



Differences in leaf traits, leaf internal structure, and spectral reflectance between two communities of lianas and trees: Implications for remote sensing in tropical environments

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ABSTRACT

Increasing dominance of lianas in many tropical forests is considered a fingerprint of global environmental change. Despite the key role they play in ecosystem functioning, lianas remain one of the least studied life forms in tropical environments. This paper contrasts leaf traits and spectral properties (400–1100 nm) of liana and tree communities from a tropical dry forest and a tropical rainforest in Panama, Central America. Differences between lianas and tree leaf traits were analyzed using spectroscopy, leaf histology and pigment extractions. Results from this study indicate that many of the biochemical, structural, and optical properties of lianas and trees are different in the dry forest site but not in rainforest sites. In the dry forest site, liana leaves exhibited significantly lower chlorophyll and carotenoid contents and were thinner than the leaves of their host trees. Specific leaf area, dry to fresh mass ratio, and mean water content of liana leaves were significantly higher when compared with tree leaves. The differences observed in the tropical dry forest site indicate that lianas may have a higher rate of resource acquisition and usage, whereas trees tend to conserve acquired resources. We suggest that our results may be indicative of the presence of a *liana syndrome* related to water availability and thus best exhibited in tropical dry forests. Our findings have important implications for using remote sensing to accurately map the distribution of liana communities at regional scales and for the continued expansion of lianas in tropical environments as a result of global change.

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1. Introduction

Tropical forest research using hyperspectral data is currently in its early stages of development. Progress has been constrained by limited access to hyperspectral data, limited access to the top of tall tropical forest canopies to provide field validation, and by the greater complexity of tropical forests as compared to temperate and boreal regions. Basic research in tropical environments on the quantification of pigments, photo-protective mechanisms as a function of different life forms, light scattering mechanisms at surface and cellular levels, or the impact of endophytes, epiphylls and galls on the spectral reflectance of leaves and canopies is, in addition, almost non-existent. Some exceptions are Lee and Graham (1986) and Lee et al. (1990) who reported correlations between leaf optical properties of sun vs. shade

leaves on a set of tree species from Costa Rica, Panama and the United States; Roberts et al. (1998), who reported the impact of leaf age on the spectral properties of tree species from the Amazon caatinga, Cochrane (2000) who explored the potential separability of Amazonian mahogany from selected background species, and Clark et al. (2005) who explore the separability between a selected number of tree species at La Selva Biological Station, Costa Rica. Zhang et al. (2006) documented the intra and inter-species variability of spectral reflectance for tree species of Mesoamérica while Castro-Esau et al. (2006) examined specific factors controlling their spectral variability. Gamon et al. (2005) documented contrasting photo-protective strategies among trees within a single Panamanian dry forest stand. These strategies, which ranged from photosynthetic downregulation to leaf movement and leaf shedding, were all detectable with spectral reflectance, indicating the potential for remote detection of contrasting physiological function.

A unique characteristic of tropical forests is the density of species for a given area. Gentry (1991) reports a range of 21–121 tree species for various 0.1 ha plots around the Neotropics. Lianas are woody

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climbers that further increase canopy plant diversity. Lianas play a key role in the community structure and ecosystem function of tropical dry and rainforests. In particular, lianas suppress tree regeneration and promote tree mortality (Laurence et al., 2001). Studies of the dynamics of liana coverage in tropical environments indicate high percentages of tree infestation for many parts of the neotropics. Examples from the Neotropics include 43% of trees at Rio Negro, Venezuela; 47% at Barro Colorado Island, Panama; 63% at Los Tuxtlas, Mexico; 73% at La Chonta, Bolivia; and 86% at Oquirita, Bolivia (Putz, 1983, 1984; Alvira et al., 2004; Pérez-Salicrup et al., 2001; Pérez-Salicrup & de Meijere, 2005). Lianas are one of the least studied life forms in tropical forests even though their dominance is growing relative to trees in many tropical forests (Phillips et al., 2002, 2005; Wright et al., 2004) and they are considered to be one of the ten key fingerprints of global environmental change in tropical environments (Phillips et al., 2002).

Information on the optical properties of lianas and their controlling mechanisms is even more limited. Avalos et al. (1999) documented differences in absorbance and transmittance between lianas and trees from a tropical dry forest (Parque Natural Metropolitano, Panama). They examined leaf optical properties of 12 liana and 7 tree species during the rainy season and found differences among life forms for transmittance but not for absorbance and reflectance. Castro-Esau et al. (2004) explored the separability of liana and tree leaves using hyperspectral signatures collected during the dry season and reported that the two life forms were distinct at a dry forest site (Parque Natural Metropolitano, Panama) but not at a rainforest site (Fort Sherman, Panama). More recently, Sánchez-Azofeifa and Castro-Esau (2006) and Kalácska et al. (2007) have documented differences between spectral reflectance at the leaf and crown levels at liana infested sites. Because lianas may obscure or distort the optical signals of trees, it is

imperative to determine the differences in leaf-level characteristics of lianas and trees in tropical forests, and to test whether these differences are reflected in their leaf and canopy optical properties. Furthermore, determining the leaf-level attributes of lianas may shed light on their competitive strategies (Wright et al., 2001; Reich et al., 1998), which may explain their relative increase in abundance in tropical and temperate forests (Phillips et al., 2002; Wright et al., 2004; Wright & Calderón, 2006; Mohan et al., 2006).

In this paper we seek the answers to three questions: 1) Do leaf pigment concentrations and spectral reflectance differ between life forms? 2) Do leaf internal structure and near-infrared reflectance differ between life forms? and 3) Do leaf traits such as Specific Leaf Area (SLA), leaf thickness, water content, and nitrogen (N) and phosphorus (P) concentration differ between life forms? We explored these questions in the context of spectral reflectance measured between 400 and 1100 nm. This work expands previous studies by Castro-Esau et al. (2004) and Kalácska et al. (2007) who explored the use of advanced parametric and non-parametric classification approaches to evaluate the spectral separability between lianas and trees at the same sites, but without exploring in-depth the biochemical and structural drivers that contribute to such separability.

2. Materials and methods

2.1. Study area

Leaf samples were collected using two canopy cranes maintained by the Smithsonian Tropical Research Institute (STRI) in Panama. Samples were collected at the Parque Natural Metropolitano (PNM), located near the Pacific coast, and the Parque Nacional San Lorenzo (FS; Fort Sherman) located near the Caribbean coast. At PNM, annual

Table 1

List of species collected and analyzed at Parque Natural Metropolitano (dry forest) and Fort Sherman (rainforest) of Panama.

Dry forest			Rainforest		
Family	Species	Life form	Family	Species	Life form
Apocynaceae	<i>Forsteronia spicata</i>	L	Apocynaceae	<i>Odontadenia puncticulosa</i>	L
Aristolochiaceae	<i>Aristolochia maxima</i>	L	Apocynaceae	<i>Fosteronia myriantha</i>	L
Asteraceae	<i>Mikania leiostachya</i>	L	Bignoniaceae	<i>Arrabidaea verrucosa</i>	L
Bignoniaceae	<i>Amphilophium paniculatum</i>	L	Bignoniaceae	<i>Pleonotoma variabilis</i>	L
Bignoniaceae	<i>Pithecoctenium crucigerum</i>	L	Convolvulaceae	<i>Maripa panamensis</i>	L
Bignoniaceae	<i>Arrabidaea patellifera</i>	L	Dilleniaceae	<i>Dolioscarpus multiflorus</i>	L
Bignoniaceae	<i>Stizophyllum riparium</i>	L	Fabaceae-Papilionoideae	<i>Dioclea wilsonii</i>	L
Bignoniaceae	<i>Phryganocydia corymbosa</i>	L	Hippocrateaceae	<i>Tontelea ovalifolia</i>	L
Bignoniaceae	<i>Arrabidaea candidans</i>	L	Hippocrateaceae	<i>Unknown sp.</i>	L
Convolvulaceae	<i>Bonamia trichantha</i>	L	Apocynaceae	<i>Aspidosperma cruenta</i>	T
Convolvulaceae	<i>Jacquemontia perryana</i>	L	Boraginaceae	<i>Cordia bicolor</i>	T
Dilleniaceae	<i>Dolioscarpus major</i>	L	Fabaceae-Papilionoideae	<i>Lonchocarpus longifolium</i>	T
Dilleniaceae	<i>Dolioscarpus dentatus</i>	L	Meliaceae	<i>Carapa guianensis</i>	T
Dilleniaceae	<i>Tetracera portobellensis</i>	L	Moraceae	<i>Brosimum utile</i>	T
Fabaceae-Papilionoideae	<i>Machaerium milleflorum</i>	L	Moraceae	<i>Ficus nymphaeifolia</i>	T
Hippocrateaceae	<i>Prionostema aspera</i>	L	Sapindaceae	<i>Matayba apetala</i>	T
Fabaceae-Papilionoideae	<i>Machaerium riparium</i>	L	Sapotaceae	<i>Manilkara bidentata</i>	T
Hippocrateaceae	<i>Hippocratea volubilis</i>	L	Sapotaceae	<i>Pouteria reticulata</i>	T
Malpighiaceae	<i>Hiraea reclinata</i>	L			
Malpighiaceae	<i>Stigmaphyllon hypargyreum</i>	L			
Passifloraceae	<i>Passiflora vitifolia</i>	L			
Phytolaccaceae	<i>Trichostigma octandrum</i>	L			
Rhamnaceae	<i>Gouania lupuloides</i>	L			
Sapindaceae	<i>Serjania mexicana</i>	L			
Sapindaceae	<i>Serjania atrolineata</i>	L			
Vitaceae	<i>Vitis tiliifolia</i>	L			
Anacardiaceae	<i>Anacardium excelsum</i>	T			
Anacardiaceae	<i>Astronium graveolens</i>	T			
Annonaceae	<i>Annona spraguei</i>	T			
Bombacaceae	<i>Pseudobombax septenatum</i>	T			
Boraginaceae	<i>Cordia alliodora</i>	T			
Moraceae	<i>Ficus insipida</i>	T			
Moraceae	<i>Castilla elastica</i>	T			
Sapotaceae	<i>Chrysophyllum argenteum</i>	T			
Tiliaceae	<i>Luehea seemanii</i>	T			

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