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Uncertainties in fPAR estimation of grass canopies under different stress situations and differences in architecture

P. M. CRISTIANO*, G. POSSE, C. M. DI BELLA and F. R. JAIMES
Instituto de Clima y Agua, INTA, Los Reseros y Las Cabañas S/N (1686), Hurlingham, Buenos Aires, Argentina

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The fraction of intercepted photosynthetic active radiation (fPAR) is a key variable used by the Monteith model to estimate the net primary productivity (NPP). This variable can be assessed by vegetation indices (VIs) derived from spectral remote sensing data but several factors usually affect their relationship. The objectives of this work were to analyse the fPAR dynamics and to describe the relationships between fPAR and several indices (normalized difference vegetation index (NDVI), optimized soil adjusted vegetation index (OSAVI), Green NDVI (GNDVI), visible atmospherically resistant index (VARI) green, VIgreen and red edge position (REP)) under different water and nutrient treatments for two species with different canopy architectures. Two C_3 grass species with differences in leaf orientation (planophile and erectophile) were cultivated from seeds in pots. Four treatments were applied combining water and nitrogen availability. Every week, canopy reflectance and fPAR were measured. Aerial biomass was clipped to estimate final above-ground production for each species and treatment. Starting from reflectance values, the indices were calculated. Planophile species have a steeper (but not significantly) slope in VIs–fPAR relationships than the erectophile species. Water and nutrient deficiencies treatment showed no relationship with fPAR in any spectral index in the erectophile species. In the other species, this treatment showed significant relationship according to the index used. Analysing each species individually, treatments did not modify slopes except in one case (planophile species between both treatments with high nitrogen but differing in water availability). Among indices, GNDVI was the best estimator of fPAR for both species, followed by NDVI and OSAVI. Inaccurate results may be obtained from commonly reported spectral relationships if plants' stress factors are not taken into account.

1. Introduction

The rate of vegetation primary production shows a linear response to light absorbed by the canopy under ideal conditions (Monteith 1972, 1977, Landsberg 1986). The fraction of intercepted photosynthetic active radiation (fPAR) is a key variable in models used to estimate net primary productivity (NPP) of ecosystems. The fPAR can be assessed indirectly from remote sensing data. Nowadays, the use of this tool for the study of vegetation dynamics is very common since it provides a great quantity of information at different scales (from regional to landscape scale), and is easy to acquire, with relatively low costs (Tucker 1980, Gower *et al.* 1999, Paruelo *et al.* 1999, Nagendra 2001, Kerr and Ostrovsky 2003). Spectral information is commonly

*Corresponding author. Email: pcristiano@cnia.inta.gov.ar

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summarized to a single value or vegetation index (VI) for assessing vegetative characteristics.

Among numerous VIs, normalized difference vegetation index (NDVI) is the most widely used for vegetation studies. Using differences in reflectance of the photosynthetic tissues in red (R) and near-infrared (NIR) wavelengths, the NDVI allows the estimation of fPAR for different growing conditions (Daughtry *et al.* 1983, Sellers 1985, Choudhury 1987). Also, NDVI has been related to other variables like green biomass and primary productivity (Rouse *et al.* 1974, Tucker and Sellers 1986, Quattrochi and Pelletier 1991, Goward and Huemmrich 1992, Paruelo *et al.* 1997, Awaya *et al.* 2004), absorbed photosynthetically active radiation (Gamon *et al.* 1995, Di Bella *et al.* 2004), leaf area index (Vaesen *et al.* 2001, Xavier and Vettorazzi 2004), leaf chlorophyll content (Dawson and Curran 1998, Oppelt and Mauser 2004, Cho and Skidmore 2006), stocking rate of an ecosystem (Oesterheld *et al.* 1998, Posse and Cingolani 2000) and evapotranspiration (Di Bella *et al.* 2000).

However, the relation between NDVI and fPAR shows some alterations at low and high cover values (Myneni and Williams 1994, Ruimy *et al.* 1994, Joel *et al.* 1997, Viña and Gitelson 2005). Also, in the senescent phase, the relationship turns weak because canopies still intercept incident radiation but NDVI values are small due to low photosynthetic pigment concentrations in leaves (Leamer *et al.* 1978). Moreover, the relationship between fPAR and spectral indices weakens under stress situations and may be different among species with different growth habits (Colwell 1974, Jackson and Ezra 1985, Myneni and Williams 1994, Turner *et al.* 2002). In this context, some authors proposed other VIs. When green coverage is low, soil background is a major component that affects the spectral response of the integrated signal (Huete 1988, Paruelo *et al.* 1997). Under this situation, the optimized soil adjusted vegetation index (OSAVI) is proposed (Rondeaux *et al.* 1996). On the other hand, with high cover percentages, when the NDVI usually saturates (Asrar *et al.* 1985, Ruimy *et al.* 1994), the Green NDVI (GNDVI) exhibits more sensitivity to changes in fPAR (Gitelson and Merzlyak 1998, Viña and Gitelson 2005). Visible atmospherically resistant index (VARI) avoided the unclear response of NIR regarding differences in leaf orientation, because it is calculated without near-infrared values (Gitelson *et al.* 2002). In addition, inclusion of a blue band compensates for atmospheric and background effects (Huete *et al.* 1999). Another index that does not use the NIR band is the VI green index that appears to be a better estimator of fractional cover than NDVI, especially at high cover values (Gitelson *et al.* 2002). Since the Leaf Area Index (LAI) and fPAR are associated with leaf chlorophyll content, some indices that estimate it, such as the REP (red-edge position), have also been proposed. REP is the point of inflection (maximum slope) between 680 and 780 nm reflectance, known as the red-edge position (Guyot and Baret 1988, Dawson and Curran 1998, Cho and Skidmore 2006), but it has not been tested across many species; nor has its relationship with the fPAR been studied yet.

Water availability is the most important resource that affects plant growth. Green leaf area decreases under water stress, as fPAR does consequently, since leaves roll up or senesce early (Collino *et al.* 2001). Changes in NDVI values are also expected, but the magnitude of the change is uncertain. If water stress promotes the senescence of leaves, an additional factor will be present, since dead material diminishes VI and fPAR canopy values. In this case, the relative quantity of dead material present will be determinative (Di Bella *et al.* 2004). Mineral nutrition is the second restrictive factor that commonly affects vegetation growth. Nitrogen (N) is among the most limiting nutrients because it is needed in high quantities (Serrano *et al.* 2000). When plants grow with limited access to N, growth reduction takes place, and specific symptoms of deficiency are developed. A common characteristic is the increase in photosynthetic compounds assigned to roots, and the decrease in stem and leaf production (Evans and Edwards 2001). Moreover, vegetation that grows under these restrictive conditions can suffer alterations in spectral indices, since N is an important component of the chlorophyll pigment (Wylie *et al.* 2002).

The quantity of intercepted radiation depends fundamentally on the surface of green tissues and its spatial disposition. Reflectance values depend on the optic properties of leaves, but the canopy architecture is able to influence the estimation of fPAR through the VIs (Goel and Qin 1996). There is some controversy regarding the consequences of different plant architectural characteristics and the mechanisms that control the reflectance values. For example, Colwell (1974) and Jackson and Ezra (1985) found that for erectophile vegetation, more radiation is trapped within the canopy than planophile species, increasing the ability of plants to absorb radiation. On the other hand, Myneni and Williams (1994) proposed that canopies with horizontal leaves intercept more incident radiation than erect ones, producing higher reflectance values especially in the NIR wavelengths. Therefore, planophile species will have greater values of NDVI than erectophile plants with the same LAI values. In addition, NDVI is sensitive to the spatial distribution of leaf area and not simply to the absolute amount of leaf area; and the relationship with the fPAR changes with the density of leaf clumps and the distance between them (Myneni and Williams 1994).

Under natural conditions, as in Argentinean grasslands, vegetation is exposed to multiple interacting stress situations. In these grasslands, species with different growth habits coexist in time and space, and are exposed to different grazing intensities and levels of stress. Effects of particular growing conditions and differences in canopy architecture on values of different VIs are unknown. The index selected to calculate fPAR from spectral data becomes an important issue, especially to ensure reliability in the estimation of primary productivity. Considering that remote sensing is now a common tool used to estimate above-ground net primary productivity (ANPP), the objectives of this work were: (1) to find a robust spectral index that produces accurate estimations of fPAR under different water and nutrient conditions, (2) to analyse how fPAR dynamics and fPAR–VIs relationship were affected under different water and nutrient conditions and (3) to compare these results between two species with conspicuous differences in canopy architecture. Our hypotheses were that fPAR would be affected by different stress conditions and the fPAR–VIs relationships would be affected by canopy structure and restrictive water and nitrogen conditions. The predictions were that fPAR would be more affected by water than nitrogen restriction and that planophile grasses would reach the same fPAR value as erectophile grasses at lower levels of green biomass. Consequently, the slope of the fPAR–VI relationship would be different between these two growth habits. These results could help us to better understand these relationships and therefore improve ANPP estimations when satellite images are used. Indirectly, these results would improve livestock carrying capacity estimations from remote sensing data, optimizing the management of extensive cattle systems in natural ecosystems.

2. Materials and methods

2.1 *Study site and growth conditions*

This research was carried out at the experimental field of the 'Instituto de Clima y Agua' (INTA Castelar, Argentina) located at 31° 36′ S and 58° 40′ W. An experiment was designed using two C_3 grass species: perennial ryegrass (*Lolium perenne* L.) and orchard grass (*Dactylis glomerata*) with erectophile and planophile architecture, respectively, under simple visual inspection. Plastic pots of 5 litres were filled with a soil–sand mixture (2:1 v/v). Seeds were sown on 22 May 2006 (winter season) at a rate of approximately 20 seeds per pot. Germination was completed 10 days later. After emergence, we left two plants per pot to homogenize the final number and to ensure final closed canopies. We placed all pots below an open transparent polycarbonate shelter to avoid natural rainfall over plants.

2.2 *Experimental treatments*

Four treatments were applied combining water and nitrogen availability: N1W1 (high availability of nitrogen, high availability of water), N1W0 (high availability of nitrogen, low availability of water), N0W1 (low availability of nitrogen, high availability of water) and N0W0 (low availability of nitrogen, low availability of water). The experimental unit was composed of four pots which simulated a canopy. All pots were uniformly irrigated from time of germination until 73 days after sowing. Then, water treatments were implemented. In high water availability (W1), pots were watered regularly up to field capacity. Low water availability treatment (W0) was generated reducing the irrigation frequency and intensity (quantity of water per plant). Water conditions of plants in both treatments were controlled by water potential measurements of leaves with a Scholander pressure bomb (Scholander *et al.* 1965). In the high nitrogen availability treatment (N1), pots were fertilized with 4 g of NH_4NO_3 (ammonium nitrate): 2 g on day 63 and 2 g on 78 day after germination, with a final concentration of 0.8 g per kg of soil–sand mixture. This was equal to two fertilizations of 200 kg ha^{-1}. Low nutrient availability treatment was not fertilized. Analysis of soil samples from both nitrogen treatments was carried out on the first week of August to control their effectiveness. Once a week during the experiment (from May to November), all pots were rotated to avoid or reduce the border effect. Several pots belonging to the N0W1 treatment was eliminated due to problems with plant development. This imbalance between treatments ultimately caused us to discard the N0W1 treatment. We present here the results of the three remaining treatments.

2.3 *Measurements*

A canopy was constructed with four pots randomly selected and located together in two columns by two rows that covered 0.16 m^2. For each measured variable over each treatment, we used three canopies per time (replicates), where the canopy was the experimental unit. Every week, we measured fPAR and reflectance. The fraction of intercepted photosynthetically active radiation, fPAR, was defined as shown in equation (1):

$$\mathrm{fPAR} = ((\mathrm{PAR_i}) - (\mathrm{PAR_t}) - (\mathrm{PAR_r}))\,/\,(\mathrm{PAR_i})), \tag{1}$$

where PAR means photosynthetically active radiation, specifically with PAR_i being the incident PAR at the top of the canopy, PAR_t is the transmitted PAR beneath the canopy and PAR_r is the reflected PAR.

PAR radiation was measured using a linear quantum sensor (^{TM}Cavadevices, Buenos Aires, Argentina) that measures the photon flux between 300 to 1000 nm, and up to 3000 μmol m^{-2} s^{-1}, over a 1-m linear surface. Although it was measured, PAR_r can be ignored because in the PAR domain leaves absorbed most of the light (Di Bella *et al.* 2004). Thus, canopy light interception was calculated as shown in equation (2):

$$\mathrm{fPAR} = ((\mathrm{PAR_i}) - (\mathrm{PAR_t}))/(\mathrm{PAR_i}), \tag{2}$$

where PAR_i was measured locating the quantum linear sensor just above each experimental unit and PAR_t was registered below each canopy being measured. Two perpendicular measurements of PAR_i and PAR_t were made on each canopy and then averaged for the fPAR calculation.

One reflectance measurement per canopy were carried out using an Ocean Optics spectroradiometer^{TM} (1 nm spectral resolution, Ocean Optics, Florida, USA) in a small darkroom with artificial light to maintain constant illumination conditions. Four tungsten lamps of 150 W each (^{TM}Phillips Spot, R95, Amsterdam, The Netherlands) were mounted on the top of chamber. The optic fibre cable of the spectrometer was mounted in the central position between the lamps at a 50 cm height (field of view, FOV = 25), this assured us that only the entire canopy was measured. In order to calculate reflectance, a white reference of barium sulphate ($BaSO_4$) was used to normalize to absolute reflectance. These data were used to calculate six spectral indices as follows in equations (3)–(8):

$$\mathrm{NDVI}: (R_{864} - R_{671})/(R_{864} + R_{671})(\mathrm{Rouse}\ et\ al.\ 1974) \tag{3}$$

$$\mathrm{GNDVI}: (R_{800} - R_{500})/(R_{800} + R_{550})(\mathrm{Gitelson}\ et\ al.\ 1996) \tag{4}$$

$$\mathrm{OSAVI}: (1 + 0.16)(R_{800} - R_{670})/(R_{800} + R_{670} + 0.16)(\mathrm{Rondeaux}\ et\ al.\ 1996) \tag{5}$$

$$\mathrm{VARI\ green}: (R_{550} - R_{670})/(R_{550} + R_{670} - R_{490})(\mathrm{Gitelson}\ et\ al.\ 2002) \tag{6}$$

$$\mathrm{VI\ green}: (R_{550} - R_{670})/(R_{550} + R_{670})(\mathrm{Gitelson}\ et\ al.\ 2002) \tag{7}$$

$$\begin{aligned}\mathrm{REP}: &(A(\lambda_2 + \lambda_3) + B(\lambda_1 + \lambda_3)\\ &+ C(\lambda_1 + \lambda_2))/(2(A + B + C))(\mathrm{Dawson\ and\ Curran\ 1998}),\end{aligned} \tag{8}$$

where R is reflectance (%) in the different wavelengths (nm) denoted by the subscripts. REP was computed with the Lagrangian technique where λ is the wavelength, and subscripts 1, 2 and 3 denote the specific wavelength: 680, 700 and 740, respectively. A, B and C are three parameters calculated from the first-derivative values of the reflectance in these three specific wavelengths and the wavelengths values itself (for more details, see Dawson and Curran (1998)). Note that each index used a slightly different wavelength, but we used the indices as they were defined. Spectral response difference was negligible and did not affect the VIs values obtained.

Every 3 weeks, aerial biomass was manually harvested and dried for 72 h at 70°C in a drying stove. An initial measurement prior to treatment was also done. Three replicates were evaluated for every treatment through five dates. In total, six harvests were carried out during the experiment. This produced a total number of 252 pots used. To calculate and compare the treatments, final aerial biomass production was analysed.

2.4 *Data analysis*

In order to compare treatments with regard to total aerial biomass, factorial Analysis of Variance (ANOVA) tests were performed using Tukey Studentized range (HSD) at the 5% probability level. To study the relationships between fPAR and the six spectral indices, simple regression analyses were used. Values of the three replicates taken at each date were averaged to carried out this analysis. We compared R^2 values and the mean square sum (MSS) error between linear and logarithmic regressions. When the logarithmic relationship produced a better fit than the linear one, the fPAR variable was transformed, applying the natural logarithm in order to find a linear relationship. Therefore, the original value (fPAR) or the natural logarithm of fPAR (ln(fPAR)) was used as an independent variable and each of the six spectral indices as dependent variables. For each index, six linear regression models were obtained from the combinations of nutrient and water availability and species as shown in equation (9):

$$Y = \beta(\mathrm{fPAR}) + \rho + \varepsilon, \tag{9}$$

where Y was the spectral index, β was the slope, ρ was the y-intercept and ε was the random error. We tested the null hypothesis, $\beta_1 = \beta_2 = \beta_3 = \beta_4 = \beta_5 = \beta_6$, with a model as shown in equation (10):

$$Y = (\alpha\, t)(\mathrm{fPAR}) + \varepsilon, \tag{10}$$

where α was the effect of nutrient and water treatments, t was the effect of the species, and ε was the random error. Contrasts were produced for the different combinations of ($\alpha\, t$) fPAR equivalent to making an equal slope test (Weber and Skillings 2000). All data analyses were carried out with the R Soft Statistics Package (©R, 2006, University of Auckland, New Zealand). To find the best fPAR estimator, we will group treatments with significant regression for each species and index, taking into account which treatment must be excluded.

3. Results

3.1 *Variability of fPAR with time*

Final accumulated aerial dry matter differed among treatments ($p < 0.05$, factorial ANOVA) for both species (39–117 g and 32–124 g for *L. perenne* and *D. glomerata*, respectively); presenting a negative relationship with the stress level (figure 1). Green biomass of water stressed plants (N1W0) was the 60% of the maximum biomass value (N1W1) in *L. perenne* and 50% in *D. glomerata*. At the other extreme, the biomass for the combined water–nutrient stress treatment (N0W0) was 33 and 26% of the N1W1 values in *L. perenne* and *D. glomerata*, respectively.

Comparing fPAR values between both species, no differences ($p > 0.05$) were observed in the N1W1 treatment in spite of differences in plant architecture. Both species reached similar fPAR values by the end of the experiment (0.87–0.93). However, growth restriction had different consequences over the fPAR depending on treatment and species (figure 2). Although final fPAR values in the water-nutrient limitation treatment (N0W0) were similar for both species (0.55–0.64), the fPAR evolution during the experiment was different, with *D. glomerata* exhibiting lower fPAR values than *L. perenne* across all measurement periods ($p < 0.05$). Comparing final fPAR values among treatments, *D. glomerata*, reached similar values on N1W0 and N0W0 treatments (0.59–0.55, $p > 0.05$), both considerably lower than in the N1W1 treatment (0.93, $p < 0.05$) (figure 2). In *L. perenne*, both

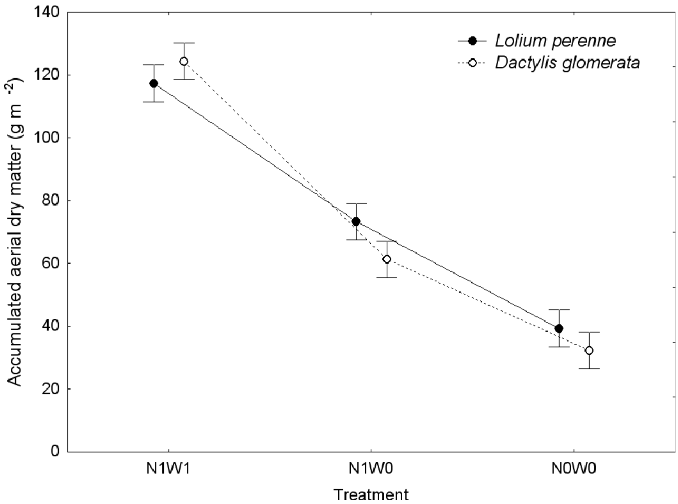

Figure 1. Accumulated aerial dry biomass for two species (-●-*L. perenne* and -○-*D. glomerata*) and treatments (N1W1, N1W0 and N0W0) analysed ($n = 3$). N1W1: higher availability of water and nitrogen; N1W0: higher availability of nitrogen and water restrictions; N0W0: nitrogen and water availability restrictions. Vertical bars denote 0.95 confidence intervals.

fertilized treatments (N1W1 and N1W0) reached similar values (0.87–0.82, $p > 0.05$), while N0W0 achieved a lower value (0.64, $p < 0.05$). Differences in fPAR values between N1W1 and both stress treatments were less in *L. perenne* (0.23) than in *D. glomerata* (0.38).

3.2 *Regression relationships between fPAR and vegetation indices*

All indices exhibited a better fit to a logarithmic function than a linear one, based on the respective coefficients of determination (data not shown). Relationships between measured fPAR values and VIs were compared through slopes and y-intercepts. Results differed according to species, treatment and the VI considered. In *L. perenne*, for example, the relationships between ln(fPAR) and NDVI, GNDVI, OSAVI and REP were significant only for N1W1 and N1W0 treatments ($p < 0.05$). VARI and VI green indices only showed a significant relationship ($p < 0.05$) in the N1W0 treatment, and no significant relationship was observed for any index in the N0W0 treatment. In *D. glomerata,* a significant relationship with ln(fPAR) was observed in most indices except the GNDVI in N0W0 and REP in N1W0 and N0W0. All indices showed the highest R^2 in N1W0 and the lowest one in N0W0 treatment, and this trend was the same for both species. When we compared slopes among treatments with significant regressions, we found no significant differences ($p > 0.05$) in *L. perenne*. In *D. glomerata*, the only significant differences in slope were observed in the N1W1 and N1W0 treatments for the relationship NDVI–ln(fPAR). No significant among-treatment or between-species differences in intercept were observed for any of the indices (table 1). To find the best fPAR estimator, we grouped treatments with significant regressions for each species and index. GNDVI was the index that best estimated the ln(fPAR), with an R^2 of 0.81 and 0.85 in *L. perenne* and *D. glomerata*, respectively (table 1).

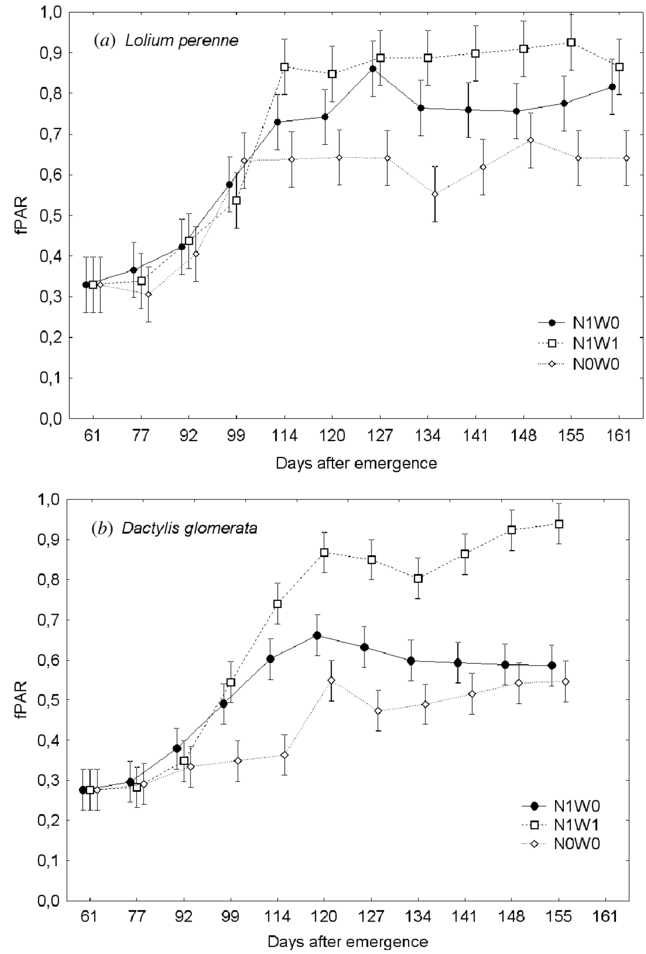

Figure 2. Fraction of photosynthetically active radiation intercepted from the canopy (fPAR) as a function of days after emergence for three treatments (-▫-N1W1, -●-N1W0 and ··◇··N0W0) for the two species with different canopy architecture: erectophile, *L. perenne* (*a*) and planophile, *D. glomerata* (*b*). Vertical bars indicate the 0.95 confidence intervals, $n = 3$.

Comparing between species, no significant differences in slopes were observed between them. Therefore, new regression analyses were performed, grouping data of both species to study the overall relationship between fPAR and each VI, without taking into account the canopy structure. For this purpose, two types of analysis were carried out: the first with the complete data set and the second only using data of treatments with significant regressions. In the last case, the data excluded were N0W0 for all indices and N1W1 for VARI and VI green of *L. perenne* and N0W0 for GNDVI in *D. glomerata*. Using all data sets, the best indices were the GNDVI ($R^2 = 0.67$), OSAVI ($R^2 = 0.64$) and NDVI ($R^2 = 0.63$). GNDVI revealed a higher R^2 value in linear relationship (0.69) than in the logarithmic one (0.67) (table 2). Taking into account only significant treatments, the best fPAR estimators were the same as those mentioned above: GNDVI ($R^2 = 0.82$) followed by the NDVI ($R^2 = 0.71$) and the OSAVI ($R^2 = 0.71$). Note that determination coefficients were higher in the second analysis (figure 3).

Table 1. Values of the parameters obtained from the simple linear regressions between the natural logarithm of fPAR (ln(fPAR)) and the six spectral indices analysed for each three treatments in *Lolium perenne* and *Dactylis glomerata*. For each index, results for all treatment data are provided as well as only the significant treatments. 'β' is the slope and 'ρ' the y-axis-intercept. R^2 was the determination coefficient, and n represented the number of data used for the regression ($n = 12$; averaged data of three replicates per 12 measurement dates per treatment). Regression was significant (or slope significantly different from zero) when the p value was <0.05.

		Lolium perenne (erectophile)					*Dactylis glomerata* (planophile)				
Vegetation indices	Treatment	R^2	β	ρ	p value	n	R^2	β	ρ	p value	n
NDVI	N1W0	0.78	0.26	0.88	0.00	12	0.88	0.45	0.97	0.00	12
	N1W1	0.46	0.18	0.89	0.01	12	0.69	0.28	0.90	0.00	12
	N0W0	0.12	0.07	0.66	0.27	12	0.59	0.27	0.80	0.00	12
	All treatments	0.44	0.23	0.85	0.00	36	0.76	0.35	0.91	0.00	36
	significant treatments	0.58	0.22	0.89	0.00	24	0.76	0.35	0.91	0.00	36
GNDVI	N1W0	0.88	0.22	0.74	0.00	12	0.87	0.30	0.77	0.00	12
	N1W1	0.73	0.19	0.76	0.00	12	0.83	0.23	0.73	0.00	12
	N0W0	0.10	0.03	0.53	0.32	12	0.29	0.11	0.57	0.07	12
	All treatments	0.54	0.21	0.71	0.00	36	0.76	0.25	0.72	0.00	36
	significant treatments	0.81	0.21	0.75	0.00	24	0.85	0.25	0.74	0.00	24
OSAVI	N1W0	0.74	0.31	1.02	0.00	12	0.87	0.56	1.13	0.00	12
	N1W1	0.47	0.24	1.03	0.01	12	0.69	0.36	1.04	0.00	12
	N0W0	0.13	0.10	0.75	0.24	12	0.63	0.37	0.95	0.00	12
	All treatments	0.44	0.29	0.98	0.00	36	0.77	0.45	1.05	0.00	36
	significant treatments	0.57	0.27	1.02	0.00	24	0.77	0.45	1.05	0.00	36
VARI green	N1W0	0.45	0.28	0.47	0.02	12	0.85	0.50	0.60	0.00	12
	N1W1	0.17	0.20	0.54	0.18	12	0.61	0.35	0.60	0.00	12
	N0W0	0.07	–0.09	0.24	0.39	12	0.80	0.42	0.52	0.00	12
	All treatments	0.27	0.28	0.46	0.00	36	0.75	0.46	0.59	0.00	36
	significant treatments	0.45	0.28	0.47	0.02	12	0.75	0.46	0.59	0.00	36
VI green	N1W0	0.47	0.19	0.33	0.01	12	0.85	0.33	0.39	0.00	12
	N1W1	0.15	0.13	0.38	0.22	12	0.61	0.23	0.40	0.00	12
	N0W0	0.08	0.07	0.17	0.38	12	0.81	0.29	0.36	0.00	12
	All treatments	0.25	0.19	0.33	0.00	36	0.75	0.30	0.39	0.00	36
	significant treatments	0.47	0.19	0.33	0.01	12	0.75	0.30	0.39	0.00	36
REP	N1W0	0.46	6.50	708.11	0.00	12	0.13	6.50	708.98	0.03	12
	N1W1	0.42	5.54	707.56	0.00	12	0.10	4.81	708.00	0.06	12
	N0W0	0.05	–4.06	696.18	0.18	12	0.02	2.90	704.06	0.43	12
	All treatments	0.15	5.54	705.76	0.00	36	0.11	5.80	707.63	0.00	36
	significant treatments	0.44	5.92	707.77	0.00	24	0.13	6.50	708.98	0.03	12

Table 2. Values of the parameters obtained from the simple regressions (linear and logarithm) between the fPAR and the six spectral indices analysed using the full data set (combined data of 12 measurement dates, three treatments and two species, $n = 72$). The slope (β), y axis-intercept (ρ) and the determination coefficient (R^2) are shown

Vegetation indices	Regression	R^2	β	ρ	n
NDVI	Linear	0.61	0.55	0.37	72
	Logarithm	0.63	0.30	0.88	72
GNDVI	Linear	0.69	0.44	0.32	72
	Logarithm	0.67	0.24	0.72	72
OSAVI	Linear	0.61	0.69	0.38	72
	Logarithm	0.64	0.38	1.01	72
VARI green	Linear	0.49	0.67	–0.10	72
	Logarithm	0.50	0.37	0.52	72
VI green	Linear	0.49	0.46	–0.06	72
	Logarithm	0.50	0.25	0.36	72
REP	Linear	0.12	9.86	697.52	72
	Logarithm	0.12	5.67	706.69	72

4. Discussion

In spite of the differences in canopy architecture, under optimal growing conditions no significant differences in fPAR values were found between *L. perenne* and *D. glomerata* (figure 2). Both species reached similar maximum fPAR values (around 0.9) on day 114 after germination. Differences appeared when some restriction was imposed to growth. The fPAR of planophile species (*D. glomerata*) was the most affected (figure 2), increasing more slowly than in the erectophile (*L. perenne*). *L. perenne* seemed to be more resistant to water deficiencies than *D. glomerata,* at least in maintaining its fPAR values. Although leaves of *L. perenne* were rolled up when water was restricted, their spatial disposition may have compensated for the reduction in leaf area, trapping more radiation among their leaves. This observation is in accordance with the results presented by Colwell (1974) and Jackson and Ezra (1985), which showed that the vertical position of leaves increases the ability of plants to absorb radiation. Therefore, fPAR values were more similar among treatments than the values in the planophile species (figure 2). This fPAR behaviour exhibited by stressed leaves in the erectophile species causes the relationship between VIs and fPAR to be more uncertain, finally showing no relationship at all in most stressed situations (table 1). On the other hand, in water-stressed canopies of *D. glomerata*, leaf tips became dry and dead, diminishing fPAR and VIs values. Therefore, the estimation of fPAR through the VIs does not exhibit important changes in this species. These differences cannot be attributed only to architectural variation, and they must be tested with other species. It must be noted that, since no differences were found in final biomass values between both species under each treatment (figure 1), the planophile species seems to be more efficient using the PAR because, even intercepting a minor quantity of light, it reaches the same productivity value as the erectophile species.

The relationship between each calculated index and the fPAR was logarithmic; although the linear approximation showed slightly lower determinant coefficients (R^2). In general, we found that *L. perenne* had weaker relationships between fPAR and most indices. Furthermore, estimation of fPAR through the indices may be

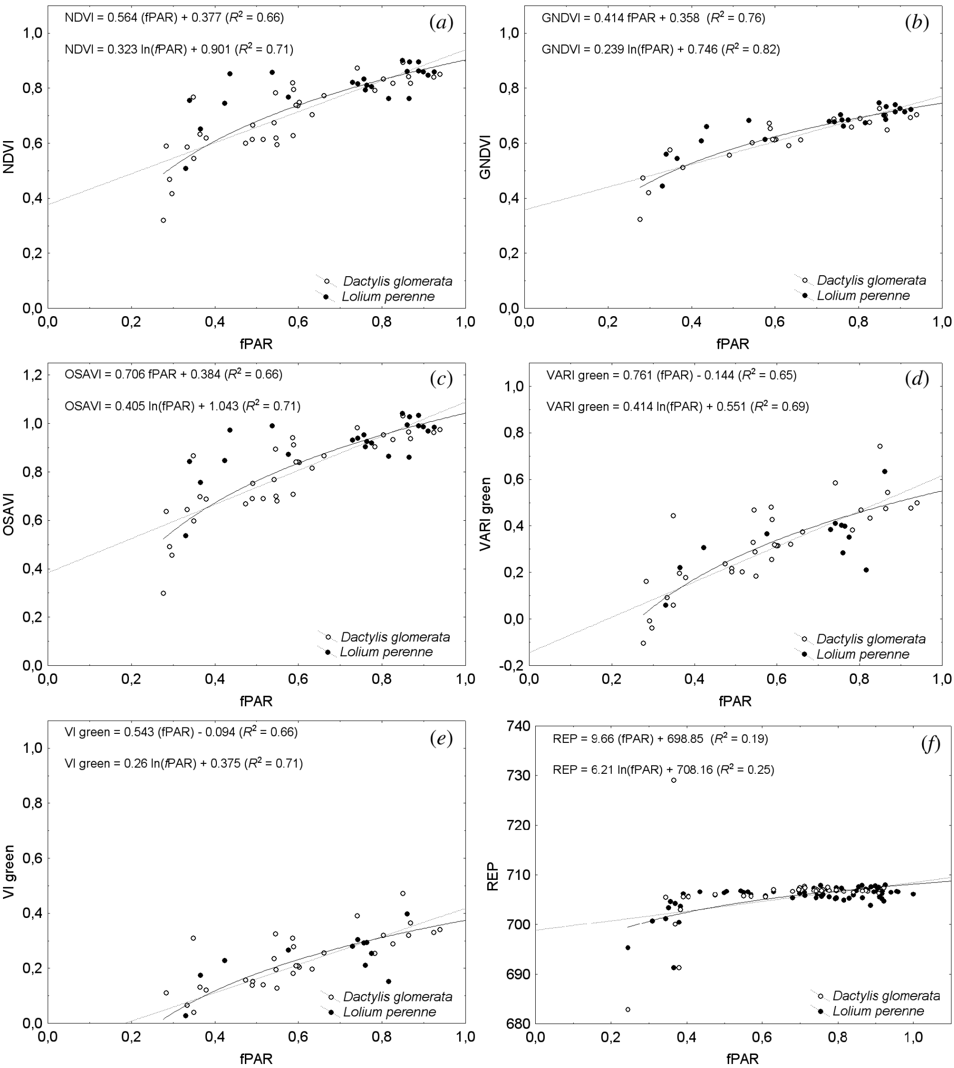

Figure 3. Global relationship (lineal and logarithm) between the fractions of photosynthetically active radiation intercepted from the canopy (fPAR) and the six spectral indices: (*a*) NDVI, (*b*) GNDVI, (*c*) OSAVI, (*d*) VARI green, (*e*) VI green and (*f*) REP for both species (○ *D. glomerata* and ● *L. perenne*). Treatments with no significant relationship ($p > 0.05$) were excluded from pooled data.

erroneous if vegetation was under a strong stress situation, since no significant relationships were found in the treatment with water and nutrient deficiencies (table 1). GNDVI was the index that best estimated the fPAR. It seems that reflectance in the green portion of electromagnetic spectrum compared with reflectance in red (GNDVI vs. NDVI and OSAVI indices), provides useful information to estimate fPAR in vegetation with differences in canopy architecture and with different resource availabilities (water and nitrogen). Nevertheless, these relationships became weak when mixed conditions (architectural and factor stress) were growing together (table 2 and figure 3). Additionally VARI index had no significant relationship in the treatment with the better growth conditions in *L. perenne*. Our observations suggest that the blue tone of leaves in plants with added nitrogen seems to alter the VARI values in this species contributing to the lack of relation since this index uses the blue portion of electromagnetic spectrum. On the other hand, *D. glomerata* revealed higher determination coefficients and low standard errors with all the indices across treatments. The single exception was the GNDVI on plants with both stresses, which had no significant relationship with the fPAR. In all cases, plants that grew with good nitrogen supply but with water restrictions (N1W0) presented the highest slopes and determination coefficients, even better than plants under optimal growth conditions (N1W1). This result could be explained because spectral indices generally exhibit sensitivity to changes in canopy chlorophyll and this pigment could be most concentrated in leaves with less water content.

For each species, there were no differences among slopes in relationships between VIs and fPAR with only one exception (NDVI – ln (fPAR) of N1W1 and N1W0 of the planophile). Thus, the stress situations did not significantly modify the relationship between VIs and fPAR. For both species, GNDVI was a better estimator of fPAR than NDVI (table 1). Gitelson *et al.* (1996) pointed out that GNDVI suffers less saturation at high values of vegetation cover than NDVI. Since we have high fPAR values in several measurement dates, the advantage of GNDVI upon the NDVI is highlighted. Comparing the general equation (grouping all treatments with significant relationships) between both architecture types, we found that the planophile species presented a little steeper slope in the relationship between VIs vs. fPAR than the erectophile species, although this trend was non-significant (table 1). Hence, species with different architecture and with the same fPAR values may have different VIs values.

After all, the difference found in this work among slopes and its significance in the estimations of fPAR through VIs might not have serious consequences, for example, when a project is carried out using coarse resolution images. After all, good regressions were obtained working with data from different canopy architectures (figure 3). A large number of published studies show that many VIs are adequate to estimate fPAR of vegetation growing under different conditions and phenological phase (Myneni and Williams 1994, Di Bella *et al.* 2004). This work, which was carried out in different stress situations (hydrological and nutritional) and canopy architectures that are common in natural systems, encourages us to use remote sensing information of moderate spatial resolution such as MODIS products. These products integrate spatial information of fPAR in pixels of 250 x 250 m, which contain vegetation with different canopy architecture and occupying different growth conditions (Fensholt *et al.* 2004, Olofsson and Eklundh 2007). However, if very detailed results were required, or an important portion of the study area suffered high stress, it will become important to take into account that the estimation of fPAR will have limited accuracy. Consequently, all the variables that were estimated from fPAR will have a great imprecision. Complementary information must be taken into account to correct the estimations that are required in each special case.

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