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INVITED PAPER

MINIREVIEW

The Scientific Development of the Physiology of Plants in the American Tropics

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Abstract: This paper is a research and journalistic work that summarizes and synthesizes the scientific development of the physiology of plants in the American tropics, also known as the Neotropics. It contains the contributions of numerous biologists interested in the physiology of tropical plants. The fabulous structural and functional diversity of tropical forests is still the major driver of research in this field. Classical physiological work involving tropical plants, such as the discovery of C4 photosynthesis in sugarcane, is invoked to exemplify the historical and current importance of physiological research in the tropics, and its applications in agriculture, forestry and conservation. An historical background describing the early and more recent development of a tradition on the physiological study of tropical plants is followed by a summary of the research conducted on the physiology of tropical crops. Common areas of interest and influence between the fields of crop physiology and plant ecophysiology are identified and exemplified with problems on the environmental physiology of crops like coffee and cassava. The physiology of tropical forest plants is discussed in terms of its contributions to general plant physiological knowledge in areas such as photosynthetic metabolism and plant water relations. Despite the impressive technical advances achieved during the past decade, the importance of continuous development of appropriate instrumentation to study and measure the physiology of plants *in situ* is stressed. Although the basic metabolic processes that underlie the mechanisms of plant responses to the environment are probably highly conserved and qualitatively similar among tropical and temperate plants, it is also apparent that tropical plants exhibit metabolic peculiarities. These include aspects of photosynthetic metabolism, phloem transport physiology, sensitivity to low temperatures, reproduction, responses to climatic seasonality, and a large variety of biotic interactions. Old and new paradigms are examined in light of recent evidence and comparative studies, and the conceptual and technical advances needed to foster the development of tropical plant ecophysiology are identified.

Key words: Plant Physiology, neotropics.

Physiological investigation reveals the mechanisms responsible for the adaptive strategies of tropical plants, and remains as the only scientific approach to explain, in physiological terms, the mechanisms by which plants adapt and persist as long-term members of tropical communities. The concerns of physiological investigations range from biochemical and organelle-scale processes to successional and evolutionary-scale events involving communities and ecosystems (Osmond *et al*. 1980).

Classical physiological work involving tropical plants, such as the discovery of C4 photosynthesis (Burr 1957, Kortschak *et al*. 1965), is frequently invoked to exemplify the historical and current importance of physiological research in the tropics and its implications in agriculture, forestry and conservation. The recent expansion experienced by diverse areas of tropical plant ecophysiology is partially the result of widespread availability of automated data-logging systems, of major technical and conceptual advances that allow the routine measurement of a variety of physiological processes in the field, and of continuous recruiting of highly capable scientists within the field. Mulkey, *et al.* (1996) summarize the state of knowledge and recognize that the study of the ecophysiology of plants under tropical conditions has achieved the stature of a mature scientific discipline, and that its development goes far beyond the interface between physiology and ecology.

The fabulous biological diversity of tropical forests that fascinates us today continues to be a major driver for research on the physiology of tropical plants. This diversity can be exemplified in 100 m^2 of tropical rain forest in Costa Rica, where 233 species of vascular plants (including 5 tree species and 102 woody seedlings) co-exist with 30 species of vines and lianas and 59 species of epiphytes (Whitmore, *et al.* 1985). Recent studies of the Amazon flora suggest that in addition to high structural and functional diversity, high physiological plasticity underlies the abundance and distribution patterns of tropical tree species (Pitman *et al.* 2001).

Why are there so many species of tropical plants? Which mechanisms allow their co-existence in tropical forests? How do these species compete and allocate limiting resources in their respective environments? How do they respond to environmental heterogeneity, herbivory and climatic unpredictability? Is functional diversity a consequence of taxonomic and morphological diversity? Research on tropical plant ecophysiology has approached those and many other important questions that require physiological explanations in an ecological context (Mulkey, *et al.* 1996). Major areas of inquiry include:

- The physical, chemical and biological environment of tropical plants.
- Water relations and gas exchange.
- Carbon assimilation and carbon balance.
- Below-ground processes and acquisition of soil resources.
- Growth and environmental effects on development.
- Competition, herbivory and other types of biological interactions.
- Stress physiology and stress adaptation.
- Physiological and environmental control of forest phenology.

This chapter is based mostly on library and journalistic field work conducted during the course OTS 01-25 “Advanced Comparative Neo-tropical Ecology” (Sept. 5 - Nov. 15, 2001) at La Selva Biological Station in Costa Rica, Barro Colorado Island in Panamá, Cocha Cashu Natural Reserve in Perú, and the Forest Fragments Project in Manaus, Brasil. Several sections represent a synthesis of my conversations with outstanding tropical ecologists and physiologists: Deborah Clark, Robin Chazdon, Rick Meinzer, Missy Holbrook, Lourens Poorter, Kaoru Kitajima, Roberto Cordero, Joe Wright, Rita Mesquita, Klaus Winter, Louis Santiago, Gordon Orians and Egbert Leigh. They kindly offered their knowledge and personal perspective of plant physiology, and I would like to acknowledge their contribution and enthusiasm for our field of research. I am responsible for the synthesis, as well as for the omissions.

Historical background

The early exploration of the American tropics by European and North American naturalists resulted in the publication of seminal work on ecophysiology, which provided for the first time a picture of the unique aspects of the physiology of tropical plants. Ernst Stahl first introduced physiological experimentation into plant ecology (Lange *et al*. 1981a). Despite the strong physiological and phytogeographic views and hypotheses of Haberlandt, Schimper, Warming and Clements (1907) on plant responses and adaptations to their environment (see Lange *et al*. 1982a for an account of early work), physiological research of tropical plants was confined to the laboratory until approximately 1925.

That generation of outstanding researchers was followed by the real founders of modern ecophysiology, which include Huber (1935) and Walter (1973) in Germany, Daubenmire (1947) and Vareschi (1953) in Latin America, and Billings (1957) in North America. Many other physiologists started the simultaneous development of research in other tropical regions of the world including Australia (Beaddle) and Israel (Evenari). They fostered the initiation of a highly prolific school of modern ecophysiologists during the 50s and throughout the 70s, removed three to four generations from Schimper. Their contribution to the field is summarized in three volumes of “Physiological Plant Ecology” (Lange *et al.* 1982).

Physiological research conducted in the field is heavily dependent on appropriate methods and instrumentation (Ehleringer *et al.* 1986; Mooney *et al.* 1987; Mooney 1991). Progress in physiological research carried out in the field in general and in the tropics in particular was the result of the ingenuity of many creative ecophysiologists, who adapted instrumentation used in industrial applications (i.e., IRGAs), and adopted techniques employed in other fields such as Meteorology and Soil Science. Parallel advances occurred in the measurement of microclimate on a scale relevant to plant responses (Monteith and Unsworth 1990, Nobel 1991). Examples of this work include studies on the transport of gases in and out of leaves (Gaastra 1959) and the development of the theory of energy balance (Gates 1962).

Similar to their colleagues working in temperate ecosystems, and following the advise of the early ecophysiologists that the relations between the environment and morpho-physiological traits of plants are better studied under extreme conditions, the exploration of physiological adaptations in Tropical America began in deserts (see Givnish 1986), alpine environments (see Rundel *et al.* 1994), and with spectacular examples of adaptations found for example in mangroves (Ball 1996), lianas, and hemi-epiphytic life forms (Holbrook and Putz 1996). This emphasis later shifted to the intensive investigation of the physiology of tropical rain forest plants that still dominates the field today (for example Medina *et al.* 1984; Clark *et al.* 1987; Mulkey *et al.* 1996).

However, the tropics hold much more than rain forests, and a variety of publications contain results of research conducted specifically on the physiology of plants in tropical alpine environments (Rundel, Smith and Meinzer 1994), savannas and seasonally dry (Bullock, Mooney and Medina 1995) and flooded forests (Fernández *et al.* 1999, Parolin 2001), cloud forests (Hamilton *et al.* 1995, Kappelle and Brown 2001), mangroves and coastal ecosystems and several other biomes (see Lüttge1997). Gone is the time when Larcher (1975) was the only reference for those interested in the physiological ecology of tropical plants.

Several attempts have been made to integrate the forest forming factors, soils and climate, into models to predict forest structure, diversity and distribution (Holdridge 1978). Modern views indicate however that such rules break down when the biological interactions are considered. This suggests that the great biological diversity of tropical forests will require a life-form approach to the study of ecosystem processes, and the use of allometric rules for scaling from physiological to ecologically-relevant scales of observation. In this direction, vascular systems have been implicated as a major force controlling allometric scaling in the size, form, and even population density of woody plants (West *et al.* 1999).

Research on the physiology of tropical crops

The early development of crop physiology in the tropics was fueled by the world-wide importance of various herbaceous (beans, corn, banana) (see Evans 1975) and perennial (coffee, cacao, rubber) crop species (see Alvim and Kozlowski 1977). Applications of physiological knowledge to crop production (see Evans 1975; Gardner *et al.* 1985) and the use of micrometeorological techniques to reliably measure processes in more uniform crop canopies (see Rosenberg *et al.* 1983), resulted in highly synthetic sets of physiologically-based recommendations to improve crop production. Crop growth models were also born and later applied to natural communities (Coombs *et al*. 1982). These pragmatic recommendations, exemplified by the Green Revolution and later replaced by more sustainable approaches, included modifications of plant architecture to increase crop photosynthesis and yield, and strategies to cope with multiple types of stress and limiting factors typically found under tropical conditions.

Important physiological and morphological adjustments were obtained during the continuous domestication of tropical crops (Heiser 1985), and successful physiological strategies to increase their yield were devised. From a physiological perspective, higher yields of tropical crops have been obtained almost exclusively through the modification of the patterns of assimilate partitioning by genetic selection or by horticultural manipulation of the source:sink ratios (Cannell and Jackson 1985).

Crop physiologists working in the tropics realized the consequences of the C4 photosynthetic syndrome discovered in sugar cane (Burr 1957) and present in other tropical grasses like sorghum, corn (Sage and Monson 1999), and some of the most aggressive weeds of the world (Holm *et al*. 1977). The local diversity of other highly productive heliophyte crops (oil palm, yams, cassava) was also exploited to generate architectural and metabolic modifications for cultivation in a variety of environmental conditions (Corley 1983). For example, deeper understanding of plant-environment interactions in traditionally shaded crops such as coffee and cacao allowed the exploitation of crop physiological plasticity in the design of management strategies suited for different sites around the world. Although agronomists recognized that shade was not an environmental requisite for the cultivation of these crops, they soon realized that cultivation under full radiation increased mineral uptake, photosynthesis, and yield, but also substantially reduced the life span of these perennial species (Carvajal 1984).

Physiological investigations provided insights into the biannual phenological behavior of tropical trees, and reliable horticultural practices to modify tree phenology were developed (Cannell and Jackson 1985). Also, important advances in our understanding of flower dormancy and bud break were obtained utilizing tropical species as experimental material (Crisosto *et al.* 1992). Conceptual and technical advances in the study of root systems (Waise, Eshel and Kafkaki 1996, Smit *et al*. 2000) and belowground processes (Hillel 1998) are still the result of the strong influence of soil science on research concerning the physiological basis of crop production and on plant eco-physiology in general.

Considerable progress has also been made in identifying and overcoming the physiological limitations to crop productivity in tropical regions. These include inefficient light interception caused by sub-optimal leaf area index, high temperatures, reduced leaf life span, and constraints on assimilate partitioning patterns (Corley 1983). Photorespiration is frequently mentioned as a major drain to biomass production of C3 crops in the tropics, because the ubiquitous year-round high temperatures and frequent water stress exacerbate this process. It has been speculated that reductions of both respiratory and photo-respiratory release of CO_2 of C3 crops is possible via the genetic modification of key respiratory enzymes and RuBisCO, respectively, or the increment of $[CO_2]$ within the crop canopy. Attempts to increase crop yields by the application of substances that reduce photorespiration (i.e. ethanol) will probably face the fact that crop yields in the tropics are more limited by inadequate agricultural practices than by physiological or environmental constraints.

Agricultural production will benefit from the continuous conceptual and technical developments experienced in field ecophysiology and outlined in the following sections. An example of this is the application of physiologically-based, “medical” approaches to solve problems in the field of plant protection and pest management (Higley *et al.* 1993).

The physiology of tropical forest plants

Several areas of physiological knowledge in general have benefited greatly from the research conducted in the tropics. These include the study of:

- Photosynthetic metabolism and ecophysiology, particularly aspects of photosynthetic differentiation in higher plants.
- Plant responses and acclimation of photosynthesis to light, including the dynamics of sunfleck utilization.
- Plant water relations, particularly the study of xylem water transport and the hydraulic architecture of trees.
- Plant-herbivore interactions.

- Adaptation to low temperature in high mountain regions in the tropics, where plants are faced with the risk of freezing temperatures year-round.

These contributions are partially the result of significant advances in technology and availability of high-precision instrumentation capable of withstanding the harshness of the tropical environments. Recent technical developments add to the widespread use of environmental-monitoring equipment, pressure chambers, autoporometers, psychrometers, and other classical physiological instrumentation, and include:

- Portable, robust gas exchange and fluorometer systems to measure *in situ* assimilation rates, photosynthetic efficiency and photoinhibition of leaves.
- Portable weather stations and equipment to measure soil water content.
- Micrometeorological approaches to study the energy balance and fluxes in plant canopies (Eddy correlation, Bowen ratio-Energy Balance technique).
- Canopy cranes to access the crowns of large trees. The first canopy crane was erected in the tropics.
- Instrumentation for sap flow measurements of plants *in situ*.
- Low flow- low pressure transduction techniques to measure hydraulic architecture parameters.
- Mini-rhyzotron imaging and ground-penetrating radars to study the structure, distribution and life span of root systems with minimum disturbance.
- Nuclear magnetic resonance imaging to non-invasively observe a variety of physiological and long-distance transport processes.
- Stable isotope techniques to trace spatial and temporal patterns of soil water uptake (D/H), and to characterize integrated gas exchange properties of leaves and other tissues ($^{12}C/^{13}C$).

Is the physiology of tropical plants unique?

Although the basic metabolic processes that underlie the mechanisms of plant responses to their environment are probably highly conserved and qualitatively similar among tropical and temperate plants, it is also apparent that tropical plants exhibit metabolic peculiarities that differentiate them from temperate species. These include aspects of photosynthetic metabolism and phloem transport physiology, sensitivity to low temperatures, reproduction, responses to climatic seasonality, and the variety of biotic interactions. For example, a higher abundance of plants exhibiting the C4 (Sage and Monson 1999) and CAM photosynthetic syndromes (Medina 1987) is found in tropical environments.

Plant growth in tropical ecosystems is not constrained by reduced temperatures. As a consequence of this, tropical plants in general and C4 species in particular do not tolerate low temperatures, which limits the latitudinal and altitudinal distribution of C4 species (Osmond, *et al.* 1982). High sensitivity of tropical plants to low temperatures has been a major field of research in post harvest physiology, because tropical fruits experience chilling injury upon exposure to temperatures typically employed in post-harvest handling of fruits and vegetables.

Pioneering explorations of the ecological implications of diversity in phloem physiology indicate that, in contrast to their temperate counterparts, tropical and subtropical trees and shrubs exhibit predominantly symplastic loading of the phloem (Gamalei 1991). This mechanism of phloem loading seems to be correlated with the dominance of axial over lateral sinks, lower growth rates typical of trees and shrubs as compared to herbs, and reduced tolerance to low temperatures. However, any generalization regarding relations between phloem physiology and other variables such as growth form and environmental temperature await confirmation in tropical ecosystems.

Tropical forests are unique in the sense that they contain an enormous diversity of environments and plant life forms, so that the range and variety of plant adaptations to these habitats are also unique. Multiple life forms are found almost exclusively in tropical forests (lianas, epiphytes, hemi-epiphytes, palms) and their adaptations to their respective environments within these forests are unique too.

Tropical forests exhibit higher functional diversity and more potential “solutions” to the same problems. This diversity can be observed even in the vertical scale, where dramatic variations in light availability and other microclimatic variables occur throughout the forest profile. Distinct canopy layers develop in different kinds of forests, where the understory vegetation seems to act as a filter that decouples processes near the forest floor from those occurring in the upper canopy.

Plant reproduction in the tropics also holds some peculiarities. Tropical trees are primarily cross-breeders and exhibit higher levels of dioecy (20%) than their temperate counterparts (10%), but the evolutionary causes of these trends are unknown (Geber *et al.* 1999). Numerous tropical plants bear flowers especially adapted to interact with Neotropical pollinators such as hummingbirds, butterflies, and bees. The variety of secondary metabolites found in tropical plants may be an expression of the diversity of plant biotic interactions with pollinators, herbivores, pathogens, symbionts, animals, and other neighboring plants.

Fine root density seems to be lower in tropical than in temperate ecosystems (see Sanford and Cuevas 1996). The implications of this finding, if confirmed, may point out to the presence of unsuspected strategies of fine root dynamics and acquisition of soil resources.

Tropical plants in general do not undergo the kind of daylength and temperature-induced dormancy that temperate zone plants experience during the winter months. Instead, they have physiological adaptations to respond to seasonality of precipitation and associated climatic changes (i.e., seasonal variation in radiation, wind speed and atmospheric humidity) (Bullock *et al.* 1995). Another physiologically-based attribute of tropical plants (especially forest trees) that distinguishes them from temperate plants is the broad continuum of their leaf phenology, defying classification into simple categories like evergreen and deciduous.

Finally, modern environmental problems like global warming may have profound impact on lowland tropical forests characterized by high temperature year-round. These ecosystems and the physiological processes that they contain have probably evolved at the edge of a subtle equilibrium between assimilation and respiration. Current global warming could result in increased respiration and decreased assimilation, altering the carbon balance of trees and other plants of these ecosystems (D. Clark, pers. comm.). The physiology of tropical herbs and other growth forms like shrubs (Wright *et al.*), epiphytes and lianas (see Mulkey, *et al.* 1996) is severely understudied in tropical forests. Details of their functions in forest ecosystems remain obscure, which does not allow mechanistic explanations of their abundance and distribution. In contrast to trees, lianas, epiphytes and palms, the diversity of tropical herbs do not surpass the diversity of herbs observed in temperate forests (Smith 1987).

Old and new paradigms

Some old, widely-held paradigms have broken as a consequence of physiological research in the tropics, and new ones have emerged. One of the major paradigm breakthroughs that arose from research on tropical plants (e.g. sugarcane) was the discovery of C4 photosynthesis (see Sage and Monson 1999 for details on the C4 pathway). Evidence for this additional metabolic pathway was met with great resistance at first (Nickell 1993). Another paradigm shift that is in progress is the recognition that despite the great diversity of species in the tropics, there is considerable functional convergence among plants that links them together along common physiological response curves and surfaces (Meinzer and Goldstein 1996). Another rather new specific paradigm is that in tropical alpine environments, leaf pubescence serves to warm the plants. The prevailing paradigm based on research in temperate deserts had been that pubescence serves to cool leaves by reflecting more light (see Meinzer and Goldstein in Givnish 1986 for a full account).

A new paradigm has also emerged from recognizing the role of Nitrogen but especially Phosphorus and other minerals in controlling key physiological processes such as assimilation rate in some tropical ecosystems. Phosphorus deficiency and aluminum and manganese toxicity become the limiting factors for plant survival and growth in some tropical soils. It has also been recognized that the magnitude of CO_2 recycling in tropical forest understories is substantial, and in agreement with early results obtained in crops (Lemon and Wright 1969), CO_2 released from the soil can act as a major source of carbon for canopy photosynthesis.

It has been indicated that ecological succession in the tropics can take different paths depending on the environmental conditions prevailing during plant establishment, and that distinct floras do not differentiate primary from secondary forests (R. Mesquita, pers. comm.). These stages of forest succession differ rather in the distribution of the species that they contain (R. Chazdon, pers. comm.). Finally, categorization of tropical trees as pioneers, mid-successional, and climax species did not lead to significant insights because most species of tropical woody plants occupy an intermediate position along the shade-tolerant /light-demanding continuum (Chazdon, *et al.* 1996).

Conceptual and technical developments in ecophysiology of tropical plants

More attention must be given to linking and reconciling measurements across different scales of observations. Many physiologists have traditionally assumed that the behavior of a single leaf in a chamber somehow represents what the whole organism is doing. As a consequence of this, early ecophysiological studies focused on processes occurring at the leaf level, and although we are moving towards a whole-plant level of inquiry, we are still far from understanding the rules of scaling from physiological to higher scales of observation (Meinzer and Goldstein 1996). It is also critical to establish links with community and population ecology (including restoration sciences) and with the study of biogeochemical processes that control carbon and nutrient cycles in the biosphere.

Key issues remain to be approached with a more intensive use of the variety of conceptual and technical tools currently available. These include the quantitative analysis in a population sense of the physiological basis of ecotypic and phenotypic differentiation and the integration of performance and survival events. Approaches of this nature will finally focus the attention on the physiological processes that are the key to ecological relations. For example, to demonstrate adaptive significance of a physical or other trait requires evidence that it confers superior fitness to one genotype compared to another. Rarely in physiological research are comparisons made with the unsuccessful genotypes, and rarely it is shown that specific traits actually confer competitive or reproductive advantage (Lange *et al.* 1982a). Therefore, progress is needed in the following areas of plant physiology:

- Resource partitioning and storage.
- Physiology of development in the field, especially the interactions between vegetative growth and reproduction.
- Phloem allometry, function and diversity.
- Below-ground processes. It is unknown if the diversity in structure and physiology observed above-ground is matched below-ground by the root systems of plants and their ubiquitous symbionts.
- Physiology of large trees.

Desirable conceptual and technical developments include:

- Wider applications of remote sensing to examine phenology, nutrient, carbon and water relations of vegetation at ecologically-meaningful scales.
- Molecular techniques applied to plant physiology, particularly in the characterization of the genetic basis of physiological diversity and plasticity.
- Portable canopy access systems and techniques to non-destructively measure leaf area of plants, trees and forests.
- Transparent substrates to study below-ground processes, root systems, and plant-mycorrhiza interactions.
- Techniques to measure nutrient fluxes, real-time resource use and storage, and non-destructive estimates of non-structural carbohydrates *in situ.*

- Instrumentation to measure the three-dimensional radiation environment of plants.
- Techniques to measure respiration rate and carbon balance of plants and plant organs in the field.

Fostering the development of physiological research in tropical countries

The paucity in progress on recruiting new scientists and developing physiological research in the American tropics (mostly Latin America) is mainly due to the allocation of very limited resources to other areas of higher priority, such as agriculture and conservation. In addition, training of field biologists has traditionally focused on natural history and ecological models that do not involve experimentation and mechanistic explanations. Research and training in plant physiology, so much dependent on expensive instrumentation and innovative technical and conceptual developments, certainly faces major difficulties in the poor, underdeveloped countries that make up the American tropics.

Training of students on ecophysiology of tropical plants should be approached with a strong foundation based on physiology and function, basic mechanisms and their implications for plant interactions with their environment and with other plants. It is a mistake to offer plant ecophysiology courses that are basically plant ecology courses that introduce a few field measurement techniques. This leads to a rather naive and unimaginative view of ecophysiology. In addition to their contribution to solve these problems, field exercises as a teaching tool would reduce the costs of teaching compared to laboratory work.

Finally, it is our responsibility as biologists to become involved in fostering the development of ecophysiology and other biological disciplines in tropical America, and to pursue the conservation of the natural tropical ecosystems where we conduct our physiological research. Under the current global *status-quo*, this will occur only if genuine partnering involving direct collaboration between local and visiting scientists from the first world is developed. This collaboration includes student involvement, literature updates and access to electronic journals, the creation of positions for local researchers at local universities and institutions, and renewed and sustained funding policies. Willingness of foreign researchers from temperate zones to accept graduate students from tropical countries and allow them to conduct their dissertation research in their own countries is an example of the kind of actions needed to promote the development of sound physiological work in Latin American institutions.

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