



## The influence of epiphylls on remote sensing of humid forests

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### ARTICLE INFO

#### Article history:

Received 23 February 2009

Received in revised form 9 April 2009

Accepted 11 April 2009

#### Keywords:

Epiphylls

Epifoliar fungi

MODIS

Amazon

Caatinga

Terra Firme

Canopy reflectance modeling

EVI

### ABSTRACT

Epiphylls – lichens, fungi, liverworts, etc. infesting leaf surfaces – are found throughout humid forests of the world. It is well understood that epiphylls inhibit light interception by host plants, but their effect on remote sensing of colonized forests has not been examined. Incorporating leaf-level spectra from *Terra Firme* (primary forest) and Amazonian *Caatinga* (woodlands/forest growing on nutrient-deficient sandy soils), we used the GeoSAIL model to propagate leaf-level measurements to the canopy level and determine their effect on commonly used vegetation indices. In *Caatinga*, moderate infestations (50% leaf area epiphyll cover), lowered simulated Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) values by 6.1% and 20.4%, respectively, largely due to near infrared dampening. Heavy infestation (100% cover) simulations exhibited decreases 1.5–2 times greater than those of moderate infestations. For *Terra Firme*, which are generally less affected by epiphylls, moderate (20% leaf area) and heavy infestations (40%) lowered EVI by 4.4% (S.D. 0.8%) and 8.1% (S.D. 1.5%), respectively. Near infrared and green reflectance were most affected at the canopy level, showing mean decreases of 10.6% (S.D. 2.25%) and 9.5% (S.D. 3.49%), respectively, in heavy *Terra Firme* infestations. Time series of Moderate Resolution Imaging Spectrometer (MODIS) data corroborated the modeling results, suggesting a degree of coupling between epiphyll cover and the EVI and NDVI. These results suggest that, without explicit consideration of the presence of epiphylls, remote sensing-based methodologies may underestimate leaf area index, biomass and productivity in humid forests.

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### 1. Introduction

Epiphylls, microepiphytes colonizing leaf surfaces, are found throughout the humid tropical forests of the world. Their presence has been documented in Central and South America (Coley et al., 1993; Gilbert et al., 2007; Richards, 1954), northern Australia (Anthony et al., 2002), Africa (Olarinmoye, 1974; Pocs, 1978), and Asia (Frahm, 1990). A wide variety of organisms may inhabit leaf surfaces, including lichens, liverworts, fungi, algae and bacteria. Owing to their considerable diversity, the role that epiphylls play in ecosystem functioning varies widely. Epiphylls have often been viewed as pathogens and parasites (Coley & Kursar, 1996; Garcia-Guzman & Dirzo, 2004), while others have documented commensalism among epiphylls and host plants (Anthony et al., 2002). Liverworts typically have a more mutualistic symbiosis with their hosts, conferring protection from herbivores via terpenoid and phenol production (Zinsmeister & Mues, 1990). Bentley (1987) suggested that blue-green algae epiphylls also practice mutualism as they provide fixed nitrogen in exchange for the epifoliar substrate. This

study focuses on fungi epiphylls, a guild of several hundred known species of widespread Ascomycetes, which generally exhibit commensal symbioses with their hosts (Fig. 1; Gilbert et al., 2007).

Several researchers have examined the effect of epiphylls on the interception of photosynthetically active radiation (PAR; 400–700 nm) by the host leaves and its consequent effect on carbon assimilation. Coley et al. (1993) found that liverworts may reduce leaf interception of PAR by as much as 55–85%. Anthony et al. (2002) encountered a mean PAR attenuation of 48% for epiphytic lichens. Roberts et al. (1998) conducted a 14-month time series of near-monthly leaf spectral measurements for both PAR and the near infrared (NIR; 700–1000 nm) for the Amazonian *Caatinga* canopy dominant, *Aldina heterophylla*. They found that as epiphyll cover increases, green and NIR absorption of mature leaves increased significantly.

Recent remote sensing-based studies of the Amazon basin have documented substantive fluctuations in canopy reflectance (Huete et al., 2006; Myneni et al., 2007; Xiao et al., 2005). These seasonal and interannual changes have been attributed to rainforest phenology and ecosystem responses to water availability. In each publication, the researchers alluded to the presence of and possible errors due to epiphyll cover, yet no thorough analysis of their effect on at-satellite radiances was made. Leaf-level measurements, as referred to above, suitably address first-order effects of epiphyll cover. They cannot account, however, for the myriad radiative interactions within a canopy, including woody-component and background reflectance, leaf area

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Fig. 1. Clean (left) and moderately fungus-coated (right) *Pradosia schomburgkiana* leaves.

index (LAI), shadowing, multiple scattering and species heterogeneity. A quantitative examination of the effect of epiphylls on remote sensing measurements must account for all of these factors. Canopy reflectance models enable the prediction of plant canopy reflectance based on a suite of canopy parameterizations. Canopy reflectance models have been used extensively in remote sensing science to estimate canopy chemistry (Gond et al., 1999), biophysical properties (Jacquemoud et al., 1995) and at-sensor radiances (Verhoef & Bach, 2003). To our knowledge, no studies have used such models to determine the role that epiphylls play in the canopy reflectance of humid forests.

This paper describes the use of leaf-level optical measurements in concert with the GeoSAIL model (Huemmrich, 2001) to estimate the effect of epiphylls on canopy reflectance and consequently, on remote sensing of epiphyll-colonized forests. Optical measurements were conducted in the field for canopy dominants in Amazonian *Caatinga* (a wooded/forested savannah–forest transition on poorly-drained leached white sands) and *Terra Firme* (primary forest on well-drained clay or loam) and serve as essential inputs into GeoSAIL. Model outputs are used to calculate the Normalized Difference Vegetation Index (NDVI; Rouse et al., 1974) and Enhanced Vegetation Index (EVI; Huete et al., 1997). We aim to address the following questions:

1. How do epiphylls affect canopy reflectance in Amazonian *Caatinga* and *Terra Firme* and how do they vary as a function of canopy phenology?
2. How do such changes impact the commonly used vegetation indices, NDVI and EVI?
3. Do such reflectance and NDVI/EVI variations impact remotely sensed imagery?

We hypothesize that epiphylls will have a strong effect on canopy reflectance of Amazonian *Caatinga* as well as a lesser but noteworthy impact on *Terra Firme* – largely a function of differing infestation rates. We anticipate that the increase in NIR absorption (Roberts et al., 1998) and simultaneous decrease in visible light in infested leaves will be mirrored or even amplified at the canopy level, affecting at-sensor radiances. The authors seek to assess the confounding effect of epiphylls on remote sensing of humid forests and the potential risk of failing to account for them.

## 2. Study region

Our study is based on foliage samples made in two biological reserves in the Manaus area in Amazonas, Brazil – the *Campina*

Reserve and *Bacia Modelo* – both of which are managed by the National Institute of Amazonian Research (INPA). The regional climate is warm and humid, with only three months having less than 100 mm of rain and average annual precipitation of ~2300 mm. Altitudes are less than 160 m above sea level. The former is a 900 ha preserve (2° 34'S, 60° 2'W) containing 25 ha of *Caatinga* woodland and forest growing on nutrient-deficient, poorly-drained white-sand podzol soils. *Caatinga* is one of the three major Amazonian vegetation types (Pires, 1974) and is characterized by 10 m (woodland) to 30 m (forest) canopies, low biodiversity and thick humus and litter layers (Anderson et al., 1975) which facilitate highly efficient nutrient cycling (Anderson, 1981). This vegetation type is largely fragmented and clustered throughout most of the Amazon basin, but covers extensive tracts of land in northwestern Amazon in the Rio Negro (along which Manaus is situated) and Rio Branco basins (Anderson, 1981). Amazon *Caatinga* is a humid vegetation formation and should not be confused with arid *Caatinga* that is common in northeastern Brazil. Dominant species in the *Campina* Reserve include *A. heterophylla* and *Pradosia schomburgkiana* (Roberts et al., 1998).

*Bacia Modelo* is part of the 21,000 ha Tropical Silviculture Experiment Station and hosts a 43 m tall flux tower which provides access to the canopy. The tower is situated on a plateau approximately 60 km northwest of the city of Manaus (2° 35'S, 60° 7'W). Soils on the plateau are leached, lateritic, well-drained, kaolinite clays which grade into sandy podzols on the surrounding slopes (Lucas & Chauvel, 1992). Undisturbed tall dense rain forest covering both the plateau and the slopes is very diverse. Over 500 tree species in 181 genera were identified in three nearby hectares (Oliveira & Mori, 1999). Most species occur at densities of less than one tree per hectare but a few families do dominate the forest. Lecythidaceae, Leguminosae and Sapotaceae contribute about 40% of all trees (Rankin-de-Merona et al., 1992).

## 3. Methods

This work employs a combination of *in situ* leaf spectral measurements and canopy reflectance modeling to estimate the effect of epiphyll infestations on remote sensing of humid forest canopies. Model predictions are then compared to time series of Moderate Resolution Imaging Spectrometer (MODIS) imagery to detect the influence of epiphylls on remotely sensed imagery.

### 3.1. Leaf-level spectral measurements

Leaf samples for Amazonian *Caatinga* and *Terra Firme* species were harvested destructively in the field and measured in the laboratory. Leaf sampling from four *A. heterophylla* trees in the INPA *Campina* Reserve was conducted over a 15-month period – July 1993 to September 1994 (Roberts et al., 1998). On July 14, 1993, separate sets of clean and infested *Aldina* leaf samples were collected which were used in *Caatinga* mixed canopy simulations. Repeated visits were made on a monthly basis, excluding December 1993 and February, May and August 1994, to determine the effects of leaf aging and progressive epiphyll development on leaf-level spectral and biophysical properties. Samples from the initial sampling period (July 1993 for plants 1–3 and August 1993 for plant 4) were omitted from this study to ensure inclusion of only mature leaves. On each tree, six sunlit branches were tagged for consistency in foliar collections. During each visit, three leaves from each tree were randomly selected from the tagged branches, harvested and placed into sealed plastic bags with 100% humidity. Samples were stored in Styrofoam containers and kept in the dark with consistent humidity until spectroradiometric measurements were made, within 24 h (see Roberts et al., 1998 for more details). *Terra Firme* field samples were collected on September 13, 1992, using the canopy access tower at *Bacia Modelo*. Leaves were harvested from the mid to upper levels of the canopy using a pruning pole. Branch samples were collected in the field, then stored in a

**Table 1**

Leaf genera and species measured in the field and utilized in GeoSAIL canopy simulations.

Genus (species)	Vegetation type	Degree of infestation		Sampling site
		Upper	Lower	
<i>Aldina heterophylla</i>	Caatinga	Moderate coating	Clean	Reserva Campina
<i>Protium heptaphyllum</i>	Caatinga	Light film	Clean	Reserva Campina
<i>Pradosia schomburgkiana</i>	Caatinga	Medium coating	Clean	Reserva Campina
<i>Byrsonima cf poeppigiana</i>	Terra Firme	Clean	Heavy coating	Bacia Modelo
<i>Inga cf sertulifera</i>	Terra Firme	Thin film	Clean	Bacia Modelo
<i>Porouma tomentosa</i>	Terra Firme	Clean	Light film	Bacia Modelo
<i>Protium cf polybotryum</i>	Terra Firme	Clean	Light film	Bacia Modelo

Degree of infestation indicates fungal thicknesses on upper and lower leaf surfaces.

moistened plastic bag for transport to the laboratory. Species-level *Terra Firme* identifications were made by INPA parobotanists (see Acknowledgements).

Leaf samples were transported to the laboratory to measure reflectance and transmittance from both surfaces (Roberts et al., 1998). In 1992, only a single set of spectra were measured for each leaf. In 1993, replicates were collected for all species. Each leaf was visually assessed to determine relative age (young, mature, old) and the extent of leaf damage and epiphyll thicknesses (Fig. 1). Leaf squares approximately 1.5 cm<sup>2</sup> in size were cut from the right and left side (avoiding the mid-vein) of the leaves for spectral measurements. Depending on variability in leaf quality (i.e. age, and epiphyll cover) and the availability of material, between one and three leaves were measured for each species. Leaf samples primarily exhibited fungal epiphylls. The most common species encountered was *Pestalotia*, which, unlike most fungal symbionts, is considered a plant pathogen (Roberts et al., 1998). Yellow and rose pigmented bacteria were also observed but were not identified.

Spectroscopic measurements were conducted within 24 h of field sampling. Leaf spectra were measured using a portable Analytical Spectral Devices (ASD, Boulder, Colorado) Personal Spectrometer II attached to a Licor integrating sphere (Model 1800-12, Licor, Lincoln, Neb., USA). The ASD Perspec II has a nominal range between 329 and 1051 nm, collected in 512 bands at a sampling interval of 1.4 nm. In practice, poor sensor response restricted the usable range to 400 to 1020 nm. Spectra were standardized using a barium sulfate reflectance standard and illuminated using the calibrated light source supplied by Licor. Prior to each set of measurements, integrating sphere performance and stray light contamination were tested, demonstrating that errors due to contamination were less than 0.2% reflectance for most spectra.

3.2. GeoSAIL canopy reflectance modeling

Scaling leaf reflectance and transmittance measurements to the canopy level was achieved with the GeoSAIL model (Huemmrich, 2001). The model is a variation of the widely used SAIL (Scattering of Arbitrarily Inclined Leaves; Verhoef, 1984) model (e.g. Asner, 1998; Jacquemoud et al., 1995; Verhoef & Bach, 2003). Both models predict canopy reflectance based upon parameterizations of leaf/branch/background optical properties, LAI, canopy architecture, and viewing/solar geometry; GeoSAIL also accounts for canopy shadowing (Huemmrich, 2001). The model is well suited for this study, as it accounts for multiple scattering (secondary and higher order reflectance of radiation which has already been transmitted by other leaves).

Three Amazonian *Caatinga* and four *Terra Firme* dominant species were selected for modeling simulations (Table 1). These species were chosen for the availability of both clean and infested samples. Three classes of GeoSAIL simulations were employed to model *Caatinga* and *Terra Firme* canopy reflectance: Class 1) 14-month time series of a pure *A. heterophylla* *Caatinga* canopy for each of four sampled trees; Class 2) mixed *Caatinga* canopies with graduated epiphyll cover; Class 3) mixed *Terra Firme* canopies with graduated epiphyll cover (Table 2). For Class 2, mixed *Caatinga* canopies were created by combining equal proportions of leaf spectral measurements for *A. heterophylla* with those of *P. schomburgkiana* as well as with those of *Protium heptaphyllum*. Similar species combinations were created for Class 3, employing six different pairings of *Byrsonima cf poeppigiana*, *Inga cf sertulifera*, *Protium cf polybotryum*, and *Porouma tomentosa* (Table 2).

For all GeoSAIL simulations (Table 2), we used a cylindrical canopy model and plagiophile leaf angle distribution (based on field observations for *Caatinga*; Wirth et al., 2001 for *Terra Firme*). Branch and background were modeled using a *Laetia procera* bark spectrum and a dry litter layer of *Goupia glabra* (*Terra Firme*) leaves, respectively. Simulations were executed for the visible and NIR (400–1000 nm) with 1.4 nm-wide bands, yielding 429 bands per run. Plant Area Index (PAI; LAI and Branch Area Index) of *Caatinga* canopies is parameterized as 5 (Klinge & Herrera, 1983) and PAI of *Terra Firme* is parameterized as 6 (BigFoot, 2002; McWilliam et al., 1993). PAI was kept constant throughout the simulations, although we recognize it is likely to vary seasonally. Using a 0.25 woody-to-total area ratio, the branch component of PAI was assumed to be 2.5%, as only 10% of branch material is visible from above in broadleaf canopies (Kucharik et al., 1998).

At each time step of the Class 1 simulations, the canopy was simulated as composed entirely (i.e. 100%) of *A. heterophylla* leaves. Epiphyll cover and thicknesses are a function of leaf age and consequent fungal development in the sampled leaf spectra, with a trend of consistently increasing fungal cover over the 14 month (August 1993–September 1994) sampling period. The input leaf

**Table 2**

GeoSAIL parameterizations for the three classes of simulations.

Parameter	Class 1: <i>Caatinga</i> <i>Aldina</i> time series	Class 2: <i>Caatinga</i> mixed canopies	Class 3: <i>Terra Firme</i> mixed canopies
% infestation	100, (bi)monthly measurements	0, 25, 50, 75, 100	0, 10, 20, 30, 40
Species pairings	<i>A. heterophylla</i>	<i>A. heterophylla</i> / <i>P. schomburgkiana</i> <i>A. heterophylla</i> / <i>P. heptaphyllum</i>	<i>B. poeppigiana</i> / <i>I. sertulifera</i> <i>B. poeppigiana</i> / <i>P. polybotryum</i> <i>B. poeppigiana</i> / <i>P. tomentosa</i> <i>I. sertulifera</i> / <i>P. polybotryum</i> <i>I. sertulifera</i> / <i>P. tomentosa</i> <i>P. polybotryum</i> / <i>P. tomentosa</i>
PAI	5	5	6
LAD	Plagiophile	Plagiophile	Plagiophile
BAD	Planophile	Planophile	Planophile
Solar zenith angle	0	0	0
Canopy geometry	Cylindrical	Cylindrical	Cylindrical
Background spectrum	<i>Caatinga</i> litter	<i>Caatinga</i> litter	<i>Caatinga</i> litter
Branch spectrum	<i>Laetia procera</i>	<i>L. procera</i>	<i>L. procera</i>

PAI = plant area index; LAD = leaf angle distribution; BAD = branch angle distribution; see text for explanation and sources.

spectrum is the only changing variable in the time series – all other parameters are kept constant throughout Class 1 simulations. The latter classes, however, require a range of probable estimates of epiphyll infestation. In the *Caatinga* forest, leaf fall/flush was nearly synchronous for the four sampled plants and initial epiphyll colonization was not observed until two months after leaf maturation (Roberts et al., 1998). Observed epiphyll cover increased steadily over the course of the year and in the final two field sampling periods, 93% and 77% ( $n=29$  and 30, respectively) of the sampled leaves were colonized by epiphylls. Spectral measurements of infested leaf samples are treated as representations of uniform epiphyll cover. Therefore, graduated leaf area infestation rates are achieved by parameterizing varying LAI proportions to clean and infested samples. Hence, Class 2 epiphyll infestation (% leaf area) rates are modeled as: 0% (no infestation), 25% (light), 50% (moderate), 75% (high), and 100% (heavy). Proportions must also account for the branch contribution to canopy reflectance. For example, a mixed *Aldina/Protium* with >50% infestation would be modeled as 2.5% branches, and 24.375% each of

clean/infested *Aldina* and *Protium*. Changing the number of canopy elements can effect small but noticeable (<5%) changes in canopy reflectance. Thus, for consistency in model behavior, 0 and 100% simulations were still modeled as a mixed canopy, necessitating infestation rates of 1% epiphylls (with 99% clean leaves) and 99% (with 1% clean leaves), respectively.

We do not have field estimates of epiphyll cover for *Bacia Modelo*. In Barro Colorado Island, Panama, which has a drier climate, Gilbert et al. (2007) showed that 16.1% of plant samples in the overstory had epifoliar fungi on them. Working in the same reserve, Coley and Kursar (1996) reported leaf area epiphyll cover exceeding 50%. Likewise, Roskoski (1981) reported infestation rates as high as 38% in the upper 1 meter of tropical coffee canopies in Veracruz, Mexico. Rogers et al. (1994) encountered mean leaf area epiphyll cover of 40% in a subtropical Australian rainforest palm canopy, with some leaf samples bearing 100% coverage. Consequently, Class 3 infestation rates (% leaf area) are modeled as: 0% (no infestation), 10% (light), 20% (moderate), 30% (high) and 40% (heavy). The disparity in epiphyll cover between *Terra Firme* and *Caatinga*

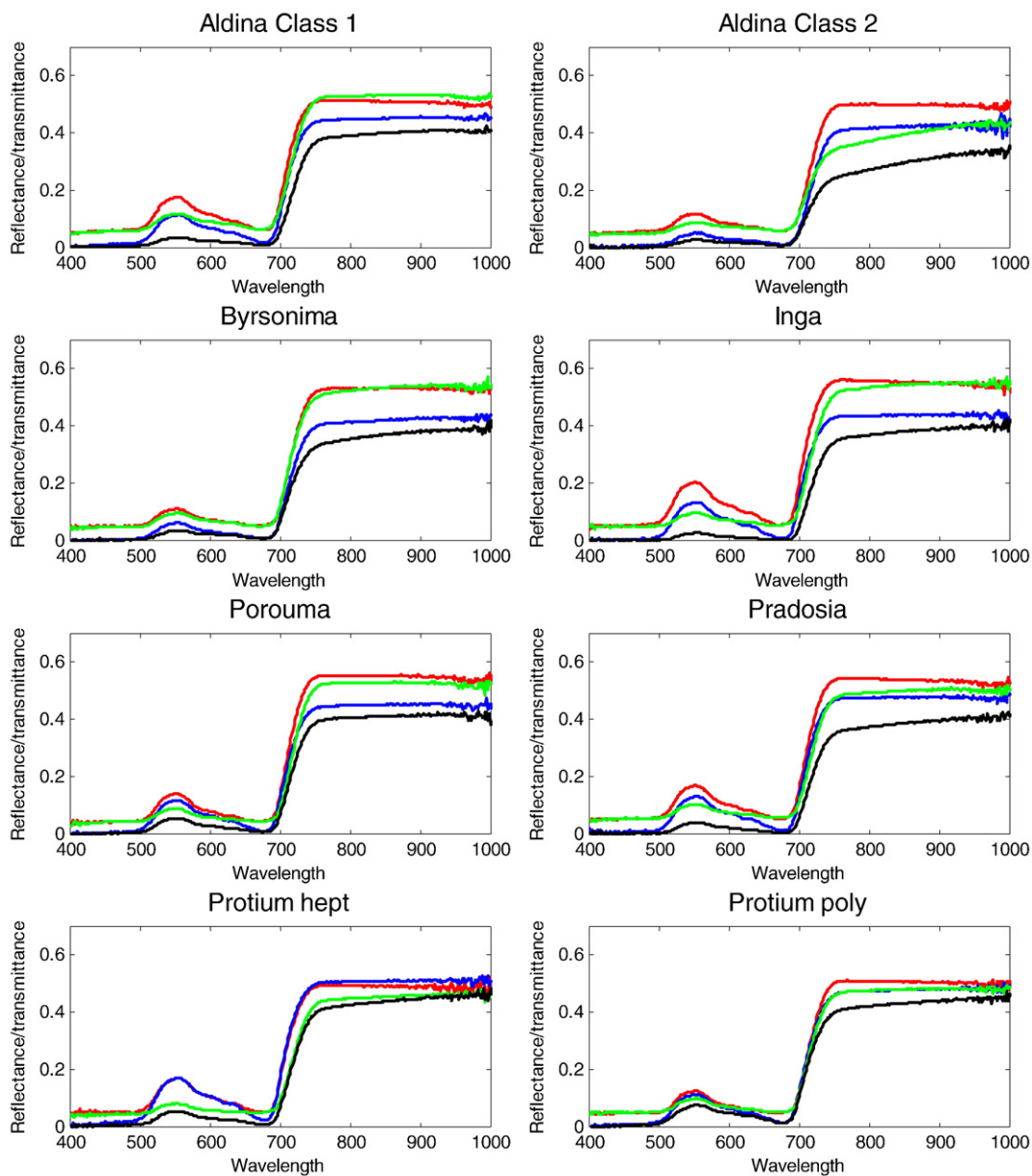


Fig. 2. Leaf spectral measurements for clean, mature leaves and colonized leaves. The Aldina Class 1 plot illustrates spectral changes in Plant 3 between the first sample in the time series (clean) and the final sample (colonized). Red and blue are reflectance and transmittance, respectively, of clean leaves. Green and black are reflectance and transmittance, respectively, of colonized leaves. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

may be explained by leaf morphology. The conspicuous absence of drip-tips in *Caatinga* vegetation (Anderson, 1981) may account for enhanced susceptibility to fungal growth (Coley & Kursar, 1996) since drip-tips facilitate draining of liquid water from the leaf surface. Manipulation experiments of epiphyllous lichen development using artificial leaves, however, suggest that drip-tips may not impede colonization (Lucking & Bernecker-Lucking, 2005). Thus, the cause for the difference in infestation rates has not yet been identified but may otherwise be related to humidity (Coley & Kursar, 1996) and leaf longevity (Reich et al., 2004).

The GeoSAIL model was executed in such a way to reproduce the full spectral resolution of the original field spectra. As much of the remote sensing literature focuses on the use of vegetation indices for the derivation of biological information, GeoSAIL model outputs were resampled to the spectral response functions of three common remote sensing platforms, Landsat Thematic Mapper, MODIS, and SPOT (*Système Probatoire pour l'Observation de la Terre*) and used to calculate two commonly used vegetation indices, the NDVI (Rouse et al., 1974) and EVI (Huete et al., 1997):

$$NDVI = \frac{\rho_{NIR} - \rho_{RED}}{\rho_{NIR} + \rho_{RED}}$$

$$EVI = \frac{2.5 \cdot (\rho_{NIR} - \rho_{RED})}{(1 + \rho_{NIR} - 6 \cdot \rho_{RED} + 7.5 \cdot \rho_{BLUE})}$$

where  $\rho$  is reflectance. The EVI and NDVI have been commonly employed for studies of Amazonian humid forests (e.g. Huete et al., 1997, 2006; Myneni et al., 2007; Saleska et al., 2007; Xiao et al., 2005).

### 3.3. MODIS imagery

GeoSAIL predictions of canopy reflectance and vegetation indices are compared with time series of MODIS imagery. Two full years, 2002–2003, of daily MODIS 500 m Surface Reflectance (MOD09GHK) data were downloaded and temporally composited into 16-day segments using the Dennison et al. (2007) algorithm, yielding 44 images. These specific years were chosen for similar temporal patterns and quantity of precipitation as the original field season, based on World Data Center for Meteorology data (Manaus weather station, 82331; <http://www.ncdc.noaa.gov/oa/wdc/index.php>). One  $10 \times 10^\circ$  tile ( $1.24 \times 10^6$  km<sup>2</sup>) was used in this study, h11v09. The MODIS time series was used to sample pixel values for Amazonian *Caatinga* and *Terra Firme* as delineated by vegetation cover data obtained from the Brazilian Institute of Geography and Statistics (<ftp://geofp.ibge.gov.br/mapas/>). For each of two distinct vegetation formations: Amazonian *Caatinga* forest without palms, and dense, low-land *Terra Firme* rainforest with emergent canopy, we made a sampling of 300 random pixels. Individual band values were extracted from each image in the time sequence and used to calculate NDVI and EVI values. Time series data were smoothed using a 3-composite window (48 days).

## 4. Results

### 4.1. Leaf-level measurements

Epiphyll colonization induced substantive decreases in NIR transmittance and minor changes in reflectance in all species sampled

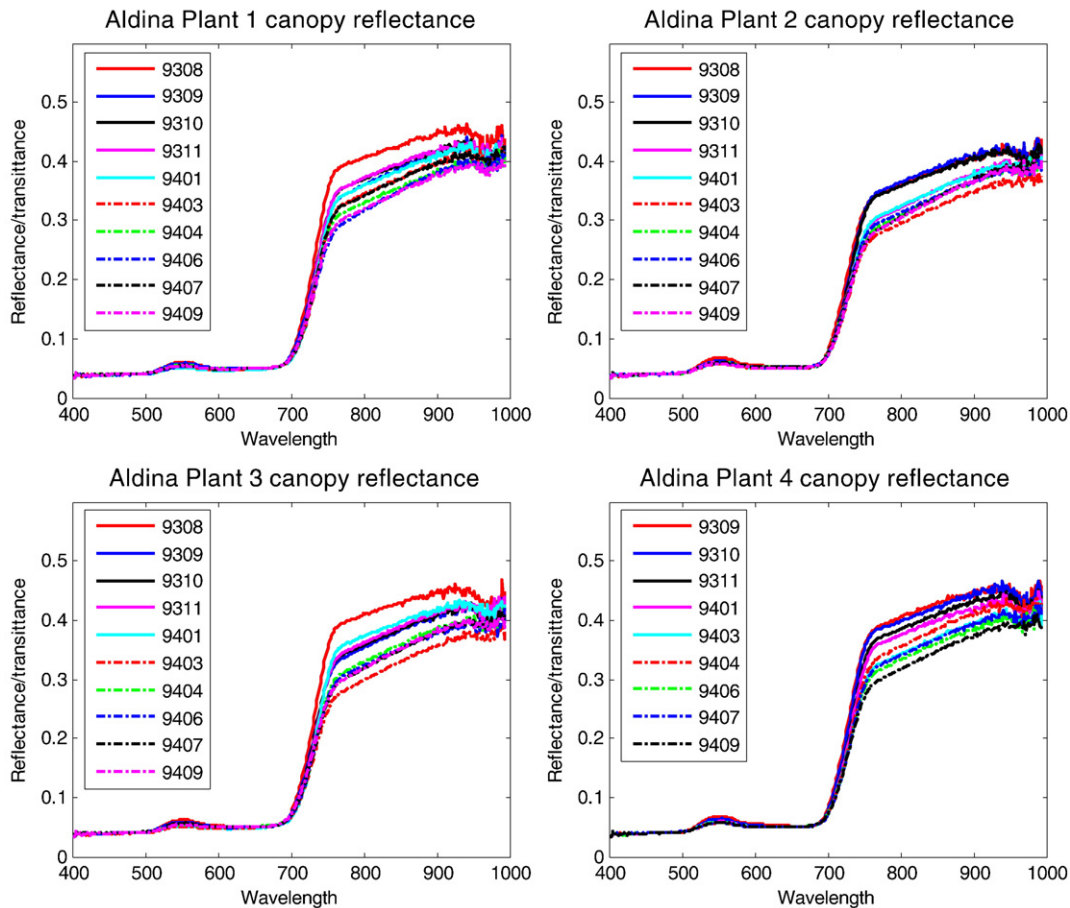


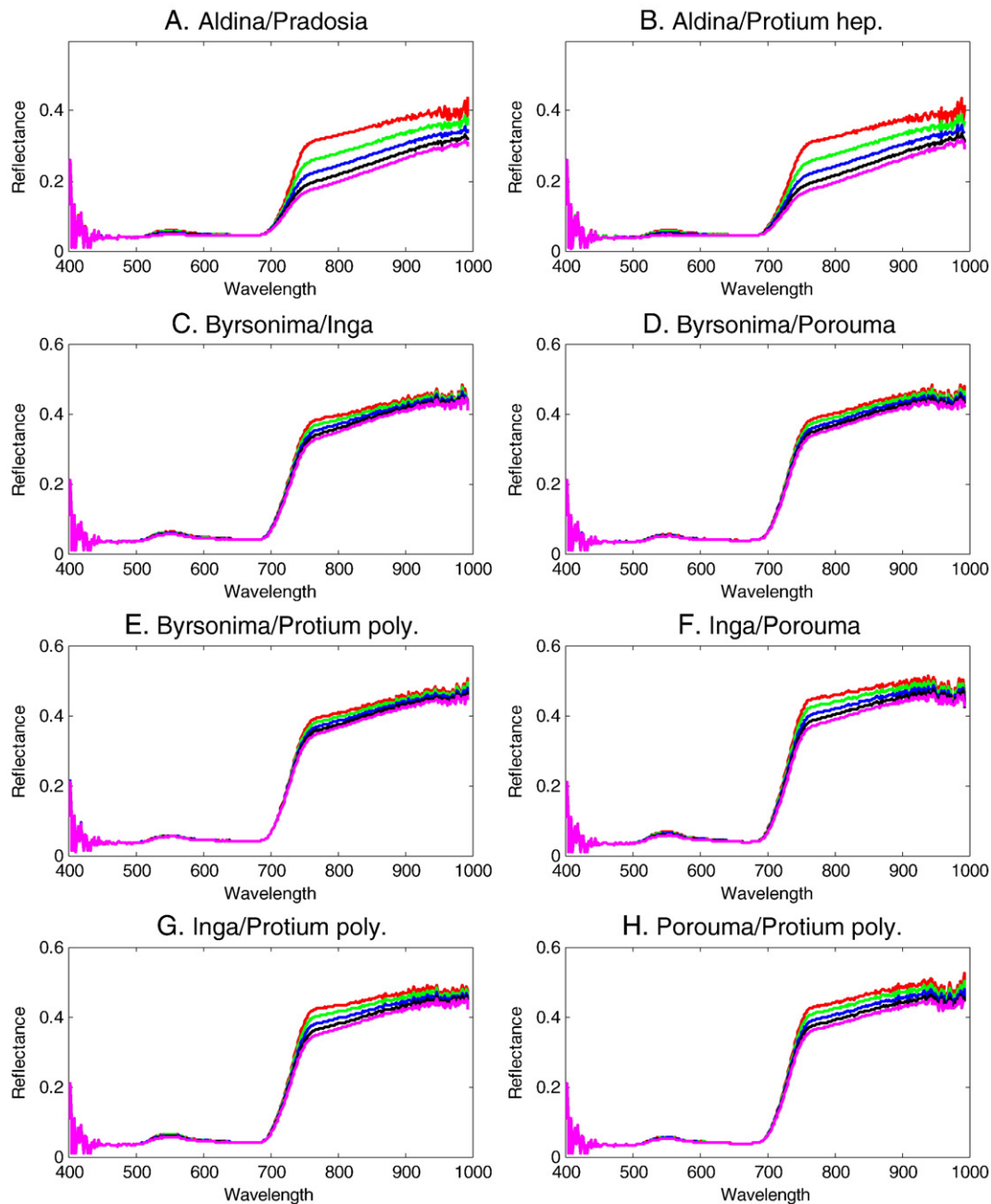
Fig. 3. GeoSAIL simulations of canopy spectral reflectance for the *Aldina heterophylla* time series (Class 1). Dates are labeled in YYYY format. For each, the first spectrum represents mature, clean leaves; the second shows the first occurrence of fungi.

(Fig. 2). All percent changes reported below are relative change compared to clean leaves. Thus, a decrease in absolute reflectance from 50% to 45% would be reported as a 10% relative decrease in reflectance. NIR midpoint (850 nm) transmittance decreased 8.4% (*Porouma*) to 29.4% (*Aldina*), with an average decrease of 14.5% (S.D. 6.7%). Reflectance changes were relatively minor, ranging from slight increases (4.0% in the *Aldina* time series) to decreases in *Pradosia* and (non-time series) *Aldina* (6.7% and 21.0% respectively). Mean NIR reflectance decrease was 5.3% (S.D. 7.5%). The visible spectrum – the green portion in particular – underwent large changes when expressed as relative differences. Green midpoint (550 nm) reflectance decreased 13.7% (*Byrsonima*) to 52.8% (*Inga*), with a mean of 34.3% (S.D. 13.9%). Transmittance decreases in the green were even greater, ranging from 35.5% (*Protium polybotryum*) to 81.9%, in the case of the *Aldina* time

series, with a mean decrease of 58.9% (S.D. 15.9%). Red transmittance also decreased substantially, while reflectance changes were relatively minor. A shift in the “red edge” toward longer wavelengths, commonly associated with vegetation stress (Boochs et al., 1990), as noted among all species, and was especially pronounced in the *Inga* and *Aldina* spectra. Despite higher relative differences in the visible spectrum, absolute changes were significantly lower and less likely to affect canopy reflectance as a result.

#### 4.1.1. Canopy level GeoSAIL model simulations

GeoSAIL simulations of the *Aldina* time series illustrate a clear and consistent dampening effect on NIR with increasing epiphyll cover (Fig. 3). All percent changes reported below are relative change compared to clean canopies (0% infestation). By the end of the time



**Fig. 4.** GeoSAIL simulations (Classes 2 and 3) of canopy spectral reflectance for mixed *Caatinga* (A and B) and *Terra Firme* (C–F). Red, green, blue, black and magenta represent 0%, 10% (25%), 20% (50%), 30% (75%), and 40% (100%) infestations in *Terra Firme* (*Caatinga*) forests. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 3**  
Predicted NDVI (A) and EVI (B) for mixed *Caatinga* and *Terra Firme* canopies.

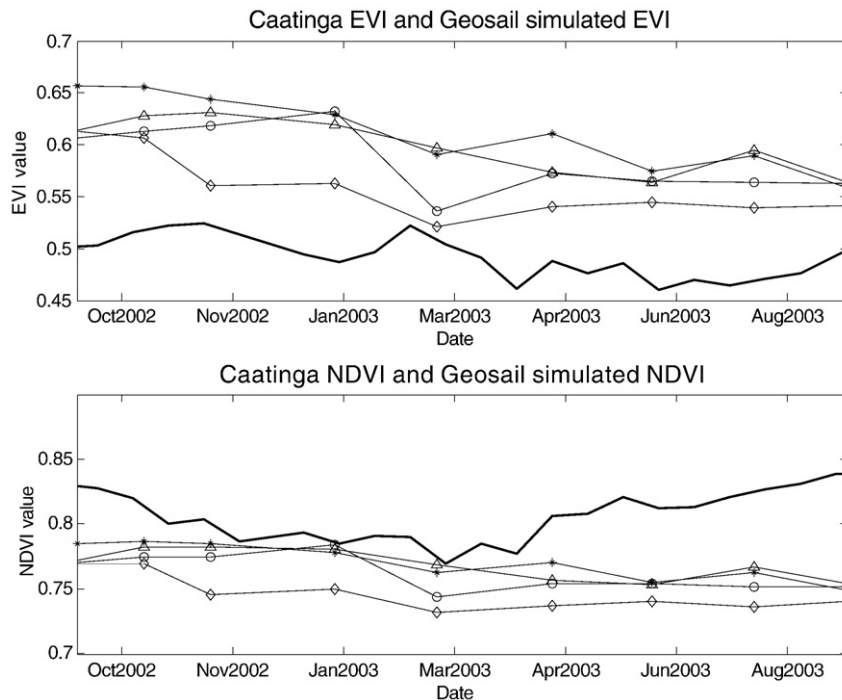
A.								
Degree of infestation	<i>Aldina/Pradosia</i>		<i>Aldina/Protium</i> hept.		<i>Byrsonima/Inga</i>		<i>Byrsonima/Porouma</i>	
0%	0.794		0.791		0.835		0.850	
10% (25%)	0.767	3.4%	0.766	3.2%	0.833	0.3%	0.847	0.3%
20% (50%)	0.744	6.3%	0.744	5.9%	0.830	0.6%	0.844	0.8%
30% (75%)	0.723	9.0%	0.724	8.4%	0.828	0.9%	0.841	1.1%
40% (100%)	0.704	11.3%	0.707	10.5%	0.826	1.2%	0.838	1.4%
B.								
Degree of infestation	<i>Aldina/Pradosia</i>		<i>Aldina/Protium</i> hept.		<i>Byrsonima/Inga</i>		<i>Byrsonima/Porouma</i>	
0%	0.615		0.607		0.702		0.725	
10% (25%)	0.543	11.7%	0.537	11.5%	0.691	1.6%	0.712	1.8%
20% (50%)	0.489	20.5%	0.484	20.2%	0.678	3.5%	0.697	3.8%
30% (75%)	0.446	27.5%	0.442	27.2%	0.666	5.0%	0.685	5.5%
40% (100%)	0.411	33.1%	0.408	32.7%	0.656	6.5%	0.673	7.1%
C.								
Degree of infestation	<i>Byrsonima/Protium</i> poly.		<i>Inga/Porouma</i>		<i>Inga/Protium</i> poly.		<i>Porouma/Protium</i> poly.	
0%	0.842		0.855		0.847		0.862	
10%	0.839	0.4%	0.852	0.4%	0.843	0.5%	0.858	0.5%
20%	0.835	0.8%	0.848	0.9%	0.839	1.0%	0.853	1.1%
30%	0.832	1.2%	0.845	1.2%	0.835	1.4%	0.848	1.6%
40%	0.829	1.6%	0.842	1.6%	0.832	1.8%	0.844	2.1%

Percentages indicate the amount of decrease in the index relative to a clean canopy. Parentheses denote the higher infestation rates for Class 2 simulations.

series, NIR decreases of about 12.0–17.8% were encountered, although in Plants 2 and 3, the lowest NIR was found in March 1994–15.8% and 21.4% decreases respectively. These anomalies are primarily due to

especially low NIR transmittance during that collection. Green reflectance had significant decreases of 10.5–14.9%; changes in the blue and red were negligible. The “red edge” shift, however, (Fig. 2), propagates to the canopy level (Fig. 3). In each of the three simulation classes, there is a trend of increasing NIR reflectance with increasing wavelength (Figs. 3 and 4), which differs from the classic, flat NIR spectral shape often found in leaf-level spectra. This increasing trend is the result of influence of the background and branch reflectance and is commonly observed in branch-scale and canopy-scale hyperspectral measurements (Roberts et al., 2004). With increasing epiphyll cover the slope of the NIR “plateau” increases, indicating that epiphyll infestations more effectively dampen the albedo of shorter wavelength NIR (~700–800 nm) than longer wavelength NIR (~900–1000 nm).

In mixed *Caatinga* canopies, comparable dampening effects on NIR reflectance were observed for both species pairings (Fig. 4). Substantive alterations to canopy reflectance occurred in the light (25%) and moderate (50%) infestation categories, where NIR decreased an average of 13.0% and 22.3%, respectively, relative to an uncolonized canopy. With added epiphyll cover, NIR decreases in notable, but smaller increments, spurring average decreases of 29.4% (high) and 34.9% (heavy). Green reflectance behavior also mirrors that of the *Aldina* time series, exhibiting mean decreases of 10.5, 15.6 and 20.4% in moderate, high and heavy infestations, respectively. Changes in blue and red reflectance were less than 1% for *Aldina/Pradosia* but slightly higher for *Aldina/Protium* hept. – 3.5 and 3.3%. Simulations of *Terra Firme* mixed canopies do not demonstrate as dramatic effects (Fig. 4) as the *Caatinga*, despite the higher simulated LAI (LAI = 6 vs. 5). This was presumably due to the lower degrees of infestation for *Terra Firme* forest. Mean NIR decreases for moderate and heavy infestations were 5.8% (S.D. 1.31%) and 10.6% (S.D. 2.25%), respectively; average green decreases were 4.7% (S.D. 1.76%) and 9.5% (3.49%), respectively. The *Porouma/Protium* poly. canopy exhibited the greatest change, undergoing NIR decreases of 3.5, 7.2 and 13.1% for light, moderate and heavy epiphyll cover, respectively. Interestingly, simulations containing *Inga*, the only sample with adaxial epiphylls, did not exhibit the strongest effects. Red and blue reflectance at the canopy scale is largely unaffected, hardly exceeding



**Fig. 5.** Modeled vegetation index values for the *Aldina heterophylla* time series (Class 1) are superimposed on observed MODIS values (solid line). Marker symbols of the sampled plants 1–4 are: triangles, diamonds, circles and asterisks, respectively. Numbers of observations are equivalent to those in Fig. 6. See text (Section 4.2, first paragraph) for explanation of the MODIS-GeoSAIL EVI discrepancies in the above graph.

changes of 1%. The simulated mixed canopies did not exhibit the same pronounced red edge shift observed in the *Aldina* time series.

#### 4.1.2. Vegetation indices

Results of all GeoSAIL simulations were resampled to the visible and NIR bands of three sensors widely used in terrestrial remote sensing, Landsat TM, MODIS and SPOT. Correlation among the three sensors was extremely high, ( $R^2 > 0.99$ ) and as such, only the results for MODIS are shown here. Broadly, the EVI demonstrated much greater sensitivity to the presence of epiphylls than NDVI (Table 3). In simulations of increasing epiphyll cover in *Caatinga* canopies, EVI decreased at approximately three times the rate of NDVI; in *Terra Firme* canopies, EVI decreased at nearly five times the rate of NDVI. For the *Aldina* time series, EVI reductions ranged from 9.1 to 15.1%, while NDVI reductions among the sampled plants ranged from 4.0 to 5.6% (Fig. 5). Temporal dynamics of *Caatinga* vegetation indices are dis-

cussed in greater detail in the following section discussing MODIS time series. EVI declines were especially strong in mixed *Caatinga* forests, where moderate and heavy infestations spurred decreases of approximately 20.2–20.5% and 33.1–32.7%, respectively. *Terra Firme* vegetation indices are not as responsive to simulated infestations. Mean EVI decreases for moderate and heavy infestations are 4.4 and 8.1%, respectively; mean NDVI decreases are 0.9 and 1.6%, respectively. Indeed, for the *Porouma/Protium* poly. canopy, which showed the strongest declines, heavy infestations (40%) produce vegetation index reductions smaller than those for light (25%) *Caatinga* infestations (9.9% vs. 11.6% EVI decreases, respectively). These results suggest that fungal thicknesses observed in *Caatinga* leaves are accounting for the differential behavior among the two humid forest types. In addition, all *Caatinga* samples exhibited fungus on the upper surfaces, while only one of the *Terra Firme* species, *Inga cf. sertulifera*, had adaxial coatings.

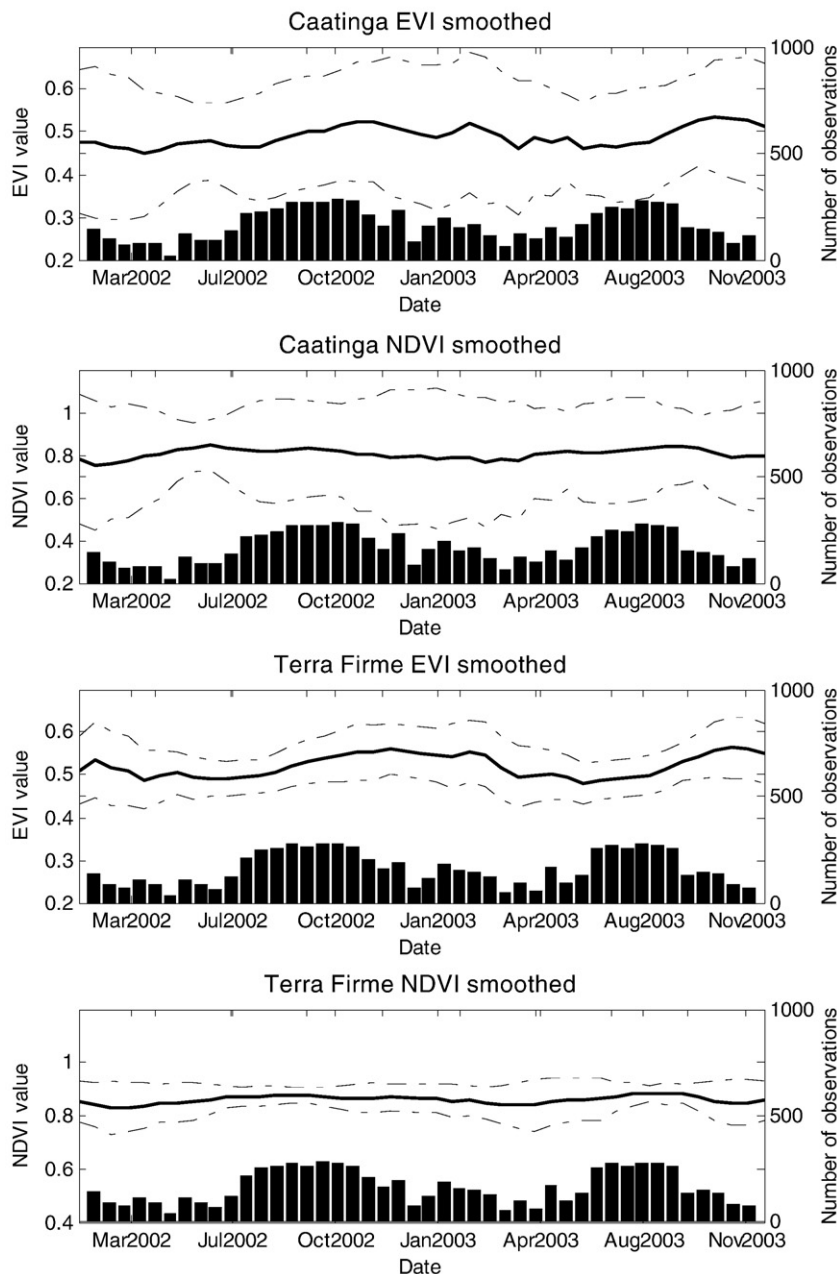


Fig. 6. MODIS EVI and NDVI time series for *Caatinga* and *Terra Firme*. Mean values are shown as solid heavy line,  $\pm 1$  standard deviations with dashed lines. Numbers of observations are shown at the bottom.

## 4.2. MODIS NDVI and EVI patterns

Time series of MODIS 500 m Surface Reflectance imagery were used to calculate vegetation index trajectories for Amazonian *Caatinga* and *Terra Firme* formations, using 300 randomly sampled pixels for each. Persistent cloud cover greatly reduced the number of observations during the wet season running from October to April (Fig. 6). Temporal EVI patterns demonstrated greater sensitivity to intra-annual changes in *Caatinga*, whereas NDVI was considerably more constant throughout the two year period. EVI minima and maxima were 0.45 and 0.54, making a range that is 16.7% of peak value. In contrast, the dynamic range (0.76–0.84) of NDVI was only 9.5% of peak value. *Aldina* EVI and NDVI time series from Class 1 simulations were superimposed over the corresponding months of MODIS imagery (Fig. 5). Predicted EVI values for the four plants demonstrated similar temporal patterns to the MODIS imagery, with a pre-colonization maximum, then steadily declining throughout the wet season. Individual trends are quite different at the beginning of the time series – MODIS EVI demonstrates a rapid rise in the August–October period. Such a discrepancy is anticipated, as the modeled results show the patterns for a new flush of leaves, whereas MODIS is detecting reflectance for the entire canopy. There was a tendency for overestimation of the EVI by GeoSAIL, on the order of 0.05–0.1. We attribute this discrepancy to surprisingly low MODIS blue band reflectances, with an average of 1.5% reflectance throughout the time series, opposed to the GeoSAIL mean of 4.0%. Errors in atmospheric corrections and reflectance calculation of the MODIS imagery have been shown to induce inaccuracies in the blue band (Vermote & Kotchenova, 2007). Heavy weighting of the blue band (7.5) in the EVI equation causes this disparity to have a substantive effect on the absolute value of the index. The *Aldina* NDVI time series also followed a similar pattern to the MODIS data, exhibiting relatively consistent but shallowly declining values throughout the sampling period. The slight increase in MODIS NDVI at the beginning of the dry period in 2003 was likewise reflected in a plateau or subtle increase in Plants 1–3.

Comparable temporal patterns for both indices were observed in *Terra Firme*. EVI is more sensitive to intra-annual changes, increasing during the mid-late summer, reaching peaks in November–January. The EVI decreased during the late wet season, with a low at the beginning of the dry period (Fig. 6). EVI minima and maxima were 0.47 and 0.56, constituting a range of 14.9% that of peak value. NDVI exhibited a smaller dynamic range, as in *Caatinga*, with slight increases beginning in the late spring that remain high until the end of the dry season. NDVI minima and maxima were 0.83 and 0.88, with a range that is 6.3% of peak value.

## 5. Discussion

### 5.1. Leaf-level measurements and canopy simulations

As hypothesized, GeoSAIL simulations of Amazonian *Caatinga* and *Terra Firme* canopies indicate that remote sensing of humid forests may be affected by varying epiphyll cover. Although the former undergoes more dramatic changes in canopy albedo, the results indicate that epiphyll infestations in primary forest are not dismissible. Observed leaf-level changes in NIR reflectance and transmittance were largely mirrored at the canopy scale, and the interaction of the two is paramount. Though the net effect of epiphyll colonization is a reduction in NIR reflectance, some leaf-level spectra had only very minor decreases or even small increases in NIR reflectance, in the case of *Byrsonima* (Fig. 2), underscoring the importance of transmittance when predicting canopy albedo. This point is further supported by the fact that simulations including *Inga*, the only *Terra Firme* leaf sample with upper surface epiphylls, did not yield the strongest decreases in NIR reflectance. The net decrease can be attributed to multiple scattering, or leaf additive reflectance, whereby radiation transmitted

through a leaf may be reflected by a lower leaf in the canopy, increasing above-canopy reflectance. As a result, heavy epiphyll infestations may reduce NIR reflectance in *Caatinga* and *Terra Firme* by as much as 33.1% and 9.9%, respectively. Given the evidence of very high infestation rates in some high humidity environments (Coley & Kursar, 1996; Rogers et al., 1994), it is possible that some primary forests may well exhibit albedo changes similar to those of moderate *Caatinga* (50% leaf area cover), especially where epiphylls primarily inhabit upper leaf surfaces. Our results are slightly higher than those of Myneni et al. (2007) who estimated a change in leaf reflectance of only 5% in one year old *Aldina* leaves based on the original results of Roberts et al. (1998). It is difficult to directly compare these results, though, as Myneni et al. do not specify the derivation of their figures.

Changes in visible reflectance were not observed at the canopy level, most likely due to the high vegetation density simulated, background reflectance and the fact that all but one of the *Terra Firme* samples exhibited epiphylls on the lower surface. The green band demonstrated the only substantive change in the visible spectrum. Nonetheless, leaf-scale decreases of 68–82% (*Aldina*, *Pradosia*, *Inga* and *Protium* hept.) are only faintly replicated at canopy scale (18–22% for heavy-infestation, mixed *Caatinga* canopies). Modeled spectra produce commensurate changes in the vegetation indices, EVI and NDVI. Sensitivity of individual bands to epiphyll cover is somewhat diminished when incorporated into vegetation indices, especially in the NDVI. For example, heavy *Inga/Protium* poly. infestations exhibit reductions of 13.1, 9.2 and 1.8% in the NIR, EVI, and NDVI respectively. The reason for this is that the direction of change with epiphyll increases is almost uniformly negative across the spectral range. That is to say, an identical decrease, regardless of magnitude, in the red and NIR would effect a 0% change in the NDVI. Hence, the EVI, with its inclusion of the blue band and differential weighting of the input bands, is more sensitive to the presence of epiphylls. Researchers should take note of the reflectance changes exhibited across the full spectrum (Fig. 4) and not just the sensitivity of the tested indices.

This work focused on two of the most commonly used vegetation indices for remote sensing of forests, the NDVI and EVI. The latter is especially well suited to humid forests due to its relative insusceptibility to saturation in closed canopies (Huete et al., 1997). These are only two of a wide suite of vegetation indices that have been developed and tested for numerous applications (see Jensen, 2007 for review). It is probable that vegetation index behavior will be very different with a wider array of indices. Vegetation indices incorporating the green band (e.g. VARI, Gitelson et al., 2002) may be much more sensitive to epiphyll cover than those that include only the red and/or blue. Our field spectra were limited to the range of 329–1051 nm, entirely missing the shortwave infrared (SWIR), which is highly sensitive to leaf water content (Woolley, 1971). The SWIR has demonstrated great utility for remote sensing of leaf biochemical and biophysical properties (e.g. Gao, 1996; Huete et al., 2002; Toomey & Vierling, 2005) and further research should include measurement, modeling and remote sensing of epiphylls in the SWIR. In addition, full range spectra (400–2500 nm) of epiphylls in isolation may enhance the detection of unique spectral features that could guide hyperspectral remote sensing of their distribution and infestation rates.

The leaf samples utilized in this study were primarily infested by epifoliar fungi. *Pestalotia*, a fungal pathogen, was the most commonly identified genus (Roberts et al., 1998). Lichens and liverworts, the most common epiphylls (Coley & Kursar, 1996) were not identified in any of the samples, although they may have been present (Roberts et al., 1998). When extrapolating our results to other colonized forest communities, one must consider the spectral differences and biodiversity of epiphylls. For example, Anthony et al. (2002) report significant differences in PAR transmission between light and dark lichens – 30–70%, respectively. Mean attenuation among all lichens sampled, 48%, is considerably lower than that of liverworts – 55–85% (Coley et al., 1993).

## 5.2. MODIS observations and ecological implications

Time series of MODIS imagery for the Manaus area appear to affirm our third hypothesis — epiphyll colonizations are detectable from space. Also, satellite observations corroborate our findings that EVI is more sensitive to epiphyll cover than NDVI. Modeled *Aldina* EVI time series demonstrate a degree of synchronicity with measured MODIS EVI and NDVI (Fig. 6). This interpretation is based on the assumption of a high degree of leaf turnover during the dry season for Amazonian *Caatinga*. Boubli (2005) reported that in *Caatinga* stands in the Pico da Neblina National Park, Amazonas, Brazil, 24% of the trees produced more than 50% or more of their crown capacity in a month-long period beginning of the dry season. Coomes (1997) showed that *Caatinga* stands in the Orinoco basin, Venezuela, demonstrate very similar litter fall timing to *Terra Firme*, with peaks in Aug–Sept. Roberts et al. (1998) observed near synchronous leaf turnover for the four trees examined in this study. Recent field observations (January 2009) of 18 *Aldina* trees in the *Campina* Reserve indicate that five underwent near synchronous turnover in the mid to late dry season (July–September 2008); 10 of the remaining trees appeared to have flushed at the beginning of the 2007 dry season, but a precise leaf age estimation was not possible.

We may also infer *Terra Firme* and *Caatinga* epiphyll growth cycles from the EVI pattern of low values during the late wet season (Feb–July) and peak values in the late dry season/early wet season. The steady decline in EVI values throughout the wet season may reflect increasing canopy epiphyll cover as would be expected with readily available moisture (Coley & Kursar, 1996). This trend occurs until the start of the dry season (July–August) when peak litterfall occurs (Roberts et al., 1998; Wright & Cornejo, 1990; Xiao et al., 2005), which would serve to disproportionately remove aging and epiphyll covered leaves from the canopy — especially those harboring pathogenic or parasitic epiphylls (Coley & Kursar, 1996; Garcia-Guzman & Dirzo, 2004; Reich, 1995). Thus, EVI of the canopy would begin to increase as new leaves are flushed and would continue until the onset of the next wet season. Discrepancies between MODIS and GeoSAIL at the beginning of the *Aldina* time series (Fig. 5) illustrate this pattern, where observed EVI values rise rapidly from July to October, following the turnover of infested leaves and flush of new leaves. This contrasts with the maximum EVI value in the model simulations, as these represent clean, mature leaves. By October–November, both GeoSAIL and MODIS EVI values start to decline simultaneously, until the beginning of the 2003 dry period, when the same MODIS cycle repeats itself. Here again, the two diverge, as the measured leaves would be expected to exhibit decreasing reflectance and EVI with increasing epiphyll cover. Amazonian *Caatinga* leaf lifespans are quite long, 2.5 to 4.2 years (Reich et al., 2004), facilitating very heavy epiphyll loads which may reduce NIR reflectance and transmittance by as much as 60% (Roberts et al., 1998). Such extreme cases were excluded from this modeling study due to their rarity.

Other authors have noted similar seasonal fluctuations in EVI retrievals. Xiao et al. (2005) report variable seasonal dynamics among the two vegetation indices for *Terra Firme*. EVI values were found to be low during the onset of the dry season (June–July) and peaked near the end, whereas the NDVI reached and sustained a plateau throughout the dry season. The June–July EVI low coincides with an expected epiphyll cover maximum before the dry season litterfall (Xiao et al., 2005). Similarly, basin-wide *Terra Firme* EVI time series of Huete et al. (2006) demonstrate a clear decline in EVI beginning in March that continues until the start of the dry season, in July. Saleska et al. (2007) detected a similar phenological pattern in basin-wide estimates of Amazonian EVI during the 2005 drought, in which peak EVI occurs during the July–September drought peak. We do not suggest that all of the EVI fluctuations reported by the above authors or in this study are derived from epiphyll cover, yet the declines in *Terra Firme* of up to 9% (similar to some of the high- and heavy-infestation *Terra Firme* simulations) suggest that they may play a part. Additional data are needed on epiphyll biogeography and phenology

to ascertain their complete role in the EVI patterns being reported in the literature.

In the MODIS time series, the dynamic range of EVI values is slightly higher (16.7% vs. 14.9%) for *Caatinga* than for *Terra Firme*. This difference was expected, considering the higher degrees of infestation that were simulated, but not as high as the disparities predicted by GeoSAIL. This might be explained by the fact that our GeoSAIL simulations do not account for atmospheric sources of error such as water vapor and aerosols. The Dennison et al. (2007) temporal compositing algorithm used here automatically removes any pixels contaminated by cloud cover via the 1 km surface reflectance quality product (MOD09GST). Any inaccuracies in the MODIS data quality is thus manifested in the composites. Our data do not suggest that cloud cover is adversely affecting accuracies of the vegetation indices, since the number of observations (a surrogate for cloud cover) does not covary with EVI/NDVI values (Fig. 6). Nevertheless, atmospheric noise may account, in part, for the less dramatic fluctuations of observed vegetation indices. As discussed above (Section 4.2), the low MODIS blue reflectance (~1.5%) may signify overcorrection for atmospheric aerosols. The MODIS atmospheric correction algorithm used for MOD09 has been shown to perform poorly with band 3, the blue band (Vermote & Kotchenova, 2007). Such low values decrease the dynamic range of the blue band and consequently, the EVI.

Vegetation indices are merely a means to an end and do not necessarily have inherent biological meanings. Our results suggest that epiphyll infestations may have a confounding effect on vegetation index applications, although the effect is variable. Conferred inaccuracies in the derivation of biophysical parameters are expected to be direct, provided that such calculations are based on fundamental principles of light interaction with plant canopies. The effect on biological processes such as photosynthesis is less clear. Many researchers have made the intuitive assumption that PAR-attenuating epiphylls reduce photosynthesis (Coley et al., 1993; Roskoski, 1981), but there is little experimental evidence confirming this. Anthony et al. (2002) reported shade acclimation among lichen-covered Australian palms, noting increased chlorophyll content in infested leaves and no detectable change in carbon assimilation. Epiphylls in tropical coffee plantations (*Coffea arabica*) have little effect on leaf area (Jimenez, 1979) and coffee yields are actually higher in shady areas with heavy epiphyll cover (Jimenez & Martinez, 1979). Sand-Jensen (1977) offer equivocating experimental evidence, reporting a 31% photosynthesis reduction in eelgrass (*Cocconeis scutellum*) by inhibition of carbon uptake and limiting PAR interception by epiphytic diatoms. If photosynthetic carbon uptake decreases proportionally with epiphyll cover, little compensation must be made when relating reflectance to GPP. Additional data are needed, though, to confirm the limits of shade acclimation and the implications for remote sensing of ecological processes.

## 6. Conclusions

A combination of leaf-level spectral measurements, canopy reflectance modeling, and multitemporal remote sensing techniques were employed to explore the potential effects of epiphylls on canopy reflectance and remote sensing of humid forests. Two epiphyll-colonized vegetation types were examined — Amazonian *Caatinga* (woodland/forest on nutrient-deficient sandy soils) and *Terra Firme* (primary forest on poor lateritic clay soils) — two of the three major vegetation types of the Amazon basin (Pires, 1974). The GeoSAIL canopy reflectance model (Huemmrich, 2001) was utilized to scale the leaf spectra to above-canopy reflectance as well as predict values of the EVI and NDVI. We found that Amazonian *Caatinga* canopies may undergo major decreases in NIR reflectance (22.3–34.9%) under moderate to heavy infestations (50 and 100% leaf area cover, respectively), while green reflectance decreases 10.5–20.4%. A 14-month time series simulating the effects of aging and epiphyll growth on the theoretical

*A. heterophylla* (*Caatinga*) canopy albedo exhibits similar but less severe reductions in the NIR and green – up to 21.4% and 14.9%, respectively. *Terra Firme* did not demonstrate the same degree of albedo changes, with NIR decreases of 5.8% (S.D. 0.66%) and 10.6% (S.D. 2.25%) for moderate and heavy infestations. These results were not unexpected, as *Caatinga* (Roberts et al., 1998) incurs a higher degree of infestation than *Terra Firme* (Coley & Kursar, 1996; Rogers et al., 1994; Roskoski, 1981) and the simulations were parameterized as such.

There is a need for more quantitative research on distribution and rates of infestation of tropical rainforests. Figures were adapted from other humid forests in Australia and Panama as well as a coffee plantation and were applied somewhat conservatively. The findings of Coley and Kursar (1996) and Rogers et al. (1994) suggest that in very humid rainforests, infestation may exceed our maximum infestation of 40%. Their data are not explicit about canopy position of the epiphylls, and it is assumed that epiphyll infestations in the mid to upper canopy will have the strongest effect on canopy reflectance. In addition, our *Terra Firme* samples included only one species, *Inga cf. sertulifera*, which exhibited epiphylls on the upper surface, lessening their effect on canopy reflectance, especially in the visible. *Terra Firme* canopies with substantive upper leaf surface infestations may exhibit reflectance changes on the order of light (25%) *Caatinga* infestations or even higher.

Vegetation indices were predicted from the GeoSAIL outputs for an assessment of the impact of epiphylls on the oft-used EVI and NDVI as well as for comparison with MODIS satellite observations of the study area. Both the model predictions and MODIS data illustrated greater sensitivity of the EVI to intra-annual changes in canopy reflectance. The extent to which epiphylls contribute to the index fluctuations cannot be determined from our data alone, yet the synchronicity of MODIS EVI/NDVI time series and modeled *Caatinga* suggest a causal relationship. EVI was slightly overestimated by the model, which we have attributed to inaccurate atmospheric corrections in the MODIS blue band (Vermote & Kotchenova, 2007). Temporal vegetation index patterns were quite similar to those of recent studies of MODIS-based EVI/NDVI and LAI in the Amazon basin (Huete et al., 2006; Myneni et al., 2007; Saleska et al., 2007; Xiao et al., 2005). These trends are in accordance with expected cycles of epiphyll growth, as dictated by moisture/precipitation (Coley & Kursar, 1996), litterfall dynamics (Reich, 1995; Roberts et al., 1998; Wright & Cornejo, 1990; Xiao et al., 2005), and leaf longevity (Reich et al., 2004). Our findings indicate that epiphylls have a substantive effect on the remote sensing of *Caatinga* canopies and a lesser, but notable effect on *Terra Firme*. Therefore, remote sensing-based studies of biophysical parameters and ecological processes in humid forests should account for their presence.

## Acknowledgments

This work was funded by NASA Terrestrial Ecology grant, NNX08AM89G. We thank José Lima dos Santos, José Ferreira Ramos, and Thaise Emilio Lopes de Sousa for their help with *Terra Firme* species identifications. We also thank Christopher Still, Sara Baguskas, and an anonymous reviewer for their helpful comments and suggestions.

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