
2 Remote Sensing and Plant Functional Groups

Physiology, Ecology, and Spectroscopy in Tropical Systems

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2.1 PLANT FUNCTIONAL GROUPS IN TROPICAL SYSTEMS

The term “functional groups” was proposed by Cummins [1] to classify species playing similar roles or performing analogous processes in the ecosystem. Plant functional types may describe groups of plants with common responses to certain

environmental influences [2,3] and have been applied to several ecosystem functions such as biochemical cycles, fire resistance, invasion resistance, acquisition and use of resources, defense against herbivory, pollination, and seed dispersal, among others [4].

In general, functional grouping of species allows us to simplify biodiversity into components capable of explaining patterns or processes in a certain system [5]. This concept has been useful to predict the types of responses of vegetation to environmental changes even without detailed information about each species [6]. Thus, functional groups are often used in global models of vegetation [7,8] and climatic change [9].

The most important approaches to plant functional groupings are based on the use of functional characteristics and have been used by ecologists for decades [10–14]. According to Reich et al. [6], there are four main kinds of functional groupings. The first one is based on categorical qualitative approaches that classify groups of plants based on certain characteristics such as life form and type of photosynthesis, among others. The second one groups species along a continuum of quantitative characteristics such as growth rate, specific leaf area, maximum photosynthetic capacity, etc. [15,16]. The third model is based on a combination of quantitative characteristics that may influence each other such as leaves, seeds, and tree height [17]. Finally, a fourth model groups plant species based on their responses to specific environmental factors; a good example of this is the classification of tropical plant species proposed by Mulkey, Wright, and Smith [18] on the basis of their shade tolerance or the C-S-R scheme of plant strategies proposed by Grime [10].

2.1.1 STUDIES ON FUNCTIONAL GROUPS

In general, the number of studies regarding functional groups has increased over the last two decades. An important number of these studies have focused on plant groups associated to successional stages after anthropogenic disturbance; another set of studies evaluated the response of predefined functional groups to global increments of CO₂ and temperature due to climate change; and a third group of studies evaluated the importance of functional diversity in synthetic or natural communities. Most of these studies, however, have been conducted in temperate regions rather than in tropical forests where biodiversity is higher and ecosystems are fragile [19]. The few studies in the tropics suggest that the quantity of plant functional groups is potentially very high and more complex [20]. Most of the studies in the tropics have been conducted in tropical rain forests with few in tropical dry and cloud forests [21–24]. Tropical systems other than tropical rain forests have been largely overlooked in the scientific literature [25].

In an extensive review, we surveyed the literature from different databases using a combination of the following keywords: “plant functional group,” “plant functional type,” and “tropical.” Searches were conducted in the Science Citation Index and Biological Abstracts databases as well as in the main editorials (Blackwell Science, Springer–Verlag, Elsevier) and scientific societies of the most important indexed journals of ecology, physiology, and conservation biology. In this revision we found a total of 50 studies that analyze plant functional groups in tropical systems. Fifty-four percent of the studies use data of tropical plants in combination with data

from other ecosystems to analyze three main aspects of functional groups related to (1) theoretical generalizations of ecological processes [2,6,26–30]; (2) performance of morphological and physiological characters and of their interrelationships [31–36], among others; and (3) the role of functional groups on the dynamics of communities and ecosystems [2,37–40]. The remaining 46% of these studies exclusively analyze tropical species to identify functional groups *de novo* or to evaluate the performance and consistency of functional groups previously defined for the tropics.

Ecophysiological characteristics are among the most used plant traits to classify functional groups. In tropical systems these traits have been mainly used for grouping plant species on the basis of (1) shade tolerance [41–43]; (2) maximum potential height [44–46]; (3) increment in diameter used as an indicator of growing rate [20,44,47–50]; (4) elements related to photosynthetic capacity [15,51]; and (5) water status and/or water use efficiency (i.e., water storage stems [21]), stomatal conductance [51], C isotopic composition ($\delta^{13}\text{C}$) [52,53], or the difference between the air and leaf temperatures (ΔT) (i.e., indicator of heat dispersion capacity [23]).

Some other classifications including ecophysiological characteristics are based on species responses to different environmental factors such as plant response to abnormal patterns of drought and rain [22] or the response to changes in the landscape (i.e., structure of forest fragments [54]). Other studies have identified a combination of various other characteristics to define functional groups. These include reproductive traits, life forms and patterns of distribution in forests in different successional stages [55], demographic characteristics such as mortality rate [44], and, in the case of invasive species, the impact on native species [56]. In summary, we can classify the studies of functional groups of tropical plants in the following groups: (1) studies that characterized plant species associated to different successional stages, (2) studies that classify plants based on growth patterns, and (3) studies that classify plants based on water stress, water storage capacity, and heat dissipation.

The analysis of functional plants under succession has been emphasized due to the increasing importance of tropical secondary forests. There is increasing knowledge that recognizes different strategies of groups of plants specialized to regenerate in different successional stages; these studies have become crucial for the conservation of tropical systems [57,58]. Another set of studies emphasized the use of growth patterns to determine functional groups because growth rate is a trait that is correlated with ecophysiological characteristics of great importance for species performance [59]. Finally, some studies classify plants based on water use mechanisms because this resource plays a decisive role in species distribution and diversity gradients in tropical forests [60]. Water availability is an important determinant of species distribution in tropical dry forests [61].

As shown thus far in this review, most studies in tropical systems have analyzed single or a combination of a few ecophysiological characters for the discrimination of tropical functional groups. However, an analysis considering an assemblage of characteristics with ecological relevance that determine the establishment of species in a given habitat would be more realistic. Thus, we consider that a possible combination of plant traits should include plant growth rate, leaf longevity, specific leaf area, photosynthetic capacity, leaf water content, water use efficiency, and certain reproductive parameters. The use of this kind of assemblage would generate more

consistent information about a great number of species in order to detect tropical functional groups. The information generated in most studies until now did not consider a multivariate approach of both vegetative and reproductive parameters. Therefore, there is a lack of comprehensive analyses of functional groups in tropical systems—communities that are highly diverse and complex.

2.2 SOLAR IRRADIATION AND LEAF OPTICAL PROPERTIES

Solar electromagnetic radiation reaches the Earth's outer atmosphere with an energy of 1366 W m^{-2} . During its trajectory to the planet's surface, approximately 40% of the energy is attenuated, with an essentially absolute filtering of wavelengths below 200 nm and above 10,000 nm [62,63]. Considering that such radiation can be absorbed, transmitted, or reflected at different wavelengths, remote sensing takes advantage of the net reflected radiation by the various objects on the surface of the Earth, allowing for applications, for instance, in tropical ecology, as discussed later in this chapter. In the present section we will consider some of the factors that result in the range of reflected wavelengths registered by remote sensing satellites, with a special focus on leaf-level properties.

2.2.1 SOLAR IRRADIANCE AND RADIATION SOURCES

The wavelengths of the solar radiation reaching the outer layers of the atmosphere approximately range from 200 to 1600 nm, with most of the incident energy within the range of visible light [62,63]. Various components of the atmosphere attenuate such solar irradiance. For instance, the stratospheric ozone layer filters out wavelengths below 350 nm [64]. Water vapor, in turn, absorbs infrared radiation with major bands at 900, 1100, and above 1200 nm [63]. CO_2 has narrow absorption bands at 2700, 4300, and 15,000 nm [65]. In fact, the infrared absorption properties of water vapor and CO_2 are widely utilized for the measurement of real-time gas exchange (i.e., CO_2 uptake and transpiration by plants).

In addition to the aforementioned solar irradiance attenuation by absorption, air and suspended particles further attenuate it by scattering, a phenomenon of special relevance for visible light. Indeed, when a light beam's trajectory is intercepted by an object, some of its energy is lost on impact and the rest is re-irradiated concentrically [66]. In fact, the sky's brightness and blue color during clear days are due to the scattering of light by air molecules—a phenomenon known as Rayleigh scattering—while larger particles, such as dust, further reduce the light's energy, as can be observed during red-sky sunsets due to Mie scattering [63,66].

In any case, six sources of radiation can reach an object (e.g., a leaf) on Earth's surface. First is direct solar irradiation or *sunlight*, for which most of its energy comes from visible light and whose range largely coincides with photosynthetically active radiation (wavelengths of 400–700 nm), with a special enrichment in yellow-orange (approximately 560–640 nm) wavelengths [62,63]. Due to scattering and absorption by the atmosphere, *skylight* also reaches the surface of the Earth during clear days, with energy of only 10% of that of direct solar irradiation with a peak wavelength near 400 nm [63,67]. Finally, visible *cloudlight*, with a peak around 500 nm, results

from the transmission through clouds of irradiance [67]. The optical properties of the objects encountered by direct sunlight, skylight, and cloudlight result in reflected long-wave radiation that also reaches objects such as leaves. Thus, the three remaining radiation sources can be identified as *reflected sunlight*, *reflected skylight*, and *reflected cloudlight*.

2.2.2 LEAF OPTICAL PROPERTIES

In the previous section we considered the six sources of radiation that can reach a leaf. Now we will discuss some leaf optical properties that result in the wavelength ranges, or bands, that are actually registered by remote sensors and some of their ecophysiological implications.

Pigments are highly conjugated biological molecules that absorb light at certain wavelengths. The most obvious pigment for studying plants is chlorophyll, which has absorption peaks in the blue and, especially, red regions of the visible spectrum, while light absorption of intermediate wavelengths is substantially reduced, especially in the green region. As a result, most of the red and blue radiation is absorbed by leaves, while most of the green light is reflected, conferring the familiar color to plants and vegetation in general. In this respect, remote sensors are able to detect a depletion in the red region that can be correlated with chlorophyll content (e.g., Castro-Esau, Sanchez-Azofeifa, and Caelli [68]). Higher chlorophyll contents, as suggested by remotely measured red-light depletion, can be indicators of higher canopy density or a more complex community structure. Another possibility is that such depletion indicates higher nitrogen content in the plant tissue. This is due to the fact that the most abundant protein in plants and on Earth is responsible for CO₂ fixation. Thus, chlorophyll content can be used as a proxy for determining protein and nitrogen content for plant tissue, as well as soil nitrogen levels [69,70].

While chlorophyll's maximum absorption occurs in the red region, accessory pigments absorb light of shorter wavelengths and, in consequence, of higher energy [63,70]. Of particular importance for tropical and subtropical forests, where the solar angle leads to higher irradiances than at higher latitudes, pigments that absorb in the blue-green region can be mentioned. In addition to funneling energy toward photosynthesis they also double as photoprotective pigments. First, as a result of photochemistry, a very reactive form of oxygen can result from an interaction with chlorophyll molecules. Carotenoids can quickly absorb the energy from such *free radicals*, thus preventing cellular damage. The second photoprotective function of carotenoids, specifically linked with the xanthophyll cycle, is nonphotochemical quenching. In this case, excited chlorophyll molecules can return to a basal state either by fluorescence (i.e., emitting light) or by transferring the excitation energy directly to other molecules. When exposed to high-light environments, a finite number of chlorophyll molecules become saturated, as illustrated by the numerous light response curves of net CO₂ uptake available in the literature, and such excess energy can inhibit or damage the photosynthetic machinery. In this respect, under high light the xanthophyll violaxanthin (absorption occurs in the blue region) is converted to zeaxanthin (absorption occurs in the green region), which in turn is converted back to violaxanthin when the light decreases [70].

Leaves also absorb infrared radiation, mainly from reflected light, which can increase their temperature. As a response, transpiration rates may also increase, taking advantage of the cooling effect resulting from evaporation. Nevertheless, because all objects with a temperature higher than absolute zero emit radiation, in addition to reflected radiation, leaves irradiate in the infrared [63]. The wavelength in which they maximally irradiate can be predicted, as a function of their surface temperature, by the Wien displacement law, $\lambda_{\max} T = 3.67 \times 10^6 \text{ nm K}$, on a photon basis, where λ_{\max} is the wavelength of maximum photon flux density, and T is the surface temperature of an object. For instance, the sun's surface temperature is 5800 K; according to Wien's displacement law, it maximally irradiates at 630 nm, while a leaf at 30°C would maximally irradiate at 35,631 nm. The relative importance of emitted vs. reflected infrared radiation in terms of the spectral signature of vegetation registered by remote sensors is not yet known. Yet, because infrared is absorbed by water, such bands can be utilized for assessing the water status of vegetation (e.g., Castro-Esau et al. [68] and Hunt, Rock, and Nobel [71]).

Plant anatomy also influences the optical properties of leaves. For instance, leaves from xeric environments may be more reflective of shorter wavelengths due to the higher contents of silicates in their leaves. In addition, some species present calcium oxalacetate crystals, which are believed to dissipate excess energy [63,72]. Also, the thickness of a leaf's mesophyll influences the amount of absorbed light as a consequence of the multiple layers of cells per leaf unit area [63,72]. Studies about the particular influences of cuticle composition, trichomes, and mesophyll thickness on leaf reflectance are recent and scarce, so further studies characterizing various functional groups may improve our understanding of the biological implications of remotely sensed spectra.

2.3 HYPERSPECTRAL DATA APPLICATIONS ON FUNCTIONAL GROUP DETECTION IN TROPICAL FORESTS: CASE STUDIES

Hyperspectral data are narrowband information on the reflectance of an object on Earth gathered by remote sensing analysis from in situ, airborne, or satellite sensors. This state-of-the-art technology allows for a detailed analysis of objects in the landscape from air and space; an example is provided by two hyperspectral satellites, Hyperion and Proba, now in orbit [73].

In hyperspectral imagery it is possible to subdivide the spectral range into over 200 intervals, each approximately 10–20 nm in width. If a radiance value is obtained for each interval, then a spectral curve of the wavelength intensity can be generated from the reflectance of each object in the landscape. The area covered by each hyperspectral image (and spatial resolution) varies by sensor; for example, Hyperion's ground coverage is 7.5 by 100 km with a resolution of 30 m per pixel [73]. Hyperspectral imaging is, then, a powerful and versatile means for continuous sampling of broad intervals of the spectrum.

The capability of hyperspectral sensors to detect numerous narrow bands can be applied to detect from space characteristic chemical and anatomical properties of vegetative and reproductive tissues of plants. A number of recent studies have indicated the advantages of using discrete narrowband data (i.e., hyperspectral data)

from specific portions of the spectrum, rather than broadband data (i.e., multispectral data), to obtain the most sensitive quantitative or qualitative information on vegetation or crop characteristics (i.e., references 74 through 77). For example, Thenkabail et al. [76] established the advantages of using narrowband Hyperion data over broadband IKONOS, ETM+, and ALI data in studying rainforest vegetation. When compared to broadband data from IKONOS, ETM+, and ALI sensors, Hyperion's narrow bands explained 36–83% more of the variability in biomass and increased by 45–52% land use/land cover (LULC) classification accuracies as verified by ground truthing. The overall accuracy in classifying nine rainforest LULC classes was 96% and was achieved by using 23 Hyperion wavebands. In comparison, the overall accuracies were only 48% for IKONOS (four bands), 42% for ETM+ (six nonthermal bands), and 51% for ALI (nine multispectral bands). Similarly, Lee et al. [78] and Kalacska et al. [79] indicated that the large number of narrow bands of hyperspectral data is an advantage for the estimation of structural and functional canopy characteristics.

Given the fact that 47% of the global forest cover is in the tropics [80], where the most biodiversity can be found, it is necessary to apply modern techniques to describe and study functional attributes of tropical plant communities using a large-scale landscape approach that can be corroborated with ground truth data at the species level. Thus, exploration of the role of hyperspectral remote sensing in the assessment and determination of functional traits in the tropics is an important task in order to evaluate current and future applications of these technologies in ecological sciences. At present, however, hyperspectral imaging techniques have been poorly applied in tropical zones, with only a few efforts to detect and study plant functional groups. In order to exemplify applications of hyperspectral remote sensing in this respect, in the following sections we will describe some case studies regarding identification of different kinds of vegetation based on functional attributes of species.

2.3.1 DISCRIMINATION OF SUCCESSIONAL STAGES

The area covered by secondary forests has increased over the last decades worldwide, encouraging the interest in successional studies and the development of new techniques oriented to detect these habitats using remote sensing images (e.g., Landsat, SAR, MODIS, AVIRIS). Thus, studies in this respect could involve the detection and characterization of plant successional groups, which would be of crucial importance for conservation purposes [25].

In general, recent forest clearings are spectrally distinct as they have higher reflectance than mature forest in visible, near, and middle infrared wavebands used by satellite sensors. In forest succession, red reflection exhibits a slight decrease as increasing leaf area absorbs rising amounts of radiation in this range; meanwhile, near-infrared reflectance (NIR) increases as additional leaf layers are added to a canopy as a result of the increasing reflectance from the spongy mesophyll. Nevertheless, subsequent canopy maturation, characterized by the acquisition of more layers and complexity, reduces reflectance, given that shadowing traps incoming energy. Shadowing also depresses shortwave infrared reflectance (SWIR). Provided that the SWIR is influenced by water absorption, increasing canopy moisture content also leads to a decrease in SWIR through secondary forest succession. In fact, several

studies have indicated that SWIR bands contain most of the information relevant to plant regeneration [81].

At present, a few attempts have been made to discriminate tropical forest successional stages by using hyperspectral remote sensing. For example, Thenkabail et al. [76] used hyperspectral imaging in order to detect different types of LULC in several ecoregions of West Africa, including humid forests. Specifically, they classified primary forests without evidence of anthropogenic disturbance, degraded primary forest with some evidence of anthropogenic disturbance, young secondary forest between 9 and 15 years old, mature secondary forest between 15 and 40 years old, and mixed secondary forest with significant anthropogenic disturbance. They also attempted to identify LULC classes of agricultural lands recently abandoned with regrowth vegetation between 1 and 8 years old. Only seven to nine Hyperion bands were required to separate pristine vs. degraded primary forest, young vs. mature vs. mixed secondary forest, and fallows of 1–3, 3–5, or 5–8 years old. When all rain-forest vegetation was pooled, approximately 23 Hyperion bands were required to achieve adequate separability.

Indeed, examination of average reflectance spectra for the different vegetation types indicated that the Hyperion data provided many possibilities for separating vegetation categories using specific narrow bands throughout the 600- to 2350-nm spectral range. The most important wavebands were early mid-infrared (EMIR; 1300–1900 nm) bands followed by far near-infrared (FNIR; 1100–1300 nm), far mid-infrared (FMIR; 1900–2350 nm), and red (600–700 nm) wavebands. The results of this study showed that the two most frequently occurring wavebands sensitive to predicting forest biomass were centered at 682 and 1710 nm. Consequently, this study reaffirms the importance of using bands near 680 nm, as previously established by Thenkabail, Smith, and De Pauw [82], that are within a maximal absorption region for crops and vegetation. Some of the most important bands useful for detecting different vegetation types in this study were those related to leaf biochemical and physical traits such as content of water, chlorophyll, starch, lignin, cellulose, and proteins. Biophysical characteristics of vegetation such as biomass, vegetation growth, and leaf types were also important to obtain this segregation. Provided that most of these traits do differ among species in tropical forests [72], the potential use of hyperspectral remote sensing in the tropics to identify groups of species displaying different functional attributes associated to specific successional stages is clear.

2.3.2 DISCRIMINATION OF VEGETATION TYPES

Hyperspectral remote sensing has already shown important capabilities to differentiate vegetation types, especially when combined with data from other sensors such as radar that provide concurrent information about forest structure. An example for high-diversity mangrove systems is provided by Held et al. [83]. The study emphasizes the potential of hyperspectral scanners for identifying groups of species occurring under different grades of environmental stress. Provided that every group of species shares an assembly of physiological, anatomical, and ecological characteristics that allows survival under particular conditions, the differences among such groups

should be detected by hyperspectral sensors facilitating the discrimination of plant functional groups.

In mangrove ecosystems, gradients in salinity, tide action, and drainage often cause major differentiation in species composition and structure across a linear spatial arrangement from the water edge to inland. Thus, high-diversity mangrove systems can contain up to 30 different species, broadly segmented into “mangrove zones” [83]. In order to describe these ecosystems accurately and objectively in terms of their zonation, productivity, and diversity patterns, Held et al. [83] conducted an analysis combining high spatial (3-m pixels or less) and spectral resolutions by using SAR (synthetic aperture radar) and the airborne hyperspectral scanner CASI (compact airborne spectrographic imager).

Although SAR data separated the vegetation into its general structural groups quite well, it had difficulty discriminating any further detail; thus, the SAR-only analysis correctly classified 57.9% of the mangrove types. The CASI-only data, on the other hand, provided finer detail but exhibited considerable confusion between structurally different vegetation classes—specifically, between the sand-dune vegetation and mixed stands of the plant *Bruguiera* sp. The CASI-only analysis classified 71% of the mangrove types present in the subset. However, when the data from both sensors were considered together, the classification accuracy increased to 76%. There are only a few cases where mangrove types have been classified at this level of detail within an individual estuary. This study, therefore, showed that there is considerable scope in use of high-resolution hyperspectral data for detecting, mapping, and monitoring mangroves at the necessary level of detail for mangrove diversity, ecological, and even ecophysiological studies. This study also shows the potential of a combination of remote sensing techniques for increasing the level of accuracy in the detection of vegetation types.

2.3.3 LIFE FORM DISCRIMINATION

A specific case attempting to discriminate between species with different biochemical properties and ecological traits with hyperspectral data is the study of Castro-Esau et al. [68]. The objective of this study was to determine if it is possible to distinguish between lianas and supporting trees, at the leaf level, using hyperspectral reflectance measurements taken for two communities of tropical liana/tree species from a tropical dry forest (Parque Natural Metropolitano, Panama) and from a tropical wet forest (Fort Sherman, Panama). The study showed that lianas and trees from the tropical dry forest are distinguishable based on their spectral reflectance at the leaf level with the use of pattern recognition techniques. It is suggested that the chlorophyll concentration of liana leaves is lower than for tree leaves and that this difference is highly significant, resulting in an increase in reflectance at 550 nm as liana quantity/coverage increases.

Differing levels of water or nutrient stress (i.e., nitrogen) between lianas and trees could also have induced the differences observed in leaf reflectance between lianas and trees, and/or possibly differences in photosynthetic capacity between the two structural groups. Indeed, lianas typically were forming monolayers above tree crowns, favoring high light interception and low light transmission. Trees, in

contrast, favor greater light transmission [68]. According to the authors, further study is required to clarify the physiological mechanisms between the two groups and whether such differences are maintained throughout the year. It must be emphasized, however, that in this case hyperspectral data effectively reflected general physiological differences between species with different ecological traits. Information produced in this respect could be useful for mapping species or communities with applications in biodiversity assessment studies. Indeed, mapping of lianas would be helpful for carbon budgets' estimation, because carbon sequestration is impeded in areas where liana proliferation obstructs tree regeneration to the point, in some cases, that a net release of CO₂ can be measured for some tropical forests [84,85].

2.3.4 DISCRIMINATION OF BIOPHYSICAL PROPERTIES

Hyperspectral remote sensing has proven to be useful in distinguishing biophysical properties of tropical forests, which usually differ among vegetation types. Kalacska et al. [79], for instance, examined forest structure and biodiversity of tropical dry forest from satellite imagery. They addressed the inference of neotropical dry forest biophysical characteristics (i.e., structure), biomass, and species richness directly from hyperspectral remote sensing imagery acquired over three seasons: wet, transition, and dry. They also examined six narrowband spectral vegetation indices that were sensitive to canopy characteristics in other ecosystems: normalized difference vegetation index (ND705), canopy normalized difference vegetation index (NDcanopy), single ratio (SR705), canopy single ratio (SRcanopy), modified single ratio (MSR), and canopy structure index (CSI). The results of this study showed that all canopy characteristics share similarities in shortwave infrared, except for biomass, which had important spectral regions in the visible, near infrared, and shortwave infrared. In addition, for species richness, the shortwave infrared was also heavily favored with the exception of one wavelength from the visible.

In contrast, for canopy height, basal area, and the Holdridge complexity index (HCI), none of the wavelengths were from the visible range, but instead all wavelengths were from the near infrared and shortwave infrared (743–2257 nm). Differences in canopy openness and structure among seasons were considered the most important factor in predicting biomass. According to the authors, low-canopy leaf area index (LAI) observed in the dry season exposed woody material, leaf litter, and soil with minimal to no contribution from green leaves, accounting then for the importance of the shortwave- and near-infrared regions. The intermediate stage had an important contribution of woody material and dry leaves, of less importance of the soil and green leaves; while in the late stage the green leaf was an important contribution to the spectral response in the visible region of the spectrum.

These studies provide new techniques to identify groups of species with functional differences by their particular biophysical properties, especially when such differences are reflected at the phenological level. In this sense, hyperspectral technology would allow for more accurate quantification of forest biophysical and biochemical attributes, which is essential for biodiversity assessment, land cover characterization, biomass modeling, and carbon flux estimation [86].

2.4 HYPERSPECTRAL REMOTE SENSING AND FUNCTIONAL GROUP STUDIES: PRESENT AND FUTURE APPROACHES

The capability of hyperspectral remote sensing to discriminate among plant functional groups has already been explored directly or indirectly, as mentioned in the previous section. However, such a discriminatory capability has several potential applications that have not been properly explored at present in the tropics: for example, differentiation of land vegetation/forest types, carbon flux estimates, description of ecosystem status, and assessment of vegetation functional changes, among others. Now we will briefly explain some of these potential applications in order to present a general view of future approaches for studies on tropical vegetation.

2.4.1 VEGETATION TYPE DISCRIMINATION ON TROPICAL LAND VEGETATION

Vegetation surveys in tropical forests are difficult and time consuming because plant species diversity is extremely high, their taxonomy is known only by a few specialists, and remote areas are logistically difficult to work in. As a result, it is difficult to collect field data that cover the area of interest sufficiently [87]. Remote sensing data are then an alternative technique that could be applied for separating vegetation types [88].

Provided that tree species composition is related to soil differences [89], spectral characteristics may behave similarly because they are mostly determined by the forest canopy. For example, Salovaara et al. [87] were able to separate floristically defined terra firma forest classes in Amazonia from Landsat ETM+ images with a reasonable accuracy. On the other hand, inundated and noninundated forests have been mapped and discriminated with high accuracy by Hess et al. [90]. Hyperspectral data, however, could help discern unique spectral patterns of different vegetation types and could be useful in extracting biophysical information such as biomass. These data will then be extremely useful for vegetation studies since they can contribute to tropical functional group differentiation. Indeed, hyperspectral remote sensing would be especially helpful for this purpose in complex tropical rain forests, where the distribution patterns of individual species are poorly known and a high level of accuracy is required. This type of datum could additionally offer valuable information for sustainable resource use and biodiversity conservation, where vegetation types can be used as surrogates for modeling the distributions of species and communities [91].

2.4.2 CARBON FLUX ESTIMATIONS

Globally, terrestrial vegetation sequesters some 100 Pg of carbon from the atmosphere each year for the production of organic matter through photosynthesis, half of which occurs in the tropics. The role of the various major forest ecosystems in the carbon cycle must therefore be assessed, particularly as carbon sinks that may be managed to reduce the atmospheric carbon load. Currently, attention is focused on tropical forests, which cover 7% of the Earth's land surface, playing a major but poorly understood role in the cycling of carbon [92].

Many studies have used remote sensing analysis to discriminate between mature tropical forest and nonforest areas [93] because monitoring of secondary forest

regrowth may be important in the carbon balance of the tropics. Tropical secondary forests that follow nonforested stages have the facility to decrease atmospheric carbon concentrations to some degree in relatively short periods of time [94]. Recent special attention to tropical secondary forests may then be attributed to their capacity to act as carbon sinks and their potential role to serve as regulators of climate change. A secondary forest may actually have higher net primary production than a mature forest and may rapidly sequester carbon from the atmosphere, converting it to biomass. The strength of this carbon sink and the size of the resulting carbon pool depend on a range of factors, such as species composition and, remarkably, on the age of the regenerating forest [95]. Thus, to understand the role of regenerating forests as carbon sinks, information about their age, species composition, location, and extent is required. The most feasible way to derive this information is through remote sensing [92].

In order to analyze the progress and future potential of research to monitor carbon sequestration, Castro-Esau, Sanchez-Azofeifa, and Rivard [96] reviewed the attempts for estimating secondary forest biomass from space-borne data in the neotropics. This review states that considerable progress has been made in classifying neotropical secondary forests according to age using Landsat TM data. Currently, most Landsat TM studies of secondary forests have separated few broad regrowth classes of fairly young age (usually up to 20 years old or less) and with varying degrees of accuracy. The majority of studies analyzed have involved multitemporal images of sites in the Brazilian Amazon. Foody et al. [92], for instance, investigated ability of Landsat TM data to identify different successional stages of tropical rain forest in Amazonia. A range of forest classes (11) varying in strength as carbon sinks was identified accurately from these data. Their results also indicated that the youngest age class may be more variable in composition and spectral response than the older forest. This could be a function of a range of successional pathways being followed.

These results demonstrated that it is possible to use image classifications to scale up point measurements of carbon flux between regenerating forest classes and atmosphere over large areas. Moreover, the dynamics of the forest succession was to some extent manifested in the remotely sensed data. Castro-Esau et al. [96] stated that, although much research is required, it is possible that accurate classification of secondary forests in tropical areas will necessitate the use of imagery with higher spectral resolution (i.e., hyperspectral data) from which unique spectral signatures (i.e., for certain common crops) might be determined for their distinction from secondary forests. Furthermore, the capability of hyperspectral remote sensing to discriminate the dominant species within a regenerating forest would refine carbon accounting models, increasing classification accuracy of regeneration stages. Hyperspectral remote sensing could then be used to classify regenerating tropical forest classes accurately and even to identify different successional pathways.

Hyperspectral data will also be especially useful in highly heterogeneous sites, where pixels with mixed classes would be abundant and an entire area of interest with secondary forests of varying ages might occupy only a few pixels [96]. However, we must consider that the use of only hyperspectral data could eventually fail when discriminating different secondary forests, especially when dealing with highly homogeneous areas. An example of such limitation is the study performed by

Lucas et al. [97], who made the first attempt at mapping tropical forest regeneration stages using only hyperspectral data in the Brazilian Amazon and failed to obtain an acceptable level of accuracy for further estimation of biomass and carbon accumulation rates. Thus, the combination of hyperspectral imagery with data from other sensors is recommended. The integration of Landsat TM data with selected Hyperion scenes, for instance, may be useful for the separation of secondary forests from land cover types that have appeared spectrally similar [96]. Nonetheless, the determination of secondary forest biomass content from remote sensing data with greater precision would provide a better understanding of the role of secondary forests in global biogeochemical cycles as well as of their potential for mitigating atmospheric carbon [96].

2.4.3 DIRECT DETECTION OF PLANT FUNCTIONAL TYPES

Hyperspectral data have directly been used to discriminate plant functional types in nontropical zones. Studies carried out by Schmidlein and Sassin [98] used hyperspectral remote sensing to analyze gradual floristic differences difficult to assess by conventional field surveys. They ranked species according to their functional responses and successfully modeled gradients in the appearance of plant functional response groups. These modeled gradients served to map species distributions. The results from this study indicate the potential of hyperspectral remote sensing and gradient analysis for mapping of continuous gradients in species assemblages. Of course, longer-term work with multitemporal data is needed to determine whether the approach can become a useful supplement to ground surveys. Such investigation must also be performed in the tropics in order to analyze functional diversity.

A specific attempt to discriminate tropical plant functional groups is currently being performed in a Mexican tropical dry forest by the authors. In order to identify and characterize secondary forest we are determining functional groups of plant species from different successional stages in the tropical dry forest of Chamela, a highly diverse tropical system located on the Pacific coast of Mexico. To define functional groups we decided to evaluate different morphological and physiological attributes highly involved in resource acquisition mechanisms, such as maximum photosynthesis, leaf dynamics, relative growth rate, and various leaf traits (specific leaf area, blade shape, thickness, water content, and chlorophyll content).

Preliminary results suggest that attributes such as water content, photosynthesis, specific leaf area, and chlorophyll content account for a substantial part of the functional differences observed among species from different successional stages, as well as among individuals of the same species growing in different stages. The phylogenetic origin of species appears to be an important factor for the variability of functional traits among evaluated stages. However, species growing in the different successional stages showed important differences in such traits, providing evidence of the response of certain functional traits to specific environmental factors associated with successional change. Variability of evaluated functional traits must be reflected at the spectral level, as demonstrated by Castro-Esau et al. [72]. Thus, by relating these attributes to the spectral reflectance of each species, we will be able to recognize the different types of secondary tropical dry forests (successional stages)

by hyperspectral remote sensing. This kind of information is crucial for the understanding of the natural regeneration process as well as to determine the area covered by secondary vegetation in the tropics.

2.4.4 CHANGES IN FUNCTIONAL PROPERTIES OF ECOSYSTEMS

As mentioned previously, remote sensing can provide accurate estimates of functional features of tropical forests. Studies assessing changes in functional properties of the tropics by using remote sensing have been performed with coarse-resolution imagery by Koltunov et al. [99]. Provided that changes in forest function can be expressed as changes in forest phenology, these changes can be detected via remote sensing. Koltunov et al. used MODIS imagery to show that removal of timber species during selective logging changes forest composition and structure. Imagery analysis showed changes sufficiently large in magnitude to alter biosphere–atmosphere exchange of CO₂, water vapor, and energy in the logged regions of the Amazon basin. These changes could, in turn, alter a range of biogeochemical processes in the region and may have cascading effects on the regional climate system.

In the same sense, in order to understand canopy gap dynamics following selective logging, Asner et al. [100] used a spectral mixture analysis of the Landsat ETM data to estimate damage as well as to monitor intensity and canopy closure following timber harvests in eastern Amazon forests. They evaluated the impacts of different kinds of logging in terms of the canopy gap formations and showed that approximately one-half of the canopy opening caused by logging is closed within 1 year of regrowth following timber harvests. As stated by Asner et al., forest canopy damage monitored by remote sensing has several applications at the regional level—for example, to predict the location of fire-prone sites and respiration hotspots likely to result from coarse woody debris and damaged roots. Spatial and temporal dynamics of faunal species can also be linked to forest disturbance. Thus, an understanding of the components of canopy recovery will be important both for carbon balance as well as for other ecological and biogeochemical functions of the system [100]. These findings highlight the need for using higher resolution data to carry out a detailed analysis of the consequences of selective logging or other anthropogenic disturbances that may cause changes in the functional properties of tropical systems.

2.5 CONCLUSIONS

The current conservation status of tropical forests demands systematic approaches to study functional diversity. Such approaches must focus on the discrimination of coherent (consistent) plant functional groups as representative as possible of the great diversity of these systems. Assemblages of ecophysiological characteristics are considered of great utility to characterize tropical functional groups. These characteristics are susceptible to being detected and analyzed with modern techniques such as hyperspectral remote sensing, which allows for studying vegetation at a landscape level. At present, the capability of hyperspectral remote sensing to detect anatomical, biochemical, and biophysical properties of vegetation has been applied to tropical forests to discriminate successional stages, structural characteristics, life

forms, and vegetation types, among others. Thus, the high accuracy and discriminatory capability of this technique on the detection of information of ecological relevance could be used for the discrimination of plant functional groups in the tropics. Such an approach would generate valuable knowledge about tropical functional diversity, would constitute a powerful tool for the study of forest dynamics, and would contribute to our understanding of the responses of tropical vegetation to human disturbance and climatic change.

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