

University of Alberta

Leaf Area Index in a Tropical Dry Forest in Mexico

by

Yingduan Huang

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Sciences

Earth and Atmospheric Sciences

©Yingduan Huang

Spring 2012

Edmonton, Alberta

Permission is hereby granted to the University of Alberta Libraries to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only. Where the thesis is converted to, or otherwise made available in digital form, the University of Alberta will advise potential users of the thesis of these terms.

The author reserves all other publication and other rights in association with the copyright in the thesis and, except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatsoever without the author's prior written permission.

Abstract

Tropical dry forests are important ecosystems for their high species richness, endemism and their important role in sustaining earth's system. This thesis utilized leaf area index measurements to characterize tropical dry forest successions and their seasonality in a tropical dry forest in Mexico, explored its linkage with MODIS LAI and the factors that drive the variation of MODIS LAI. The objectives were: 1) To estimate LAI field measurements across three stages of succession in this tropical dry forest and evaluate the linkage between LAI and ecosystem structure and composition, 2) To estimate seasonal dynamics of the tropical dry forest by optical LAI measurements, and to evaluate the performance of MODIS LAI in estimating LAI in the tropical dry forest, 3) To evaluate the effects of subpixel land surface characteristics on the phenological pattern derived from MODIS LAI time series. Results found significant difference in LAI as well as in composition among successional stages. Seasonal dynamics were well captured by both optical measurements and MODIS LAI however discrepancy in values was found between these two variables. Further study in exploring subpixel characteristics found the amount of forest cover within a MODIS pixel, along with the mean aspect had a significant impact on MODIS LAI values as well as phenological characteristics derived from its time series. This thesis contributed to future research in the application and validation of remotely sensed LAI from both a biological perspective and a remote sensing perspective.

Acknowledgements

I would like to thank Dr. Arturo Sánchez-Azofeifa for providing me the opportunity to participate in the Inter-American Institute for global change research project in tropical dry forests, and learn a lot from him and his team. He has been so patient, encouraging, and always believes in me. I benefit a lot from my graduate program and working with him. He is a wonderful supervisor. It's such an honor being one of his students.

I would like to thank the Inter-American Institute for global change research and the University of Alberta for the institutional and financial support to my program.

Thank you to Dr. Benoit Rivard and his students for sharing the knowledge and experience, which helps me especially when starting my program.

Thank you to Dr. Mauricio Quesada and his group at the Universidad Nacional Autónoma de México for providing me accommodation, transportation and all the support to my field work. They tried everything they could to help me and shared their knowledge of this specific ecosystem.

I would like to thank everyone in the Earth Observation Systems Laboratory (EOSL) and other professors and friends in the Department of Earth and Atmospheric Sciences for their support.

At last, a big thank to all my family members for their support.

Table of Contents

Chapter One: Introduction.....	1
Tropical Dry Forests	1
Chamela-Cuixmala Biosphere Reserve, Mexico	3
Study Area	4
Leaf Area Index	4
Objectives	7
Significance.....	8
Literature Cited.....	10
Figure	17
 Chapter Two: Linkages between ecosystem structure, composition and leaf area index along a tropical dry forest chronosequence in Mexico.....	 18
1. Introduction.....	18
2. Methods.....	23
2.1. Plot Design.....	23
2.2. Field Data Collection and Analysis	24
2.3. MODIS Data Extraction and Analysis.....	26
3. Results.....	27
3.1. Species Composition.....	27
3.2. Estimation of Wood Area Index	28
3.3. Estimation of Plant Area Index.....	28
3.4. Estimation of Leaf Area Index and Seasonality	29
3.5. MODIS LAI.....	30

4. Discussion	31
5. Conclusion	35
Literature Cited	37
Figures and Tables	47

Chapter Three: Effects of subpixel land surface characteristics on MODIS

LAI phenology in a tropical dry forest in Mexico.....	62
1. Introduction.....	62
2. Methods.....	64
2.1. Imagery	64
2.2. Methodology	65
2.2.1. MODIS LAI Time Series.....	65
2.2.2. TIMESAT	66
2.2.3. Land Cover Classification.....	67
2.2.4. Topography.....	67
2.2.5. ANOVA	68
3. Results.....	69
3.1. Phenological Pattern of MODIS LAI	69
3.2. Land Cover.....	70
3.3. Topography and Solar Radiation	70
3.4. Effect of Land Surface Characteristics on MODIS LAI Phenological Pattern	70
4. Discussion.....	72
5. Conclusion	74

Literature Cited	76
Figures and Tables	81
Chapter Four: Conclusion.....	86
Contribution and Future Insight.....	87
Chapter Two: Linkages between ecosystem structure, composition and leaf area index along a tropical dry forest chronosequence in Mexico	87
Chapter Three: Effects of subpixel land surface characteristics on MODIS LAI phenology in a tropical dry forest in Mexico	89
Overall Significance.....	91
Literature Cited	92

List of Tables

Table 2-1.	Main characteristics of plots.....	58
Table 2-2.	Average Morisita–Horn index within and between successional stages.....	59
Table 2-3.	Morisita–Horn index between sites in the early stage.....	59
Table 2-4.	Morisita–Horn index between sites in the intermediate stage.....	59
Table 2-5.	Morisita–Horn index between sites in the late stage.....	59
Table 2-6.	WAI in June, LAI in July and August, and dominant species of the 9 plots of three successional stages.....	60
Table 2-7.	Comparison between <i>In Situ</i> LAI and MODIS LAI. The MODIS land cover types for the 9 sites are listed.....	61
Table 3-1.	Training and testing regions – number of polygons and number of pixels per land cover class.....	84
Table 3-2.	Highest and lowest values of phenological parameters among the 48 MODIS pixels.....	85
Table 3-3.	p values of a two-way ANOVA – effects of forest cover and aspect on phenological parameters.....	85
Table 3-4.	Least square means of phenological data in non-parametric two-way ANOVA – effects of forest cover and aspect on phenological parameters (ranks).	85
Table 3-5.	Mean annual solar radiation (WH/m ²) in the 4 groups in a two-way ANOVA.....	85

List of Figures

Figure 1-1.	Study area: Chamela-Cuixmala Biosphere reserve in the state of Jalisco, Mexico.....	17
Figure 2-1.	Location of 9 sampling plots (3 plots per successional stage) in the Chamela-Cuixmala Biosphere reserve, Mexico.....	47
Figure 2-2.	Illustration of leaves development from the dry season to the rainy season of the year.....	48
Figure 2-3.	Sampling schemes for WAI and PAI collection for the 30m × 60m plots.....	49
Figure 2-4.	Comparison of WAI of the three successional stages.....	50
Figure 2-5.	Comparison of PAI values across successional stages.....	51
Figure 2-6.	Comparison of PAI values of the 9 plots in July (a) and in August (b)	52
Figure 2-7.	Comparison of LAI values across successional stages.....	53
Figure 2-8.	Comparison of LAI values of the 9 plots in July (a) and in August (b)	54
Figure 2-9.	Relation between LAI and the altitude of the plots in each stage of succession.....	55
Figure 2-10.	WAI in June, LAI in July and in August for the 9 plots.....	56
Figure 2-11.	<i>In situ</i> and MODIS LAI relationship in July (a) and in August (b)	57
Figure 3-1.	Study area, covered by the QuickBird image obtained in April 2003, just north to the Chamela-Cuixmala Biosphere Reserve...	81

Figure 3-2.	Some of seasonality parameters derived in TIMESAT.....	82
Figure 3-3.	MODIS LAI time series of two pixels with different percentage of forest cover from year 2000 to 2010.....	83

Chapter One: Introduction

Tropical Dry Forests

Tropical dry forests are important ecosystems for their intimate relation to climate system dynamics, atmospheric composition, and their environmental services that benefit human welfare and help to sustain the earth's system, including renewal of soil fertility, purification of water, and carbon sequestration that aids in mitigation of climate change (Sánchez-Azofeifa et al., 2001; Sánchez-Azofeifa et al., 2007).

Tropical dry forests are defined by Sánchez-Azofeifa et al. (2005b) as a vegetation type dominated by deciduous trees where more than 50% are drought deciduous, the mean annual temperature is $>25^{\circ}\text{C}$, total annual precipitation ranges between 700 and 2000 mm, and there are three or more dry months every year when precipitation is < 100 mm. Tropical dry forests comprise approximately 42% of all tropical forests (Brown and Lugo, 1982; Miles et al., 2006), among which approximately 54% are located in the Americas, from Mexico to Northern Argentina, which are referred to as Neotropical dry forests (Miles et al., 2006). A recent study conducted by Portillo-Quintero and Sánchez-Azofeifa (2010) revealed the current extent of Neotropical dry forests as 519,597 km^2 , based on the results of a supervised classification using MODIS surface reflectance product at 500-m spatial resolution.

Tropical dry forests maintain high levels of species diversity (Portillo-Quintero & Sánchez-Azofeifa, 2010), and are even more diverse structurally and physiologically than wet forests (Medina, 1995; Sánchez-Azofeifa et al., 2003). They have higher endemism than wet forests which refers to species unique to the area (Kalacska et al., 2005a; Rzedowski, 1991). Gentry (1995) found endemism to be as high as 76% in South American dry forests.

In spite of their high species richness, endemism and their important role in sustaining earth's system and human development, tropical dry forests are among the most vulnerable and threatened ecosystems in the Americas due to intensive human disturbance (Janzen, 1988; Hoekstra et al., 2005) given that historically they were preferred for agricultural activities, human settlement and development in the tropics (Maass, 1995; Quesada et al., 2009; Sánchez-Azofeifa et al., 2005b). At the global level, approximately 48.5% of the tropical dry forest has been converted to other land uses (Hoekstra et al., 2005). In the Americas, 66% of the ecosystem has been reduced caused by the timber industry, agricultural development and cattle ranching, leaving a total of 519,597 km² tropical dry forests across North and South America, among which only 4.5% (23,417 km² out of 519,597 km²) are protected by nature reserves (Portillo-Quintero & Sánchez-Azofeifa, 2010). As a result of deforestation, tropical dry forests exist as fragments embedded in matrices of transformed land covers (Portillo-Quintero & Sánchez-Azofeifa, 2010). It is indicated that most mature forests will disappear and secondary forest patches in different successional stages will take the lead eventually (Quesada et al., 2009; Sánchez-Azofeifa, 2005b).

While most studies have focused on tropical rain forests, tropical dry forests are one of the least well studied tropical ecosystems (Stoner & Sánchez-Azofeifa, 2009). Few efforts have been put towards the conservation and sustainable management of tropical dry forests (Sánchez-Azofeifa, 2005b). There are only a few national parks and biological reserves (Sánchez-Azofeifa et al., 2005a), and only 4.5% of Neotropical dry forests are under protection compared to 16-18% protected area for tropical humid forests (Hoekstra et al., 2005; Portillo-Quintero & Sánchez-Azofeifa, 2010).

Chamela-Cuixmala Biosphere Reserve, Mexico

Mexico has the largest extend of tropical dry forests in the Americas, although 71% has been converted to other land uses due to agriculture and cattle ranching (Portillo-Quintero & Sánchez-Azofeifa, 2010). The current extend is 181,461 km² in Mexico representing 38% of the Neotropical dry forests (Portillo-Quintero & Sánchez-Azofeifa, 2010). However, despite the fact that tropical dry forests in Mexico are important for their highest diversity and endemism (Short 1974; Janzen 1983), they are among the least protected, with only 336 km² (0.2%) protected area (Miles et al., 2006; Portillo-Quintero & Sánchez-Azofeifa, 2010). One of the protected areas for tropical dry forest in Mexico is the Chamela-Cuixmala Biosphere Reserve, located on the Pacific coast of Mexico, in the state of Jalisco. The climate is influenced by tropical cyclones which have led to a highly variable annual rainfall pattern (Garcia-Oliva et al., 1991). The Chamela-Cuixmala Biosphere Reserve is a protected area of approximately 131 km² (Maass

et al., 2005), with 92.1% of tropical dry forest, 4% of riparian forest and mangroves and 3.7% of deforestation area (Sánchez-Azofeifa et al., 2009b). The surrounding areas within a 5 km distance from the reserve also maintain as high as 80% of tropical dry forest (Sánchez-Azofeifa et al., 2009b).

Study Area

This study was conducted in the tropical dry forest in the Chamela-Cuixmala Biosphere Reserve, located at 19°30' N, 105°03' W (Figure 1-1), where mean annual temperature is 25°C (Maass et al., 1995), mean annual precipitation is 748 mm with 80% falling between July and October (Balvanera et al., 2002; Maass et al., 2005). Due to human activities and forest recovery, this area is mainly comprised of tropical dry forests of three successional stages (Kalacska et al., 2005): early stage – secondary dry forest of 3-5 years old, intermediate stage – secondary dry forest of 8-12 years old and late stage – mature tropical dry forest.

Leaf Area Index

Seasonality is one of the significant characteristics of tropical dry forests (Sánchez-Azofeifa et al., 2009a). During the dry season, the majority of the woody plant species is drought deciduous (Frankie et al., 1974; Lobo et al., 2003) and sheds the leaves due to the lack of water availability (Borchert, 1994). At the end of the dry season and when the rains begin, leaves start growing for most of the species in tropical dry forests (Murphy and Lugo, 1995; Arroyo-Mora et al., 2005). Leaf Area Index (LAI) is a variable introduced to measure the amount of

foliage, which is defined as the total one-sided area of photosynthetic tissue per unit ground surface area for broad-leaved trees (Jonckheere et al., 2004). LAI is not only important in monitoring and studying seasonality of tropical dry forests (Kalacska et al., 2005b), but also essential in the studies of primary production, carbon sequestration, energy and water vapor exchange between canopy and atmosphere (Clark et al., 2008; Gower et al., 1999).

There are direct and indirect methods of estimating leaf area index (Gower et al., 1999). Direct measurements include: (1) Area harvest – collect foliage sample, use the ratio of leaf area to dry mass in deriving leaf area index. This approach is good for ecosystems that are homogeneous spatially, e.g., grassland, crops. (2) Allometric equation – collect foliage sample and use the relation between leaf area and stand diameter data to derive leaf area index. (3) Litter fall - collect litter fall, use the ratio of leaf area to dry mass to calculate the leaf area index. All the direct methods are considered accurate but laborious.

Alternatively, an indirect optical approach is less labor intensive and preferred in recent studies (Welles, 1990; Welles & Cohen, 1996). Optical instruments such as digital hemispherical cameras and the LICOR-2000 Plant Canopy Analyzer capture the radiation from beneath the canopy. Leaf area index is derived based on the analysis of light transmission through canopies (Jonckheere et al., 2004). Optical measurements include the contribution of not only foliage, but also woody material such as trunks and branches (Kucharik et al., 1998). The concept of wood area index was introduced by Chen et al. (1997) to

represent the amount of wood materials. Leaf area index is calculated by subtracting wood area index from the optical measurement defined as the plant area index (Chen et al., 1997; Sánchez-Azofeifa et al., 2009a). Clumping is another factor that affects LAI optical measurements especially for canopies where branches are non-randomly distributed such as conifers. Random distribution of foliage is assumed in tropical forest canopies due to practical reasons. Since indirect methods are considered less accurate than direct methods thus the latter are often used as calibration tools for indirect measurements (Jonckheere et al., 2004).

In addition to the direct and indirect field measurements of leaf area index, remote sensing techniques have been used in estimating leaf area index (Chen et al., 2002; Cohen et al., 2003; Eklundh et al., 2003; Meroni et al., 2004). Using remotely sensed data is a rapid way in LAI assessment, much more cost-effective for large areas (Kalacska et al., 2005b; Weiss et al., 2004), and is essential in providing information on water and energy exchange, and momentum flux between canopy and atmosphere at regional and global scales (Morisette et al., 2006). One of the most popular remotely sensed LAI products is NASA's MODIS (Moderate Resolution Imaging Spectroradiometer) LAI. MODIS LAI is derived from MODIS atmospherically corrected surface reflectance and is provided as a 8-day composite product at 1-km spatial resolution since February 2000. MODIS LAI has provided near real-time estimates of leaf area index globally (Heinsch et al., 2006).

MODIS LAI has been used in scientific studies for indirect LAI observation and monitoring seasonal dynamics. Compared with field measurements (Fensholt et al., 2004; Wang et al., 2004; Wang et al., 2005) as well as with LAI maps derived from higher spatial resolution satellite images (Fang and Liang, 2005), MODIS LAI was found to capture well seasonal dynamics yet overestimate LAI in some studies (Fensholt et al., 2004; Heinsch et al., 2006; Wang et al. 2005). In regard to the process of deriving LAI, errors could be introduced at any stage of remotely sensed image acquisition or image analysis (Jonckheere et al., 2004) thus validation of remotely sensed LAI by utilizing field measurements is essential in order to refine algorithms that derive LAI and advance the development and application of remotely sensed LAI (Yang et al., 2006).

Objectives

The objectives of this thesis are:

1. To evaluate the impacts of ecosystem structure and composition on LAI field measurements across different stages of succession in a tropical dry forest, estimate seasonal changes using LAI measurements made by optical methods, and to evaluate the performance of MODIS LAI in estimating LAI for this tropical dry forest.
2. To evaluate the effects of subpixel land surface characteristics on the phenological patterns captured by MODIS LAI in the tropical dry forest,

including subpixel land cover, topographic features such as slope and aspect.

Significance

Most scientific studies have focused primarily on the protection of humid forests in the tropic, while little attention has been paid to tropical dry forests (Sánchez-Azofeifa et al., 2005b). This study will help to increase knowledge of tropical dry forests and its succession. Succession is critical in understanding tropical dry forests given that secondary forests of different levels of succession will eventually replace mature tropical dry forests in the future (Quesada et al., 2009). However, few scientific studies address tropical dry forest succession – less than 1/7 compared to studies in tropical rain forest succession (Quesada et al., 2009).

This thesis categorizes the tropical dry forest in the Chamela-Cuixmala Biosphere Reserve into three successions – early, intermediate and late, and examines the difference in LAI measured by optical methods across the three successional stages. It helps to increase our knowledge of the structural and compositional difference among successions, how tropical dry forests respond to environmental changes, i.e. seasonal water availability. By evaluating the performance of MODIS LAI in capturing seasonal variability, and exploring the factors driving the discrepancy between MODIS LAI and field measurements,

this research outlines aspects to be considered with attention when applying MODIS LAI in ecological studies.

Literature Cited

- Arroyo-Mora, J. P., Sánchez-Azofeifa, A., Kalacska, M. E., and Rivard, B. (2005). Secondary Forest Detection in a Neotropical Dry Forest Landscape Using Landsat 7 ETM+ and IKONOS Imagery. *Biotropica*, 37(4), 497-507.
- Balvanera, P., Lott, E., Segura, G., Siebe, C., and Islas, A. (2002). Patterns of β -diversity in a Mexican tropical dry forest. *Journal of Vegetation Science*, 13, 145-158.
- Borchert, R. (1994). Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, 75, 1437-1449.
- Brown, S., and Lugo, A. E. (1982). Storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica*, 14, 161-187.
- Chen, J. M., Blanken, P. D., Black, T. A., Guilbeault, M., and Chen, S. (1997). Radiation regime and canopy architecture in a boreal aspen forest. *Agricultural and Forest Meteorology*, 86, 107-125.
- Chen, J. M., Pavlic, G., Brown, L., Cihlar, J., Leblanc, S. G., and White, H. P., Hall, R. J., Peddle, D. R., King, D. J., Trofymow, J. A., Swift, E., Van der Sanden, J., and Pellikka, P. K. E. (2002). Derivation and validation of Canada-wide coarse-resolution leaf area index maps using high-resolution satellite imagery and ground measurements. *Remote Sensing of environment*, 80, 165-184.
- Clark, D.B., Olivas, P.C., Oberbauer, S.F., Clark, D.A., and Ryan, M.G. (2008). First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity. *Ecology Letters*, 11 (2), 163-172.
- Cohen, W. B., Maiersperger, T. K., Yang, Z., Gower, S. T., Turner, D. P., Ritts, W. D., Berterretche, M., and Running, S. W. (2003). Comparisons of land cover and LAI estimates derived from ETM+ and MODIS for four sites in North America: A quality assessment of 2000/2001 provisional MODIS products. *Remote Sensing of Environment*, 88, 233-255.

Eklundh, L., Hall, K., Eriksson, H., Ardo, J., and Pilesjo, P. (2003). Investigating the use of Landsat thematic mapper data for estimation of forest leaf area index in southern Sweden. *Canadian Journal of Remote Sensing*, 29, 349-362.

Fang, H., and Liang S. (2005). A hybrid inversion method for mapping leaf area index from MODIS data: experiments and application to broadleaf and needleleaf canopies. *Remote Sensing of Environment*, 94, 405-424.

Fensholt, R., Sandholt, I., and Rasmussen, M. S. (2004). Evaluation of MODIS LAI, fAPAR and the relation between fAPAR and NDVI in a semi-arid environment using in situ measurements. *Remote Sensing of Environment*, 91, 490-507.

Frankie G. W., Baker, H. G., and Opler, P. A. (1974). Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *The Journal of Ecology*, 62, 881-919.

Garcia-Oliva, F., Ezcurra, E., and Galicia, L. (1991). Pattern of Rainfall Distribution in the Central Pacific Coast of Mexico. *Geografiska Annaler. Series A, Physical Geography*, 73, 179-186.

Gentry, A. H. (1995). Diversity and floristic composition of neotropical dry forests. In: Bullock, S.H., Mooney, H.A., and Medina, E. (Eds.) *Seasonally dry tropical forests* (pp. 146-194), Cambridge: Cambridge University Press.

Gower, S. T., Kucharik, C. J., and Norman, J. M. (1999). Direct and indirect estimation of leaf area index, fAPAR, and net primary production of terrestrial ecosystems. *Remote Sensing of Environment*, 70, 29-51.

Heinsch, F. A., Zhao, M., Running, S. W., Kimball, J. S., Nemani, R. R., Davis, K. J., Bolstad, P. V., Cook, B. D., Desai, A. R., Ricciuto, D. M., Law, B. E., Oechel, W. C., Kwon, H., Luo, H., Wofsy, S. C., Dunn, A. L., Munger, J. W., Baldocchi, D. D., Xu, L., Hollinger, D. Y., Richardson, A. D., Stoy, P. C., Siqueira, M. B. S.,

Monson, R. K., Burns, S. P., and Flanagan, L. B. (2006). Evaluation of remote sensing based terrestrial productivity from MODIS using regional tower eddy flux network observations. *IEEE Transactions on Geoscience and Remote Sensing*, 44 (7), 1908-1925.

Hoekstra, J., Boucher, T., Ricketts, T., and Roberts, C. (2005). Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters*, 8, 23-29.

Janzen, D. H., editor. (1983). Costa Rican natural history. University of Chicago Press, Chicago.

Janzen, D. H. (1988). Guanacaste National Park: tropical ecological and biocultural restoration. In: Cairns, J.J. (Ed.), *Rehabilitating Damaged Ecosystems* (vol. II pp. 143-192). Boca Raton, FL: CRC Press.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., and Baret, F. (2004). Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology*, 121, 19-35.

Kalacska, M., Calvo-Alvarado, J. C., and Sánchez-Azofeifa, G. A. (2005a). Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession. *Tree Physiology*, 25, 733-744.

Kalacska, M., Sánchez-Azofeifa, G. A., Calvo-Alvarado, J. C., Rivard, B., and Quesada, M. (2005b). Effects of Season and Successional Stage on Leaf Area Index and Spectral Vegetation Indices in Three Mesoamerican Tropical Dry Forests. *Biotropica*, 37(4), 486-496.

Kucharik, C. J., Norman, J. M., and Gower, S. T. (1998). Measurements of branch area and adjusting leaf area index indirect measurements. *Agricultural and Forest Meteorology*, 91, 69-88.

Lobo, J. A., Quesada, M., Stoner, K. E., Fuchs, E. J., Herrerías-Diego, Y., Rojas, J., and Saborío, G. (2003). Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. *American journal of botany*, 90, 1054-1063.

Maass, J. M., Vose, J. M., Swank, W. T., and Martinez-Yrizar, A. (1995). Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. *Forest Ecology and Management*, 74, 171-180.

Maass, J., Balvanera, P., Castillo, A., Daily, G. C., Mooney, H. A., Ehrlich, P., Quesada, M., Miranda, A., Jaramillo, V. J., García-Oliva, F., Martínez-Yrizar, A., Cotler, H., López-Blanco, J., Pérez-Jiménez, A., Búrquez, A., Tinoco, C., Ceballos, G., Barraza, L., Ayala, R., and Sarukhán, J. (2005). Ecosystem services of tropical dry forests: insights from long-term ecological and social research on the Pacific Coast of Mexico. *Ecology and Society*, 10(1), 17-39.

Medina, E. (1995). Diversity of life forms of higher plants in Neotropical dry forests. *Seasonally Tropical Forests*. Cambridge University Press, UK.

Meroni, M., Colombo, R., and Panigada, C. (2004). Inversion of a radiative transfer model with hyperspectral observations for LAI mapping in poplar plantations. *Remote Sensing of Environment*, 92, 195-206.

Miles, L., Newton, A., DeFries, R., Ravilious., C., May, I., Blyth, S., Kapos., V. and Gordon, J. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, 33, 491-505.

Morisette, J. T., Baret, F., Privette, J. L., Myneni, R. B., Nickeson, J. E., Garrigues, S., Shabanov, N. V., Weiss, M., Fernandes, R. A., Leblanc, S. G., Kalacska, M., Sánchez-Azofeifa, G. A., Chubey, M., Rivard, B., Stenberg, p., Rautiainen, M., Voipio, P., Manninen, T., Pilant, A. N., Lewis, T. E., Iiames, J. S., Colombo, R., Meroni, M., Busetto, L., Cohen, W. B., Turner, D. P., Warner, E. D., Petersen, G. W., Seufert, G. and Cook, R. (2006). Validation of Global Moderate-Resolution LAI Products: A Framework Proposed Within the CEOS

Land Product Validation Subgroup. *IEEE Transactions on Geoscience and Remote Sensing*, 44 (7), 1804-1817.

Murphy, P.G. and Lugo, A.E. (1995) Dry forests of Central America and the Caribbean. Seasonally dry tropical forests (ed. by S.H. Bullock, H.A. Mooney and E. Medina), pp. 9-34. Cambridge University Press, Cambridge.

Portillo-Quintero, C.A. and Sánchez-Azofeifa, G.A. (2010). Extent and conservation of tropical dry forests in the Americas. *Biological Conservation*, 143, 144-155.

Quesada, M., Sánchez-Azofeifa, G. A., Alvarez-Anorve, M., Stoner, K. E., Avila-Cabadilla, L., Calvo-Alvarado, J., Castillo, A., Espirito-Santo, M. M., Fagundes, M., Fernandes, G. W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L. P. C., Powers, J. S., Neves, F. S., Rosas-Guerrero, V., Sayago, R., and Sánchez-Montoya, G. (2009). Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, 258, 1014-1024.

Rzedowski, J. (1991). El endemismo en la flora fanerógamica mexicana: una apreciación analítica preliminar. *Acta Botánica Mexicana*, 15, 47-64.

Sánchez-Azofeifa, G.A., Harriss, R.C., and Skole, D.L. (2001). Deforestation in Costa Rica: a quantitative analysis using remote sensing imagery. *Biotropica*, 33, 378-384.

Sánchez-Azofeifa, A., Kalacska, M. E., Quesada, M., Stoner, K. E., Lobo, J. A., and Arroyo-Mora, P. (2003). Tropical Dry Climates. *Phenology: An integrative environmental science*. (pp. 121). The Netherlands: Kluwer Academic Publisher.

Sánchez-Azofeifa, A., Kalacska, M. E., Quesada, M., Calvo-Alvarado, J., Nassar, J. M., and Rodriguez, J. P. (2005a). Need for Integrated Research for a Sustainable Future in Tropical Dry Forests. *Conservation Biology*, 19 (2), 285-286.

Sánchez-Azofeifa, G. A., Quesada, M., Rodriguez, J. P., Nasser, J. M., Stoner, K. E., Castillo, A., Garvin, T., Zent, E. L., Calvo, J. C., Kalacska, M., Fajardo, L., Gamon, J., and Cuevas-Reyes, P. (2005b). Research priorities for Neotropical dry forests. *Biotropica*, 37(4), 477-485.

Sánchez-Azofeifa, G.A., Pfaff, A., Robalino, J. A., and Boomhower, J. P. (2007). Costa Rica's Payment for Environmental Services Program: Intention, Implementation, and Impact. *Conservation Biology*, 21 (5), 1165-1173.

Sánchez-Azofeifa, A., Kalacska, M. E., Espirito-Santo, M. M., Fernandes, G. W., and Schnitzer, S. (2009a). Tropical dry forest succession and the contribution of lianas to wood area index (WAI). *Forest Ecology and Management*, 258, 941-948.

Sánchez-Azofeifa, G. A., Quesada, M., Cuevas-Reyes, P., Castillo, A., and Sánchez-Montoya, G. (2009b). Land cover and conservation in the area of influence of the Chamela-Cuixmala Biosphere Reserve, Mexico. *Forest Ecology and Management*, 258, 907-912.

Short, L. L. (1974). A zoogeographical analysis of the South American Chaco avifauna. *Bulletin of the American Museum of Natural History*, 154, 165-352.

Stoner, K. E. and Sánchez-Azofeifa, G. A. (2009). Ecology and regeneration of tropical dry forests in the Americas: Implications for management. *Forest Ecology and Management*, 258, 903-906.

Wang, Q., Tenhunen, J., Granier, A., Reichstein, M., Bouriaud, O., Nguyen D., and Breda, N. (2004). Long-term variations in leaf area index and light extinction in a *Fagus sylvatica* stand as estimated from global radiation profiles. *Theoretical and Applied Climatology*, 79, 225-238.

Wang, Q., Tenhunen, J., Nguyen Q. D., Reichstein, M., Otieno, D., Granier, A., and Pilegarrrd, K. (2005). Evaluation of seasonal variation of MODIS derived leaf

area index at two European deciduous broadleaf forest sites. *Remote Sensing of Environment*, 96, 475-484.

Weiss, M., Baret, F., Smith, G. J., Jonckheere, I., and Coppin, P. (2004). Review of methods for in situ leaf area index (LAI) determination Part II. Estimation of LAI, errors and sampling. *Agricultural and Forest Meteorology*, 121, 37-53.

Welles J. M. (1990). Some indirect methods of estimating canopy structure, *Remote Sensing Reviews*, 5(1), 31-43.

Welles, J. M. and Cohen, S. (1996). Canopy structure measurement by gap fraction analysis using commercial instrumentation. *Journal of Experimental Botany*, 47, 1335-1342.

Yang, W., Tan, B., Huang, D., Rautiainen, M., Shabanov, N.V., Wang, Y., Privette, J.L., Huemmrich, K.F., Fensholt, R., Sandholt, I., Weiss, M., Ahl, D.E., Gower, S.T., Nemani, R.R., Knyazikhin, Y., and Myneni, R.B. (2006). MODIS leaf area index products: from validation to algorithm improvement. *IEEE Transactions on Geoscience and Remote Sensing*, 44 (7), 1885-1898.

Figures



Figure 1-1. Study area: Chamela-Cuixmala Biosphere reserve in the state of Jalisco, Mexico.

Chapter Two: Linkages between ecosystem structure, composition and leaf area index along a tropical dry forest chronosequence in Mexico

1. Introduction

Tropical dry forests (TDFs) are transitional ecosystems between savanna and moist forest, and comprise 42% of the earth's tropical and subtropical forests ((Murphy and Lugo, 1986). TDFs are defined as a forest type dominated by deciduous trees, with a mean temperature $> 25^{\circ}\text{C}$, a total annual precipitation between 700 mm and 2000 mm, and three or more dry months when the precipitation is less than 100 mm (Sánchez-Azofeifa et al., 2005). The seasonal changes in phenological characteristics of a tropical dry forest are determined primarily by the seasonal variation in water availability (Reich and Borchert, 1984). Although tropical dry forests have less tree species (Murphy and Lugo, 1986), they have more structural and physiological diversity (Medina, 1995; Sánchez-Azofeifa et al., 2003), and they have higher endemism than tropical wet forests (Rzedowski, 1991 as cited by Kalacska et al., 2005).

Being disturbed frequently and severely due to human activity and economic pressures (Brooks et al., 2009; Janzen, 1986, 1988; Kalacska et al., 2004; Mooney et al., 1995; Quesada and Stoner, 2004), tropical dry forests are considered the most endangered major tropical ecosystem (Janzen, 1988, Portillo and Sánchez-

Azofeifa, 2010). Land cover change in TDFs in the Americas is generally driven by expansion on the agricultural frontier, extensive and intensive cattle ranching and tourism development (Portillo and Sánchez-Azofeifa, 2010). Though the conservation of tropical dry forest has been advocated (Sánchez-Azofeifa et al., 2005), little has been done and only a handful of national parks and biological reserves exist in the Americas (Portillo and Sánchez-Azofeifa, 2010).

In tropical dry forests, phenological characteristics such as leaf shedding, shooting, flowering, present a higher degree of variability than in other tropical ecosystems (Burnham 1997; Borchert 1994). It has been recognized that the principal element controlling the phenology of tropical dry forests is soil moisture availability (Reich and Borchert, 1984; Longman and Jenik, 1974; Doley, 1981), which is highly related with the seasonal variation in rainfall (Schimper, 1898; Bullock and Solis-Magallanes, 1990). The phenological expression from temporal changes associated to the environmental factors mentioned above, can be characterized via the quantification of the temporal changes in Leaf Area Index (LAI). LAI, defined as the total one-sided area of photosynthetic tissue per unit ground surface area (Watson, 1947 as cited by Jonckheere et al., 2004), has been widely used as a convenient way to quantify leaf phenology, gross primary productivity, and carbon and water cycle processes (Chena et al., 2002; Chen at al., 1991; Maass et al., 1995, Asner et al., 2003; Xiao et al., 2004,; Asner et al., 2003; Mccarthy et al., 2007).

Estimation of LAI can be direct or indirect (Jonckheere et al., 2004; Weiss et al., 2004). Among those methods, the indirect optical techniques are preferred because they are relatively rapid and accurate (Dufrene and Breda, 1995). Hemispherical canopy photography and LAI-2000 are two of the optical instruments to estimate LAI by measuring the canopy gap fraction – the fraction of view that is not obstructed by canopy in any particular direction (Welles and Cohen, 1996). Hemispherical canopy photography captures photographs through a fisheye lens from beneath the canopy, while LAI-2000 measures the gap fraction through the ratio between diffuse radiation under and above the canopy (Jonckheere et al., 2004). However, optical instruments are not able to distinguish foliage from trunks and branches (Kucharik et al., 1998) and estimate the overall contribution of leaves and woody components, which is defined as Plant Area Index (PAI) (Chen et al., 1991). The contribution of woody components is defined as Woody Area Index (WAI) (Chen et al., 1997; Leblanc and Chen, 2001; Wang, 2005). LAI is then calculated as (Chen et al., 1997; Frazer et al., 2000; Leblanc and Chen, 2001; Sánchez-Azofeifa et al., 2009; Wang, 2005):

$$LAI = L_p(1 - WAI) = \frac{L_e(1 - WAI)}{\Omega}$$

where L_p is the total plant area index, WAI is the ratio of wood area contribution. L_e is the effective PAI obtained from optical methods (Chen et al., 1991). Ω is the clumping factor, which is significant for non-random foliage such as conifers,

but can be assumed to be 1 in many studies in tropical environments due to practical reasons (Clark et al., 2008; Sánchez-Azofeifa et al., 2009).

Beside the *in situ* methods, remote sensing techniques have also been used as tools for indirect LAI estimations (Chen et al., 2002; Cohen et al., 2003; Eklundh et al., 2003; Meroni et al., 2004; Myneni et al., 2002). The Moderate Resolution Imaging Spectroradiometer (MODIS) provides 1-km moderate spatial resolution and 8-day temporal resolution LAI product to monitor phenology (Huemmrich et al., 2005). Many researchers have applied MODIS LAI in their studies (Ahl et al., 2006; Fensholt et al., 2004; Wang et al., 2004; Wang et al., 2005). Discrepancy has been found between MODIS LAI and *in situ* LAI (Ahl et al., 2006; Cohen et al., 2003; Fensholt et al., 2004; Wang et al., 2004). Spatial scale is one of the factors leading to the discrepancy (Ahl et al., 2006). One MODIS pixel at 1-km spatial resolution may contain fractions of different land cover types (Tian et al., 2002) that combine to form spectral reflectance of the pixel (Peddle et al., 1999) which affects the derivation of MODIS LAI. Other factors include temporal compositing of MODIS LAI and understory vegetation that could explain the discrepancy between MODIS LAI and *in situ* LAI (Ahl et al., 2006).

Though many studies have aimed to develop techniques to quantify LAI, most of this work has been conducted for crops (Demarez et al., 2008), temperate forests (Behera et al., 2010; Gower and Norman, 1991; Macfarlane et al., 2007; Sonnentag et al., 2007; Spanner et al., 1990) and boreal forests (Chen et al., 1997; Deblonde et al., 1994). For example, Demarez et al. (2008) estimated LAI of

crops with hemispherical photographs in France. Gower and Norman (1991), Behera et al. (2010) used LAI-2000 Plant Canopy Analyzer to estimate LAI in temperate forests. Sonnentag et al. (2007) applied both LAI-2000 and a destructive sampling method to measure LAI in a temperate shrub canopy in Canada. Macfarlane et al. (2007) conducted LAI estimation with hemispherical photography in a temperate forest in western Australia. Spanner et al. (1990) applied remote sensing techniques in estimating LAI in a temperate forest. As to studies in boreal forests, Barr et al. (2004) measured LAI with LAI-2000 in a boreal forest in Canada. Deblonde et al. (1994) conducted an experiment for LAI measurement in pine stands; Chen et al. has been observing LAI in boreal forests using optical and remotely sensed methods since 1990s.

Only a few estimations have been made for tropical forests in general (Asner et al., 2003). Kalacska et al. (2005) used both an optical method and litterfall data to estimate seasonal LAI in different successional stage in a tropical dry forest in Costa Rica. Maass et al. (1995) also used both methods to assess LAI for a three-year period in a tropical dry forest in west Mexico while Asner et al. (2003) synthesized LAI measurements from more than 1000 published estimates in 15 biomes including arid, temperate, tropical and boreal ecosystems.

The main objectives of this study were to estimate seasonal changes in LAI in a tropical dry forest in Mexico, evaluate the impacts that ecosystem structure and composition have on the seasonal changes by comparing LAI values obtained

in different stages of succession of the tropical dry forests, and evaluate the ability of the current MODIS algorithm to estimate LAI for tropical dry forests.

2. Methods

2.1. Plot Design

A total of 9 plots representing three successional stages (three plots per successional stage) were selected in this study area (Figure 2-1). The forest plots were characterized as early (3-5 years old), intermediate (8-12 years old), and late (mature forests) stages. Table 2-1 presents the main characteristics of each of the selected plots. Tejon 1 and Tejon 2, two sites characterized as old growth, were the only two located inside the Chamela Biological Station.

Ripley's K function was used to test the random spatial distribution for the selected 9 sites at different scales. Our results indicated that all the 9 sites were randomly distributed at 100 simulated scales within the 99.9% confidence intervals.

Three 30m × 60m plots were set up for each successional stage. The plot size was the same as that used by Kalacska et al. (2005) in the same region, and was designed to allow for comparison with her work. A grid sampling design was used to collect woody area index. Measurements of plant area index were conducted

spatially using a triangular offset-grid sampling scheme developed by Kalacska et al. (2005) to be used specifically for the optical instrument LICOR-2000.

2.2. Field Data Collection and Analysis

From a strict phenological point of view June marks the dry season and the majority of canopies are leafless, July represents the greening season and August is considered the season with full foliage when most of the precipitation falls in the region (Figure 2-2).

Woody Area Index (WAI) information was acquired using a Nikon CoolPix 995 camera (Chen et al., 1991) during June 2005 when it was the dry season. Deciduousness was 100% during the acquisition of the hemispherical camera data. A grid sampling method (Figure 2-3-a) was designed for WAI acquisition with a fisheye lens which captures a hemispherical view of the canopy. WAI was extracted from color hemispherical photos by calculating the gap fraction using the software Gap Light Analyzer 2.0.

Plant Area Index (PAI) measurements were conducted using a LAI-2000 Canopy Analyser (Gower and Norman, 1991) between the months of July and August in 2005. Measurements were carried out under diffuse light conditions, either at twilight or under cloudy skies to reduce the radiation scattered by the foliage, which overestimates the below canopy readings resulting in underestimates of LAI. A 45° view cap was used to eliminate the influence of the

operator from the field of view. Diffuse radiation was measured below the canopy at different measuring points per successional stage (Figure 2-3, b through d). Readings above the canopy were also acquired to calculate PAI on canopy gaps close to each one of the plots. Measurements with the LAI-2000 were made in July when the growing season started and in August when the leaves were fully developed. PAI was estimated by the following equation (Jonckheere et al., 2004):

$$L = -2 \sum_i \ln[T_i] \cos \theta_i W_i$$

where L is PAI, i is 1-5 representing the five distinct angular bands of the fisheye light sensor, T is the light transmission, θ is the zenith angle, and W_i are the weighting factors, which are 0.034, 0.104, 0.160, 0.218 and 0.484 respectively (Jonckheere et al., 2004). When a canopy is clumped, a clumping factor Ω resulting from the nonrandom distribution of foliage is considered (Leblanc and Chen, 2001; Nilson, 1971; Sánchez-Azofeifa et al., 2009). As Ω is generally unknown, Chen et al. (1991) introduced the effective PAI (L_e), which is the PAI obtained from optical methods:

$$L_e = \Omega L$$

Ordinary Kriging (Luna et al., 2006) was applied to spatially interpolate effective PAI and WAI values. This application was conducted in the software ArcGIS 9.0. Continuous surfaces of PAI or WAI of the plots were created. By subtracting WAI from PAI, the effective LAI was then obtained.

Normality of the data was tested using the Kolmogorov-Smirnov test (Lilliefors, 1967). Paired t-test was applied to find if difference existed between: (1) LAI measured in July and in August for each plot; (2) LAI in July and in August for each successional stage; and (3) LAI obtained from all the plots of the three successional stages in July and in August. The one-way ANOVA and independent t-test were carried out to compare WAI/PAI/LAI between the three successional stages.

The Morisita–Horn index that takes into account the differences in total basal area per species among sites was calculated to examine the differences in species composition which could affect LAI values across sites. The Morisita–Horn index ranges between 0 and 1, where 0 means no similarity and 1 means total similarity between each pair of sites.

2.3. MODIS Data Extraction and Analysis

Moderate Resolution Imaging Spectroradiometer (MODIS) provides the 8-day composite LAI product at 1-km spatial resolution. MODIS LAI was derived from MODIS spectral reflectance through a three-dimensional radiative transfer model (main algorithm) which provides good quality LAI product (Tian et al., 2000). If the main algorithm fails, a backup algorithm is applied to derive LAI with relatively poor quality based on the relation between the normalized difference vegetation index (NDVI) and LAI (Aragão et al., 2005). To obtain MODIS LAI values for comparison with ground LAI measurements, MODIS LAI

images corresponding to the locations and dates of ground measurements were selected. LAI values were extracted from the 9 pixels where the 9 plots were located and compared to ground LAI values.

3. Results

3.1. Species Composition

Results showed that on average, similarity in species composition was much higher within late stage (Morisita–Horn index = 0.69) and moderate within early stage (Morisita–Horn index = 0.45), while within intermediate stage, the Morisita–Horn index indicated very low similarity estimates (0.10) (Table 2-2). Species composition greatly differed between each successional stage, with the Morisita–Horn index between 0.09 and 0.19 (Table 2-2). The largest compositional difference was found between intermediate and early stage (0.09) (Table 2-2).

In the early stage, the three sites were moderately similar in species composition with Morisita–Horn index ranging between 0.35 and 0.64 (Table 2-3). Similarity was very low in the intermediate stage with Morisita–Horn index between 0.04 and 0.17 (Table 2-4). Caiman 8-12 and Ranchitos 8-12 were found to be most different in composition within the intermediate stage (0.04) (Table 2-4). The three sites in the late stage showed compositional similarity (the Morisita–Horn index > 0.5) (Table 2-5), with the highest Morisita–Horn index value of

0.85 between Tejon 1 and Tejon 2, the two sites inside the Chamela Biological Station (Table 2-5).

3.2. Estimation of Wood Area Index

WAI was significantly different between the three successional stages ($F = 48$, $p < 0.0001$). Through the comparison, the late stage was found to have the largest amount of woody material followed by the intermediate stage and then the early stage (Figure 2-4). WAI of the late stage was higher than that of the intermediate stage ($p < 0.1$), and the early stage ($p < 0.0001$). Also, WAI was higher in the intermediate stage compared to the early stage ($p < 0.0001$).

3.3. Estimation of Plant Area Index

The comparison of effective PAI values across successional stages also indicated that significant difference existed both in July ($F = 37$, $p < 0.0001$) and in August ($F = 58$, $p < 0.0001$). However, the highest effective PAI values were observed in the intermediate stage in July (Figure 2-5-a) and in August (Figure 2-5-b). PAI of the intermediate stage was significantly higher than that of the early stage and late stage in both months ($p < 0.0001$). PAI of the late stage was found higher than that of the early stage in July ($p < 0.001$) and in August ($p < 0.01$).

In each successional stage, PAI varied between the three plots (Figure 2-6). For the early stage, PAI of Caiman 3-5 was higher than PAI of Santa Cruz 3-5,

and than that of Ranchitos 3-5. For the intermediate stage, Caiman 8-12 had higher PAI than Santa Cruz 8-12 and than Ranchitos 8-12. In the late stage, Gargollo had higher PAI than the two plots inside the Chamela Biological Station, between which PAI of Tejon 2 was higher.

3.4. Estimation of Leaf Area Index and Seasonality

Effective LAI was found to have a similar pattern to PAI both at the stage level and the plot level (Figure 2-7 and Figure 2-8). A significant difference was observed between successional stages in July ($F = 19, p < 0.0001$) and in August ($F = 34, p < 0.0001$). In July, the intermediate stage had a higher LAI value than the late stage ($p < 0.001$) and the early stage ($p < 0.0001$). In August, the LAI value of the intermediate stage was significantly greater than the LAI value of the late stage and than that of the early stage (both p values < 0.0001).

At the plot level, the highest LAI values were observed in Caiman 3-5 of the early stage, Caiman 8-12 of the intermediate stage and Gargollo of the late stage respectively, when compared to the other two plots within the successional stage (Figure 2-8; Table 2-6). For the early stage, LAI values were ranked in the order of Caiman 3-5 > Santa Cruz 3-5 > Ranchitos 3-5; for the intermediate stage, the order was Caiman 8-12 > Santa Cruz 8-12 > Ranchitos 8-12; for the late stage, LAI was ranked as Gargollo > Tejon 2 > Tejon 1. Since both the 9 LAI values in July and the 9 values in August (Table 2-6) are not normally distributed ($p < 0.05$), a Spearman Rank Order Correlation was applied to examine the correlation

between LAI values and elevation of the 9 plots. The LAI values were found to be inversely correlated to elevation of the 9 plots with a correlation coefficient of -0.767 ($p < 0.05$) in July and -0.667 ($p < 0.05$) in August. Segregating LAI by successional stages makes the linear relation between these two variables more significant with R^2 ranging from 0.78 to near 1 (Figure 2-9).

One-way ANOVA was applied to compare LAI of the three plots in each successional stage in July and August. A significant difference was found between plots in the early and intermediate stages ($p < 0.0001$). But the difference between plots in the late stage was not significant ($p = 0.28$) because there was not much difference between the altitude of the two plots inside the Chamela Biological Station – 71m for Tejon1 and 78m for Tejon2 (Table 2-1).

Seasonal LAI measurements showed an increase in LAI values from July to August for the 9 plots (Table 2-6; Figure 2-10). Results of the t-test proved that a significant increase existed in the LAI values from July to August for most of the plots ($p < 0.05$), except for the intermediate plot Caiman 8-12 (increased from 3.51 to 3.64) and the late plot Tejon 2 (increased from 1.13 to 1.22). Also, a significant increase in the LAI values from July to August was found for the early stage (all measurements of the 3 plots, $p < 0.0001$), the intermediate stage ($p < 0.0001$) and the late stage ($p < 0.001$), and for all the measurements taken from the 9 plots ($p < 0.0001$).

3.5. MODIS LAI

MODIS LAI pixel values were extracted and compared with *in situ* LAI (Table 2-7). Generally, both in July and August, MODIS LAI values were higher than field measurements except for two sites – Santa Cruz 8-12 and Gargollo. The discrepancy in August is bigger, which ranged between -3.48 and 3.13, while in July it ranged between -0.55 and 1.92. A linear relationship with R^2 of 0.55 was found between MODIS and *in situ* LAI of July (Figure 2-11-a). But the relationship in August was very poor with $R^2 < 0.1$ (Figure 2-11-b).

4. Discussion

The results of this study indicated that in the Chamela-Cuixmala Biosphere Reserve, the intermediate stage of the tropical dry forest had the highest effective PAI and effective LAI values among the three successional stages followed by the late stage and then the early stage. A comparison of effective LAI between successional stages in this study is consistent with results presented by Kalacska et al. (2005), who found the highest effective LAI in the intermediate stage of a tropical dry forest during the wet season (September) in Santa Rosa, Costa Rica.

The difference in effective LAI is expected because the forest structure and species composition are different across successional stages (Table 2-1). By using the Morisita–Horn index, differences in species composition were found between successional stages (Table 2-2). The largest compositional difference was found between intermediate and early stage (0.09) (Table 2-2), where the greatest difference in LAI values at the stage level was found as well (Figure 2-7).

Another explanation of the difference in LAI between successional stages could be the difference in stem density. Reed et al. (1999) found a positive relation between LAI and sapling density. According to the census of our 9 plots, the intermediate stage has the largest number of stems > 1cm (2812 stems in total), followed by the late stage (2480 stems in total), and then the early stage (1848 stems in total). Especially in the early stage, there were many gaps in the canopy.

Species composition varied between sites within each successional stage (Table 2-3, Table 2-4, Table 2-5) and it showed an impact on LAI. Similarity in species composition was found very low in the intermediate stage. Caiman 8-12 and Ranchitos 8-12, which had the highest and lowest LAI in the intermediate stage (Table 2-6, Figure 2-8), were found to be most different in species composition within the stage with a Morisita–Horn index of 0.04 (Table 2-4). The three sites in the late stage showed compositional similarity between each other (the Morisita–Horn index > 0.5). The highest Morisita–Horn index value was 0.85 between Tejon 1 and Tejon 2 (Table 2-5). *Apoplanesia paniculata Presl.* was the dominant species of both sites. LAI values of the two sites were found similar as well (Table 2-6). The comparison within each successional stage indicated that, Caiman 3-5 in the early stage, Caiman 8-12 in the intermediate stage, and Gargollo in the late stage had higher effective LAI values. Of the three plots, both Caiman 3-5 and Gargollo had *Piptadenia constricta (Micheli) Macbr.* as dominant species.

The different altitude of the plots was found in this study to be inversely related to LAI in each stage ($p < 0.05$). Murphy and Lugo (1986) found that leaf size decreased with the increase in altitude for tropical dry forests, which could be one of the reasons for lower LAI found in the plots at higher altitude.

Significant increase in LAI were observed from July to August at the plot level – LAI measured within most plots, at the stage level – LAI measured within each successional stage and at the landscape level – LAI obtained from all the plots of three successional stages. Seasonal changes of LAI in the deciduous tropical dry forests are driven by soil moisture that is related to precipitation (Maass et al., 1995; Murphy and Lugo, 1986). Precipitation is strongly seasonal in the Chamela-Cuixmala Biosphere reserve (Bullock, 1986; Maass et al., 1995; Segura et al., 2003). Our records indicated that precipitation measured at the Chamela Biological Station increased from 69.60 mm in July to 127.76 mm in August, which explains the seasonal increase in LAI from July to August found in this study.

The error of the LAI in this study would come from the errors produced in PAI and WAI measurements. The first source of error is clumping. It is a major problem that all optical instruments have since they assume that the leaves are randomly distributed in space (Dufrene and Breda, 1995). When clumping occurred, both PAI and WAI would be underestimated. Until now, clumping problem can't be satisfactorily solved (Jonckheere et al., 2004). Secondly, the WAI measured in the dry season in fact included the contribution of leaves of a

few evergreens inside the plots. This part was subtracted from PAI, leading to an underestimation of LAI. Thirdly, when taking PAI measurements in the growing season, it was difficult to obtain the diffuse radiation above the canopy in the forests. Instead, most measurements were taken in open area, which would be equal or smaller than the above canopy readings affected by the surrounding trees and thus caused the underestimation of PAI. Finally, although LAI-2000 minimizes the multiple scattering inside the canopy by collecting diffuse sky radiation < 490 nm where the foliage reflects or transmits little radiation, foliage is not perfectly “black” and scattering still occurred, which caused higher below canopy readings, and in turn, lower PAI values.

MODIS LAI was found to be higher than the field measurements in most of the cases in this study. Douglas et al. (2006) presented similar results that MODIS overestimated LAI during the onset of greenness and maturity. Understory vegetation could be one of the reasons explaining the discrepancy between MODIS LAI and *in situ* LAI (Ahl et al., 2006). Greatest discrepancy was found in the early succession where canopies were more open with more gaps which enhanced understory development (Dupuy and Chazdon, 2008).

Other factors leading to the difference between MODIS LAI and *in situ* LAI include the relatively coarse spatial resolution and temporal resolution of MODIS LAI (Ahl et al., 2006). One MODIS pixel at 1-km spatial resolution may contain several land cover types (Tian et al., 2002). All land cover types in a pixel contribute to the spectral reflectance (Peddle et al., 1999) which is used to derive

MODIS LAI (Tian et al., 2000). Land cover misclassification in this area (Table 2-7) reflects that the spectral reflectance of a MODIS pixel is affected by fractions of land cover types. Most of the pixels where the 9 plots were located were misclassified as savannas. Two of them were classified as mixed forests. Only the pixel where Tejon 2 was located was classified as deciduous broadleaf forests, where better agreement was found between MODIS LAI and field LAI. Besides, the 8-day temporal resolution of MODIS LAI may not be sufficient to detect phenological changes during the onset of greenness. Ahl et al. (2006) suggested leaf expansion could be better captured with a temporal resolution < 1 week.

The overestimation of LAI can also be partially attributed to the MODIS LAI derivation by the backup algorithm and the presence of clouds or aerosols. Among the 18 MODIS LAI values, 4 of them were retrieved using backup algorithm. The remaining 14 values were retrieved by the main algorithm with the presence of clouds. In this condition, which is difficult to avoid during the rainy season, the data quality is satisfactory but not the best.

5. Conclusion

By segregating the tropical dry forests into three successional stages, we found that not only is the species composition different between stages of succession, but LAI measurements in the field are also significantly different across the stages. A seasonal increase in LAI was captured by the ground measurements made from the dry leafless season to the rainy season. The results

not only contribute to a general understanding of the tropical dry forests in the Chamela-Cuixmala Biosphere Reserve and its stages of succession, but also may have a broad application in other tropical dry forests and other forest ecosystems.

The examination of the relation between MODIS LAI and *in situ* LAI in this study did not yield satisfactory results. The underestimates of *in situ* LAI by optical instruments and the uncertainty of MODIS LAI data (Foody and Atkinson, 2003) are the two main factors leading to the discrepancy between MODIS and *in situ* LAI. It is suggested in this study that MODIS LAI needs further validation with field measurements, which is essential to large scale applications. Deriving LAI from high resolution remotely sensed imagery and using it to link MODIS and ground LAI could be an option in further studies.

Since LAI plays an important role in calculating carbon, water and energy exchanges between terrestrial environments and the atmosphere (Sellers et al., 1997) and thus contributes to the global climate studies (Myneni et al., 1997), the data and results of this study are important not only in characterizing the tropical dry forests but also in developing conservation policies and estimating environmental services payments for the Chamela-Cuixmala Biosphere Reserve, which is also applicable in other forest ecosystems (Kalacska et al., 2008).

Literature Cited

Ahl, D.E., Gower, S.T., Burrows, S.N., Shabanov, N.V., Myneni, R.B., and Knyazikhin, Y. (2006). Monitoring Spring Canopy Phenology of a Deciduous Broadleaf Forest using MODIS. *Remote Sensing of Environment*, 104, 88-95.

Aragão, L. E. O. C., Shimabukuro, Y. E., Espírito-Santo, F. D. B., and Williams, M. (2005). Spatial validation of the collection 4 MODIS LAI product in eastern amazonia. *IEEE Transactions on Geoscience and Remote Sensing*, 43(11), 2526-2534.

Asner, G. P., Scurlock, J. M. O., and Hicke, J. A. (2003). Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Global Ecology and Biogeography*, 12, 191-205.

Barr, A. G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K., and Nesic, Z. (2004). Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agricultural and Forest Meteorology*, 126(3-4), 237-255.

Behera, S. K., Srivastava, P., Pathre, U. V., and Tuli, R. (2010). An indirect method of estimating leaf area index in *Jatropha curcas* L. using LAI-2000 Plant Canopy Analyzer. *Agricultural and Forest Meteorology*, 150(2), 307-311.

Borchert, R. (1994). Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, 75, 1437-1449.

Brooks, S., Cordell, S., and Perry, L. (2009). Broadcast Seeding as a Potential Tool to Reestablish Native Species in Degraded Dry Forest Ecosystems in Hawaii. *Ecological Restoration*, 27(3), 300-305.

Brown, S., and Lugo, A. E. (1990). Tropical secondary forests. *Journal of Tropical Ecology*, 6, 1-32.

- Bullock S.H. (1986). Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. *Meteorology and Atmospheric Physics*, 36, 297-316.
- Bullock, S. H. and Solis-Magallanes, J. A. (1990). Phenology of Canopy Trees of a Tropical Deciduous Forest in Mexico. *Biotropica*, 22, 22-35.
- Burnham, R. J. (1997). Stand characteristics and leaf litter composition of a dry forest hectare in Santa Rosa National Park, Costa Rica. *Biotropica*, 29, 387-395.
- Ceballos, G., and García, A. (1995). Conserving Neotropical Biodiversity: The Role of Dry Forests in Western Mexico. *Conservation Biology*, 9, 1349-1356.
- Chen, J. M., Black, T. A., and Adams, R. S. (1991). Evaluation of hemispherical photography for determining plant area index and geometry of a forest stand. *Agricultural and Forest Meteorology*, 56, 129-143.
- Chen, J. M. and Cihlar, J. (1996). Retrieving leaf area index of boreal conifer forests using Landsat TM images. *Remote sensing of environment*, 55, 153-162.
- Chen, J. M., Blanken, P. D., Black, T. A., Guilbeault, M., and Chen, S. (1997). Radiation regime and canopy architecture in a boreal aspen forest. *Agricultural and Forest Meteorology*, 86, 107-125.
- Chen, J. M., Pavlic, G., Brown, L., Cihlar, J., Leblanc, S. G., and White, H. P. et al. (2002). Derivation and validation of canada-wide coarse-resolution leaf area index maps using high-resolution satellite imagery and ground measurements. *Remote Sensing of Environment*, 80(1), 165-184.
- Clark, D.B., Olivas, P.C., Oberbauer, S.F., Clark, D.A., and Ryan, M.G. (2008). First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity. *Ecology Letters*, 11(2), 163-172.
- Cohen, W. B., Maiersperger, T. K., Yang, Z., Gower, S. T., Turner, D. P., Ritts, W. D., Berterretche, M., and Running, S. W. (2003). Comparisons of land cover and LAI estimates derived from ETM+ and MODIS for four sites in North

America: a quality assessment of 2000/2001 provisional MODIS products. *Remote Sensing of Environment*, 88 (3), 233-255.

Deblonde, G., Penner, M., and Royer, A. (1994). Measuring Leaf Area Index with the Li-Cor LAI-2000 in Pine Stands. *Ecology*, 75(5), 1507-1511.

Demarez, V., Duthoit, S., Baret, F., Weiss, M., and Dedieu, G. (2008). Estimation of leaf area and clumping indexes of crops with hemispherical photographs. *Agricultural and Forest Meteorology*, 148(4), 644-655.

Doley, D. (1981). Tropical and subtropical forests and woodlands. *Water Deficits and Plant Growth*, Vol. VI (Ed. by T. T. Kozlowski), 209-323. Academic Press, New York.

Douglas E. A., Stith T. G., Sean N. B., Nikolay V. S., Ranga B. M. and Yuri K. (2006). Monitoring spring canopy phenology of a deciduous broadleaf forest using MODIS. *Remote Sensing of Environment*, 104, 88-95.

Dufrene, E., and Breda, N. (1995). Estimation of deciduous forest leaf area index using direct and indirect methods. *Oecologia*, 104, 156-162.

Dupuy, J. M. and Chazdon, R. L. (2008). Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. *Forest Ecology and Management*, 255(11), 3716-3725.

Eklundh, L., Hall, K., Eriksson, H., Ardo, J., and Pilesjo, P. (2003). Investigating the use of Landsat thematic mapper data for estimation of forest leaf area index in southern Sweden. *Canadian Journal of Remote Sensing*, 29, 349-362.

Foody, G. M. and Atkinson, P. M. (2003). *Uncertainty in Remote Sensing and GIS*. Wiley.

Frazer, G. W., Trofymow, J. A., and Lertzman, K. P. (2000). Canopy openness and leaf area in chronosequences of coastal temperate rainforests. *Canadian Journal of Forest Research*, 30, 239-256.

Fensholt, R., Sandholt, I., and Rasmussen, M. S. (2004). Evaluation of MODIS LAI, fAPAR and the relation between fAPAR and NDVI in a semi-arid environment using in situ measurements. *Remote Sensing of Environment*, 91, 490-507.

Gerwing, J. J., and Farias, D. L. (2000). Integrating Liana Abundance and Forest Stature into an Estimate of Total Aboveground Biomass for an Eastern Amazonian Forest. *Journal of Tropical Ecology*, 16(3), 327-335.

Gower, S. T., and Norman, J. M. (1991). Rapid Estimation of Leaf Area Index in Conifer and Broad-Leaf Plantations. *Ecology*, 72(5), 1896-1900.

Huemmrich, K. F., Privette, J. L., Mukelabai, M., Myneni, R. B. and Knyazikhin, Y. (2005). Time-series validation of MODIS land biophysical products in a Kalahari woodland, Africa. *International Journal of Remote Sensing*, 26(19), 4381-4398.

Janzen, D. H. (1986). Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson, E.O. (Ed.), *Biodiversity* (pp. 130-137). Washington: National Academy Press.

Janzen, D. H. (1988). Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson, E.O. (Ed.), *Biodiversity* (pp. 130-137). Washington: National Academy Press.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., and Baret, F. (2004). Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology*, 121, 19-35.

Kalacska, M., Sánchez-Azofeifa, G. A., Calvo-Alvarado, J. C., Quesada, M., Rivard, B., and Janzen, D. H. (2004). Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. *Forest Ecology and Management*, 200, 227-247.

Kalacska, M., Calvo-Alvarado, J. C., and Sánchez-Azofeifa, G. A. (2005). Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession. *Tree Physiology*, 25, 733-744.

Kalacska, M., Sánchez-Azofeifa, G.A., Rivard, B., Calvo-Alvarado, J.C., and Quesada, M. (2008). Baseline assessment for environmental services payments from satellite imagery: A case study from Costa Rica and Mexico. *Journal of Environmental Management*, 88(2), 348-359

Kucharik, C. J., Norman, J. M., and Gower, S. T. (1998). Measurements of branch area and adjusting leaf area index indirect measurements. *Agricultural and Forest Meteorology*, 91, 69-88.

Leblanc, S.G. and Chen, J.M. (2001). A practical scheme for correcting multiple scattering effects on optical LAI measurements. *Agricultural and Forest Meteorology*, 110, 125-139.

Lilliefors, H. W. (1967). On the Kolmogorov-Smirnov test for normality with mean and variance unknown. *Journal of the American Statistical Association*, 62, 399-402.

Longman, K. A. and Jenik, J. (1974). *Tropical Forest and its Environment*. Longman, London.

Luna, M. Y. , Morata, A., Almarza, C. and Martín, M. L. (2006). The use of GIS to evaluate and map extreme maximum and minimum temperatures in Spain. *Meteorological Applications*, 13, 385-392.

Maass, J. M., Vose, J. M., Swank, W. T., and Martinez-Yrizar, A. (1995). Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. *Forest Ecology and Management*, 74, 171-180.

Macfarlane, C., Hoffman, M., Eamus, D., Kerp, N., Higginson, S., McMurtrie, R., and Adams, M. (2007). Estimation of leaf area index in eucalypt forest using digital photography. *Agricultural and Forest Meteorology*, 143(3-4), 176-188.

Medina, E. (1995). Diversity of life forms of higher plants in Neotropical dry forests. *Seasonally Tropical Forests*. Cambridge University Press, UK.

Meroni, M., Colombo, R., and Panigada, C. (2004). Inversion of a radiative transfer model with hyperspectral observations for LAI mapping in poplar plantations. *Remote Sensing of Environment*, 92, 195-206.

Mooney, H. A., Bullock, S. H., and Medina, E. (1995). Introduction. In: Mooney, H.A., Bullock, S.H., Medina, E. (Eds.), *Seasonally Dry Tropical Forests* (pp. 1-8), Cambridge: Cambridge University Press.

Murphy, P. G., and Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, 17, 67-88.

Myneni, R.B., Ramakrishna, R., Nemani, R., and Running, S.W. (1997). Estimation of global leaf area index and absorbed par using radiative transfer models. *IEEE Transactions on Geoscience and Remote Sensing*, 35(6), 1380-1393.

Myneni, R. B., Hoffman, S., Knyazikhin, Y., Privette, J., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G. R., Lotsch, A., Friedl, M., Morisette, J. T., Votava, P., Nemani, R. R., and Running, S. W. (2002). Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sensing of Environment*, 83, 214-231.

Nilson T. (1971). A theoretical analysis of the frequency of gaps in plant stands. *Agricultural Meteorology*, 8, 25-38.

- Peddle, D. R., Hall, F. G., and Ledrew, E. F. (1999). Spectral mixture analysis and geometric-optical reflectance modeling of boreal forest biophysical structure. *Remote Sensing of Environment*, 67(3), 288-297.
- Portillo, C., and Sánchez, A. (2010). Extent and Conservation of tropical dry forests in the Americas. *Biological Conservation*, 143, 144-155.
- Putz, F. E. 1983. Liana biomass and leaf area of a 'Tierra Firme' forest in the Rio Negro basin, Venezuela. *Biotropica*, 15, 185-189.
- Quesada, M., and Stoner, K. E. (2004). Threats to the conservation of the tropical dry forest in Costa Rica. In: Frankie, G.W., Mata, A., Vinson, S.B. (Eds.), *Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest* (pp. 266-280). Berkeley, CA: University of California Press.
- Reed, R. A., Finley, M. E., Romme W. H., and Turner, M. G. (1999). Aboveground Net Primary Production and Leaf-Area Index in Early Postfire Vegetation in Yellowstone National Park. *Ecosystems*, 2(1), 88-94.
- Reich, P. B., and Borchert, R. (1984). Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology*, 72, 61-74.
- Rzedowski, J. (1991). El endemismo en la flora fanerógamica mexicana: una apreciación analítica preliminar. *Acta Botánica Mexicana*, 15, 47-64.
- Sabogal, C. (1992). Regeneration of Tropical Dry Forests in Central America, with Examples from Nicaragua. *Journal of Vegetation Science*, 3, 407-416.
- Sánchez-Azofeifa, A., Kalacska, M. E., Quesada, M., Stoner, K. E., Lobo, J. A., and Arroyo-Mora, P. (2003). Tropical Dry Climates. *Phenology: An integrative environmental science*. (pp. 121). The Netherlands: Kluwer Academic Publisher.
- Sánchez-Azofeifa, G. A., Quesada, M., Rodríguez, J. P., Nasser, J. M., Stoner, K. E., Castillo, A., Garvin, T., Zent, E. L., Calvo, J. C., Kalacska, M., Fajardo, L.,

Gamon, J., and Cuevas-Reyes, P. (2005). Research priorities for Neotropical dry forests. *Biotropica*, 37(4), 477-485.

Sánchez-Azofeifa, G. A., Kalacska, M., Espirito-Santo, M. M., Fernandes, G. W. and Schnitzer, S. (2009). Tropical dry forest succession and the contribution of lianas to Wood Area Index (WAI). *Forest Ecology and Management*, 258, 941-948.

Schimper, A. F. W. (1898). *Pflanzengeographie auf Physiologischer Grundlage*. Fischer, Jena.

Segura, G., Balvanera, P., Durán, E., and Pérez, A. (2003). Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. *Plant Ecology*, 169(2), 259-271.

Sellers, P. J., Dickinson, R. E., Randall, D. A., Betts, A. K., Hall, F. G., Berry, J. A., Collatz, G. J., Denning, A. S., Mooney, H. A., Nobre, C. A., Sato, N., Field, C. B., and Henderson-Sellers, A. (1997). Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science*, 275, 502-509.

Silver, W. L., Ostertag, R., and Lugo, A. E. (2000). The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration Ecology*, 8, 394-407.

Singh, K. P., and Kushwaha, C. P. (2005). Paradox of leaf phenology: *Shorea robusta* is a semi-evergreen species in tropical dry deciduous forests in India. *Current Science*, 88(11), 1820-1824.

Sonnentag, O., Talbot, J., Chen, J.M., and Roulet, N.T. (2007). Using direct and indirect measurements of leaf area index to characterize the shrub canopy in an ombrotrophic peatland. *Agricultural and Forest Meteorology*, 144(3-4), 200-212.

Spanner, M. A., Pierce, L. L., Peterson, D. L., and Running, S. W. (1990). Remote sensing of temperate coniferous forest leaf area index. The influence of

canopy closure, understory vegetation and background reflectance. *International Journal of Remote Sensing*, 11, 95-111.

Tian, Y., Zhang, Y., Knyazikhin, Y., Myneni, R. B., Glassy, J. M., and Dedieu, G. et al. (2000). Prototyping of MODIS LAI and FPAR algorithm with LASUR and LANDSAT data. *IEEE Transactions on Geoscience and Remote Sensing*, 38(5 II), 2387-2401.

Tian, Y., Woodcock, C. E., Wang, Y., Privette, J. L., Shabanov, N. V., and Zhou, L., et al. (2002). Multiscale analysis and validation of the MODIS LAI product I. uncertainty assessment. *Remote Sensing of Environment*, 83(3), 414-430.

Wang, Q., Tenhunen, J., Granier, A., Reichstein, M., Bouriaud, O., Nguyen, D., and Breda, N. (2004). Long-term variations in leaf area index and light extinction in a *Fagus sylvatica* stand as estimated from global radiation profiles. *Theoretical and Applied Climatology*, 79 (3-4), 225-238.

Wang, Q., Tenhunen, J., Nguyen Q. D., Reichstein, M., Otieno, D., Granier, A., and Pilegarrrd, K. (2005). Evaluation of seasonal variation of MODIS derived leaf area index at two European deciduous broadleaf forest sites. *Remote Sensing of Environment*, 96, 475-484.

Watson, D. J. (1947). Comparative physiological studies in the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Annals of botany*, 11, 41-76.

Welles J. M. (1990). Some indirect methods of estimating canopy structure, *Remote Sensing Reviews*, 5(1), 31-43.

Welles, J. M., and Cohen, W. S. (1996). Canopy structure measurement by gap fraction analysis using commercial instrumentation. *Journal of Experimental Botany*, 47, 1335-1342.

Xiao, X., Zhang, Q., Braswell, B., Urbanski, S., Boles, S., and Wofsy, S. et al. (2004). Modeling gross primary production of temperate deciduous broadleaf

forest using satellite images and climate data. *Remote Sensing of Environment*, 91(2), 256-270.

Figures and Tables



Figure 2-1. Location of 9 sampling plots (3 plots per successional stage) in the Chamela-Cuixmala Biosphere reserve, Mexico.

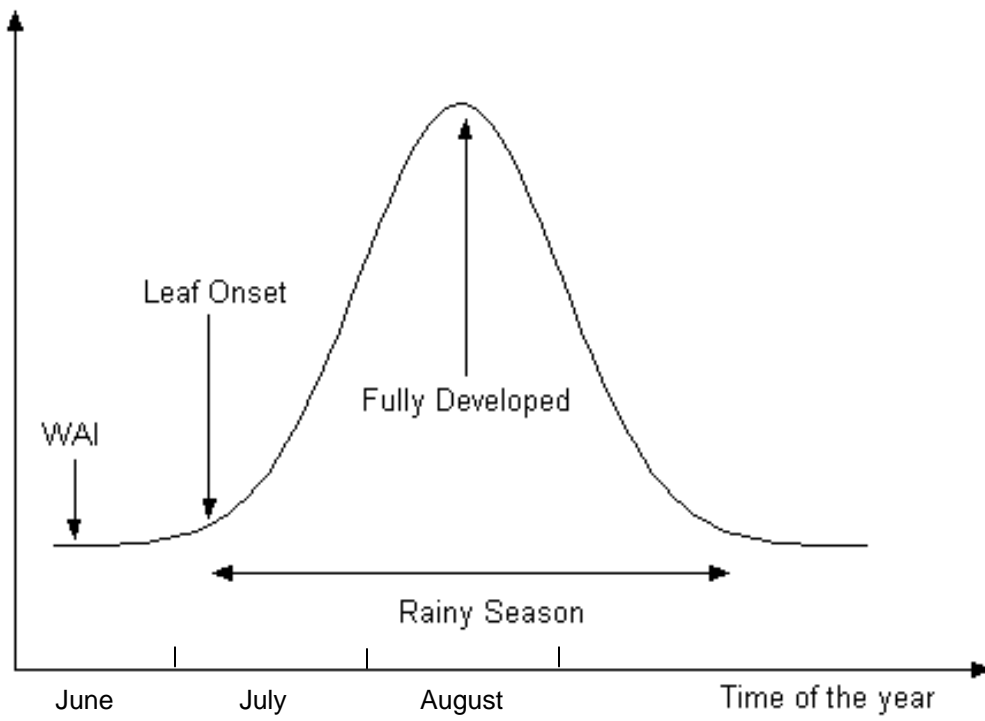


Figure 2-2. Illustration of leaves development from the dry season to the rainy season of the year.

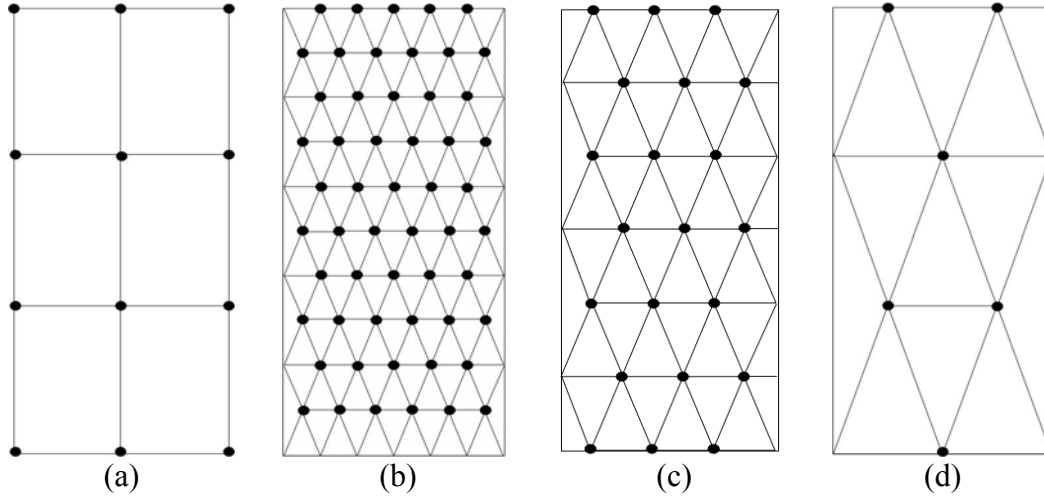


Figure 2-3. Sampling schemes for WAI and PAI collection for the $30\text{m} \times 60\text{m}$ plots. Grid sampling design for WAI collection (a); Triangular offset-grid sampling scheme based on the 45° view cap with a canopy height of (b) 6 meters, (c) 10 meters and (d) 20 meters.

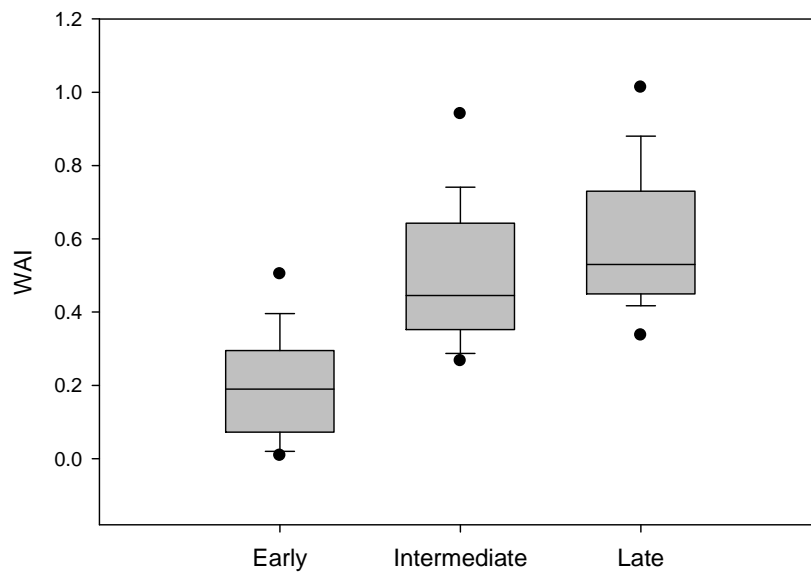


Figure 2-4. Comparison of WAI of the three successional stages. Each stage contains 36 measurements from 3 plots. Each box shows the median of WAI values of each stage, and the 25th and 75th percentiles. Black dots are outliers above the 95th and below the 5th percentiles.

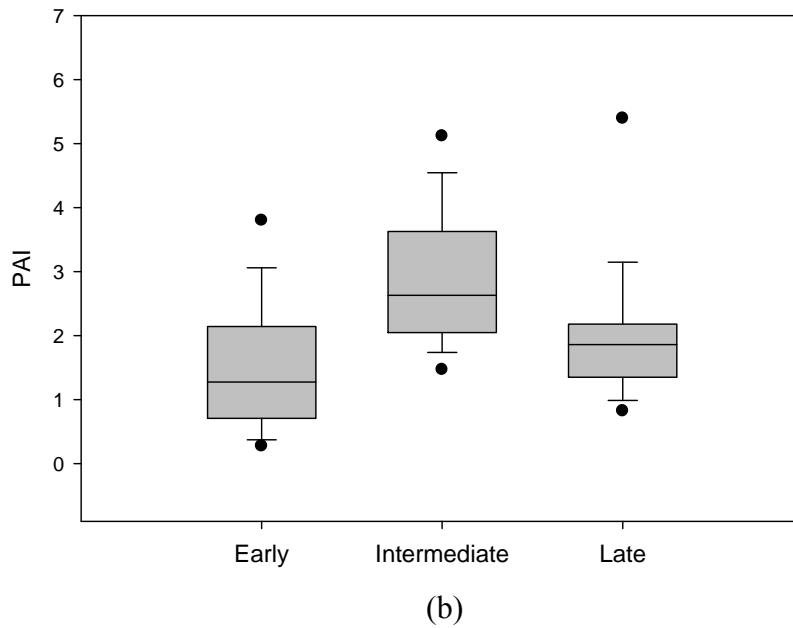
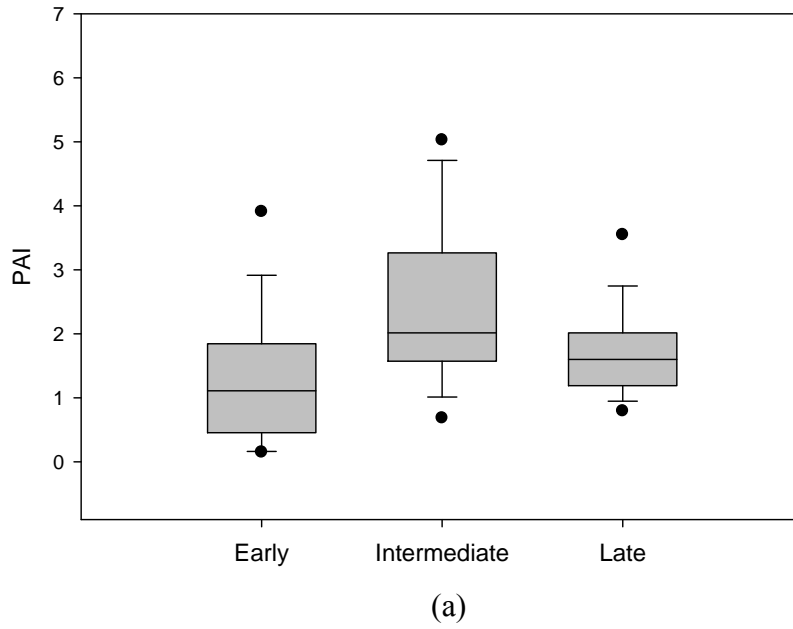


Figure 2-5. Comparison of PAI values across successional stages displayed that the intermediate stage had the highest LAI values in July (a) and in August (b) followed by the late stage and then the early stage.

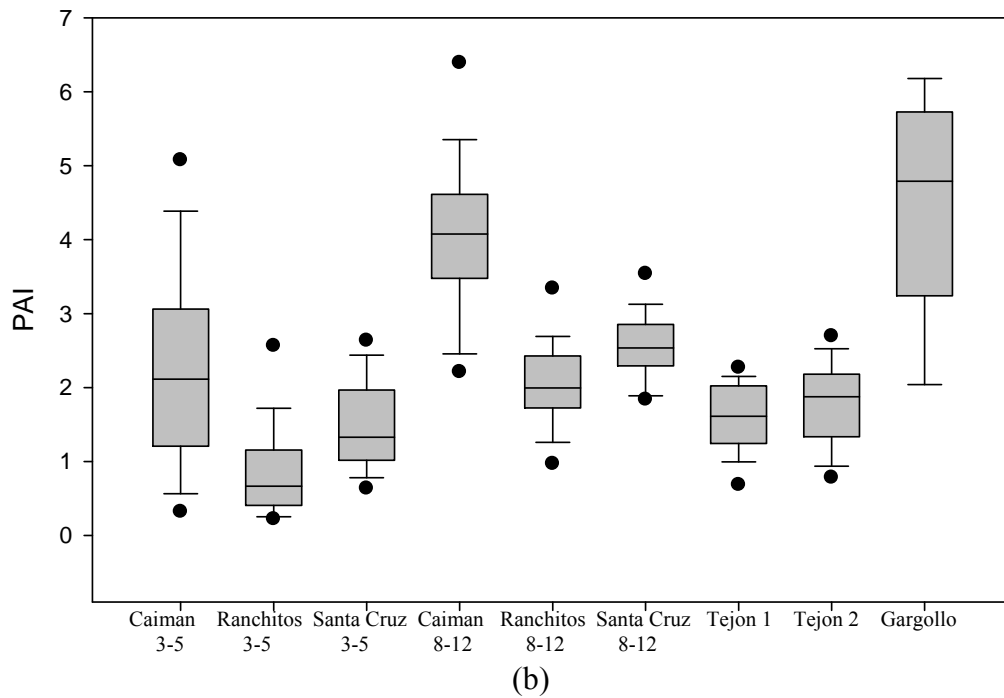
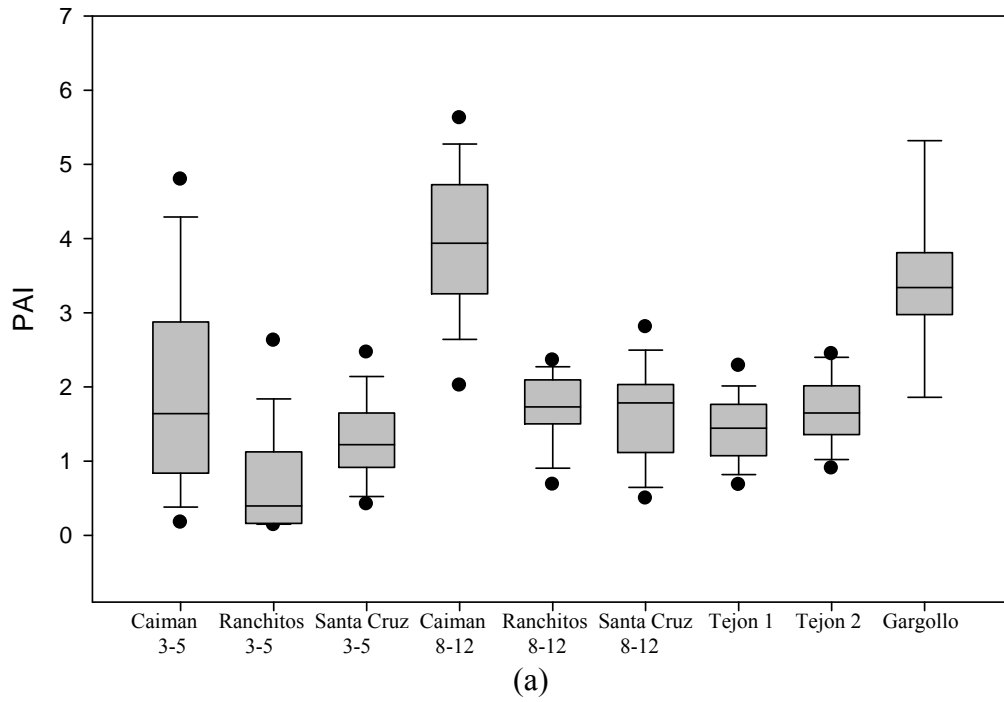
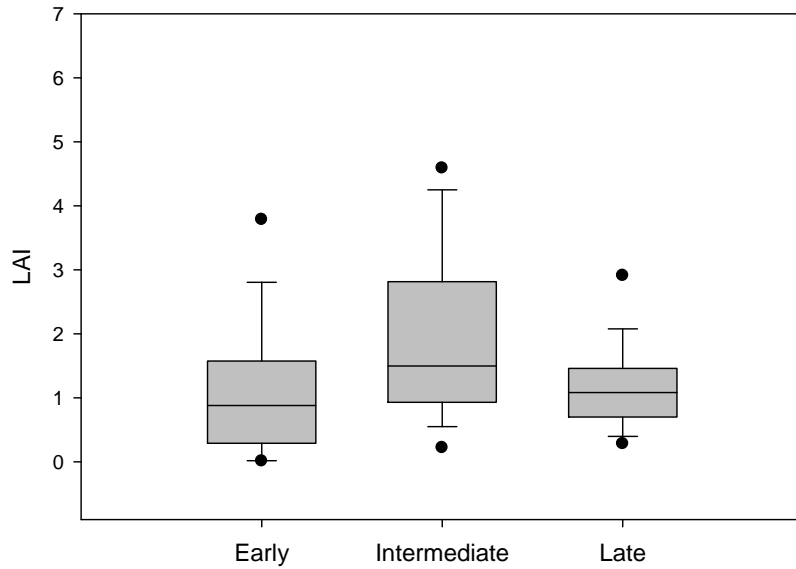
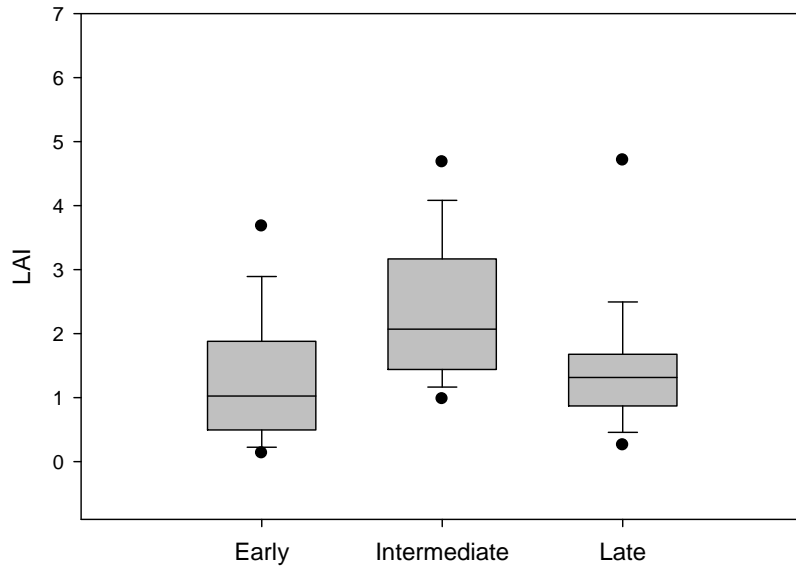


Figure 2-6. Comparison of PAI values of the 9 plots in July (a) and in August (b). Black dots are outliers above the 95th and below the 5th percentiles. Difference can be found between plots in each stage of succession.

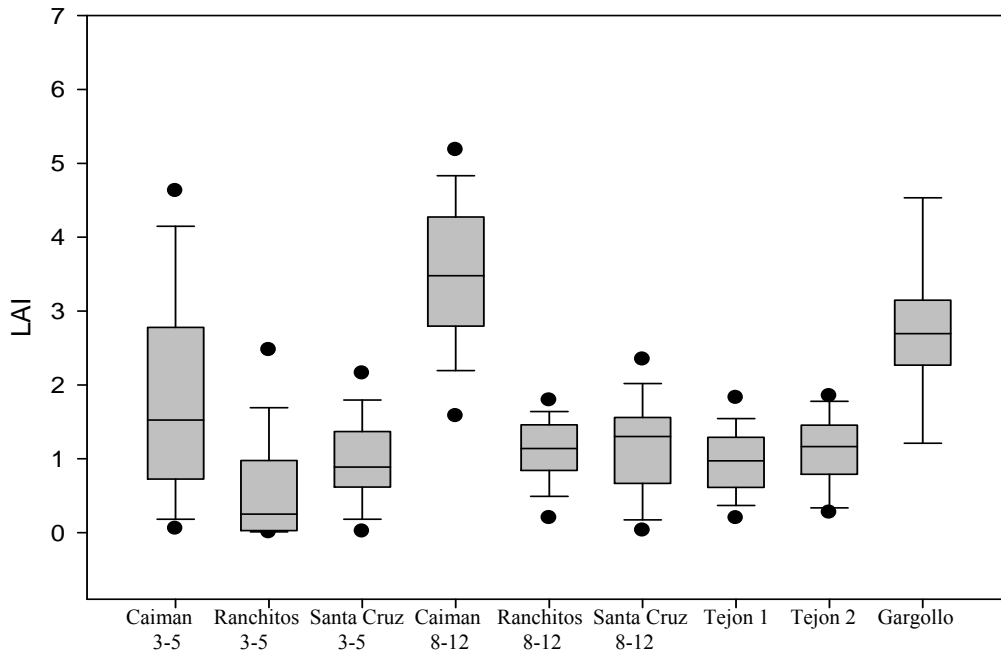


(a)

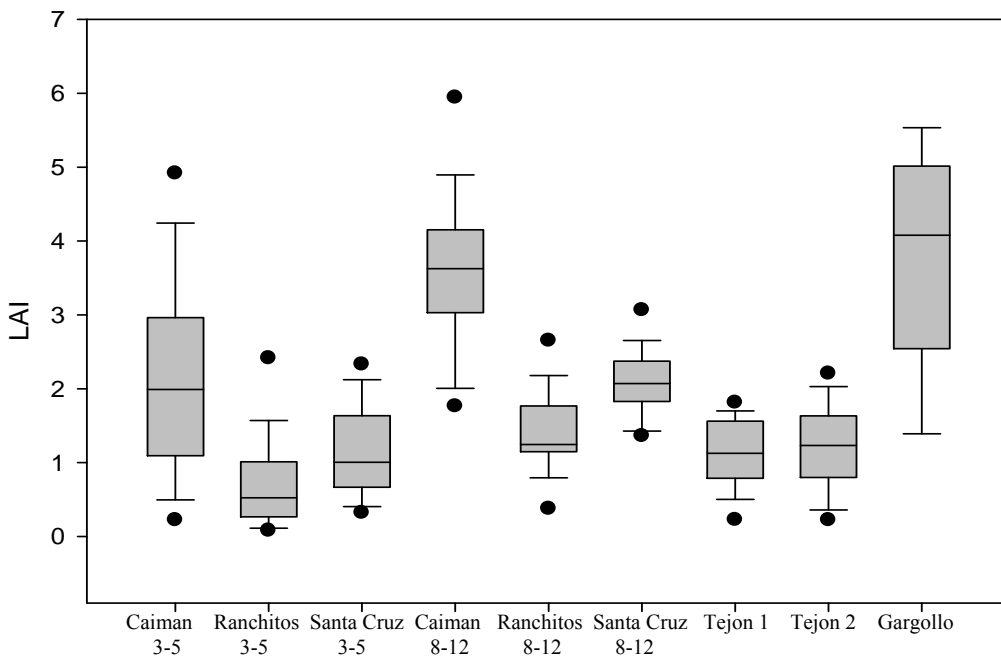


(b)

Figure 2-7. Comparison of LAI values across successional stages displayed that the intermediate stage had the highest LAI values in July (a) and in August (b) followed by the late stage and then the early stage.



(a)



(b)

Figure 2-8. Comparison of LAI values of the 9 plots in July (a) and in August (b). Black dots are outliers above the 95th and below the 5th percentiles. Difference can be found between plots in each stage of succession.

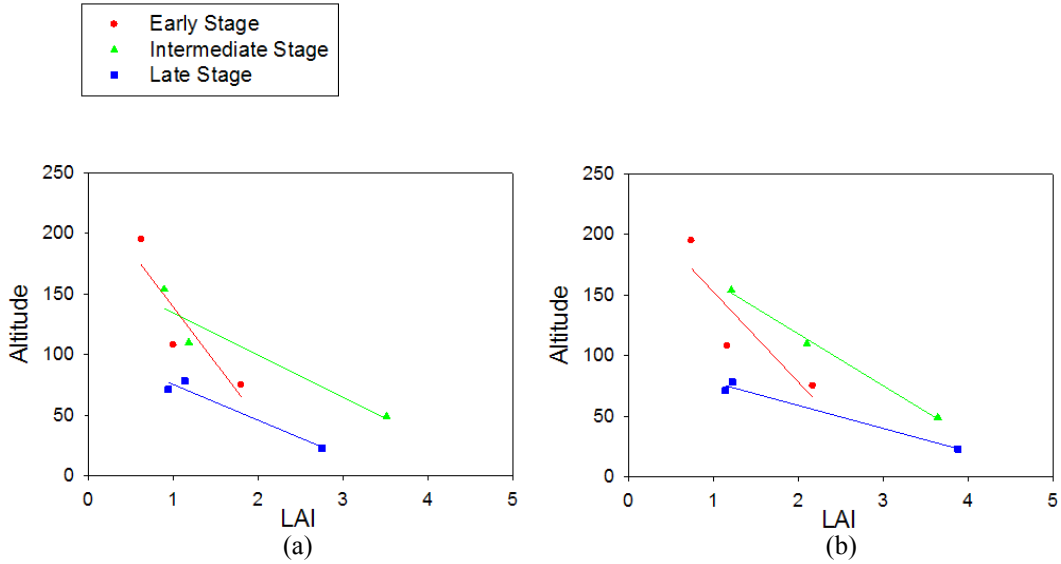


Figure 2-9. Relation between LAI and the altitude of the plots in each stage of succession. (a) In July, R^2 is 0.79, 0.9 and 0.96 for early, intermediate and late stage respectively. (b) In August, R^2 is 0.78, 1 and 0.99 for early, intermediate and late stage respectively.

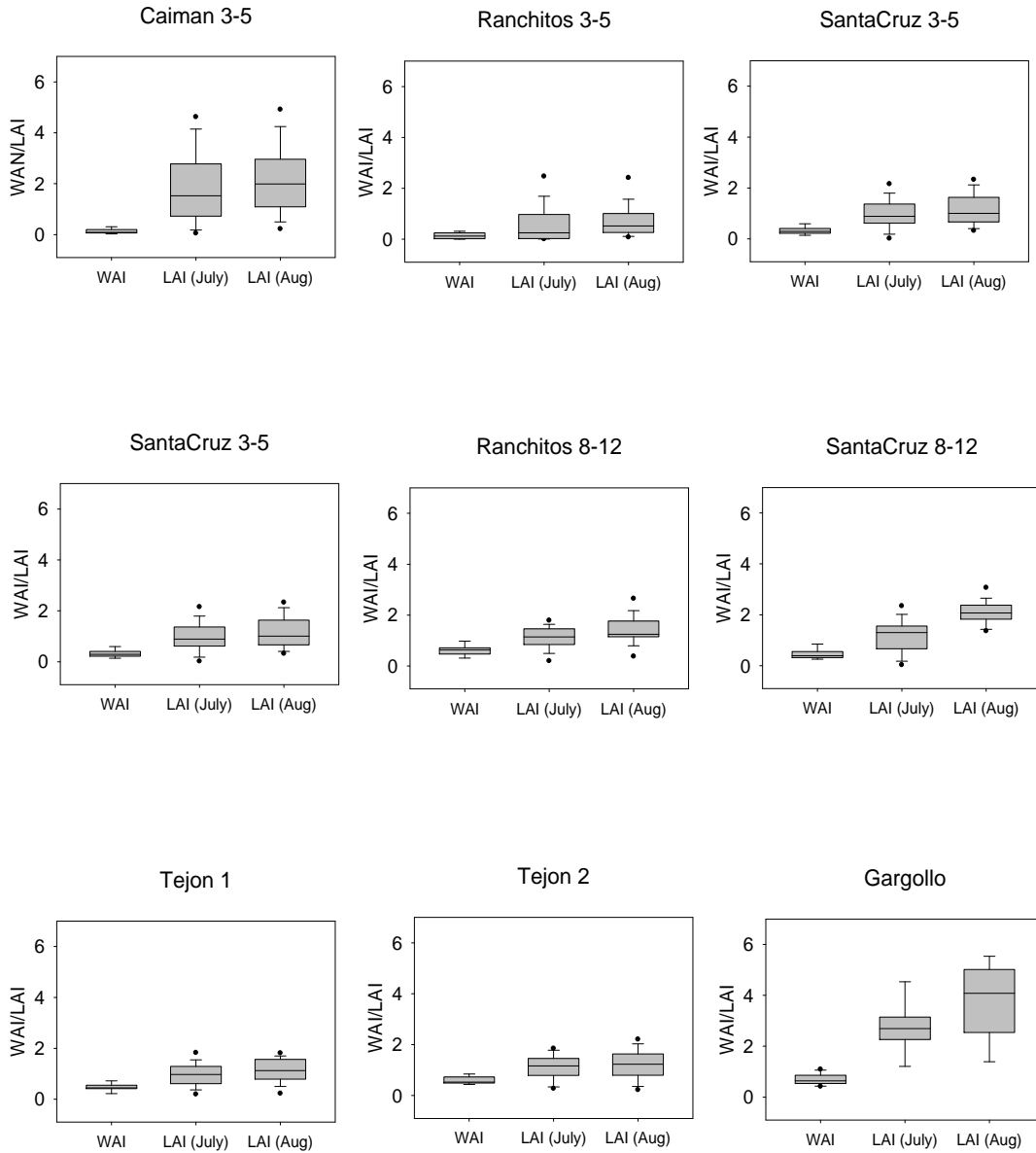


Figure 2-10. WAI in June, LAI in July and in August for the 9 plots (Early stage: Caiman 3-5, Ranchitos 3-5 and Santa Cruz 3-5; Intermediate stage: Caiman 8-12, Ranchitos 8-12 and Santa Cruz 8-12; Late stage: Tejon 1, Tejon 2 and Gargollo).

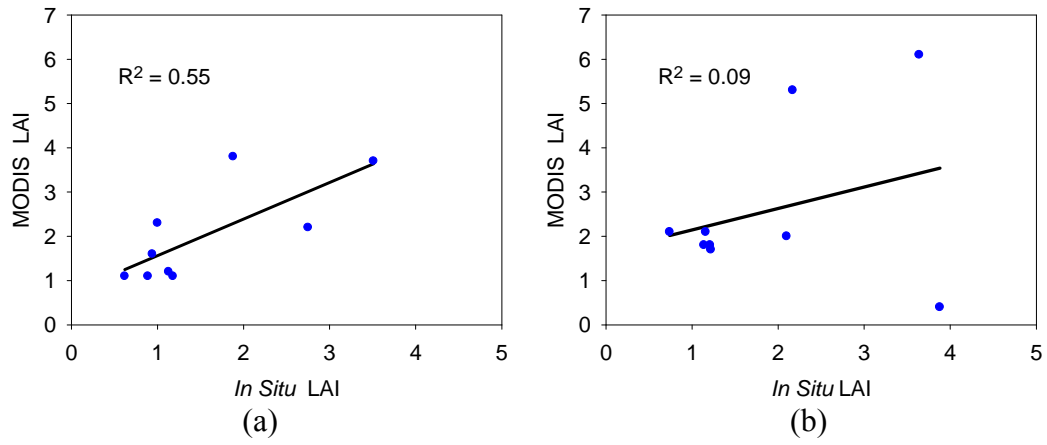


Figure 2-11. *In situ* and MODIS LAI relationship in July (a) and in August (b). The relationship in July was weak but yet with moderate $R^2=0.55$, while the relationship in August was poor with $R^2=0.09$.

Table 2-1. Main characteristics of plots

Name	Stage	Latitude Longitude	Average DBH (cm)	Average Canopy height (m)	Average Altitude (m)	Land Use History
Caiman 3-5	Early	19° 28' 40.44" N 104° 56' 5.64" W	1.91	6	75	Burned in 2001
Ranchitos 3-5	Early	19° 36' 51.12" N 105° 1' 14.88" W	1.82	6	195	Burned in 2002
Santa Cruz 3-5	Early	19° 36' 2.52" N 105° 2' 36.24" W	2.47	6	108	Burned in 2001
Caiman 8-12	Intermediate	19° 28' 3.72" N 104° 56' 13.20" W	3.29	10	49	Burned in 1997
Ranchitos 8-12	Intermediate	19° 35' 32.28" N 105° 0' 32.76" W	4.10	10	154	Burned in 1995
Santa Cruz 8-12	Intermediate	19° 35' 55.32" N 105° 2' 54.6" W	3.94	10	110	Burned in 1994
Tejon 1	Late	19° 30' 5.04" N 105° 2' 35.88" W	4.27	10	71	Undisturbed T-df
Tejon 2	Late	19° 30' 33.48" N 105° 2' 24.72" W	4.86	10	78	Undisturbed T-df
Gargollo	Late	19° 24' 18.36" N 104° 58' 57.72" W	5.01	20	23	Undisturbed T-df

Table 2-2. Average Morisita–Horn index within and between successional stages.

	Early Stage	Intermediate Stage	Late Stage
Early Stage	0.45		
Intermediate Stage	0.09	0.10	
Late Stage	0.14	0.19	0.69

Table 2-3. Morisita–Horn index between sites in the early stage.

	Caiman 3-5	Ranchitos 3-5	Santa Cruz 3-5
Caiman 3-5			
Ranchitos 3-5	0.35		
Santa Cruz 3-5	0.64	0.35	

Table 2-4. Morisita–Horn index between sites in the intermediate stage.

	Caiman 8-12	Ranchitos 8-12	Santa Cruz 8-12
Caiman 8-12			
Ranchitos 8-12	0.04		
Santa Cruz 8-12	0.10	0.17	

Table 2-5. Morisita–Horn index between sites in the late stage.

	Tejon 1	Tejon 2	Gargollo
Tejon 1			
Tejon 2	0.85		
Gargollo	0.64	0.57	

Table 2-6. WAI in June, LAI in July and August, and dominant species of the 9 plots of three successional stages

Stage of Succession	Site Name	WAI June	LAI July	LAI August	Family Name	Dominant Species	% of Dominant Species in the Plot
Early	Caiman 3-5	0.12	1.88	2.17	Leguminosae	<i>Piptadenia constricta (Micheli) Macbr.</i>	20.39%
	Ranchitos 3-5	0.14	0.62	0.74	Polygonaceae	<i>Coccoloba liebmanii Lindau</i>	27.12%
	Santa Cruz 3-5	0.32	1	1.16	Leguminosae	<i>Acacia farnesiana (L.) Willd.</i>	27.21%
Intermediate	Caiman 8-12	0.45	3.51	3.64	Euphorbiaceae	<i>Cnidoculus spinosus Lundell.</i>	27.90%
	Ranchitos 8-12	0.63	0.89	1.21	Euphorbiaceae	<i>Croton roxanae Croizat</i>	15.73%
	Santa Cruz 8-12	0.47	1.18	2.1	Leguminosae	<i>Piptadenia constricta (Micheli) Macbr.</i>	12.52%
Late	Tejon 1	0.47	0.94	1.14	Leguminosae	<i>Apoplanesia paniculata Presl.</i>	18.13%
					Euphorbiaceae	<i>Croton roxanae Croizat</i>	18.13%
	Tejon 2	0.57	1.13	1.22	Leguminosae	<i>Apoplanesia paniculata Presl.</i>	14.22%
	Gargollo	0.69	2.75	3.88	Leguminosae	<i>Piptadenia constricta (Micheli) Macbr.</i>	16.03%

Table 2-7. Comparison between *In Situ* LAI and MODIS LAI. The MODIS land cover types for the 9 sites are listed.

Stage of Succession	Site Name	LAI in July		LAI in August		MODIS Land Cover
		<i>In Situ</i> LAI	MODIS LAI	<i>In Situ</i> LAI	MODIS LAI	
Early	Caiman 3-5	1.88	3.8	2.17	5.3	Savannas
	Ranchitos 3-5	0.62	1.1	0.74	2.1	Mixed Forests
	Santa Cruz 3-5	1.00	2.3	1.16	2.1	Woody Savannas
Intermediate	Caiman 8-12	3.51	3.7	3.64	6.1	Woody Savannas
	Ranchitos 8-12	0.89	1.1	1.21	1.8	Woody Savannas
	Santa Cruz 8-12	1.18	1.1	2.10	2.0	Woody Savannas
Late	Tejon 1	0.94	1.6	1.14	1.8	Woody Savannas
	Tejon 2	1.13	1.2	1.22	1.7	Deciduous Broadleaf Forests
	Gargollo	2.75	2.2	3.88	0.4	Mixed Forests

Chapter Three: Effects of subpixel land surface characteristics on MODIS LAI phenology in a tropical dry forest in Mexico

1. Introduction

A tropical dry forest is defined as an area of seasonally deciduous forest with mean annual temperature of $> 25^{\circ}\text{C}$, and annual precipitation between 700mm and 2000 mm that mainly falls in a few months wet season, and with three or more dry months when precipitation is less than 100mm per month (Sánchez-Azofeifa et al., 2005). While tropical dry forest comprises 42% of the earth's tropical and subtropical forests (Murphy and Lugo, 1986), it's considered the most endangered ecosystem (Janzen, 1988) with for example only 0.09% of the original dry forest is present in Mesoamerica (Cascante et al., 2002; Janzen, 1988) and protected officially (Kalacska et al., 2005).

Seasonality is a main characteristic of tropical dry forests, and it is determined by seasonal water availability (Borchert, 1994; Bullock & Solís-Magallanes 1990; Reich and Borchert, 1984). Leaves grow and the productivity is high during the rainy season, while in the dry season, tropical dry forests shed their leaves due to water loss (Borchert, 1994; Reich and Borchert, 1984). Leaf area index (LAI), the one-sided green leaf area per unit ground area (Jonckheere et al., 2004; Watson, 1947), is one of the key parameters to monitor seasonal

variation of vegetation phenology, and used in most ecosystem productivity models and global models of climate, hydrology, biogeochemistry and ecology (Myneni et al., 2002; Sellers et al., 1997).

Researchers have been putting efforts to monitor forest seasonality using remote sensing techniques that are more cost-efficient (Cohen et al., 2003; Meroni et al., 2004; Myneni et al., 2002). The Moderate Resolution Imaging Spectroradiometer (MODIS) is one of the key sensors that provide moderate spatial resolution and various temporal resolution standard products for global biosphere monitoring (Cohen et al., 2003). MODIS LAI is one of the vegetation products designed to monitor phenology (Huemmrich et al., 2005) at a relatively coarse spatial resolution of 1 km and a temporal resolution of 8 days. Many researchers have applied MODIS LAI in their studies (Fang and Liang, 2005; Fensholt et al., 2004; Shabanov et al., 2003; Wang et al., 2004; Wang et al., 2005). However, some have found discrepancy between MODIS LAI and *in situ* LAI (Cohen et al., 2003; Fensholt et al., 2004; Wang et al., 2004). The discrepancy is partially due to the relatively coarse spatial resolution of MODIS LAI (1-km), pixels of which may contain fractions of different land cover types (Tian et al., 2002). Various land cover types within a pixel combine to form spectral reflectance (Peddle et al., 1999) which affects the derivation of MODIS LAI. However, no studies examined the effect of land cover mixture on MODIS LAI.

The effects of topography on vegetation distribution have been widely stated (Basnet 1992; Darmody et al., 2004; Oliveira-Filho et al., 1998; Spadavecchia et

al., 2008). Studies cover a wide range of areas from tropical rain forest (Basnet 1992), tropical dry forest (Oliveira-Filho et al., 1998), to Arctic (Darmody et al., 2004; Spadavecchia et al., 2008). However, only a few studies addressed the effects of topography on LAI. Spadavecchia et al., (2008) examined topographic effects on LAI in an Arctic ecosystem in northern Sweden. No research has been conducted on topographic effects on LAI in tropical forests.

The objectives of this chapter were to evaluate the effects of subpixel land surface characteristics on the phenological pattern of MODIS LAI time series in a tropical dry forest in Mexico. Percentage of forest cover and topographic features within a MODIS pixel were considered in the study.

2. Methods

2.1. Imagery

A high spatial resolution QuickBird multi-spectral image (2.4 m) obtained in the dry season April 2003 was used for land cover classification, which covers the a fragmented area of tropical dry forests (approximately 120 km²) located just north of the Chamela-Cuixmala Biosphere Reserve (Figure 3-1).

MODIS LAI products (8-day composite) at 1-km spatial resolution from February 2000 to September 2010 were used to derive time series and phenological characteristics. A 7×7 (pixels) MODIS LAI subset was downloaded

that is within the area covered by the QuickBird image. Geographic coordinates of the upper-left corner of each MODIS pixel were extracted and plotted on top of the QuickBird imagery. Boundaries of MODIS pixels were formed using the coordinates in vector format (Figure 3-1). There are a total of 48 MODIS pixels with one at the upper-left corner omitted since part of it was not encompassed by the QuickBird data.

The Shuttle Radar Topography Mission (SRTM) digital elevation data produced by NASA was obtained. SRTM data provides elevation at 90 m spatial resolution. The vertical resolution is less than 16 m. SRTM data was used in the analysis of topographic features of the land surface.

2.2. Methodology

2.2.1. MODIS LAI Time Series

MODIS LAI is one of NASA's MODIS land products that observe global dynamics and processes of the land. Developed by the MODIS Science Team, MODIS LAI is estimated from the main algorithm that requires the atmospherically corrected MODIS surface reflectance product and MODIS land cover product. When the main algorithm fails, a back-up algorithm is applied to estimate LAI using vegetation indices. In this study, MODIS LAI 8-day composites (1-km) were collected from February 2000 to September 2010.

Missing values were replaced by LAI obtained on the same Julian day from adjacent years.

2.2.2. *TIMESAT*

TIMESAT is a software package developed by Jönsson and Eklundh for analyzing remotely sensed data time series. TIMESAT fits smooth functions to noisy remotely sensed data and computes seasonality parameters including beginning and end of the growing season, length of season, base value, peak value, amplitude, small integral and large integral (Figure 3-2) (Jönsson and Eklundh, 2004). Base value is the average of the left and right minima in a growing season. Small integral is the area between the fitted function and the base value that represents the primary production of seasonally active vegetation. Large integral is the area between the fitted function and the zero level (Jönsson and Eklundh, 2004).

MODIS LAI time series for each of the 48 pixels were created by the Gaussian fitting function in TIMESAT. Seasonality parameters were extracted for each of the growing seasons from the MODIS LAI time series. Values of each parameter were averaged over the 11-year period to represent a pixel's phenological characteristic for comparison among pixels.

2.2.3. Land Cover Classification

Land cover classification on the QuickBird image was conducted in the ENVI image processing and analysis software using maximum likelihood supervised classification method. Maximum likelihood calculates the probability that a given pixel belongs to a specific class and assigns the pixel to the class with the highest probability. A total of 3 land cover types were classified: tropical dry forest, bare rock and roads, and water. Training regions were selected for each class to estimate the spectra of the class as the basis for classification. Testing regions were selected to evaluate the accuracy of classification (Table 3-1). The percentage of forest cover within each MODIS pixel was calculated for evaluation of its effects on the phenological pattern of MODIS LAI time series.

2.2.4. Topography

SRTM (90 m) elevation data was downloaded and mosaicked. Slope was derived in percent gradient from SRTM using ArcGIS 9. It represents the rate of maximum change in elevation from each pixel to its neighbors. Slope aspect was derived for the study area identifying the slope direction in degrees azimuth. In addition, the Solar Analyst tool developed by Fu and Rich (1999) was used to calculate solar radiation on elevation data. This modeling tool accounts for the influence of the viewshed, slope aspect and elevation, and calculates the accumulation of total direct and diffuse solar radiation throughout a year. The unit

is watt hours per square meter (WH/m²). Average slope, aspect and solar radiation within each of the 48 MODIS pixels were calculated.

2.2.5. ANOVA

Forest cover, slope, aspect and solar radiation are considered the potential factors in this study that affect the phenological pattern of MODIS LAI time series. Values of forest cover within each of the 48 MODIS pixels, ranging from 41.22% to 94.03%, were divided evenly into two levels – high and low forest cover with 24 items in each level. Similarly, 48 slope values and radiation values were divided into two levels, representing high and low values. Aspect was also grouped into two, north facing (0°-90° and 270°-360°) and south facing (90°-270°).

To explore the factors that affect phenological pattern of MODIS LAI time series, the following combinations of the above potential factors have been examined in two-way ANOVA: forest cover and aspect, forest cover and slope, forest cover and solar radiation. Due to the nature of the data, sample size is not always the same between the 4 groups in two-way ANOVA. In order to ensure data is balanced to meet the assumption before a two-way ANOVA was run, sample size of the other 3 groups was reduced to the same size as the group with the smallest number (N) of samples. The criterion of the selection was to select the highest N and lowest N values of the second factor to maximize the difference for the sake of comparison. For example, in the combination of forest cover

(factor 1) and aspect (factor 2), the smallest sample size was 8 among the 4 groups. Thus for the other 3 groups, 8 samples that were closest to 0/360 degree were selected for north facing slope aspect, and 8 samples closest to 180 degree were selected for south facing slope aspect.

The data was not normally distributed, thus was transformed into ranks in order to run a non-parametric ANOVA.

3. Results

3.1. Phenological Pattern of MODIS LAI

MODIS LAI time series were created for each of the 48 pixels using Gaussian fitting function in TIMESAT and seasonality parameters were extracted. By comparing seasonality parameters, we found that they varied among the 48 pixels. Table 3-2 shows the highest and lowest values of each phenological parameters among the 48 MODIS pixels. For example, peak LAI values varied between 2.16 and 6.27, amplitude varied between 1.74 and 5.39, and the highest primary production value of the 48 pixels is more than 4 times as much as the lowest one. Figure 3-3 shows two examples of MODIS LAI time series, where (a) was derived from a MODIS pixel with 94.03% of forest cover, and (b) with 41.22% of forest cover. Figure 3-3-a had an average of 6.27 in peak LAI value, 5.39 in amplitude and 835.03 in small integral, while Figure 3-3-b had an average of 2.33 in peak LAI value, 1.92 in amplitude and 221.02 in small integral.

3.2. Land Cover

There were 3 major land cover types in the study area: tropical dry forest (70.78%), bare rock and roads (29.18%), and water (0.04%). Overall classification accuracy was above 92%. The percentage of forest cover within each MODIS pixel was calculated, which ranged between 41.22% and 94.03%. 48 MODIS pixels were evenly divided into 2 levels – 24 pixels with high forest cover (71.02% - 94.03%) and 24 pixels with low forest cover (41.22% - 70.56%).

3.3. Topography and Solar Radiation

Slope was derived in percentage in ArcGIS. Average slope within a MODIS pixel ranged between 4.08% and 24.32% in the study area. 48 values were evenly split into two slope levels, high (4.08% - 13.94%) and low (15.03% - 24.32%). Average aspect of 90° to 270° within each MODIS pixel was considered south facing, and average aspect of 0°-90° and 270°-360° was considered north facing. There were 19 north facing MODIS pixels and 29 were south facing.

Solar radiation was calculated using the accumulation throughout a year. The unit is watt hours per square meter (WH/m²). Mean solar radiation within each MODIS pixel ranged between 1,579,390 WH/m² and 1,673,140 WH/m² and was evenly grouped into two levels, high and low.

3.4. Effect of Land Surface Characteristics on MODIS LAI Phenological Pattern

The non-parametric two-way ANOVA was run on the ranks of phenological data, with the following combination of factors: forest cover and aspect, forest cover and slope, forest cover and solar radiation.

Forest cover and aspect were found to have significant effects on the following MODIS LAI phenological parameters (Table 3-3): 1) Base value – LAI in the dry season, p values were 0.016 and 0.029 for forest cover (factor 1) and aspect (factor 2) respectively, 2) Small integral – production of tropical deciduous forest, p values were 0.004 and 0.027 for the two factors, and 3) Large integral – production of both tropical deciduous and evergreen forests, p values were 0.007 and 0.037 for the two factors. There's no statistically significant interaction between these two factors ($p > 0.1$). Results showed that MODIS pixels with high forest cover, and with north facing aspect tended to have higher phenological values (base value, small integral and large integral), while MODIS pixels with low forest cover, and with south facing aspect had lower phenological values (Table 3-4). There's no effect of forest cover and aspect on beginning or end of the growing season, length of season, peak value or amplitude.

There's no statistically significant effect of slope ($p > 0.6$) or solar radiation ($p > 0.6$) found on phenological parameters. However, results did show that MODIS pixels with north facing aspect had lower mean annual solar radiation (Table 3-5), which could be related to the variation of phenological data among the 48 MODIS pixels.

4. Discussion

Discrepancy between MODIS LAI and *in situ* LAI has been found in studies (Cohen et al., 2003; Fensholt et al., 2004; Wang et al., 2004). Subpixel land cover fraction is the main cause of problem while the landscape is not homogeneous (Asner & Heidebrecht, 2002; Kumar et al., 2008; Vikhamar & Solberg, 2003). Knowing the existing problems and the role of subpixel land cover types, this study intended to analyze land surface characteristics in a fragmented seasonally deciduous forest and how they affect seasonality in MODIS LAI. Results of a two-way ANOVA indicated that phenological parameters derived from MODIS LAI time series were affected by the percentage of forest cover within a MODIS pixel and the mean slope aspect.

In most studies, the reflectance of a pixel is assumed to be formed by the linear sum of the reflectances of all subpixel types (Asner & Heidebrecht, 2002; Vikhamar & Solberg, 2003). Thus the higher the forest cover is within a MODIS pixel, the more it contributes to the reflectance of the pixel, which leads to higher MODIS LAI values that is derived from surface reflectance, as shown in our results. Therefore, our result is considered consistent with the known theory in subpixel mixture, and should have wide applicability in explaining the spatial variation of MODIS LAI in fragmented tropical dry forest across this area.

The results also indicated the effect of slope aspect on MODIS LAI phenology, where pixels with an average of north facing aspect tend to have

higher phenological values, and pixels with an average of south facing aspect tend to have lower values. Kang et al. (2004) applied a satellite-based hydroecological model and found strong effect of topography on solar radiation, temperature, soil water and evapotranspiration. They found that south facing slopes had higher solar radiation, higher soil temperature and lower soil water content (at 10 cm soil depth) than north facing slopes. As to the tropical dry forests, seasonality is the main characteristic and is controlled by water availability which is seasonal precipitation and soil moisture (Borchert, 1994; Bullock & Solís-Magallanes 1990; Reich and Borchert, 1984). Through influencing soil water and evapotranspiration, aspect would affect the seasonality of tropical dry forests that was captured and reflected by MODIS LAI and the phenological parameters in this study,

Although there was no statistically significant relationship between solar radiation and MODIS LAI phenology, we did find an average lower solar radiation in north facing pixels. Miller (1972) stated that primary production decreased with increase in air temperature, and increasing solar radiation decreased production after reaching up to a point. This is consistent with our result showing an average lower production in south facing pixels where both temperature and solar radiation were higher than those in north facing slope.

Slope was not found to be statistically related with MODIS LAI phenology in this study. However, associated with aspect, slope is more likely to affect solar radiation, temperature, evaporation and soil water. Although in this study, a three-way ANOVA cannot be applied due to the very small sample size after balancing,

that the data cannot pass normality test nor have equal variance even after being transformed. It would be highly valuable to perform analysis on forest cover, aspect and slope in the future where it's applicable.

5. Conclusion

MODIS LAI is valuable in studies and applications for its spatial and temporal coverage. However, due to its relatively coarse spatial resolution, a large difference in spatial scale exists in practice between field measurement and MODIS data, which lead to the difficulty in MODIS data validation (Susaki et al., 2007). By using percentage of forest cover, slope, aspect and solar radiation derived from higher spatial resolution imagery, this chapter evaluated the effects of subpixel land surface characteristics on MODIS LAI and the derived phenological parameters. Results of a two-way ANOVA showed that the percentage of forest cover and mean aspect within a MODIS pixel had significant impact on MODIS LAI and the phenological parameters, with higher phenological values (base value, small integral and large integral) found in MODIS pixels with higher forest coverage and north facing slope aspect.

The results of this chapter provides a better understanding on the compositional and topographical characteristics within a MODIS pixel, how these characteristics affect spectral reflectance and so the derived LAI of a MODIS pixel from a remote sensing perspective, and how they affect the growth of vegetation through their impact on solar radiation, temperature, and soil water etc.

from a biological perspective. Validation of MODIS LAI using ground measurement should be practiced with caution. In the case of tropical dry forests, forest fragmentation and mix of land cover should be considered during the validation process. This chapter is to contribute to the discussion and so the overall goal of MODIS LAI validation.

Literature Cited

Asner, G. P., and Heidebrecht, K. B. (2002). Spectral unmixing of vegetation, soil and dry carbon cover in arid regions: Comparing multispectral and hyperspectral observations. *International Journal of Remote Sensing*, 23(19), 3939-3958.

Balvanera, P., Lott, E., Segura, G., Siebe, C., and Islas, A. (2002). Patterns of β -diversity in a Mexican tropical dry forest. *Journal of Vegetation Science*, 13, 145-158.

Basnet, K. (1992). Effect of topography on the pattern of trees in Tabonuco (Dacryodes excelsa) dominated rain forest of Puerto Rico. *Biotropica*, 24(1), 31-42.

Borchert, R. (1994). Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, 75, 1437-1449.

Bullock, S. H. and Solis-Magallanes, J. A. (1990). Phenology of Canopy Trees of a Tropical Deciduous Forest in Mexico. *Biotropica*, 22, 22-35.

Cascante, A., Quesada, M., Lobo, J. J. and Fuchs, E. A. (2002). Effects of Dry Tropical Forest Fragmentation on the Reproductive Success and Genetic Structure of the Tree *Samanea saman*. *Conservation Biology*, 16(1), 137-147.

Cohen, W. B., Maier-sperger, T. K., Yang, Z., Gower, S. T., Turner, D. P., Ritts, W. D., Berterretche, M., and Running, S. W. (2003). Comparisons of land cover and LAI estimates derived from ETM+ and MODIS for four sites in North America: a quality assessment of 2000/2001 provisional MODIS products. *Remote Sensing of Environment*, 88(3), 233-255.

Darmody, R.G., Thorn, C.E., Schlyter, P. and Dixon, J.C. (2004). Relationship of vegetation distribution to soil properties in Karkevagge, Swedish Lapland. *Arctic Antarctic and Alpine Research*, 36, 21-32.

Fang, H., and Liang S. (2005). A hybrid inversion method for mapping leaf area index from MODIS data: experiments and application to broadleaf and needleleaf canopies. *Remote Sensing of Environment*, 94, 405-424.

Fensholt, R., Sandholt, I., and Rasmussen, M. S. (2004). Evaluation of MODIS LAI, fAPAR and the relation between fAPAR and NDVI in a semi-arid environment using in situ measurements. *Remote Sensing of Environment*, 91, 490-507.

Fu, P. and P. M. Rich. (1999). Design and implementation of the Solar Analyst: an ArcView extension for modeling solar radiation at landscape scales. Proceedings of the 19th Annual ESRI User Conference, San Diego, USA, <http://www.esri.com/library/userconf/proc99/proceed/papers/pap867/p867.htm>.

Huemmrich, K. F., Privette, J. L., Mukelabai, M., Myneni, R. B. and Knyazikhin, Y. (2005). Time-series validation of MODIS land biophysical products in a Kalahari woodland, Africa. *International Journal of Remote Sensing*, 26(19), 4381-4398.

Janzen, D. H. (1988). Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson, E.O. (Ed.), *Biodiversity* (pp. 130-137). Washington: National Academy Press.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., and Baret, F. (2004). Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology*, 121, 19-35.

Jönsson, P. and Eklundh, L. (2004). TIMESAT - a program for analysing time-series of satellite sensor data. *Computers and Geosciences*, 30, 833-845.

Kalacska, M., Calvo-Alvarado, J. C., and Sánchez-Azofeifa, G. A. (2005). Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession. *Tree Physiology*, 25, 733-744.

- Kang, S., Lee, D., and Kimball, J. S. (2004). The effects of spatial aggregation of complex topography on hydroecological process simulations within a rugged forest landscape: development and application of a satellite-based topoclimatic model. *Canadian Journal of Forest Research*, 34(3), 519-530.
- Kumar, U., Kerle, N. and Ramachandra T.V. (2008). Constrained Linear Spectral Unmixing Technique for Regional Land Cover Mapping Using MODIS Data. *Innovations and Advanced Techniques in Systems, Computing Sciences and Software Engineering*, 416-423.
- Maass, J., Balvanera, P., Castillo, A., Daily, G. C., Mooney, H. A., Ehrlich, P., Quesada, M., Miranda, A., Jaramillo, V. J., García-Oliva, F., Martínez-Yrizar, A., Cotler, H., López-Blanco, J., Pérez-Jiménez, A., Búrquez, A., Tinoco, C., Ceballos, G., Barraza, L., Ayala, R., and Sarukhán, J. (2005). Ecosystem services of tropical dry forests: insights from long-term ecological and social research on the Pacific Coast of Mexico. *Ecology and Society*, 10(1), 17-39.
- Meroni, M., Colombo, R., and Panigada, C. (2004). Inversion of a radiative transfer model with hyperspectral observations for LAI mapping in poplar plantations. *Remote Sensing of Environment*, 92, 195-206.
- Miller, P. C. (1972). Bioclimate, Leaf Temperature, and Primary Production in Red Mangrove Canopies in South Florida. *Ecology*, 53, 22-45.
- Murphy, P. G., and Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, 17, 67-88.
- Myneni, R. B., Hoffman, S., Knyazikhin, Y., Privette, J., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G. R., Lotsch, A., Friedl, M., Morisette, J. T., Votava, P., Nemani, R. R., and Running, S. W. (2002). Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sensing of Environment*, 83, 214-231.

Oliveira-Filho, A. T., Curi, N., Vilela, E. A., and Carvalho D. A. (1998). Effects of Canopy Gaps, Topography, and Soils on the Distribution of Woody Species in a Central Brazilian Deciduous Dry Forest. *Biotropica*, 30(3), 362-375.

Peddle, D. R., Hall, F. G., and Ledrew, E. F. (1999). Spectral mixture analysis and geometric-optical reflectance modeling of boreal forest biophysical structure. *Remote Sensing of Environment*, 67(3), 288-297.

Reich, P. B. and Borchert, R. (1984). Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology*, 72, 61-74.

Sánchez-Azofeifa, G. A., Quesada, M., Rodriguez, J. P., Nasser, J. M., Stoner, K. E., Castillo, A., Garvin, T., Zent, E. L., Calvo, J. C., Kalacska, M., Fajardo, L., Gamon, J., and Cuevas-Reyes, P. (2005). Research priorities for Neotropical dry forests. *Biotropica*, 37(4), 477-485.

Sellers, P. J., Dickinson, R. E., Randall, D. A., Betts, A. K., Hall, F. G., Berry, J. A., Collatz, G. J., Denning, A. S., Mooney, H. A., Nobre, C. A., Sato, N., Field, C. B., and Henderson-Sellers, A. (1997). Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science*, 275, 502-509.

Shabanov, N. V., Wang, Y., Buermann, W., Dong, J., Hoffman, S., Smith, G. R., Tian, Y., Knyazikhin, Y., and Myneni R. B. (2003). Effect of foliage spatial heterogeneity in the MODIS LAI and FPAR algorithm over broadleaf forests. *Remote Sensing of Environment*, 85, 410-423.

Spadavecchia, L., Williams, M., Bell, R., Stoy, P. C., Huntley, B., and Wijk, M. T. (2008). Topographic controls on the leaf area index and plant functional type of a tundra ecosystem. *Journal of Ecology*, 96, 1238-1251.

Susaki, J., Yasuoka, Y., Kajiwara, K., Honda, Y., and Hara, K. (2007). Validation of MODIS Albedo Products of Paddy Fields in Japan. *IEEE Transactions on Geoscience and Remote Sensing*, 45(1), 206-217.

Tian, Y., Woodcock, C. E., Wang, Y., Privette, J. L., Shabanov, N. V., and Zhou, L., et al. (2002). Multiscale analysis and validation of the MODIS LAI product I. uncertainty assessment. *Remote Sensing of Environment*, 83(3), 414-430.

Vikhamar, D. and Solberg, R. (2003). Snow-cover mapping in forests by constrained linear spectral unmixing of MODIS data. *Remote Sensing of Environment*, 88(3), 309-323.

Wang, Q., Tenhunen, J., Granier, A., Reichstein, M., Bouriaud, O., Nguyen D., and Breda, N. (2004). Long-term variations in leaf area index and light extinction in a *Fagus sylvatica* stand as estimated from global radiation profiles. *Theoretical and Applied Climatology*, 79, 225-238.

Wang, Q., Tenhunen, J., Nguyen Q. D., Reichstein, M., Otieno, D., Granier, A., and Pilegarrrd, K. (2005). Evaluation of seasonal variation of MODIS derived leaf area index at two European deciduous broadleaf forest sites. *Remote Sensing of Environment*, 96, 475-484.

Watson, D. J. (1947). Comparative physiological studies in the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Annals of botany*, 11, 41-76.

Figures and Tables



Figure 3-1. Study area, covered by the QuickBird image obtained in April 2003, just north of the Chamela-Cuixmala Biosphere Reserve. Polygons overlain on the QuickBird image define the location of the 48 MODIS pixels from a 7×7 subset.

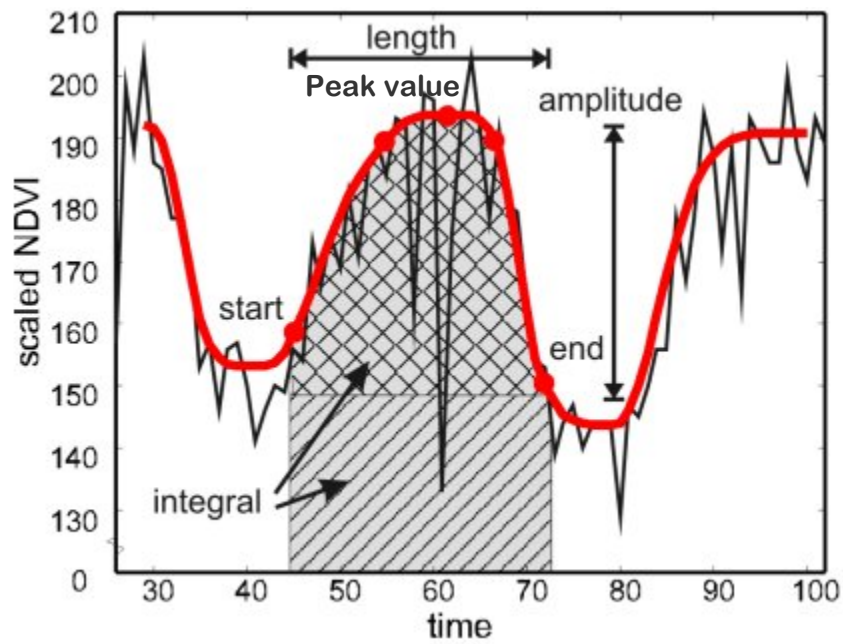
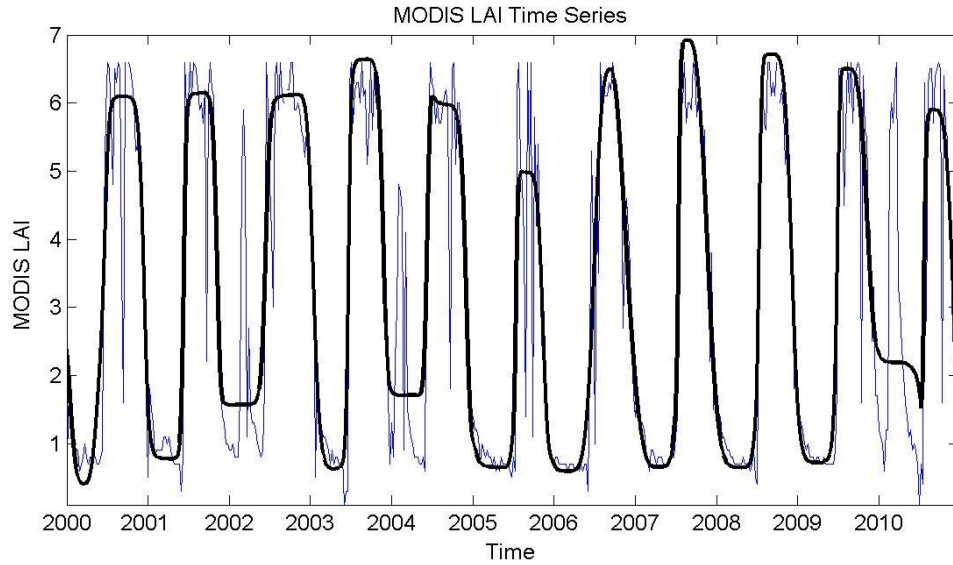
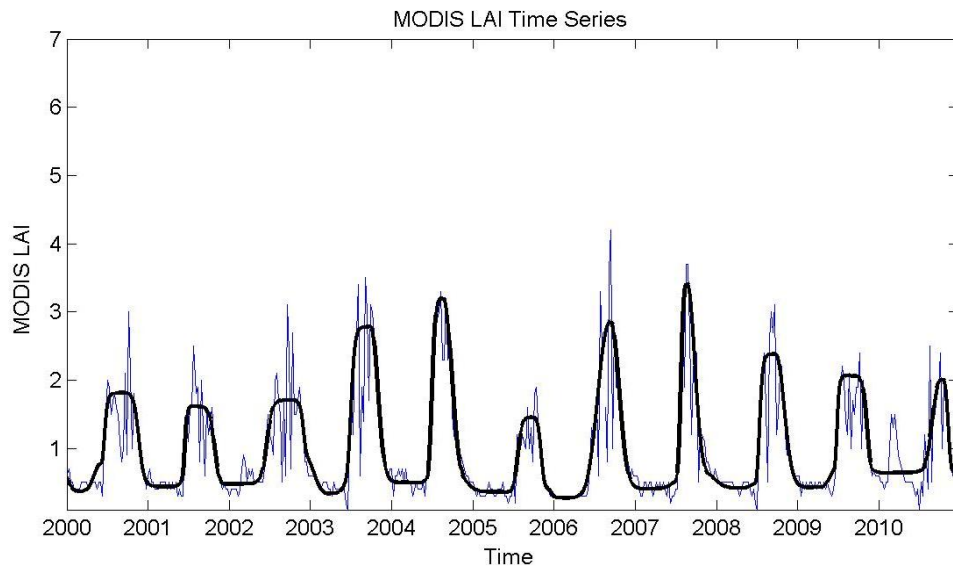


Figure 3-2. Some of seasonality parameters derived in TIMESAT, including begin of the growing season, end of the growing season, peak value, amplitude, length of season, small integral and large integral. The thin black line simply connects noisy remotely sensed data. The red line is the fitted function.

After: Jönsson and Eklundh (2004)



(a)



(b)

Figure 3-3. MODIS LAI time series of two pixels with different percentages of forest cover from year 2000 to 2010, where (a) is a time series of the pixel with 94.03% of forest cover, average peak value 6.27, amplitude 5.39 and small integral 835.03, (b) is a time series of the pixel with 41.22% of forest cover, average peak value 2.33, amplitude 1.92 and small integral 221.02. The blue line simply connects observed MODIS LAI values. The black line is a Gaussian fit estimated with TIMESAT.

Table 3-1. Training and testing regions – number of polygons and number of pixels per land cover class.

	Land Cover	Polygons	Pixels
Training Regions	Tropical dry forest	40	3,654
	Bare rock and roads	23	1,375
	Water	3	65
Testing Regions	Tropical dry forest	40	2,330
	Bare rock and roads	13	717
	Water	3	62

Table 3-2. Highest and lowest values of phenological parameters among the 48 MODIS pixels.

	Length of Season	Base Value	Peak Value	Amplitude	S. Integral	L. Integral
Min. Value	115.28	0.41	2.16	1.74	198.24	271.04
Max. Value	194.64	0.89	6.27	5.39	835.04	1019.04

Table 3-3. p values of a two-way ANOVA – effects of forest cover and slope aspect on phenological parameters.

	Effects on Base Value	Effects on L.integral	Effects on S.integral
Factor1 - Forest Cover	P = 0.016	P = 0.004	P = 0.007
Factor2 - Aspect	P = 0.029	P = 0.027	P = 0.037
Factor1 x Factor1	P = 0.233	P = 0.155	P = 0.140

Table 3-4. Least square means of phenological data in non-parametric two-way ANOVA – effects of forest cover and slope aspect on phenological parameters (ranks).

	of Base Value	of L.integral	of S.integral
High Forest Cover	20.188	20.813	20.563
Low Forest Cover	12.813	12.188	12.438
North	19.813	19.688	19.563
South	13.188	13.313	13.438

Table 3-5. Mean annual solar radiation (WH/m²) in the 4 groups in a two-way ANOVA.

	High Forest Cover	Lower Forest Cover
North	1,621,121.25	1,625,611.25
South	1,652,862.50	1,655,848.75

Chapter Four: Conclusion

Leaf area index plays a significant role in the studies of primary production, carbon, energy and water vapor exchange between canopy and atmosphere (Clark et al., 2008; Gower et al., 1999; Sánchez-Azofeifa et al., 2009). It is a variable widely used in scientific research from tropical forests, temperate forests, to boreal and Arctic ecosystems (Behera et al., 2010; Chen et al., 2002; Kalacska et al., 2005; Spadavecchia et al., 2008). Besides traditional direct and indirect methods in measuring leaf area index in the field, remotely sensed techniques especially MODIS LAI products are also important in estimating LAI in a rapid way for large areas (Weiss et al., 2004). However convenient MODIS LAI is, it is found to be able to capture well seasonal changes in LAI yet overestimates LAI in some studies when compared to field measurements (Fensholt et al., 2004; Heinsch et al., 2006; Wang et al. 2005) since errors could be produced at any stage of image acquisition, processing and analysis (Jonckheere et al., 2004). Although understanding leaf area index and the evaluation of MODIS LAI have been the interest of scientific research, most attention and studies have been paid to boreal forests and tropical rain forests. This thesis focuses on the study of leaf area index in a tropical dry forest in the Pacific coast of Mexico, which involves estimating leaf area index in the field, and evaluating the performance of MODIS LAI and the effects of subpixel land surface characteristics on MODIS LAI. The methodologies and results of this thesis are meant to develop studies in the area

of leaf area index using remote sensing for the tropical dry forests, and contribute to the scientific research of tropical dry forests in a bigger picture.

Contribution and Future Insight

Chapter Two: Linkages between ecosystem structure, composition and leaf area index along a tropical dry forest chronosequence in Mexico

Optical measurements were found to capture well seasonal changes in LAI from the dry season to the rainy season. Significant increase in LAI was found at the plot level, the stage of succession level and at the landscape level. By comparing LAI and the Morisita–Horn index among the three successional stages, we found the largest compositional difference between the early stage and the intermediate stage, where the largest difference in LAI was found as well, with the highest LAI found in the intermediate stage and the lowest values found in the early stage. Significant difference in LAI was found between all three stages of succession, which is consistent with the results produced by Kalacska et al. (2005) in a tropical dry forest in Santa Rosa, Costa Rica. Since different stages of succession exist as the main form of tropical dry forests nowadays as a result of deforestation and forest recovery, this result provides a better understanding in the structural and compositional difference across stages of succession, as well as valuable insight for the studies applying remote sensing in LAI measurement for tropical dry forests. Most scientific research has focused on applying different sensor types and algorithm in order to estimate LAI through remote sensing, mainly in boreal, temperate forests

and tropical rain forests (Fernandes et al., 2004; Maire et al., 2011; Soudani et al., 2006). Along with Kalacska's work, this chapter provides a new perspective in improving accuracy of LAI estimation for tropical dry forests given the significant difference in LAI between succession stages. A preliminary step to categorize and segregate stages of succession is recommended before estimating LAI either in the field or using remote sensing. This is significant in connecting biological findings of tropical dry forest succession with leaf area index as it is an important parameter in many predictive models.

The comparison between LAI in the field and MODIS LAI indicated a relatively low agreement between each other. The relatively coarse spatial and temporal resolution of MODIS LAI products is the main reason that accounts for the disagreement between MODIS LAI and LAI measured in the field. One MODIS pixel may contain more than one land cover types, and is a composite of data from 8 consecutive days, while field measurement was obtained in homogenous stands of a certain succession at a point in time. This result enhances the need to segregate successional stages for remote sensing LAI estimates especially using moderate and coarse resolution imagery for tropical dry forests that exist as fragments of different successions.

As implicated, in order to improve accuracy in LAI estimation through remote sensing, future research should focus on differentiating stages of succession spectrally at the canopy level. This opens up new challenges in further exploring and

developing techniques and methodologies for spectral differentiation between successions and establishing a framework for such studies in the future.

Chapter Three: Effects of subpixel land surface characteristics on MODIS LAI phenology in a tropical dry forest in Mexico

Leaf area index is a direct bioindicator and is required as an important input to many climate and ecological models (Chen & Cihlar, 1996). Validation of remotely sensed LAI is a priority in order for it to be used widely as an effective means at a larger scale (Soudani et al., 2006). Most scientific studies have retrieved remotely sensed LAI and performed validation over homogenous stands, which may increase the agreement between field measurements and image-based estimates (Soudani et al., 2006). This may not apply to some fragmented secondary dry forests where intensive human disturbance had occurred. Chapter Three explored how the within pixel land surface characteristics affect MODIS LAI and its time series. Results indicated that the percentage of forest cover and the mean aspect within a pixel showed significant impact on MODIS LAI and the phenological parameters such as primary production derived from its time series. Northing facing MODIS pixels with high forest cover had higher primary production, while south facing MODIS pixels with low forest cover had lower values.

This chapter introduced innovations in analyzing the factors driving the variation in MODIS LAI across space in tropical dry forests, including the use of

finer spatial resolution imagery for MODIS subpixel characteristics analysis, the incorporation of topographic information, and the use of phenological parameters in the analysis. Results of this chapter provide a better understanding of the subpixel land surface characteristics both from a biological perspective and a remote sensing perspective. Topography is known to affect solar radiation, temperature, soil water and evapotranspiration, which have high impacts on leaf area index in tropical deciduous forests. The percentage of forest cover within a MODIS pixel accounts for the spectral contribution that eventually affects the derived leaf area index from surface reflectance.

Since fragmentation is very common in tropical dry forests, the results and conclusions of this chapter can be applied to other tropical dry forests. Additional attention should be paid when linking MODIS LAI with *in situ* LAI based on the results of Chapter Three. Vegetation and non-vegetation land cover types should be separated prior to the validation and application of MODIS LAI. MODIS pixels containing homogeneous vegetation cover without spectral contribution by other subpixel land cover types are ideal. Along with conclusions from Chapter Two, further steps to segregate forest stands by succession should be involved in remotely sensed LAI validation if stands of each succession are larger in area than a pixel that allows this process to be feasible. However in other cases where fragmented stands are embedded in matrices of various land cover types within one pixel, *in situ* LAI measurements of forest stands do not represent LAI of the area corresponding to a pixel thus are not suitable for validation purpose. The finding of this chapter contributes to the discussion in what drives or controls the

spatial variation of MODIS LAI. It promotes an important advancement towards the goal of remotely sensed LAI validation in tropical dry forests.

Overall Significance

In the efforts advocating and promoting conservation for tropical dry forests, remotely sensed products have become more and more popular and delivered timely information to researchers and decision makers at the continental, regional and local level. In the context of leaf area index, utilizing remote sensing products is the most efficient means in providing timely results needed as input in many ecosystem productivity models and models of carbon and vapor fluxes between canopy and the atmosphere. Therefore, the development and validation of remotely sensed LAI products are of critical importance. However, most scientific work has focused on boreal, temperate and tropical rainforest ecosystems. The application and validation of LAI in the tropical dry forests are still under developing. This thesis utilized LAI in estimating difference among successions and the seasonal changes in a tropical dry forest, and analyzed the factors driving variation in MODIS LAI. The results promoted our understanding in tropical dry forest and its successions, and provided valuable information for future research when validating and applying remotely sensed LAI, with the hope of opening up new discussions and challenges in the research for tropical dry forests.

Literature Cited

Behera, S. K., Srivastava, P., Pathre, U. V., Tuli, R. (2010). An indirect method of estimating leaf area index in *Jatropha curcas* L. using LAI-2000 Plant Canopy Analyzer. *Agricultural and Forest Meteorology*, 150(2), 307-311.

Chen, J. M. and Cihlar, J. (1996). Retrieving leaf area index of boreal conifer forests using Landsat TM images. *Remote sensing of environment*, 55, 153-162.

Chen, J. M., Pavlic, G., Brown, L., Cihlar, J., Leblanc, S. G., & White, H. P. et al. (2002). Derivation and validation of canada-wide coarse-resolution leaf area index maps using high-resolution satellite imagery and ground measurements. *Remote Sensing of Environment*, 80(1), 165-184.

Clark, D.B., Olivas, P.C., Oberbauer, S.F., Clark, D.A., Ryan, M.G. (2008). First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity. *Ecology Letters*, 11 (2), 163–172.

Fensholt, R., Sandholt, I., and Rasmussen, M. S. (2004). Evaluation of MODIS LAI, fAPAR and the relation between fAPAR and NDVI in a semi-arid environment using in situ measurements. *Remote Sensing of Environment*, 91, 490-507.

Fernandes, R., Miller, J., Chen, J. M., Rubinstein, I. (2004). Evaluating image-based estimates of leaf area index in boreal conifer stands over a range of scales using high-resolution CASI imagery. *Remote Sensing of Environment*, 89 (2), 200-216.

Gower, S. T., Kucharik, C. J., and Norman, J. M. (1999). Direct and indirect estimation of leaf area index, fAPAR, and net primary production of terrestrial ecosystems. *Remote Sensing of Environment*, 70, 29-51.

Heinsch, F. A., Zhao, M., Running, S. W., Kimball, J. S., Nemani, R. R., Davis, K. J., Bolstad, P. V., Cook, B. D., Desai, A. R., Ricciuto, D. M., Law, B. E., Oechel,

W. C., Kwon, H., Luo, H., Wofsy, S. C., Dunn, A. L., Munger, J. W., Baldocchi, D. D., Xu, L., Hollinger, D. Y., Richardson, A. D., Stoy, P. C., Siqueira, M. B. S., Monson, R. K., Burns, S. P., Flanagan, L. B. (2006). Evaluation of remote sensing based terrestrial productivity from MODIS using regional tower eddy flux network observations. *IEEE Transactions on Geoscience and Remote Sensing*, 44 (7), 1908-1925.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., and Baret, F. (2004). Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology*, 121, 19-35.

Kalacska, M., Calvo-Alvarado, J. C., and Sánchez-Azofeifa, G. A. (2005). Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession. *Tree Physiology*, 25, 733-744.

Maire, G., Marsden, C., Verhoef, W., Ponzoni, F. J., Seen, D., Begue, A., Stape, J., Nouvellon, Y. (2011). Leaf area index estimation with MODIS reflectance time series and model inversion during full rotations of Eucalyptus plantations. *Remote Sensing of Environment*, 115 (2), 586-599.

Sánchez-Azofeifa, A., Kalacska, M. E., Espirito-Santo, M. M., Fernandes, G. W., Schnitzer, S. (2009a). Tropical dry forest succession and the contribution of lianas to wood area index (WAI). *Forest Ecology and Management*, 258, 941-948.

Soudani, K., Francois, C., Maire, G., Dantec, V., Dufrene, E. (2006). Comparative analysis of IKONOS, SPOT, and ETM+ data for leaf area index estimation in temperate coniferous and deciduous forest stands. *Remote Sensing of Environment*, 102 (1-2), 161-175.

Spadavecchia, L., Williams, M., Bell, R., Stoy, P. C., Huntley, B., and Wijk, M. T. (2008). Topographic controls on the leaf area index and plant functional type of a tundra ecosystem. *Journal of Ecology*, 96, 1238-1251.

Wang, Q., Tenhunen, J., Nguyen Q. D., Reichstein, M., Otieno, D., Granier, A., and Pilegarrrd, K. (2005). Evaluation of seasonal variation of MODIS derived leaf area index at two European deciduous broadleaf forest sites. *Remote Sensing of Environment*, 96, 475-484.

Weiss, M., Baret, F., Smith, G. J., Jonckheere, I., and Coppin, P. (2004). Review of methods for in situ leaf area index (LAI) determination Part II. Estimation of LAI, errors and sampling. *Agricultural and Forest Meteorology*, 121, 37-53.