of these mathematically interchangeable vegetation indices (Eq. 3).

The relationships between NDVI and all measures of canopy “greenness” (as measured by green biomass, green LAI, chlorophyll, or foliar nitrogen content) approached saturation at approximately 20% of the maximum greenness (Figs. 2 and 3). Clearly, NDVI is extremely sensitive to changes in canopy cover when the cover is low, but cannot clearly distinguish between

values of these structural or chemical indicators ranging from 20 to 100% of full scale. This illustrates one of the difficulties of using NDVI as an indicator of canopy structure or chemical content for well-developed canopies; beyond a certain canopy density (in this study, green LAI \approx 2), addition of more canopy layers makes little difference in the relative interception or reflectance of red and near-infrared radiation, and thus little difference in NDVI (Sellers 1987). Partly for this reason, NDVI poorly indicated subtle seasonal growth flushes in dense evergreens (Fig. 1A). On the other hand, NDVI is ideally suited for detecting subtle differences in cover in sparse canopies (e.g., green LAI between 0 and 2), and thus makes a sensitive index of growth in young crops, grasslands, and semi-arid regions (e.g., Tucker et al. 1979, 1991, Gallo et al. 1985, Gamon et al. 1993a).

The relationships between NDVI and various measures of canopy structure and chemical content are clearly non-linear, and can be effectively described by semi-logarithmic relationships. When these various indicators were expressed on a natural log scale (Fig. 4), linear relationships emerged between NDVI and all measures of canopy structure and chemical content. The logic of this transformation lies in the negative exponential extinction of PAR with canopy depth (Monsi and Saeki 1953, Sellers 1987). While most of the variation in Fig. 4 could be described by single linear fits in these semilog plots (Table 3), there were subtle differences in these relationships between canopy types. In particular, the grassland canopies (composed of thin-leaved herbaceous species with a predominantly vertical canopy orientation) exhibited slightly higher green leaf areas and foliar nitrogen for

TABLE 3. Pearson correlation matrix (r values) comparing vegetation indices (NDVI, SR, and \ln [SR]) to various indicators of canopy structure, chemical content, and light interception for all vegetation types together (see Table 1 for species). r values are provided as measures of linear association between spectral and canopy parameters. To validate comparison, an identical sample size ($n = 23$) was used in each case. Note that in all cases, SR yielded lower correlation coefficients than NDVI, while \ln (SR) yielded correlations similar to NDVI.

Variable	NDVI	SR	\ln (SR)
\ln (total LAI)	0.912**	0.861**	0.908**
\ln (green LAI)†	0.949**	0.899**	0.947**
\ln (N)	0.901**	0.865**	0.901**
\ln (chl)	0.944**	0.898**	0.942**
\ln (total biomass)	0.844**	0.721	0.814**
\ln (green biomass)†	0.937**	0.835**	0.914**
F_{IPAR}	0.794**	0.626	0.746*
$F_{IPAR} \times \% \text{ greenness}$	0.925**	0.902**	0.935**

* $P \leq 0.01$; ** $P \leq 0.001$ (Bonferroni-adjusted probability that $r \neq 0$).

† “Green leaf area index” (green LAI) was derived by multiplying total LAI by the “% green leaf area” values in Table 2. “Green biomass” was derived by multiplying total biomass by the “% green biomass” values in Table 2. “ $F_{IPAR} \times \% \text{ greenness}$ ” indicates fractional PAR interception multiplied by the “% green leaf area” values in Table 2.

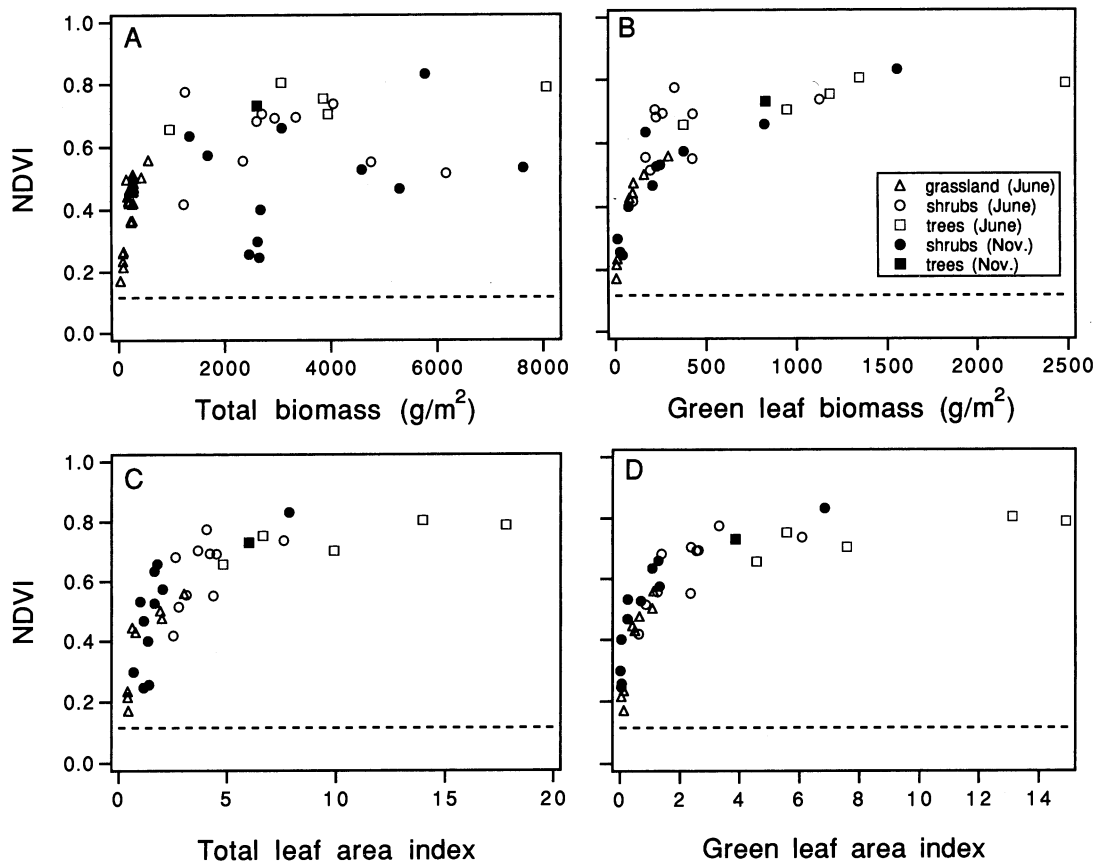


FIG. 2. Relationships of NDVI to biomass and leaf area index (LAI) for three California vegetation types at two different seasons. Panels (A) and (B), NDVI vs. aboveground biomass (dry mass basis) (A) before and (B) after correction for non-green canopy material. Panels (C) and (D), NDVI vs. LAI (C) before and (D) after correction for non-green canopy material. Total LAI (panel C) is sometimes called "plant area index" because it is the projected, one-sided area of all aboveground plant parts. Vegetation types and sampling dates are indicated in the key of panel (B). The dashed baseline illustrates the mean NDVI for bare soil.

a given NDVI than the thicker-leaved chaparral shrubs (Fig. 4B, D). Although further research would be needed to elucidate the exact cause of these variations between canopy types, these observations suggest that accurate estimation of canopy structure and composition from NDVI requires individual calibrations for distinct vegetation types.

Absorbed PAR

According to theoretical studies (Asrar et al. 1984, Sellers 1987) and empirical studies of uniform canopies (Kumar and Monteith 1981, Hatfield et al. 1984, Bartlett et al. 1990), NDVI and SR should be closely correlated with the fraction of PAR intercepted or absorbed by canopies. Our comparisons of NDVI to F_{IPAR} yielded significant but "noisy" correlations (Fig. 5A, Table 3). Scatter in the NDVI- F_{IPAR} relationship has been attributed to dead canopy material, canopy architecture, and differing soil backgrounds (Demetriades-Shah et al. 1992b). Correction of F_{IPAR} by empirical greenness factors (Table 2) improved the correlations with both indices (Fig. 5B, Table 3), demonstrating that correction

for percentage greenness alone can largely reduce between-canopy and between-site variability in the vegetation index- F_{IPAR} relationship. Remaining differences in soil background or canopy architecture apparently did not greatly affect the vegetation index- F_{IPAR} plots. These results indicate that the vegetation index- F_{IPAR} relationship is robust across a wide range of canopy architectures, and at least two soil types, after correction for dead standing biomass. This consistency supports the use of vegetation indices as universal estimators of green canopy F_{IPAR} and thus of potential photosynthetic activity.

Photosynthesis

Both NDVI and SR were good indicators of maximum CO_2 assimilation during non-stressed periods. In the annual grassland, very high correlations were found between NDVI (or SR) and peak daily canopy photosynthetic rates determined with eddy covariance at five different dates during the growing season (open symbols; Fig. 6). These five samples were comprised of four measurements at a serpentine site and one at a

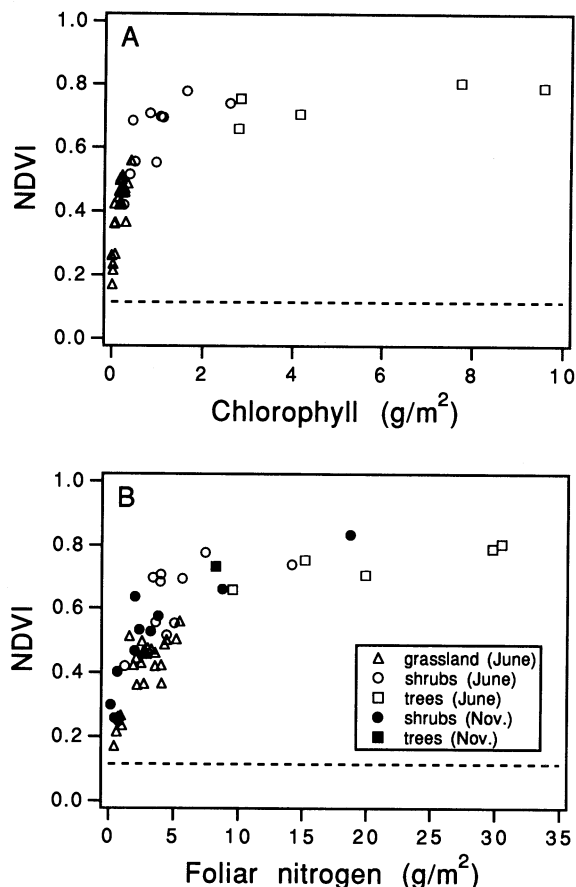


FIG. 3. Normalized difference vegetation index (NDVI) vs. foliar chlorophyll or nitrogen content (both expressed on a ground area basis) in three California vegetation types in two different seasons. Data points represent single measurements. Vegetation types and sampling dates are indicated in the symbol keys. The dashed baseline illustrates the mean NDVI for bare soil.

greenstone grassland site, and thus included two separate grassland locations. In the three evergreen oak samples, including two individuals of *Quercus agrifolia* (coast live oak) and one of *Q. durata* (leather oak), NDVI and SR yielded positive correlations with peak springtime canopy photosynthetic rates measured with a ventilated chamber (closed symbols; Fig. 6). Although the ventilated chamber (Goulden 1991, Goulden and Field 1994) and eddy covariance (Valentini et al., *in press*) techniques are dissimilar, together they yielded reasonably consistent relationships between maximum daily CO_2 flux and NDVI or SR. Similar, saturating relationships have been recently reported in comparisons of satellite NDVI with landscape-level photosynthesis derived from aircraft flux data (Cihlar et al. 1992).

While NDVI was a good indicator of non-stressed photosynthetic potential, it was a poor indicator of actual photosynthetic rates when all vegetation types and seasons were considered. In the evergreen trees and

shrubs, NDVI was completely insensitive to seasonal differences in maximum leaf-level net CO_2 uptake (Fig. 7A, B). However, in semideciduous shrubs, where canopy structure, biochemical content, APAR, and photosynthetic activity were in synchrony, seasonal changes in NDVI exhibited a significant positive correlation with seasonal patterns in maximum net CO_2 uptake (Fig. 7C). The different correlations between NDVI and photosynthetic activity among co-occurring vegetation types at this site indicate that no universal relationship exists for NDVI (or SR) and instantaneous photosynthetic fluxes.

The challenge of deriving estimates of CO_2 flux from NDVI measurements is further illustrated by an examination of seasonal photosynthetic activity in the evergreen *Q. agrifolia* (coast live oak). The maximum leaf-level net CO_2 assimilation of *Q. agrifolia* exhibited a striking seasonality, with photosynthetic rates peaking in the winter and spring, and declining to 20% of peak values by the end of the summer and fall (Fig. 8A). Because the incident PPFD levels during leaf-level measurements were similar across seasons, the seasonal photosynthetic pattern in Fig. 8A was coincident with differences in radiation-use efficiency and not primarily driven by changes in incoming radiation. A similar, but slightly delayed, seasonal pattern was evident in daily integrated fluxes at the leaf level (Fig. 8B). The seasonal pattern in daily integrated canopy flux (Fig. 8B) can be explained by a combination of changing radiation-use efficiency and APAR, and the similarity with the pattern of leaf-level photosynthetic rates suggests that alterations in radiation-use efficiency were largely responsible for the seasonal course in canopy photosynthesis. NDVI failed to capture these seasonal dynamics in photosynthetic activity measured at the leaf or the canopy level. Clearly, NDVI-based estimates of PAR absorption would be an insufficient indicator of the dynamic photosynthetic fluxes for the evergreen vegetation of this site.

DISCUSSION

Canopy structure and PAR absorption

Although NDVI and SR were poor indicators of total biomass or F_{IPAR} due to the varying abundance of non-green biomass, they were good indicators of green biomass and fractional PAR interception by green canopy material, even across many canopies with varying structure and seasonality. The good correlation with all measures of canopy structure and chemical content supports the view based on economic theory (Bloom et al. 1985) that a canopy's investment in chlorophyll, nitrogen, green leaf area, and green leaf biomass represents an economically conservative balance between several components of the photosynthetic machinery. To the extent that these structural and chemical measures represent surrogate variables for photosynthetic capacity, NDVI, and SR should also be good measures of po-

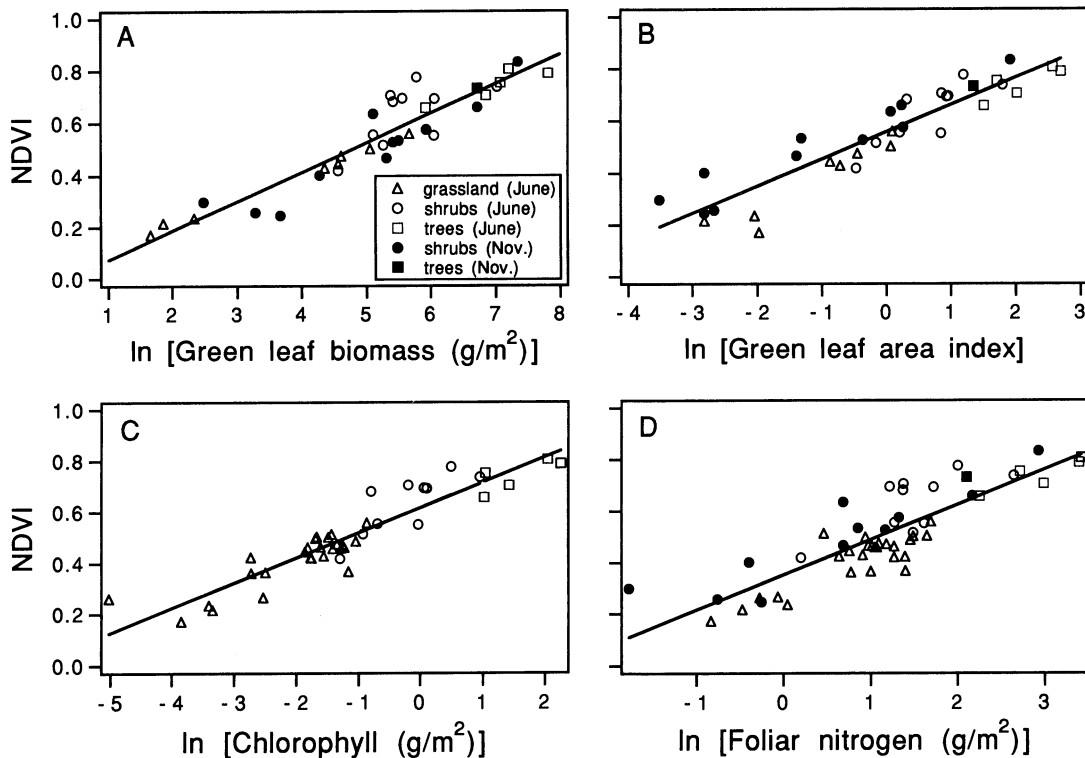


FIG. 4. Relationship between NDVI and various canopy parameters (expressed on a natural log scale) for three different California vegetation types in two seasons. Replotted from data presented in Figs. 2B, 2D, and 3. Solid lines represent first-order (linear) regressions for all species and sampling dates together. Vegetation types and sampling dates are indicated in the key, and regression statistics are indicated in Table 3.

tential photosynthetic activity (Gamon et al. 1993a, Yoder and Waring 1994). The strong relationships between NDVI, canopy structure, chemical content, and F_{IPAR} (after correction for percentage greenness) for all species from three vegetation types at different seasons support the use of vegetation indices as indicators of potential photosynthetic production at the landscape and global scales, where complex mixtures of species and vegetation types often occur. Examination of seasonal patterns in vegetation indices could also be useful in distinguishing functional vegetation types (e.g., evergreen vs. deciduous; DeFries and Townshend, *in press*).

Correction for dead biomass entailed tedious and lengthy harvests, which may not be practical under many situations. Most ground-based methods for estimating F_{IPAR} or F_{APAR} employ broadband PAR sensors (e.g., line quantum sensors, Hatfield et al. 1984, Gallo et al. 1985, Bartlett et al. 1990, Demetriades-Shah et al. 1992b) that cannot readily distinguish interceptance by live and dead biomass. Spectrally based optical estimates of dead standing biomass, possibly using spectral mixture analysis to estimate green and non-green vegetation fractions (Roberts et al. 1993), might provide rapid, non-destructive corrections of F_{IPAR} measurements for canopy greenness.

In this study, NDVI saturated at much lower LAI

values than in some other studies (e.g., Running 1990, Spanner et al. 1990). Many factors can affect the NDVI-LAI relationship, including soil background, canopy senescence, sensor or sun position, and amount of shadow intercepted by the sensor (Curran 1983). Correction for non-green (dead and structural) canopy material alone can easily cause a two-fold variation in LAI for a given NDVI (Fig. 2C, D). The scale of measurement can affect the degree of shadow intercepted by the sensor. By concentrating on canopy tops, our study tended to minimize shadow effects that might be more prevalent in landscape-scale studies (Running 1990, Spanner et al. 1990). The method used to estimate LAI, and whether it considers leaf orientation, foliage clumping, and other structural features, can also be important. Our study employed direct area measurements on harvested material, while others have used allometric methods that can overestimate LAI (Spanner et al. 1990). These problems illustrate the difficulty of accurately estimating LAI from NDVI and the danger in LAI-based models of photosynthetic fluxes that use NDVI as a driving variable. The simpler, near-linear relationship between NDVI and fractional PAR intercepted by green canopy material (Fig. 5B) suggests that LAI-independent, IPAR- or APAR-based photosynthetic models (e.g., Potter et al. 1994) would be more reliable than LAI-based models.

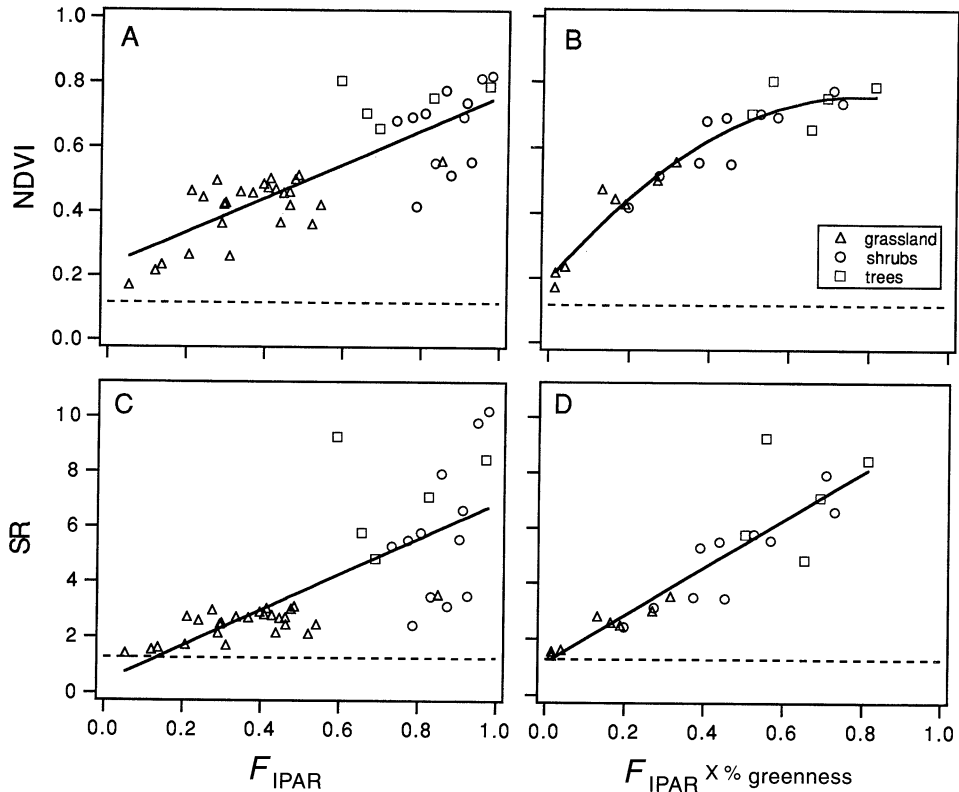


FIG. 5. Normalized difference vegetation index (NDVI) or simple ratio (SR) vs. fractional intercepted PAR (F_{IPAR}). (A, C); F_{IPAR} was not corrected for non-green canopy material and thus includes interception by non-photosynthetic tissues. (B, D); F_{IPAR} was corrected by the “% green leaf area” values in Table 2 to indicate PAR intercepted by green material only. Vegetation types (all sampled in May–June 1991) are indicated in the legend. In panel (B) only, addition of a second-order term to the regression model was statistically significant ($P \leq 0.01$). Correlation coefficients for the regressions illustrated are as follows: panel (A), $R = 0.823$ ($n = 43$); panel (B), $R = 0.964$ ($n = 23$); panel (C), $R = 0.737$ ($n = 43$); panel (D), $R = 0.902$ ($n = 23$). Pearson correlation coefficients are indicated in Table 3. The dashed baseline illustrates the mean NDVI or SR for bare soil.

NDVI vs. SR

The relative merits of NDVI and SR as indicators of canopy structure, light absorption, and potential photosynthetic activity have been the subject of some discussion in the literature. Some authors report slightly curvilinear relationships between NDVI (or SR) and F_{IPAR} (e.g., Choudhury 1987, Sellers 1987). Others report strong linear correlations between NDVI and F_{IPAR} (e.g., Bartlett et al. 1990, Demetriades-Shah et al. 1992b). In our study, NDVI did not necessarily support a more linear regression model than SR, but it yielded less scatter than SR, especially at high values (Fig. 5), resulting in similar linear correlations between these two indices and F_{IPAR} after correction for percentage greenness (Table 3). The choice of SR vs. NDVI appears to be an arbitrary one based upon the particular purpose at hand, and not upon absolute, theoretical limitations of either index.

CO_2 flux and radiation-use efficiency

When integrated over long time periods (e.g., an entire growing season), NDVI yields good correlations

with integrated carbon gain (NPP) for a wide variety of vegetation types (Goward et al. 1985), suggesting that a constant ϵ may be a reasonable approximation even for mixed vegetation types if long enough time periods are considered. This assumption of a relatively constant ϵ (e.g., Kumar and Monteith 1981, Russell et al. 1989) may work well in annual and deciduous vegetation where canopy structure and light absorption change in synchrony with canopy-level fluxes (Gamon 1993a). However, even in annual canopies, stress-induced declines in ϵ have been detected (Bartlett et al. 1990, Steinmetz et al. 1990, Demetriades-Shah et al. 1992a, Valentini et al., *in press*). In our study, evergreen species showed striking seasonal variability in instantaneous photosynthetic radiation-use efficiency. Recent model simulations illustrate a similar uncoupling between NDVI and photosynthetic productivity due to a changing ϵ in evergreen forests (Running and Nemani 1988). Although physiological factors affecting radiation-use efficiency are relatively well understood from controlled studies at the leaf level (Ehleringer and Pearcy 1983, Genty et al. 1989, Demmig-Adams and

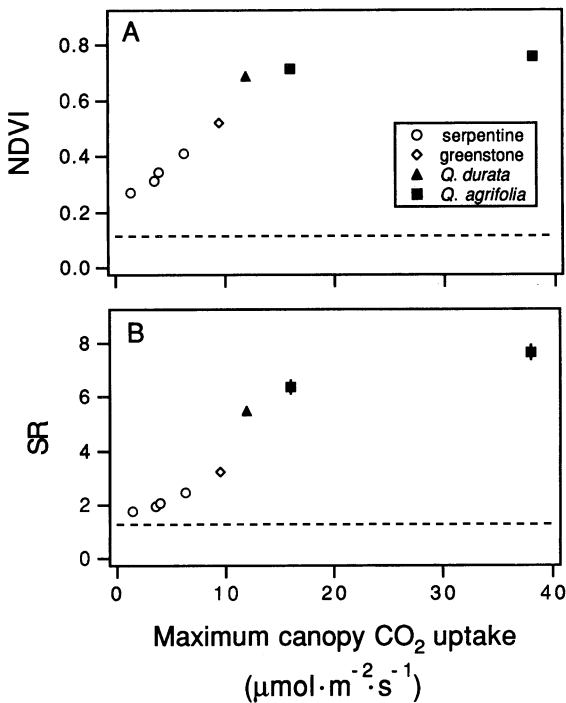


FIG. 6. (A) normalized difference vegetation index (NDVI) or (B) simple ratio (SR) vs. maximum daily canopy CO_2 flux measured either with eddy covariance in two types of annual grassland (Gamon et al. 1993a, Valentini et al., *in press*) or with a ventilated canopy chamber on two evergreen oak species (Goulden 1991, Goulden and Field 1994). Grassland fluxes were measured at five different times in the growing season (between February and May 1991) at two different sites with different soil types (serpentine and greenstone). Carbon dioxide uptake by oak was measured on three individuals between 4 and 16 April 1991, during the season of peak photosynthetic activity for both species. Squared correlation coefficients (R^2) were 0.99 (NDVI) and 0.97 (SR) for grassland only, and 0.67 (NDVI) and 0.81 (SR) for both grassland and oaks together.

Adams 1992, Overhuber et al. 1993), it is less clear how these physiological processes are translated into spatial and temporal patterns of ϵ at the canopy and larger levels.

Strong correlations between NDVI and NPP (e.g., Goward et al. 1985) do not necessarily indicate that NDVI is a reliable or direct measure of current or future instantaneous photosynthetic fluxes. Vegetation indices are more a measure of integrated past photosynthetic activity (and resulting canopy structure) than present photosynthetic activity, and the ability of NDVI to predict future fluxes or NPP depends both on the time scale of interest and the degree to which past environmental and physiological conditions are good indicators of future conditions. Variation in above- and belowground carbon allocation, a factor rarely considered in estimates of production, could further perturb the relationships between NDVI, photosynthetic rates, and NPP. Presumably over sufficiently long (i.e., ontogenetic and evolutionary) time scales, canopy PAR ab-

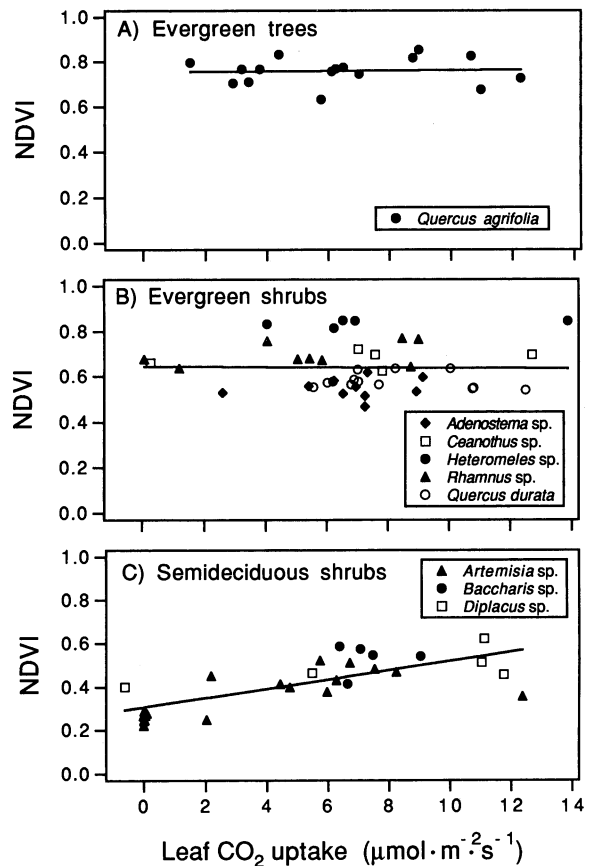


FIG. 7. Normalized difference vegetation index (NDVI) vs. leaf level net CO_2 uptake measured at different seasons for (A) evergreen trees, (B) evergreen shrubs, and (C) semideciduous shrubs. Each data point represents a single measurement. Lines represent first-order fits for all species within a type. The fit for the semideciduous shrubs is the only significant regression ($R = 0.733$, $P \leq 0.001$).

sorption adjusts to resource availability so that a "functional convergence" exists between NDVI, PAR absorption, and carbon gain (Field 1991, Field et al. 1994).

The results of this study indicate that it would be erroneous to predict that canopies of similar seasonal NDVIs are necessarily similar in their fluxes of CO_2 or water vapor, particularly over the shorter time scale of hours to weeks. The varying relationships between NDVI, canopy structure, and seasonal photosynthetic activity among different vegetation types confounds simple predictions of CO_2 fluxes from vegetation indices alone, especially in heterogeneous landscapes.

Clearly, the estimation of actual photosynthetic rates from NDVI requires sophisticated approaches that consider stress-induced changes in vegetation physiology. One approach uses vegetation indices in combination with environmental and physiological variables (Running and Nemani 1988, Bartlett et al. 1990, Running 1990, Sellers et al. 1992, Running and Hunt 1993, Pot-

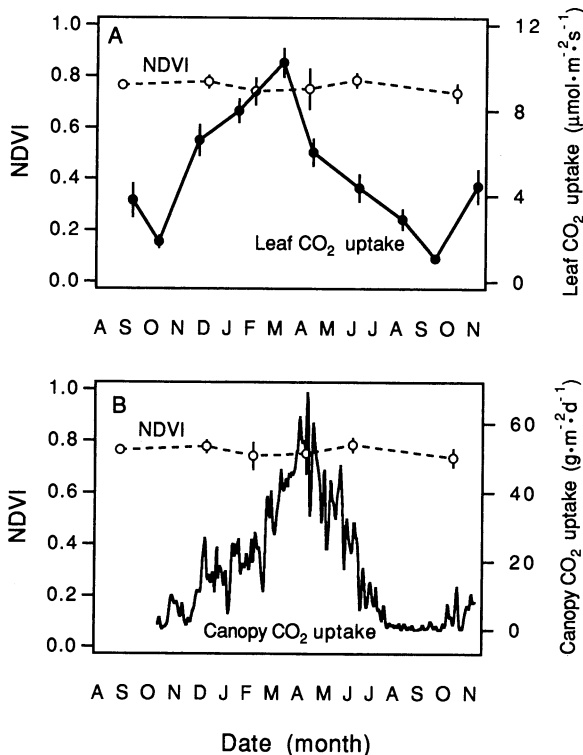


FIG. 8. Seasonal course of NDVI and both leaf- and canopy-level net CO₂ uptake in the evergreen oak *Quercus agrifolia* (coast live oak) from August 1989 to November 1990. Panel (A) indicates light-saturated net CO₂ uptake measured between mid-morning and midday on top canopy leaves at similar incident PFDs (1436–1736 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Thus, changes in leaf CO₂ uptake primarily reflect differences in photosynthetic radiation-use efficiency. Each point illustrates the mean ± 1 SE for five to eight individual canopies, and a minimum of three leaves per canopy. Panel (B) indicates daily integrated canopy fluxes averaged for two canopies (daytime hours only) using the sap-flow approach outlined by Goulden (1991) and Goulden and Field (1994). Seasonal variation in canopy fluxes include the effects of changing physiology and daily integrated canopy radiation exposure, and thus are not strictly comparable to leaf level fluxes.

ter et al. 1994, Runyon et al. 1994) or estimates of leaf biochemical content or physiological capacity (Collatz et al. 1991) as inputs to simulation models. A complementary approach might be to directly derive information on in situ photosynthetic rates or radiation-use efficiencies from chlorophyll fluorescence (Bolhar-Nordenkamp et al. 1989) or from "physiological reflectance indices" derived from spectral reflectance using high spectral resolution sensors (Gamon et al. 1990, 1992, 1993b, Peñuelas et al. 1994, Field et al. 1994). In the near future, these optical assays of physiology may be limited to ground-based applications at the leaf to canopy scales. In some cases, measurements of photosynthetic fluxes at the landscape scale (e.g., via eddy covariance or aircraft sampling) can be combined with spectral reflectance to derive CO₂ flux estimates at larger scales (Cihlar et al. 1992, Desjardins

et al. 1992, Gamon et al. 1993a). Spectral mixture analysis of narrow-band reflectance imagery (Gamon et al. 1993a, Roberts et al. 1993) could supplement applications of NDVI and assist in developing ecologically and structurally meaningful interpretations of vegetation that correlate with patterns of carbon flux.

Considerable challenges remain in the estimation of CO₂ fluxes from remote sensing, particularly in cases where environmental stresses reduce photosynthetic fluxes without parallel declines in canopy greenness. It is unclear whether such stress periods have significant effects on the global carbon budget as many global CO₂ flux calculations involving NDVI (e.g., D'Arrigo et al. 1987, Fung et al. 1987) have not explicitly considered possible asynchrony of canopy structure and physiology associated with changing radiation-use efficiency.

CONCLUSIONS

The vegetation indices NDVI and SR derived from canopy reflectance in the red and near-infrared wavebands are useful indicators of canopy structure, chlorophyll content, nitrogen content, fractional intercepted or absorbed PAR, and potential photosynthetic activity across a wide range of vegetation types. While NDVI is especially sensitive to differences in canopy cover in sparse canopies (green LAI between 0 and 2), it loses sensitivity in moderate and dense canopies. Estimation of canopy biomass and NPP from NDVI or SR may require additional estimation of percentage non-green tissue, which can be the dominant canopy component in some vegetation types. Despite their good correlation with fractional intercepted PAR and several measures of canopy structure and chemical content (and thus potential photosynthetic activity), these indices are not always reliable indicators of instantaneous photosynthetic rates because of varying synchrony between green canopy development and photosynthetic fluxes across vegetation types. Accurate estimation of evergreen canopy photosynthetic rates from remote sensing may require careful, independent evaluation of seasonally changing radiation-use efficiency. If judiciously used with additional information, these vegetation indices can be powerful tools for scaling a physiologically-based estimate of photosynthesis to the landscape and global levels.

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