Preface

Our World is changing rapidly, yet, how tropical forests will respond to this change and in turn dampen or accelerate its ripple effects is essentially a physiological question. Addressing important questions regarding the impacts of changes in land utilization, such as deforestation, and effects of global climate change will require specific information on tropical tree physiology. Earth system modeling scientists are clamoring for more physiological data from tropical trees. It seems that the scarcity of information on the physiological responses of trees is the greatest source of uncertainly in predicting how the tropical rain forests will respond to increasing greenhouse gases and in particular increasing atmospheric CO_2. For example, tree species can adjust their physiological behavior to increasing global temperatures or decreases in precipitation, or they can be replaced by other species better adapted to the new environmental conditions. It is also true that the physiology of tropical trees has not been as well-studied as the physiology of trees from temperate regions, leading to major gaps in our understanding of how tropical trees interact with the Earth system over a range of scales.

It is known that the physiological behavior of both tropical and temperate trees is regulated by similar mechanisms. The differences, however, are related to the unique selective pressures to which tropical trees have been subjected during the evolutionary process and its adaptive consequences. The idea put forward by Theodosius Dobzhansky in the 1950s that tropics and temperate zones are areas where selection operates differently, generated fruitful lines of thinking and research. His contention was that in temperate areas mortality was essentially climatically determined, with little or no competition pressure, while in the tropics, where the environment is relatively more constant, at least in terms of seasonal changes in temperature, mortality is the result of the effects of population size and competition. This paradigm of evolutionary pressures has changed substantially but some aspects of it still remain as a guide for understanding differences in patterns of adaptation between temperate and tropical plants. Negative density dependence prevents any single tree species from dominating most tropical forest ecosystems. The reasons for this must be sought not only in ecological and demographic processes but also among the highly diverse physiological characteristics of tropical trees. In the tropics, seasonal temperature variations are relatively small compared to diurnal temperature changes and if soil water is available, growth and metabolic activities can be maintained throughout the entire year. Heavy herbivore pressure is continuous and the adaptive responses of tropical plants to herbivory are impressive. The physiological implications of various types of mutualisms found among tropical trees are also important. Many trees have a relatively short life span of less than 200 years in the wet tropics compared to more than a 1000 years in some temperate-zone trees.

There has been a substantial increase in the number of studies of tropical tree physiology during the last few decades. The reason for this is not only that trees are the dominant growth form in most tropical ecosystems, but also because of increasing availability and refinement of equipment such as portable photosynthesis systems and instruments for studying water relations of plants. Furthermore, a substantially larger number of tropical biologists are now involved in more mechanistic studies. The use of tower cranes during the last 25 years has allowed scientists to reach the canopy of tropical forests, one of the ultimate frontiers for unveiling not only new organisms but also new processes that were unthinkable just a few years ago.

A distinct feature of tropical trees is not only their high species diversity but also the large variety of life history traits and growth forms that are mostly unique to the tropics such as hemiepiphytic trees, stem succulent trees such as baobab trees, mangroves, palms and other arborescent monocots, and unusual arborescent plants near tree line that are not traditional trees. The wide range of shade tolerance from rapidly growing pioneer trees during gap-phase regeneration to species that can survive by growing slowly in deep shade contribute to this diversity.

Tropical trees tend to grow in habitats where soil water availability is high all year round or at least in habitats were it is seasonally available. They grow in arid environments were they access deep soil water such as in the case of phreatophytic trees. They also occur along altitudinal gradients within the tropics up to the upper tree line and in some cases, such as the caulescent giant rosette plants, they can grow above the continuous forest line. They extend to the subtropics, and in many cases they share close phylogenetic relationships with subtropical tree species, and the structure and function of subtropical forests are in many cases similar to tropical forests, in regards to gap-phase regeneration and the high abundance of lianas.

Through 20 chapters authored by 55 people, this book captures the current state of knowledge of the main physiological characteristics of tropical trees. The book was as a way to not only to provide information gathered during the last few years across the world, but also for laying the foundation for discussing controversial paradigms and new hypothesis of physiological process and mechanisms of trees. Thus this book will surely capture the attention not only of tropical biologists but also of biologists working in many different types of environments around the globe. Physiological consequences of global environmental change will permeate most book chapters, as it provides a dynamic arena for tropical trees to respond. The book is organized in six main parts. The first one is on the physiology of unique tropical growth forms. This group of conspicuous plants is extremely important for understanding the structure, function, and dynamics of tropical forests, as well as understanding why certain species live where they do and not elsewhere. Hemiepiphytic trees with an unusual progression of life stages and obligate epiphytes with a unique photosynthetic pathway, are plants that capture the environmental and demographic wonder of forest ecosystems: Do they start their life cycle (as in the case of hemiepiphytic trees) or spend their entire life cycle (as in the case of obligate epiphytes) in the upper canopy to utilize higher levels of incoming solar radiation or to escape the shady understory with high chances of damage by falling debris and exclusion by competition with other plants? Stem succulents trees, such as the fat-stemmed baobabs, which have captured the imagination and attention of writers, such as in the case of "the little prince" by Antoine de Saint-Exupéry, are fascinating trees occurring mostly in seasonally dry forests. The enlarged stem with photosynthetic surfaces, leaves that drop during the dry season and with little biomass allocation to root systems, appear to have a combination of physiological and anatomical traits that at first sight is difficult to understand. Do their low wood density trunks represent conspicuous water storage? Is stored stem water used for new leaf growth near the end of the dry season or to maintain stem conductance during the rainy season? Does the large size of the stem serve a biomechanical role for providing stability to tall mature trees? Palms are another unique growth form, nearly always associated with tropical environments. The hydraulic architectures of these monocots have long intrigued physiologists working on plant water relations and hydraulic architecture. How can trees that do not have secondary growth, and thus cannot produce new xylem tissue after the plants start growing in height, cope with intensive droughts and the dysfunction of cavitated xylem vessels? Finally lianas, which have solved the problem of reaching the upper canopy without investment in a large diameter stem, can move large amounts of water to transpiring leaves. How did these plants solve this important water economy constraint imposed by a relatively narrow stem?

The second part of the book deals with adaptive responses of trees growing in habitats that are unique to the tropics. Mangrove trees occur in coasts across all tropical regions with roots taping seawater. Floodplain trees tolerate freshwater inundation for several months in inland tropical regions and in some cases are completely covered by water. At high elevation, tropical giant rosette plants represent one of the most fascinating cases of evolutionary convergence among tropical alpine climates that are characterized as "summer during the day and winter at night."

The third part of the book discusses emergent paradigms on hydraulic architecture and water relations. The high diversity of tropical tree species allows the use of a wide array of physiological and morphological traits. This provides fertile ground for testing new hypothesis on the adaptive significance of physiological mechanisms for how trees cope with drought, and how they may avoid or repair cavitated xylem vessels, or how close they are to their physiological limits of water availability in the face of extreme climatic events.

The fourth part of the book deals with important responses of trees to a limitation common in tropical soils: low amounts of available nutrients. How valid is the paradigm of widespread phosphorous limitation? What can be inferred from litter manipulation and fertilization experiments in tropical forests? What are the dynamics and the roles of litter accumulation and decomposition? What is the main distinctive characteristic of nutrient cycling in tropical ecosystems dominated by trees? Do nutrients limit the ability of tropical trees to respond to climate change, or can trees adjust and adapt to nutrient limitations to carry on the process of photosynthetic carbon assimilation? Do N and P equally limit the photosynthetic process in tropical trees?

Carbon economy and biomass allocation patterns in tropical trees and forests are the focus of the fifth part of the book. Important issues related to carbon cycling and the strength of carbon sinks across terrestrial ecosystems worldwide are analyzed. In particular, the continuum of physiological traits from high light requiring pioneer trees to slow growing shade-tolerant trees is discussed in terms of primary and secondary succession in tropical forests and gap-phase regeneration. These two groups of trees are considered as the extremes of a gradient of species requiring high light levels for photosynthesis and rapid growth and in species tolerant to diffuse light and the use of light flecks for carbon assimilation. Are there trade-offs in carbon allocation between defense against herbivores and growth? Compared to tropical and temperate forests, subtropical forests have received little attention until now, and the contribution of this region to the global carbon cycle has not been fully assessed. In this part the carbon balance of subtropical forests at different spatial and temporal scales will be analyzed. The reader will be surprised to know that many subtropical forests are strong carbon sinks, and perhaps the strongest when compared to other terrestrial ecosystem.

In the last part, ecophysiological processes at different spatial and temporal scales are analyzed. Until recently the trunks of tropical trees in lowland areas were assumed not to have tree rings. Several studies have found that this is not the case, particularly in seasonally dry environments, which opens a window of opportunities for using tree rings to acquire insights into the ecology and climate sensitivity of tropical trees as well as the possibility of obtaining the age of individual trees. This part also addresses biomechanical characteristics of tree, with special references to the constraints of being a tropical tree. Do tropical trees adhere to the same biomechanical laws as temperate trees?

In the past 20 years since we began working together, we have seen tropical ecophysiology evolve from single species studies to large comparative works that embrace the high diversity of tropical forests. We have seen a transition from descriptive and natural history studies, which provided an important foundation, to advanced quantitative and modeling approaches that reveal broader patterns in space and time. Plant ecophysiology in the tropics has also developed strong linkages to disciplines that focus on larger spatial scales, including community ecology, ecosystem ecology, and landscape ecology, as well as smaller spatial scales such as molecular biology, stable isotope ecology, and genomics. This book represents the work of a community of leading tropical ecophysiologists, many of whom are colleagues and collaborators. We hope that it will provide a useful resource for understanding, conserving, and sustainably managing tropical forests, as well as predicting how these ecosystems will respond to future climate change.

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