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Global Change and Tropical Forests:

Functional Groups and Responses of Tropical Trees to Elevated CO_2

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M. Sc. Thesis
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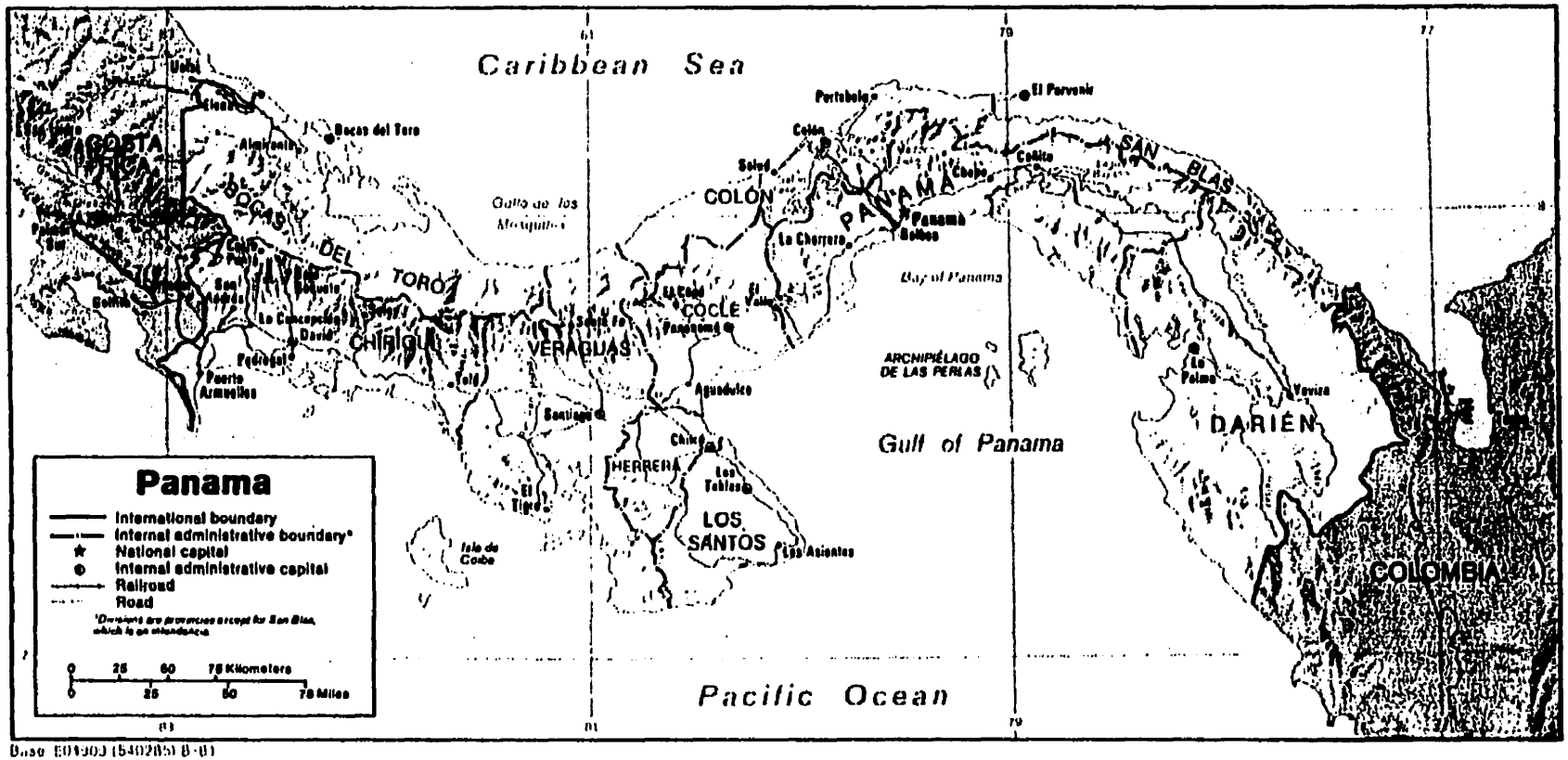
A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements of the degree of Masters in Science, Biology.

To my grandmothers...

One of whom who has nurtured my love of nature
and the other who has sparked my interest in Latin America



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THESIS ABSTRACT

The paradox of tropical forests is that they are simultaneously the most diverse, the least understood, and the most imperiled terrestrial ecosystem in the world. While other anthropogenic dangers to the forest such as deforestation manifest themselves physically, one has biochemical effects. Dramatic increases in the atmospheric carbon dioxide (CO_2) concentration threaten to adversely affect fundamental climatic and ecosystem processes, gradually changing many things which we do not yet understand. Although the impacts of this rise have been studied in temperate areas, little research has investigated tree responses in the tropics, especially under natural forest conditions. This thesis examines three central issues in tropical ecophysiology and global change. First, it investigates the feasibility of *in-situ* measurements of several physiological traits under heterogeneous environmental conditions in a Panamanian rainforest. Second, it studies whether physiological traits differ among species and which traits are most consistent with ecological niche. Finally, it explores how variable species are in response to elevated CO_2. If ecologically-defined functional groups were toremain physiologically similar under increased CO_2, they could be useful in accurately representing the variation at the species level in a global change model of system-level responses.

The first chapter demonstrates that variation in several physiological traits is detectable under heterogeneous environmental conditions and ambient CO_2 (365 $\mu L\ L^{-1}$). It further shows that groups of ecologically-related species also share physiological traits. Together, these findings indicate that both ecological and physiological traits of these species can be represented by groups. Subsequently, global carbon models under ambient CO_2 could be parameterized using groups rather than individual species. The second chapter examines the leaf-level responses of tropical trees to elevated levels of atmospheric CO_2 (~750 $\mu L\ L^{-1}$). Photosynthetic and water use enhancements resulting from CO_2 are detectable under natural conditions. All species increase their photosynthetic rates when exposed to elevated CO_2, though the magnitude of this enhancement varies significantly. However, though the first chapter supports the use of functional groups as robust descriptors of the ecology and physiology of many species, the second illustrates that this is no longer valid under elevated CO2. Groups are not reliable estimators when attempting to detect changes due to elevated CO_2.

These results challenge the paradigm that physiological differences among species will be undetectable within the variable forest conditions and clearly show that

the effects of elevated CO_2 cannot be entirely assessed by measurements controlled conditions and are not uniform across species. Although these results represent leaf-level responses, they suggest that the global rise in CO_2 will play a significant role in the physiology and, subsequently, the ecology of tropical forests in the coming decades.

RÉSUMÉ

Les forêts tropicales sont sont parmi les habitats les plus riches en espèces de la planète. Cependant ils sont parmi les écosystèmes les plus menacés et les processus écologiques qui y prennent place sont toujours mal compris. Si la déforestation constitue une menace directe pour les forêts tropicales, l'augmentation de la concentration de dioxyde de carbone (CO_2) atmosphérique risque à plus long terme de perturber le fonctionnement de ces écosystèmes. L'impact de l'augmentation du CO_2 atmosphérique a été bien étudiée dans les régions tempérées mais peu ou pas sur les arbres tropicaux en conditions naturelles. Ce mémoire de maîtrise explore trois thèmes clefs à la frontière de l'écophysiologie tropicale et des problématique lié aux changements climatiques.

Premièrement, nous avons étudié la faisabilité de mesures physiologiques *in situ* au sein d'un environnement naturellement hétérogène dans une forêt tropicale humide. Deuxièmement, nous avons cherché à quantifier l'importance des différences physiologiques existant entre des individus issus de groupes fonctionnels (définis sur une base écologique) différents ou d'espèces différentes au sein du même groupe fonctionnel. Ceci nous a permis d'évaluer dans quelles mesure des espèces provenant de groupes fonctionnels différents avaient également des physiologie très différentes. Ces différences conditionnent la pertinence de tels groupes fonctionnels pour la modélisation de l'impact dune augmentation de CO_2 sur le fonctionnement des écosystèmes.

Le premier chapitre démontre la possibilité de mettre en évidence des différences physiologiques significatives, même au sein d'un environnement naturellement hétérogène avec un niveau de CO_2 ambiant (365 $\mu L\ L^{-1}$), entre les groupes fonctionnels. De plus, ceci justifie le regroupement d'espèces en groupes fonctionnels et la pertinence de ces groupes pour modéliser la réponse de couverts végétaux à une augmentation du CO_2 atmosphérique. Le deuxième chapitre examine l'effet d'atmosphères enrichies en CO2 (~750 $\mu L\ L^{-1}$) sur les réponses physiologiques au niveau foliaire mesurées en condition naturelles. Toutes les espèces étudiées montrent des niveaux accrus (et statiquement significatifs) de photosynthèse et d'efficacité d'utilisation de l'eau. Mais on a mis également en évidence des différences significatives de réponse physiologique entre espèces pour ces deux caractères.

Alors que le premier chapitre démontre la pertinence des groupes fonctionnels pour discriminer les espèces au niveau écologique et physiologique, le deuxième chapitre montre que cette classification n'est plus pertinente dans les cas atmosphères enrichies en CO_2. Ces résultats ébranlent donc le paradigme selon lequel on ne peut mettre en évidence de différences significatives entre espèces lorsque l'on effectue des mesures en dehors d'environnement contrôlés. De plus, bien que ces résultats soient uniquement basés sur des mesures effectuées au niveau foliaire, ils suggèrent que les augmentations de concentration de CO_2 atmosphérique auront un impact non négligeable sur les couverts forestiers tropicaux et les processus écophysiologiques qui s'y déroule.

RESUMEN

La paradoja de los bosques tropicales es que ellos son simultaneamente los mas diversos, los menos entendidos y al mismo tiempo el ecosistema terrestre en mayor peligro en el mundo. Mientras, otros peligros antropogénicos al bosque como deforestación son manifestados fisicamente, en el dramático incremento atmosférico del bioxido de carbono (CO_2), cuyas altas concentraciones amenazan con romper los procesos fundamentales del ecosistema, destruyendo gradualmente lo que nosotros todavía no entendemos. Aunque los impactos de este incremento han sido estudiados antes en areas templadas, pocas investigaciones se han hecho sobre las respuestas de los arboles en los tropicos, especialmente sobre condiciones naturales del bosque tropical.

Esta tesis examina tres puntos centrales en la ecofisiología tropical y cambio global. Primero, se investigó la posibilidad de hacer medidas *in situ* de diversas características fisiológicas bajo condiciones ambientales heterogéneas en un bosque lluvioso panamaño. Segundo, se estudio si las características físicas difieren entre las especies, y cuales características son las más consistentes dentro de su nicho ecológico. Finalmente se exploro si grupos funcionales definidos ecologicamente son fisiologicamente similares, y si pueden ser usados adecuadamente para representar la variación a nivel de especie en un modelo de respuestas al incremento de CO_2.

El primer capítulo demuestra que la variación en diferentes características fisiologicas es detectado bajo condiciones ambientales heterogeneas y concentraciones de CO_2 normales (365 $\mu L\ L^{-1}$). Además se muestra que grupos relacionados ecologicamente comparten las mismas características fisiológicas. Estos resultados indican que tanto las características ecológicas y fisiológicas pueden ser representadas por grupos, los cuales pueden ser subsecuentemente usados con el proposito de crear modelos a nivel de población bajo condiciones ambientales de CO_2 normales. El segundo capítulo examina los efectos del CO2 a nivel de hoja en los arboles tropicales bajo condiciones ambientales de CO2 elevadas (~750 $\mu L\ L^{-1}$). La mejoría en la fotosíntesis y eficiencia del uso del agua como resultado de CO_2 son detectados bajo condiciones naturales. Todas las especies incrementan su tasa fotosínteticas cuando son expuestas a concentraciones elevadas de CO2, aunque la magnitud de ese mejoramiento varía significativamente entre especies. Sin embargo, aunque el primer capítulo soporta el uso de grupos funcionales como descriptivos de la ecología y fisiología de muchas

especies, el segundo ilustra que esto no funciona así bajo concentraciones de CO_2 elevadas. Los grupos no son buenos indicadores cuando se trata de detectar cambios debidos a concentraciones elevadas de CO_2.

Estos resultados desafian el paradigma sobre las diferencias fisiologícas entre especies, las cuales no son detectadas bajos las condiciones variables del bosque. Esto claramente muestra que los efectos del CO_2 elevado no son percibidos por completo bajo condiciones controladas. Por lo cual, es necesario hacer más proyectos bajo condiciones naturales. Aunque éstos resultados representan repuestas a nivel de hoja, dichos resultados sugieren que el cambio global alvsnzado en CO_2 va a jugar un papel importante en la fisiología y, subsequentamente, la ecología de los bosques tropicales en las proximas decadas.

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Author's note: Because a bibliography and literature review are integrated into each chapter, they do not appear individually. Although both works represent intellectual collaborations with Dr. Catherine Potvin and Dr. Steve Hubbell, the writing is entirely the author's. Thus, although plural first person pronouns appear in the manuscripts, their use does not imply any written contribution by these collaborators whatsoever.

GENERAL INTRODUCTION

Tropical forests are under increasing pressure from human civilization and activities. There can no longer be any doubt that clear-cutting and slash-and-burn agriculture exact a heavy ecological toll, jeopardizing the futures of forests and people. Less clear, however, is the effect of another anthropogenic force, namely elevated atmospheric carbon dioxide (CO_2). Worldwide sampling has demonstrated that the CO_2 concentration in the earth's atmosphere is rising dramatically (Figure 1 a-b). At the current rate of increase, the atmospheric CO_2 concentration is expected to double from current levels of 365 $\mu L\ L^{-1}$ to ~700 $\mu L\ L^{-1}$ by the middle of the next century (IPCC 1990). Scientists have described a variety of climatic and vegetational side effects related to this dramatic rise in CO_2. As the world's output of CO2 continues relatively unabated, it is becoming increasingly important to ascertain the potential impact of elevated CO2 at the ecosystem level, especially in areas of high diversity and complexity such as tropical forests.

This thesis explores whether species with similar ecologies, assembled into functional groups, share fundamental physiological traits such as photosynthesis, water use efficiency and nitrogen content. Second, it reports on the photosynthetic response of these species and functional groups to elevated CO_2. In doing so, it also asks whether the ecologically-defined functional groups differ in their response to CO_2 and examines the possibility that these groups could be used in lieu of individual species as a means of community simplification to parameterize global carbon models.

Why study photosynthesis?

$$CO_2 + H_2O \xrightarrow{light} (CH_2O)_x + O_2 + H_2O \qquad \textit{Equation 1}$$

Arguably the most fundamental chemical reaction on earth, photosynthesis is the process by which plants convert solar radiation and mineral nutrients into chemical energy (Equation 1). Without photosynthesis, life as we know it would not exist: no plants, no animals, no trees, no oxygen, no humans. Necessary natural resources such as petroleum, coal, and firewood are all products of the conversion of solar energy into chemical energy via photosynthesis. Ironically, it is the human usage of these sources of carbon that is primarily responsible for the increase in

atmospheric CO_2. It seems that photosynthetic creations have become the causal agents of the current perturbations to the process itself.

In sum, it is crucial to understand the mechanisms and dynamics of photosynthesis given that multicellular life relies on it and the profound impact it has on the makeup of our atmosphere. This is especially true if we are to understand fully the impact of carbon dioxide and other "greenhouse gases" on the photosynthesis and the systems it supports. Because most life relies on photosynthesis, any perturbation to photosynthetic systems is serious, and should be a major concern and focus of scientific investigation on the part of society. This is especially true when society is principally responsible for the changes.

The rising level of CO_2 and its impact on plants

In the last half century, society has begun to change our world drastically. Although global atmospheric carbon dioxide concentrations have been in a natural state of flux since the earth cooled and marine algae began to prosper, the spread of human habitation and technological advances changed both the period and the amplitude of the flux. Ice core data has revealed that since the late 1840's and the latter part of the Industrial Revolution, the global atmospheric CO_2 concentration has risen from pre-industrial levels of around 260-280 $\mu L\ L^{-1}$ to 360 $\mu L\ L^{-1}$ today with predictions of drastically higher CO_2 concentrations in the next 30-50 years (Figure 1 a-b; IPCC 1990, Andrews *et al.* 1996). While the current atmospheric CO_2 content remains well below the 2 - 8 times current levels that the earth reached in previous geological periods such as the Cretaceous or Carboniferous (> 1000 $\mu L\ L^{-1}$; Barron *et al.* 1993), what is alarming is the rate at which the increase has occurred — a century versus millennia. Even more striking is the realization that we humans are the cause of this ecological threat.

Physiologically, the mechanisms behind photosynthesis reveal why this atmospheric change is of consequence to biological systems. Plants need gaseous CO_2 as an outside source of carbon because the initial reaction between CO_2 and RuBP limits the rate of photosynthesis. Therefore, a change in CO_2 abundance can drastically affect the physiological processes of a given plant and, in turn, the entire plant community (Figure 2). Knowing the manner in which plants absorb CO_2 is central to an understanding of how elevated CO_2 affects photosynthesis and the life

history of plants. Because most trees and flowering plants (C3 species) invest the majority of their photosynthetic organelles or chloroplasts in energy-producing tissues such as leaves, the plant must have a means of supplying these tissues with CO_2. Like pores in our skin, stomates are the variable-aperture valves on the leaf's surface through which CO_2 can be introduced into the interior of the leaf and through which water can be evaporated to cool the plant. When a leaf's stomates are open, CO_2 enters the leaf's internal (parenchymal) tissue through these pores where the gas is then covalently linked to RuBP through the catalytic actions of the enzyme Rubisco. The greater a plant's stomatal aperture, the more CO_2 a plant can absorb and make available to the chloroplasts for continued photosynthesis. Yet, at the same time, the wider stomates are open, the more evapotranspirative water loss the plant experiences. After a certain point during the hot or dry periods of a typical summer day, the trade off between water loss and carbon gain forces the plant to shut its stomates to conserve water. Without available incoming raw materials, photosynthesis halts.

The classes of plants (C3, C4, CAM) are differentiated on the basis of their initial CO_2-absorption mechanism. Hence, the effects of elevated CO_2 can be expected to differ among these three classes. We have already noted that an increase in available CO_2 in ambient air would facilitate the extraction of CO_2, thereby decreasing the need for RuBP carboxylase (Rubisco) activity in C3 plants (most trees and flowering plants). In contrast, C4 plants (grasses, corn, etc.) have shown little fertilization effect as a result of elevated CO_2, presumably because of their inherent ability to concentrate CO_2 (Dahlman *et al.* 1985, Ziska *et al.* 1991). C4 plants derive this ability to concentrate CO_2 because they fix CO_2 to a PEP molecule, which is then moved into a bundle-sheath cell where it accumulates and subsequently releases the CO_2. This process, while exacting a higher energetically cost in addition to concentrating the CO_2, allows C4 plants to avoid the wasteful photorespiration co-process which, in C3 plants, re-oxidizes fixed carbon. The effects of elevated CO_2 on the third approach to CO_2-fixation — Crassulacean Acid Metabolism or CAM (cacti, pineapple, and other succulent plants) — are not yet clear but, on the basis of one study, appear to only exhibit minor CO_2-related photosynthetic and growth increases (Ziska *et al.* 1991). Although this thesis only involves C3 plants, it is useful to note that because the means of carbon absorption vary widely among the plants of different biochemical types, the responses of the various classes to a CO_2 increase may also vary.

Global change, elevated CO_2, and environmental effects

Since the realization in 1957 that the global atmosphere was changing, many researchers have sought to identify the extent and causes of the increase. New studies have shown that despite the provisions of the Montréal Protocol, anthropogenic releases of CO_2 have continued to increase. According to a recent IPCC report, even if the global output of CO_2 were maintained at 1994 levels, atmospheric levels would continue to rise for over two centuries, eventually reaching 500 $\mu L\ L^{-1}$ (IPCC 1995). Since the term "global change" refers to the multiple effects of this rise in atmospheric CO_2 on the biosphere, research in this area includes temperature and precipitation changes as well as changes in animal and plant communities. Research has centered around climatic changes resulting from this CO_2 increase. Although virtually all predictions differ somewhat from one another, a few general conclusions can be drawn from these research efforts. First, as early as 50 years from now, the average temperature may be 3-5°C higher across much of the world (Schneider 1989, 1993; IPCC 1990). This represents a tremendous increase in global mean temperature over such a short time. Second, as a result of this warming, the world's precipitation patterns are expected to change significantly, with drying occurring over Central America, the Amazon basin, and west Africa coupled with rainfall increases in Southeast Asia and Australia (*see* Bawa and Markham 1995). As a result of the first prediction, the effects of elevated CO_2 on the global biosphere are collectively referred to in common parlance as "global warming." While many gases contribute to this warming (i.e. CH_4, N_2O), CO_2 has by far the largest impact (IPCC 1995).

Significantly, the effects of elevated CO_2 are not limited to the climatic realm. Carbon is constantly cycling through every ecosystem on the planet (Figure 3). In its gaseous phase, carbon is assimilated by the land-based vegetation and deep-ocean algae. Conversely, carbon is restored to the atmosphere by decaying organisms and soil respiration, and by the combustion of stored solid carbon such as in fossil fuels and wood. As shown in Figure 3, the respiratory (catabolic) processes now exceed the assimilation processes. However, as is common in cyclical processes, an increase in one variable (the atmospheric CO_2 concentration) may well prompt a response from another constituent of the cycle. In other words, the deep ocean or vegetation may begin to sequester more carbon due to its higher concentration in the atmosphere. This project, however, is limited in scope to vegetation, specifically trees and their ability to increase their rate of carbon assimilation.

Under conditions of warm temperatures and adequate light, water, and nutrients, the rate of photosynthesis may be limited by carbon dioxide. Hence, it was reasonably assumed that an increase in the ambient CO_2 concentration of the air would cause higher photosynthetic rates, a so-called CO_2 fertilization effect. While this prediction has been borne out by research around the globe (*see* Ceulemans and Mousseau 1994, Lloyd and Farquhar 1996), several confounding factors have been noted. First, although the conclusions or implications of the studies have been aimed at natural environments, the vast majority of the studies have been conducted under controlled conditions (Ceulemans and Mousseau 1994). Although these conditions are conducive to a more detailed investigation of individual plant responses, the extent to which their results are applicable to larger scale environments, such as natural communities, remains an open question. Secondly, few elevated CO_2 projects have been conducted in the tropics, despite its prominence in the global carbon cycle (Ceulemans and Mousseau 1994, Ziska *et al.* 1991, McKane *et al.* 1995). Temperate studies that indicate large-scale changes in species responses or ecosystem function reasonably lead to the prediction that similar effects would occur in the tropics. This work addresses both issues. Not only were all measurements conducted under natural environmental conditions, but the species and the site were both tropical. Consequently, the results of this project may help further understanding of how tropical forest species respond to elevated CO_2 compared to other biomes. Beyond this, it may provide tools with which to begin to apply species-level results to communities.

Why study tropical rainforests?

Although tropical forests are the repositories for the majority of the Earth's known species, they represent the least understood biome, perhaps surpassed in scientific ignorance only by arctic ecosystems. But unlike arctic ecosystems, tropical forests also have the dubious honor of being the most rapidly disappearing habitat on the planet. This combination of diversity, unfamiliarity, and immediate peril has recently served to focus more attention on the tropics and is the impetus for this work.

The importance of tropical forests in climate change and conservation cannot be overstated. A recent survey found that tropical forests currently cover 2.2×10^9 ha

or 17% of the earth's land surface (Melillo *et al.* 1993). If left undisturbed, tropical forests of this size would account for nearly 40% of the CO_2 flux between the atmosphere and the terrestrial biosphere, far more than any other biome. Put another way, tropical forests are reported to represent 46% of the terrestrial living carbon on the planet (Brown and Lugo 1982). As such, tropical forests are considered a crucial element in the global carbon cycle. Although undisturbed forests have little net carbon exchange with the atmosphere, forest clearing and subsequent burning can lead to tremendous 'pulse' releases of carbon into the atmosphere. Under natural conditions, the newly-liberated carbon would be re-assimilated into biomass as the forest regenerated. A recent estimate of carbon accumulation rates for tropical forests found a storage rate of 6 mol C m^{-2} yr^{-1} which is 2-6 times higher than either temperate or boreal forests (Lloyd and Farquhar 1996). Yet, the capacity of the world's tropical forests to process and sequester carbon has been crippled as a result of over a century of wide-spread, unsustainable deforestation for agriculture and timber. If the soil is degraded or if tree recruitment is otherwise impeded, the carbon remains in the atmosphere.

In this way, both the decline in carbon fixing potential of tropical ecosystems and the increasing CO_2 content of the atmosphere can be traced to deforestation in the tropics. Not only does the reduction in the overall number of trees reduce the capacity of the forest to assimilate and sequester carbon, but since deforestation is frequently followed by burning of the felled vegetation, deforestation can lead to a net increase in atmospheric carbon. In fact, the burning of tropical forests is estimated to produce an amount of CO_2 equal to 35-50% of the CO_2 produced yearly by worldwide petroleum combustion (Houghton 1990). In this sense, the problem is doubly harmful; it both subtracts from one side of the equation and simultaneously adds to the other.

Tropical forests are also significant in terms of their contribution to the global resource supply. In addition to comprising a large percentage of the species on the planet, tropical forests support approximately a fifth of the world's population. Tropical areas also support the most rapidly growing populations (Keyfitz 1989). This is one of the primary reasons why rainforests are currently at the center of conservation debates regarding the preservation of biodiversity. Conventional wisdom of the past ten years has held that the best way to conserve the biological wealth is to limit or prevent clear-cutting, hunting, development, or other types of

human disturbance. In this way, it was believed that these areas would be refuges for local species, places where they could escape the impact of human activities. Certain anthropogenic influences, however, are not physical in nature yet equally disruptive. Changes in the atmosphere are international in effect, respecting no boundaries. Society must realize that in the coming years, anthropogenic global changes have the potential to alter entire ecosystems and ecologies wherever they might be located. And this is regardless of any protective measures these ecosystems might have against physical disturbances.

Consequently, to offset these changes, conservation work in the tropics has evolved not only to protect the genetic wealth but also to maintain the carbon storage and sequestration ability of the forests. Yet, despite their disproportionately large impact on the terrestrial carbon cycle and endangered status, the impact of elevated CO_2 on tropical forests has received relatively little attention until recently.

Barro Colorado Island and Las Pavas

All of the field research for this thesis was conducted in the República de Panamá between September 1994 and December 1995 on Barro Colorado Island (BCI; Figure 4 a-b). The island is a 15.6-km^2 former hilltop situated midway between the Atlantic and Pacific Oceans (9°09' N, 79° 51' W). It was isolated from the mainland in 1914 as a result of the construction of the Panama Canal. BCI sits at 476 ft (145m) above sea level and receives an average of nearly 2700 mm of precipitation each year with a strong dry season lasting from January to April. Temperatures average 27 - 32°C throughout the year and the humidity hovers between 81 - 95% on the forest floor, depending on the season (Wong and Ventocilla 1995).

The forest on the island varies in age from less than 100 years to more than 400 years old, producing a gradient of successional stages. Half of BCI's forest has not been significantly disturbed for hundreds of years. The other half, though, was disturbed to varying degrees during the construction of the canal, thus producing the gradient in forest age. Emergent tree canopies in older areas of the forest can reach 40+ meters tall and diameter at breast height of trunks can exceed 2 meters. Geologically, the majority of BCI consists of sandstone, basaltic lava, and conglomerates interspersed with some marine limestone deposits. The soils of BCI

are fairly organically- and minerally-poor oxisols with a thin humus covering. Considering these physical characteristics, BCI is comparable to other Central and South American forests (Leigh *et al.* 1982).

The diversity of life on the island is also comparable to other well-known neotropical forests. The island is home to a large number of species of all kinds: more than 1200 native plant species, 93 mammals, 373 bird species, 106 reptiles and amphibians, 409 trees and shrubs, and untold numbers of insects, bacteria, and fungi. (*see* Gentry 1993, Wong and Ventocilla 1995). Recently, the area has been shown to be floristically similar to forests of the upper Amazon basin, with 82% of the 327 genera of woody plants found on the island also occurring in the Manu floodplain of Peru (Foster 1993). As a result of its association with the Smithsonian Tropical Research Institute for over half a century, the island has been the focus of a staggering number of research efforts (well over 1500 to date). The end result is that BCI is undoubtedly the best-studied tract of tropical forest in the world.

Research for this project was also conducted in the small agricultural community of Las Pavas, situated close to the boundaries of the Barro Colorado Nature Monument. The reforestation plots at this site offered easy access to some species either unavailable or rare on BCI. Additionally, it offered a different set of environmental conditions in which to assess CO_2 fertilization. The site exists as a collaborative effort between the village of Las Pavas and the Center for Tropical Forest Science (CTFS). It was established in an effort to rehabilitate previously-farmed land and re-establish patches of forest from which timber could be sustainably harvested. The plots contain many tree species, most of which are native to the Canal zone and all of which have both an ecological and economic value. The plots are situated on farm land that is now abandoned, a common practice resulting from the poor soil quality common to the tropics. Once abandoned, these old fields are soon colonized by pioneer species, fast-growing plants such as an imported grass species (*Saccharum* spp., a.k.a. "paja blanca") that take root and often competitively exclude other species. One aspect of the CTFS reforestation research is to ascertain which tree species are hearty enough to compete with weeds and grasses and which have both good wood quality and a fast growth rate, necessary qualities for a tree to be an economically viable crop. By examining the physiological traits of these species, this work can supplement the ecological observations.

Contributions of this thesis

This thesis is composed of two separate experiments. The common thread linking them is that both studies explore species differences in physiological traits of tropical trees. The first looks at many traits and whether patterns of trait differences are meaningful. Because of the diversity of tropical trees, it does so by combining species into ecologically-defined functional groups. By establishing that functional groups share both ecological *and* physiological traits, the first chapter sets the stage for an examination of both a species and a group response to elevated CO_2. That examination is detailed in the second chapter which tests the impact of CO_2 at the species and the functional group level. It shows that changing the CO_2 level will affect species to different degrees but these species differences are not apparent if species are lumped into ecological groups. The results of these two experiments are discussed in terms of their applicability to ecological "scaling-up" techniques and their use in global change models.

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FIGURE LEGENDS

FIGURE 1: Documentation of the rise in atmospheric carbon dioxide concentration from two sampling methods: (a) yearly air sampling from Mauna Loa Observatory atop an inactive volcano in Hawaii and (b) analysis of air bubbles trapped in Antarctic ice cores. Although they cover different periods of time, both illustrate the sharp increase. The top graph (a) shows the how steadily and rapidly the increase in CO2 concentration has been just since the late 1950's. The bottom graph (b) covers a longer time scale and shows the exponential nature of the increase. It also adds another dimension by illustrating the close relationship between atmospheric CO_2 and global mean temperature (temperature shown by the jagged line). Data in (a) from Keeling *et al.* (1995) and (b) from the Climatic Research Unit at the University of East Anglia, Great Britain.

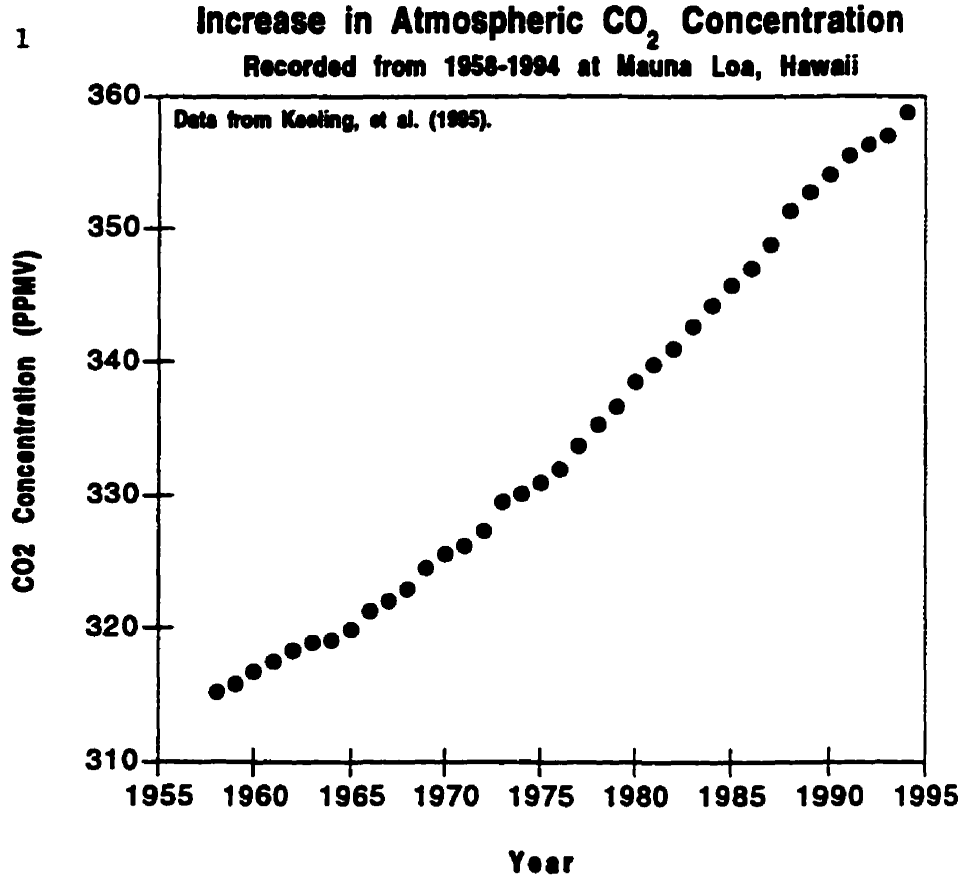
FIGURE 2: Schematic representation of the flow of energy, nutrients, and water through a tree. Dotted lines denote energy and resource inputs to photosynthesis and the solid line represents the flow of photosynthate (complex carbon structures like sugars). In the leaf tissue, the site of photosynthesis, light (here shown as photosynthetically active radiation, PAR) and carbon dioxide combine with water and mineral nutrients absorbed by the roots. The plant's photosynthetic rate is determined by the relative availability of these inputs as well as the capacity of the photosynthetic machinery. When all the raw materials are in excess, the maximum photosynthetic rate becomes dictated only by this photosynthetic capacity. For the solid line, accompanying arrowheads indicate different areas of phytosynthate storage, such as to the leaves, trunk, and roots. (*after Ceulemans and Mousseau 1994*).

FIGURE 3: Global carbon flux through terrestrial, marine, and atmospheric systems. Arrows indicate location and direction of carbon flow. Corresponding numbers with each system are estimates of the amount of carbon stored by its constituent species and processes (in billions of metric tons). Thus, by far the greatest amount of carbon is currently sequestered in the oceans. But only one system has the ability to re-convert gaseous carbon to its solid form: the vegetation. However, as illustrated here, the amount of carbon released by the combined processes of combustion and respiration now exceeds the amount of carbon fixed by photosynthesis. (*after Raven et al. 1992*).

FIGURE 4: Geography of Barro Colorado Island and environs in central Panamá. (a) The shaded areas, including the island, denote the Barro Colorado Nature Monument (BCNM), which has been managed and protected by the Smithsonian Tropical Research Institute (STRI) since 1923. It is bordered to the east by Parque Nacional Soberania, one of Panama's largest national parks and to the east by local communities, including the village of Las Pavas. Dots indicate the location of BCI's laboratory complex and the reforestation project in Las Pavas. (b) A detailed map of the island reveals the 50-ha plot (rectangle) and the trail network. Field sites were primarily in the 50-ha plot and vicinity but were also located towards the end of Standley and Armour trails.

FIGURE 1

(a)


Increase in Atmospheric CO_2 Concentration
Recorded from 1958-1994 at Mauna Loa, Hawaii
Data from Keeling, et al. (1995).
CO2 Concentration (PPMV)
360
350
340
330
320
310
1955
1960
1965
1970
1975
1980
1985
1990
1995
Year

(b)

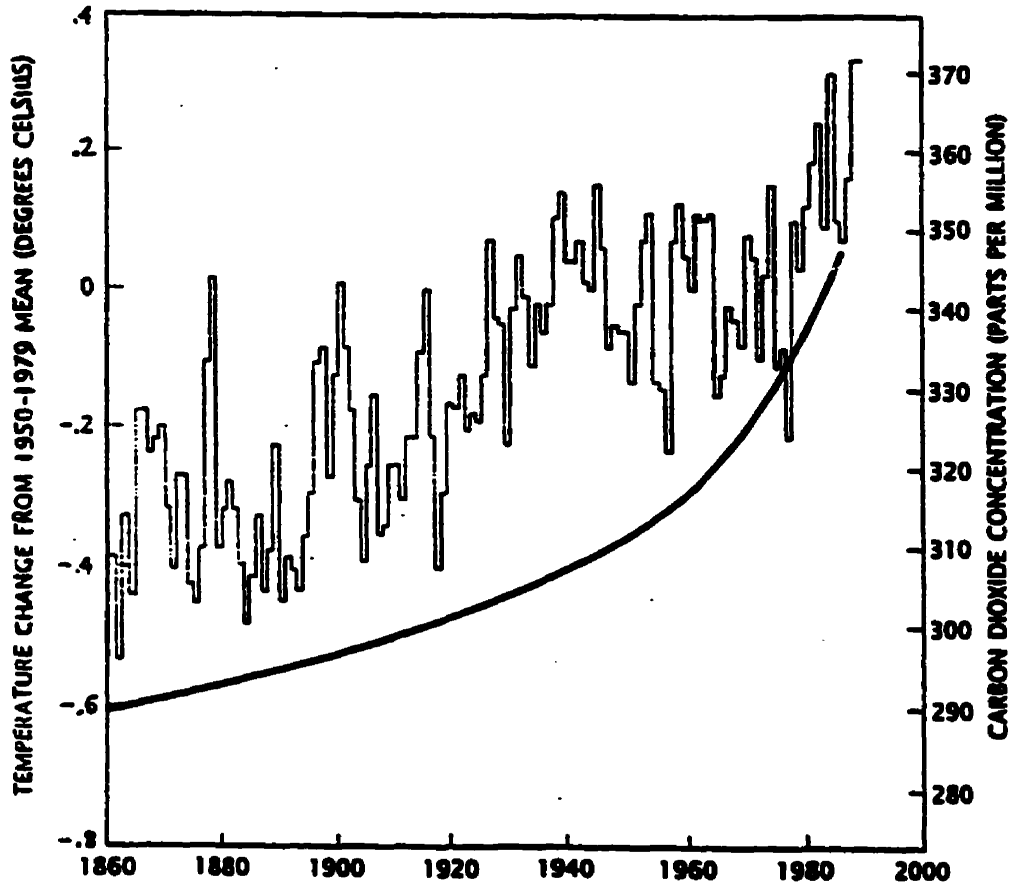

TEMPERATURE CHANGE FROM 1950-1979 MEAN (DEGREES CELSIUS)
.4
.2
0
-.2
-.4
-.6
-.8
CARBON DIOXIDE CONCENTRATION (PARTS PER MILLION)
370
360
350
340
330
320
310
300
290
280
1860
1880
1900
1920
1940
1960
1980
2000

FIGURE 2

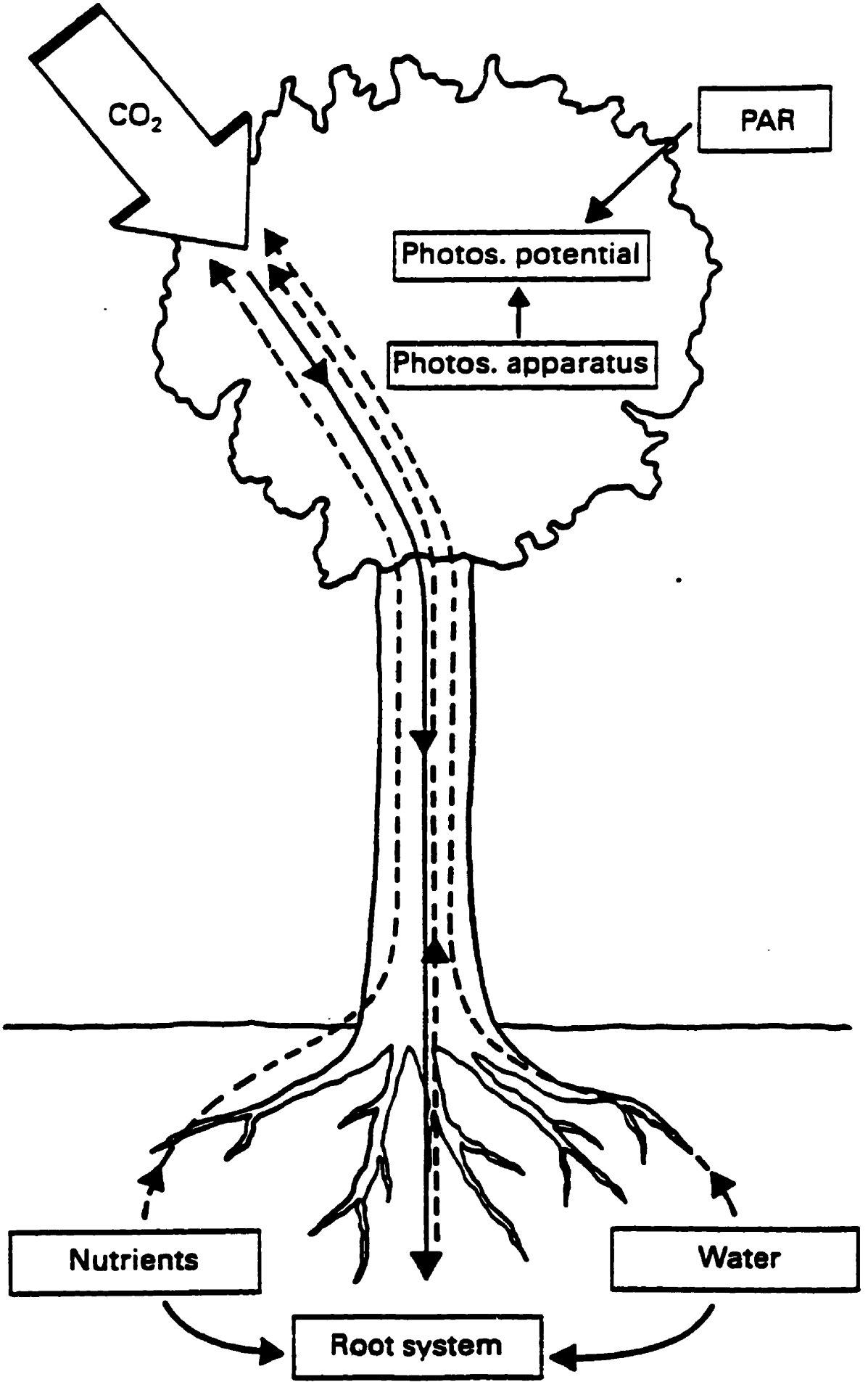

CO_2
PAR
Photos. potential
Photos. apparatus
Nutrients
Water
Root system

FIGURE 3

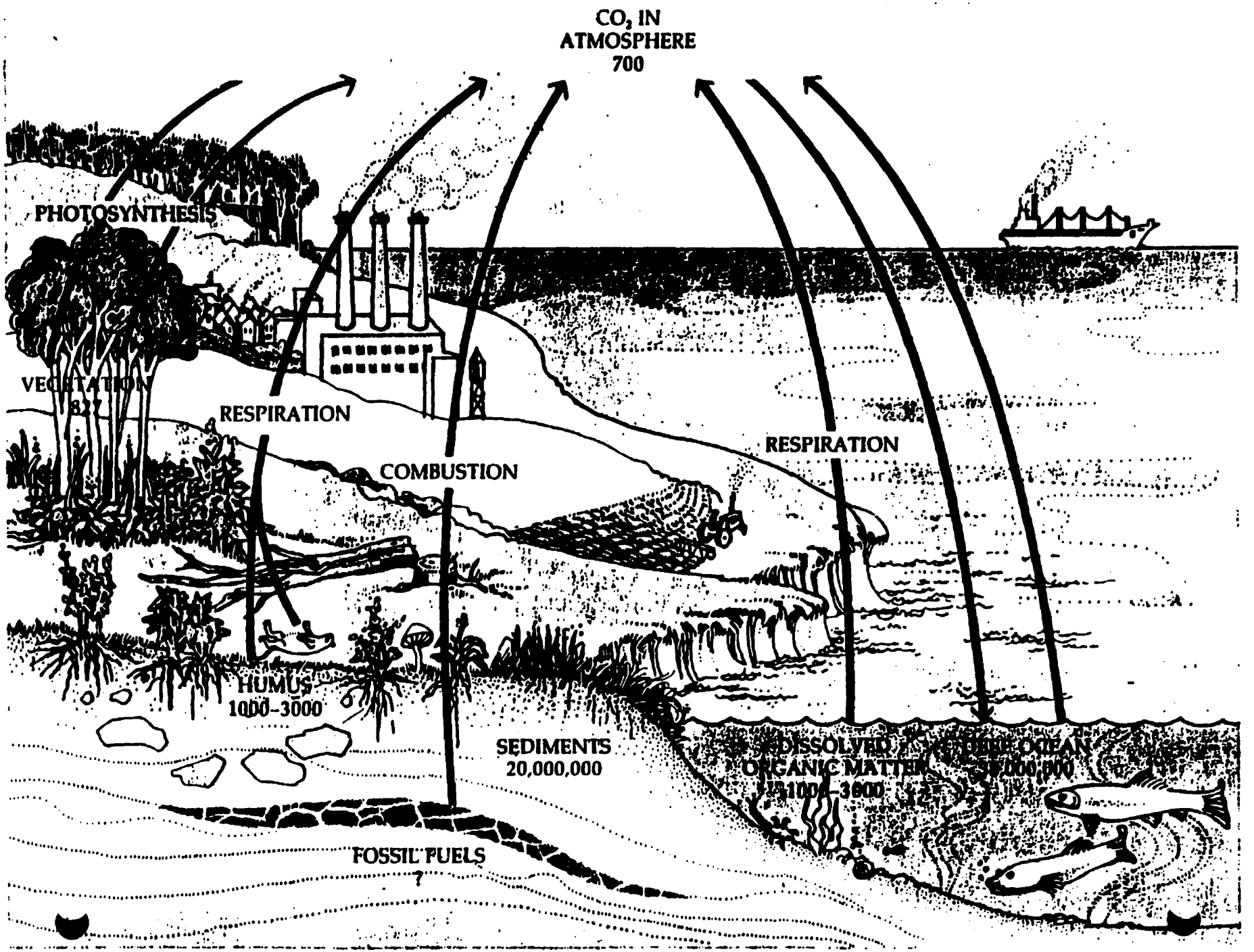
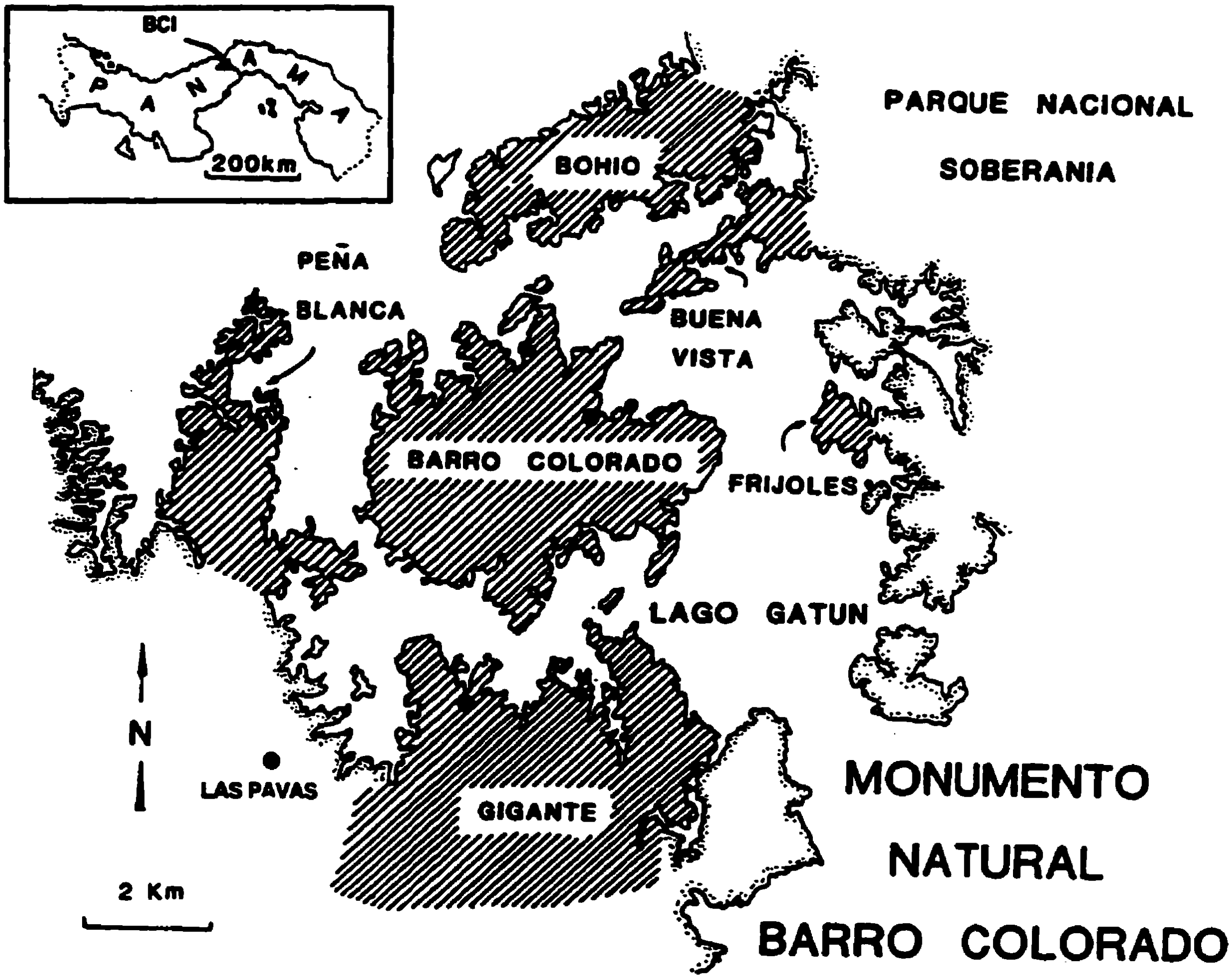
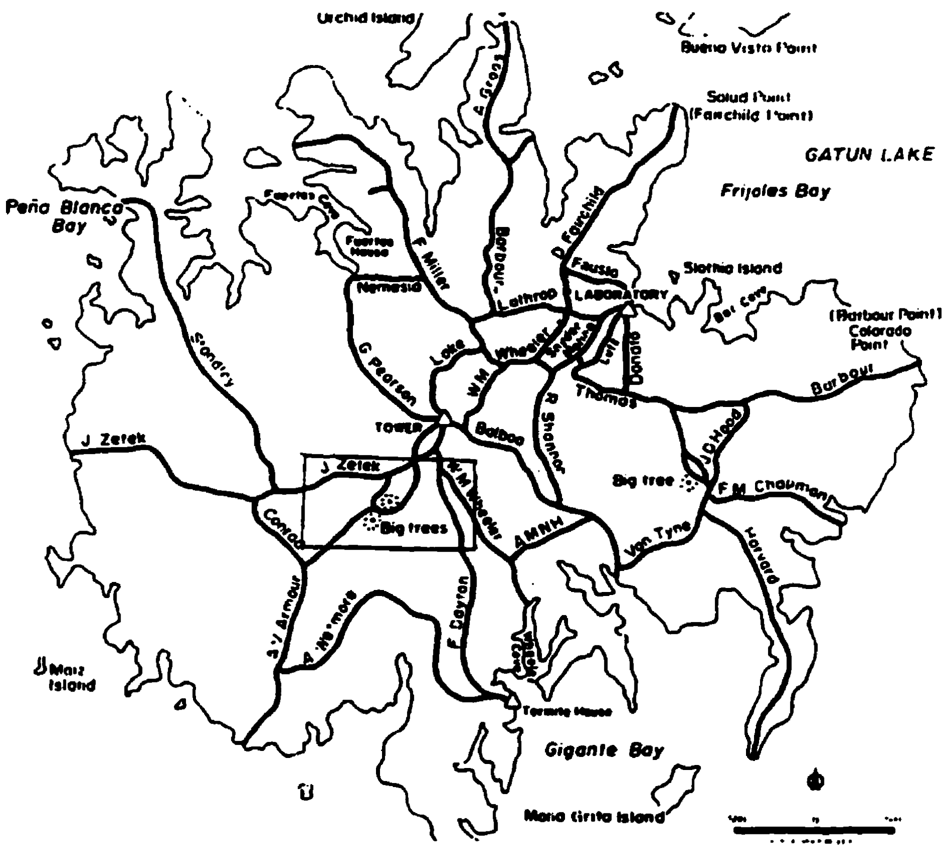

CO_2 IN
ATMOSPHERE
700
PHOTOSYNTHESIS
VEGETATION
RESPIRATION
COMBUSTION
RESPIRATION
HUMUS
1000-3000
SEDIMENTS
20,000,000
DISSOLVED
ORGANIC MATTER
1000-3600
DEEP OCEAN
FOSSIL FUELS
?

FIGURE 4

A.


BCI
P A N A M A
200km
PARQUE NACIONAL
SOBERANIA
BOHIO
PEÑA
BLANCA
BUENA
VISTA
BARRO COLORADO
FRIJOLES
LAGO GATUN
N
LAS PAVAS
GIGANTE
2 Km
MONUMENTO
NATURAL
BARRO COLORADO

B.


Orchid Island
Bueno Vista Point
Salud Point
(Fairchild Point)
GATUN LAKE
Frijoles Bay
Peña Blanca
Bay
Standley
F Miller
Barbour
D Fairchild
Fausto
Slothia Island
LABORATORY
(Barbour Point)
Colorado
Point
Nemesia
Lathrop
Wheeler
Lake
G Pearson
Donato
Barbour
Thomas
TOWER
Balboa
R Shannor
J Zetek
J Zetek
J D Hood
Big tree
F M Chapman
Conrad
Big trees
W M Wheeler
AMNH
Van Tyne
Harvard
Armour
F Drayton
Maiz
Island
Termite House
Gigante Bay

A Physiological Basis for Ecological Groups in a Tropical Forest

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Running header: Functional Groups in Tropical Forests

Key Words: tropical trees, functional groups, physiology, photosynthesis, water use efficiency, nitrogen, growth, tropical succession.

ABSTRACT

Tropical forest community ecology and physiology have traditionally addressed different biological questions with few studies examining the connection between the two disciplines. This work describes a field ecophysiological experiment linking ecology and physiology by demonstrating that ecologically similar species share some physiological traits. Twenty-one tree species from a Panamanian rainforest were assigned to one of three functional groups (pioneer, intermediate, or shade tolerant) on the basis of existing ecological data on recruitment and abundance for both mature forest and treefall gap environments. Steady-state, leaf-level grand mean photosynthesis (A_{ave}) and water use efficiency (WUE_{ave}) were measured exclusively in light gaps on 8 in-situ trees per species in both the wet and dry seasons on Barro Colorado Island, Panamá. Maximal photosynthetic rate (P_{max}) and rate of change of photosynthesis with light ("slope") were extracted from photosynthetic light response curves (A/PAR). Leaf samples were analyzed for elemental nitrogen (% N) and carbon (% C) content, and specific leaf area (SLA).

Despite the environmental variability inherent to field studies, highly significant differences in gas exchange and water use traits were detected ($p < 0.0001$). Leaf elemental composition also differed significantly at the species level ($p < 0.0001$). Among groups, three traits showed significant differences: A_{ave}, P_{max}, and % N. Pioneer species exhibited a higher photosynthetic rate (mean: 15.7 μmol CO_2 m^{-2} s^{-1}) than intermediates (12.5) and both had higher mean photosynthetic rates than shade tolerant species (8.9). Intermediate species had the highest leaf N content (2.86%) followed by pioneers (2.69%) and then shade tolerants (2.42%). WUE_{ave} and slope of the light curves did not differ significantly across all groups although differences in response between pioneers and shade tolerants were noted. Groups did not differ in either % C or SLA. A strong positive correlation between diameter growth rate and photosynthetic rate ($r^2 = 0.55$, $p = 0.004$) is observed across the species. A discriminant function analysis allowed multiple physiological traits to be considered simultaneously and identified A_{ave} and % N as the major distinguishing factors between functional groups (canononical coeff. = 0.893 and 0.655).

Our results indicate that field physiological measurements, which are extensively sampled over a broad range of natural conditions, can elucidate significant functional group and species differences. Members of ecologically-defined groups share physiological traits such as similar rates of photosynthesis and leaf N content. This work supports the use of functional groups constructed on the basis of ecological data as potential descriptors of physiological traits at the community level.

INTRODUCTION

Although they are repositories for nearly two thirds of the world's known species, tropical rainforests remain poorly understood physiologically (Mooney *et al.* 1980, McKane *et al.* 1995, Bawa and Markham 1995, Ziska *et al.* 1991). In contrast, the ecology of tropical forests has been better studied (e.g. Whitmore 1991, McDade *et al.* 1994). Integrative efforts such as those of Leigh (1982) and Gentry (1990) illustrate that while the ecological traits are relatively well known for many rainforest animal and plant species, their physiological processes are not. This study focuses on tropical trees and seeks to build on existing ecological knowledge by exploring physiological trait differences among ecologically similar species.

An early effort to examine tropical forest physiology with respect to ecological observations was conducted by Koyama (1981). However, he encountered two principal problems in conducting photosynthetic research in Pasoh, a Malaysian rainforest. The first was a suite of technical difficulties relating to the available gas exchange equipment and having to work on excised leaves. The second complication was associated with working in a highly diverse ecosystem and involved methods of species selection that would allow him to "scale up" the results and make broader conclusions. While the first problem has largely been eliminated by technological improvements, the second still bedevils tropical biologists. Recently, it has been argued that improving the generality and predictive power of tropical ecophysiology will require defining functional groups that combine species with common features or processes in order to reduce the dimensionality of diverse tropical forests in a more meaningful way (Körner 1993). Functional groups are already widely used in tropical forest ecology from taxonomy to theory. They are typically defined as assemblages of species based on successional, form, or life-history criteria (*see* Schulze 1982, Ellsworth and Reich 1996). Selecting the appropriate grouping criteria is crucial to the validity of the conclusions. The literature contains numerous approaches of functional group categorization (Solbrig 1993, Whitmore 1989), but functional groups are frequently defined on the basis of growth, shade-adaptation, or successional status (Mulkey *et al.* 1993, Reich *et al.* 1995, Bazzaz and Pickett 1980). Indeed, functional groups are increasingly called upon in tropical community ecology as a means of reducing the complexity of plant

or animal communities for modeling and estimating purposes (Körner 1993 a,b; McKane *et al.* 1995), but they are less commonly used in tropical ecophysiology.

Functional groups may represent an effective approach to organize the great diversity of tropical trees into guilds on the basis of ecological or physiological traits, producing a representation of the adaptive traits of the constituent species (Mooney *et al.* 1980, Solbrig 1993, Körner 1993a). The general grouping philosophy behind this technique is that since individual species can exhibit plasticity in response or behavior, the characteristics of a community or ecosystem can be better understood at a broader level such as through examining groups or assemblages of species. Criteria for determining functional group membership have been explored extensively (*see* Schulze 1982, Whitmore 1989) but ultimately are dictated by the function of the study (Solbrig 1993). Consequently, our groups were selected based on their ecology since our project sought to build links between existing ecological data and physiology. We used recruitment and relative abundance data from both high and low light regions of the forest (Welden *et al.* 1991) to categorize the trees as pioneer, intermediate, or shade tolerant species (also called "climax"; *see* Whitmore 1989).

Evidence indicates that such ecologically-defined groups, especially successional groups, may also be related physiologically (Mooney *et al.* 1980, Bazzaz and Pickett 1980). Some studies (Ellsworth and Reich 1996, Reich *et al.* 1995, Chazdon 1992) have found strong photosynthetic similarities among secondary successional groups in the field. Interspecific variation in canopy photosynthesis with some similar group responses has recently been demonstrated (Hogan *et al.* 1995). One study, which measured induction times on naturally-occurring shade tolerant plants, reveals intra-group variation under forest conditions (Kursar and Coley 1993). But most studies limit their scope to one segment of species (Ellsworth and Reich 1996) or contrast two extremes: a shade species and a gap species (Chazdon 1992). Studies of multiple tropical species are almost exclusively conducted under rigorously controlled laboratory or greenhouse conditions (Ceulemans and Mousseau 1994, Dahlman *et al.* 1985), providing little evidence regarding the physiological traits of successional groups in natural environments (Ellsworth and Reich 1996). Instead, field studies of the type conducted by Reich *et al.* (1995) are needed to examine several physiological traits involving multiple species having a range of ecological requirements and measured in similar environments. The aim of this work was to encompass a broad range of both

species and environmental conditions and to evaluate whether ecologically-defined groups share physiological traits.

Species-specific variation in physiological traits, especially photosynthesis, is well documented among plant species ranging from crops to evergreens (Lambers and Poorter 1992, Hogan *et al.* 1995, Zelitch 1982), and in a range of successional classes (Ellsworth and Reich 1996, Reich *et al.* 1995, Chazdon 1992). Many other physiological and biochemical properties of a plant such as growth, conductance, mineral nutrient content, and production of secondary chemicals have been demonstrated to vary among species, even among those with similar ecological characteristics (Lambers and Poorter 1992, Poorter and Bergkotte 1992, Huante *et al.* 1995). Yet, because the majority of these studies establishing species-specific physiological differences have been conducted under controlled conditions, field measurements are recognized as complementing and verifying these laboratory and growing house experiments. Indeed, as physiological data are increasingly being called upon to parameterize global carbon or forest dynamics models, the need for companion data gathered under natural conditions has become clear (Pitekla 1994, Bawa and Markham 1995, McKane *et al.* 1995). But the large environmental variation inherent in field studies may make detecting species differences difficult. It remains unclear whether these physiological differences remain detectable when the species are sampled under naturally varying ambient environmental conditions.

The present study examines eight physiological traits with respect to functional groups and species. We hypothesized that when we assembled species into groups based on ecological site preferences or light-dependent recruitment (i.e. gap *v.* shade plants), the members of each group would also have comparable physiological traits, reflecting a group trend. Furthermore, we believed that individual species would show some variation in some physiological traits, especially in photosynthetic rate and water use efficiency. These species differences would be due to demonstrated limits on plasticity and contrasting life histories (Langenheim *et al.* 1984, Chazdon 1992).

MATERIALS AND METHODS

Study Sites

The field research was conducted on and around Barro Colorado Island (BCI) in the Republic of Panamá. BCI is a 15.6-km^2 former hilltop situated midway between the Atlantic and Pacific Oceans (9°09' N, 79° 51' W). The island was isolated from the mainland in 1914 as a result of the construction of the Panama Canal. There has been no human disturbance of the forest on the island since its designation in 1923 as a biological reserve and subsequent management by the Smithsonian Tropical Research Institute (STRI). As a result, the tropical moist forest (Holdridge Life-Zone System) ranges from 80 to 500 years in age (Foster and Brokaw 1982). The island has a mean annual rainfall of about 2700 mm concentrated during the eight month wet season (May through December). A mean of 88 mm of rain falls during the pronounced four month dry season which lasts from January through April (Windsor 1990). Field measurements were also taken in large reforestation plots on abandoned farm lands in Las Pavas, a small village located near BCI. A full description of the flora and fauna of Barro Colorado and its environs can be found in Croat (1978), Leigh, *et al.* (1982) and Gentry (1990).

Study Species and Functional Groups

This study focused on twenty-one neotropical tree species representing sixteen tropical plant families (Table 1). All of these species have medium-to-large evergreen leaves and are classified as either understory treelets or canopy trees (Croat 1978, Hubbell and Foster 1986). With the exception of *Ochroma* and *Swietenia*, the selected species are all native to the island and co-occur in a range of growth habitats (i.e. both closed and open canopy forest). Seven of our species had well over 1000 stems > 1 cm DBH in the 1985 and 1990 re-censuses and are among the most common local species (Hubbell and Foster 1991, Condit *et al.* 1995b). Specific morphological and taxonomic characteristics for each can be found in Croat (1978) and Gentry (1993).

For our analyses, we classified the 21 species into one of three successional guilds or functional groups using existing ecological data. We defined our functional groups on the basis of their degree of light-dependence for recruitment and overall

forest stem abundance. These data were obtained from the BCI 50-ha plot (Welden *et al.* 1991, Hubbell *et al. in prep*). Species with a high recruitment in high-light areas (> 60% of new saplings found) but low overall abundance in mature forest (< 500 stems in the plot) were considered gap or pioneer species, while trees exhibiting low recruitment in gaps (< 20% of new saplings found) but a high abundance in mature forest (> 1000 stems in the plot) were considered shade tolerant. Species exhibiting a relatively neutral or non-gap recruitment (20-55% of new saplings found) and abundance (500-1000 stems) were classified as intermediates.

While indicative of relative successional timing, the functional group classification of a species as either a pioneer, intermediate, or shade tolerant is not necessarily a reflection of its growth form or vertical position in the forest. Under the right conditions, a pioneer species such as *Cecropia* can reach the canopy. Likewise, a shade tolerant species is normally part of the understory for many years before ascending. Thus, while the this type of functional group analysis is meaningful in terms of succession, such classifications are not intended to describe the vertical dimensionality of the forest.

Forest Gaps and Environmental Heterogeneity

Gas exchange measurements were taken exclusively in forest gaps on 8 individuals per species. Work was conducted in gap environments because they are the sites of interspecific competition that determines future canopy composition, making gaps the epicenters of forest regeneration (Whitmore 1989, Hubbell *et al. in press*). Also, they experience a wide range of light, humidity, and temperature levels, and provide a common environment in which to measure many co-existing species. For the purposes of this study, a gap was defined as a break in the forest canopy, caused by the death of at least one emergent tree such that the area formerly occupied by the crown was now open to the sky. Sampling was only conducted in > 1.5 yr. old gaps that encompassed an area of at least 15m in diameter and included at least 6 co-occurring study species.

A total of eight gaps were selected on BCI, each containing at least six co-existing species. Due to difficulties in locating juveniles of *Hura* and *Dipteryx* in sufficient quantities on BCI, the majority of measurements for these species were conducted in the Las Pavas plots. The Las Pavas trees were 2.5 yr. old saplings

planted in two principal reforestation plots surrounded by patches of secondary forest. We also included *Swietenia macrophylla* ("mahogany"), a species not naturally occurring on BCI but of significant economic interest *A priori*, we classified *Swietenia* as an intermediate species but due to the lack of BCI ecological data, we were uncertain of how the species would fit in to the three ecological groupings.

Measurements were made on trees 1-10 cm diameter at breast height (DBH) and leaves were selected to be fully-expanded and mature with a minimum of herbivore damage. Since all gaps measurements were conducted under naturally heterogeneous environmental conditions, extensive sampling was conducted to record both the environmental variables and the plant's response. This allowed us to assess photosynthesis and water use efficiency on each species in the range of natural growing conditions they experience daily and yearly.

Physiological Measurements

Grand mean carbon assimilation rate (A_{ave}, *in* μmol CO_2 m^{-2} s^{-1}) and water use efficiency (WUE_{ave}, *in* μmol CO_2 / mmol H_20) were measured using a portable leaf chamber and an open-system infrared gas analyzer (ADC model LCA-2, Hoddesdon, England). System air flow was controlled by a mass flow pump (ADC model A-SUM II, Hoddesdon, England) and an external air mixing chamber, drawing in outside air from approximately the same height as the leaf being measured. Concurrent with the CO_2 differential measurements, relative humidity and temperature of both the leaf and the air were also recorded. To be accurate in the tropics, the span of the cuvette humidity sensor was adjusted for maximum sensitivity in the range of 65 - 95% humidity rather than the default setting of 35 - 85% (A. Brady, Nortech, *pers. comm.*). Readings that were outside this range were not used in the calculations or analyses. Thus, WUE_{ave} was calculated from a reduced dataset. Light, reported as photosynthetically active radiation (PAR, *in* μE m^{-2} s^{-1}), was measured using a cuvette-mounted filtered selenium quantum sensor (ADC, sensitivity over 400-700nm) and temperature was measured with both a leaf thermocouple and a cuvette-mounted thermistor (ADC, ± 0.3°C over 0° - 45°C). Both the gas analyzer and the cuvette sensors were calibrated weekly. Photosynthetic and water use traits were calculated according to the equations found in von Caemmerer and Farquhar (1981) and are reported on a per unit leaf area basis.

After clamping the cuvette on a leaf, the gas exchange system was allowed to stabilize for at least three minutes or until it reached steady-state. Afterwards, photosynthetic measurements were recorded each minute for 8-10 minutes. All leaf-level readings were recorded twice daily to account for diurnal plant and environmental variation (*i.e.* light and temperature fluxes, stomatal closure). Measurements were recorded in the morning between 0830 and 1200h and again in the afternoon between 1230 and 1530h of the same day. In addition to daily replication, gas exchange measurements were recorded in the dry season (January - April 1995) and repeated in the wet season (September - December 1995) on the same individual trees to assess seasonal shifts. For a given individual, the gas exchange measurements over the 8-10 minute periods in both the morning and afternoon are averaged. These values for all eight individuals per species, in both seasons, are subsequently averaged to create the grand mean photosynthetic rate (A_{ave}) for the species. Therefore, A_{ave} incorporates all of the approximately 280 measurements that were made on each species, or nearly 2000 gas exchange readings per functional group.

Photosynthetic Response to Light

Light curves were produced from the PAR data gathered simultaneously with the gas exchange measurements to determine differential photosynthetic responsiveness to increasing light. Since measurements were taken throughout the year and without bias to sunny or cloudy days, they attempt to represent the light conditions experienced by trees that year. The response curves were constructed using the highest photosynthetic rates observed within each light interval. Here, incremental light intervals of 50 $\mu mol\ m^{-2}\ s^{-1}$ were chosen, allowing for a minimum of 7 photosynthetic values per curve. Short sunflecks, characteristic of tropical forests, may be insufficient to fully induce non-canopy leaves, producing sub-maximal gas exchange measurements (Pearcy, *pers. comm.*). Conversely, periods of less than an hour of high light can lead to photoinhibition and sharp decreases in photosynthetic rate (Mulkey and Pearcy 1992). As a result, some of the A_{ave} values collected were a result of either non-induced or photoinhibited leaves. These readings were not considered when constructing the envelope curves. The light environment of a leaf was not a factor in its selection for measurement. Therefore, the range of light levels for a given species is a result of natural environmental variation rather than investigator selection.

Since all measurements were taken in gaps under natural light conditions (sunny/cloudy), photosynthetic measurements were recorded over a range irradience levels, ranging from very low light (< 1 - 20 μmol m^{-2} s^{-1}) to high light (1300 - 1500 μmol m^{-2} s^{-1}) levels for every species. The data were fitted with a member of a family of hyperbolic models commonly used to describe leaf photosynthetic response to light radiation:

$$P = P_{max}\left[1 - e^{-\left(\frac{\alpha \cdot PAR}{P_{max}}\right)}\right]$$ (Thornley 1976).

This model requires the estimation of two parameters: the rate of change in photosynthesis due to light (slope or α), and P_{max}, the highest sustained or maximal photosynthetic rate recorded. The two parameters (slope and P_{max}) were estimated using an iterative least squares approximation routine which employs the Brent numerical minimization routine (Ramsay, *pers. comm.*).

Growth Measurements

Relative growth data for each species was obtained from the 1985-1990 census of the 50-ha plot on BCI from Dr. Rick Condit. Growth rates were calculated by the Forest Dynamics Project as diameter at breast height (DBH) increment over time: ln (dbh2 / dbh1) / time, also known as the instantaneous relative growth rate (Condit *et al.* 1993, Condit *et al.* 1995a). All growth data is taken from trees in the same size class as those measured, i.e. < 10 cm DBH. The species measured predominantly at Las Pavas (*Hura, Dipteryx* and *Swietenia*) are not included in the growth analyses because in-situ growth rates were not yet available.

Leaf Characteristics

Leaf discs were collected from four individuals per species in both the wet and dry seasons for a total of 8 leaves per species. The discs were of fixed, known diameter and represent a random subset of the experimental trees. They were oven dried at 70°C, and then weighed to assess thickness, commonly described by specific leaf area (SLA; in cm^2/g dry weight). These discs were then analyzed for carbon and nitrogen content in a Fison Instruments Eager 1108 CHNS-O analyzer. Both

chemical (Acetaniline, Fison Instruments) and vegetative standards (*Acer*, National Bureau of Standards) were used repeatedly for calibration purposes.

Statistical Analyses

Gas exchange, water use efficiency, and leaf composition data were analyzed with a 3-way nested ANOVA using both the General Linear Models procedure in SAS 6.08 (SAS Institute 1988) and the ANOVA module in StatView 4.5 (Abacus Concepts 1994). Photosynthetic and water use data were log-transformed prior to analysis following the results of normality tests. The model considered main effects and interactions for season, functional group (FG), and species nested under functional group. This design necessitated specification of certain error terms. Error terms for the FG and SEASON * FG effects were SPECIES (FG) and SPECIES (FG) * SEASON. Tukey post-hoc tests ($\alpha = 0.05$) specified the type and degree of significance of each effect. Testing for significant clumping of species was accomplished with Kruskal-Wallis rank order tests on the basis of the rank order of each functional group for a given physiological trait. The robustness of group means was tested with a delete-one jackknife technique. This test assesses the impact of the removal of one or three species from the group mean. Species to be removed from a group were chosen at random. For both the one and three-species removal tests, three jackknife iterations were performed. Growth and photosynthetic relationships were analyzed by linear regression.

We also statistically examined relationships among all eight physiological traits using a discriminant function analysis. This multivariate test employed various characteristics of a given species to explore group and species relationships and assess which characteristics were most responsible for group separation or connections. The test was conducted using the MGLH-Discriminant Analysis module of SYSTAT (SYSTAT, 1992) with eight dependent variables: grand mean photosynthesis, WUE, %N, %C, SLA, P_{max}, the slope of the light curve, and growth rate.

RESULTS

Photosynthesis and WUE

Grand mean photosynthesis (A_{ave}) varied from 7 to 19 μmol CO_2 m^{-2} s^{-1} or as much as 1.5 times across all species (Figure 1, Appendix 1). In addition to varying at the species level, photosynthetic rates differed significantly among the functional groups (Figure 2). Pioneer species such as *Trema*, *Ochroma*, and *Cecropia* exhibited the highest photosynthetic rates of the trees examined (18.9 to 18.1 μmol CO_2 m^{-2} s^{-1}; Figure 1). Shade tolerant species like *Poulsenia*, *Anacardium*, and *Protium* had very low rates in contrast (7.3 to 8.6 μmol CO_2 m^{-2} s^{-1}). Overall, pioneer species had a significantly higher grand mean photosynthetic rate than intermediate species and both were higher than shade tolerant species (Figure 2, Table 2). Jackknife analyses indicate that all three group means are robust, and not significantly altered by the removal of one or even half of the constituent species (Table 3). This suggests that group means are not heavily dependent on one or a few species.

In addition, species in the same functional group tended to have A_{ave} rates that were more similar to others in their group than to non-group species. This produced a significant clustering of species into their functional groups (Figure 1; Kruskal-Wallis, $H = 13.54$, $p = 0.001$). However, variation in A_{ave} is also significant at the level of species within groups (Table 2). Thus, although groups tended to cluster together, the constituent species still differed in their grand mean photosynthetic rates.

Seasonal differences in ambient light conditions are evident in gaps, with an overall mean light level across all species during the wet season of 318 μE m^{-2} s^{-1} compared to 485 μE m^{-2} s^{-1} for the dry season. However, no overall seasonal differences in grand mean photosynthetic rates or season by functional group interactions were observed (Table 2).

Across species, grand mean water use efficiencies (WUE_{ave}) did not vary as widely as did A_{ave} (Figure 3). Here, the species with the highest WUE_{ave} values were intermediate and shade tolerant species such as *Palicourea* (4.4 μmol CO_2 m^{-2} s^{-1} / mmol H_2O), *Simarouba* (4.1), and *Faramea* (4.0), the same species that exhibited relatively low photosynthetic rates. The lowest observed water use efficiencies were

for *Zanthoxylum* and *Dipteryx* (2.6-2.9 μmol CO_2 m^{-2} s^{-1} / mmol H_2O; Figure 3). Unlike photosynthesis, WUE_{ave} was not strongly group-specific (Table 2). Yet, the clustering of species into groups remained significant and in the reverse order from photosynthesis. The rank order analysis separated shade tolerants species with the highest WUE_{ave} values (mean = 3.80 μmol CO_2 m^{-2} s^{-1} / mmol H_2O) from pioneers (3.50) and intermediates (3.41), which were equivalent (p = 0.1742). Species-level differences were highly significant (Table 2). As an illustration, the WUE_{ave} of *Palicourea* is 1.5 times greater than *Dipteryx*, though both are intermediate species. In addition, seasonal fluctuations in WUE_{ave} were observed across all species, with WUE_{ave} values consistently higher in the wet season. These seasonal changes in WUE accounted for the largest percentage of the observed variation (Table 2).

Photosynthetic Response to Light

Group and species differences are observed in the curvilinear responses of photosynthesis to light for the 21 species. Maximal photosynthetic rate as a function of light (P_{max}) varied significantly (F = 10.1, p = 0.001) across all three functional groups (Figure 4 a-c). Average P_{max} for pioneer trees (37 μmol m^{-2} s^{-1}) was significantly higher than that of intermediate trees (28 μmol m^{-2} s^{-1}; p = 0.044) and that of shade tolerant trees (23 μmol m^{-2} s^{-1}; p = 0.001). Significant clustering into groups is evident among all species (Figure 5 a; Kruskal-Wallis, H = 9.90, p = 0.007), though the distribution of both intermediate and shade tolerant species is less tight than pioneers. *Hura* and *Faramea* exhibit higher P_{max} values than would be expected by their group membership (Figure 5 a).

Although the slope of the curves is not strongly significantly different among groups (Figure 5 b; F = 2.67, p = 0.096), there is a significant inverse relationship between P_{max} and slope (Fisher's r to z Correlation = -0.53, p = 0.011), indicating that species with high P_{max} values also have gradual slopes. This trend becomes apparent upon examination of the species light response curves organized by functional group (Figure 4 a-c). Some species, such as *Croton*, *Hura* and *Faramea* have unusual curves in comparison to the other members of their functional group. In general, though, all the curves of pioneer species (Figure 4 a) are tall, gradual arcs, achieving a high maximal photosynthetic rate but requiring more light to do so. This type of curve is strongly contrasted by the shade tolerant species such as *Poulsenia* and *Protium* which are characterized by curves that rise quickly to a low maximum

(Figure 4 c). As is evident from their slopes, shade tolerant species achieve their P_{max} much faster than pioneers, though its magnitude is lower. Intermediate species tend to exhibit a low P_{max} like a shade tolerants but also have a gradual slope like a pioneer (Figure 4 b). Both *Hura* and *Anacardium* have unexpectedly low slopes, though *Hura* has a high P_{max} and *Anacardium* also has a low P_{max}.

Photosynthesis and Growth

A strong relationship was observed when the grand mean photosynthetic rates of each species were regressed against their relative growth rates (Figure 6; $r^2 = 0.55$, $p = 0.0004$). The trend indicates that fast-growing species like *Ochroma*, *Trema*, and *Cecropia* photosynthesize at a high level while *Protium*, *Simarouba*, and *Poulsenia* are slow-growers and slow photosynthesizers. Clustering into functional groups is visible along the regression line with the pioneer species tending towards the high photosynthesis/growth strategy ($A_{ave} > 12$ and RGR > 10) while the shade tolerant and intermediate species co-occur in the low photosynthesis/growth region. When examined within groups, the relationship between A_{ave} and growth disappears (data not shown).

Leaf Characteristics

Our analysis of leaf composition included both elemental analysis (% N and % C) and thickness (SLA). A wide range of nitrogen values was obtained, led by the N-rich leaves of *Palicourea* which contained 2.3 times more nitrogen than *Anacardium*, the species with the least foliar nitrogen (Figure 7). The clumping of species into functional groups and rank order of groups is also significant (Kruskal-Wallis, H = 8.83, $p = 0.012$). In decreasing order of leaf N content, the groups were arranged as intermediate species (mean % N content = 2.86%), pioneer species (2.69%), and shade tolerant species (2.42%). As with A_{ave}, leaf N content not only varied among groups but was also highly species-specific (Table 4). Among groups only a small degree of scatter is observed, with *Alseis* and *Anacardium* have more and less foliar N respectively than would be expected by their group rank (Figure 7). No strong seasonal effects were noted, though a moderate overall increase in leaf N was recorded during the wet season. While no overall correlation was found between leaf nitrogen and P_{max} ($r^2 = 0.04$), weak relationships between the two traits exist

within each functional group (pioneers, $r^2 = 0.30$; intermediates, $r^2 = 0.21$; shade tolerants $r^2 = 0.20$).

There was a significant species effect for both foliar carbon content and specific leaf area (SLA) but no significant functional group effect for SLA (Table 4). Leaf carbon also varied among groups but the range of variation among groups was small (2.3% difference between intermediate and pioneer groups). Likewise, among species, the range of variation in leaf carbon was small in comparison to leaf nitrogen, ranging from the highly carbon-filled *Dipteryx* leaves (51.8%) to the relatively carbon-depauperate *Poulsenia* (38.3%). SLA, on the other hand, shows a 261% difference between the thick leaves of *Swietenia* and the thin leaves of *Alseis*. Furthermore, neither leaf carbon content nor SLA varied between seasons. No correlation was found between SLA and photosynthesis ($r^2 = 0.019$) or between SLA and growth rate ($r^2 = 0.022$) in these species.

Discriminant Analysis

Group differences, which have been observed for several physiological attributes, become even more apparent when a suite of physiological traits are considered simultaneously (Figure 8). Eight variables were entered as predictors into a multivariate discriminant function analysis. They were: A_{ave}, WUE_{ave}, %N, %C, SLA, P_{max}, slope of the light response curve, and growth rate. The scores representing Factor 1 explain 89.3% of the variance that exists among the groups while Factor 2 explains 65.5%. By the nature of the test, these two axes or factors are wholly statistically independent of one another, thereby describing two separate dimensions of variation.

The multivariate discriminant analysis suggests a pattern of group organization, with Factor 1 separating the three classes of species on the basis of photosynthesis and light response. The canonical loadings for photosynthetic and growth traits (canon. coeffs. = 0.708 and 0.562 respectively) separate pioneer species to the left on Factor 1 while light and water parameters such as slope and WUE (canon. coeffs. = 0.223 and 0.139 respectively) draw intermediate and shade tolerant species in the opposite direction. Group separation is strongest by this factor and result from photosynthesis and growth differences. Factor 2 is less explicit in terms of what it separates but appears to differentiate among intermediate species and

the two more extreme strategies on the basis of leaf biochemical traits. The intermediates load positively, indicating a strong characterization by leaf % C and N. Conversely, strong differences in WUE or slope of the light response curve differentiate pioneer or shade tolerant species. Of the 21 species that were classified *a priori* into functional groups based on ecological criteria, 18 would also have been classified that way based on their physiological traits (Table 5). Note that *Croton, Cordia,* and *Anacardium* are all indicated as potential members of other groups based on their physiological traits.

DISCUSSION

Environmental Stochasticity and Gas Exchange Measurements

The ecology of the tropical moist forest on Barro Colorado Island (BCI) where this project was conducted is relatively well known. Growth and distribution of over 300 tree species, including the study species, have now been documented for 15 years as part of the ongoing Forest Dynamics Project 50-ha plot (Hubbell and Foster 1986). In addition, a great deal of research has explored BCI's animal and plant communities (Leigh *et al.* 1982). Thus, from an ecological standpoint, BCI represents perhaps the most thoroughly studied and the best understood tropical forest in the world. In addition to the extensive ecological research, a considerable amount of ecophysiology research has been conducted on the island (*see* Mulkey *et al.* 1993, Kursar and Coley 1993, Ziska *et al.* 1991), providing the foundations for our type of field research. These legacies of research and knowledge make BCI an ideal setting in which to test whether physiological traits are related to ecological characteristics of trees.

To relate physiology to ecology, we conducted all of the physiological measurements of this study under the conditions in which the ecological traits had been measured. Many environmental factors such as light level, nutrient and water availability, and temperature fluctuate widely within the forest and are recognized to affect photosynthetic performance (Hogan *et al.* 1995, Pearcy 1987, Strauss-Debenedetti and Bazzaz 1991). Different experimental strategies have been employed to handle this variation. Highly controlled experiments seek to precisely document the physiological capabilities of one or a few species in greenhouse or lab environments (see Königer *et al.* 1995, Ögren and Sundlin 1996, Kitajima 1994). Semi-controlled

experiments allow for limited environmental variation in the field but manipulate certain variables such as light or water level (Chazdon and Field 1987, Mulkey *et al.* 1993). Finally, non-controlled experiments, such as the present study, record and use the environmental variation rather than manipulating it.

Under natural conditions, extensive sampling of species and environmental conditions are needed in order to incorporate the range of natural variation present in the habitat (Abrams *et al.* 1994, Ellsworth and Reich 1996). Our field measurements sampled individual trees growing together within a forest ecosystem. Over the course of a year, we sampled from 8 individuals per species over several days under many light, soil, water, and temperature regimes, taking an average of 278 measurements per species. As a result, we were able to calculate an average measure of photosynthesis, A_{ave} per species. These A_{ave} rates are consistent with other studies (Kursar and Coley 1993, Ellsworth and Reich 1996, Reich *et al.* 1995), though, for a few species, they are < 5 $\mu mol\ m^{-2}\ s^{-1}$ higher than previously reported by two experiments using more controlled methodologies (Oberbauer and Strain 1985, Kitajima 1994). A possible explanation for this small difference may be that the aforementioned experiments were conducted on seedlings under regulated temperature and light regimes. Photosynthesis measured in-situ on canopy leaves differs from our results only for one species (Hogan *et al.* 1995).

Our approach differs from most previous work in that it does not extrapolate from the biochemical level or from the precise capabilities of a few species up to larger systems, but rather accepts natural variation and concentrates on the species and group levels in order to make conclusions regarding the system. We understand that field measurements in and of themselves cannot not provide a full understanding of the physiology of a species. Rather, we believe they are a necessary complement to the controlled experiments conducted in the lab or greenhouse. Sampling under idealized conditions is necessary to elucidate mechanistic and biochemical processes along with species' capabilities but does not establish a clear link to the natural environment. Field measurements are subject to environmental fluctuations but provide the ability to understand questions in community ecology rather than about biochemical or mechanistic processes. Since no single approach is recognized as being complete, a detailed understanding needs to come from both perspectives

Physiological Trends among Functional Groups

An essential aim of our work was to extract mean physiological differences among species that correlate with mean differences in their population biology. In doing so, we observed species differences in photosynthesis, WUE, and leaf elemental content. However, detecting strong differences in response to light was especially important. It echoes previous findings for both tropical and temperate species showing that the efficiency of light capture and use varies widely among plants (Ögren and Sundlin 1996, Walters and Field 1987, Strauss-Debenedetti and Bazzaz 1991, Pearcy 1987, Chazdon 1992, Kubiske and Pregitzer 1996). By comprehensively sampling plants in disparate light environments, we were able to build curves that accurately describe the maximal performance as well as the sub-maximal. Short sunflecks, characteristic of tropical forests, may be insufficient to fully induce some fast-growing sun plants (Ögren and Sundlin 1996) or species with long-lived leaves (Kursar and Coley 1993), producing sub-maximal gas exchange measurements. Conversely, extended periods of high light, even of less than an hour, can lead to photoinhibition and reduce the photosynthetic rate (Mulkey and Pearcy 1992). Because we sampled trees at multiple times of day under ambient light conditions, our measurements include photoinhibited or non-maximally induced readings. Although only the maximum values were used in the construction of the envelope curves, sub-optimal conditions are encountered daily by most plants and are thus necessary components in an extrapolation of grand mean carbon assimilation.

Photosynthetic response to light was found to be moderately correlated with successional status. However, some species, principally shade tolerants, did not exhibit significantly increased levels of photosynthesis in the dry season. This may be because, at the mean light level of the wet season (318 $\mu E\ m^{-2}\ s^{-1}$), many species were already at $\geq 80\%$ of their P_{max} so the increase in light during the dry season did not benefit them as much as a species further from its light saturation point. Such differences in light response curves and saturation points across functional groups have also been found by experimenters working under controlled conditions. Oberbauer and Strain (1984) report that their two classes of gap species were not light saturated until over 1000 $\mu E\ m^{-2}\ s^{-1}$ while the shade tolerant species reached their photosynthetic capacity at half that intensity. In addition, several other tropical studies support our finding of group-specific variation in response to light (Koyama 1981, Fetcher *et al.* 1987, Strauss-Debenedetti and Bazzaz 1991). The finding that pioneer

species tend to have a higher P_{max} than other groups is further supported by these previous experiments, as is the determination of a lower P_{max} for shade tolerant species. Likewise, the relationship between increasing curve steepness with increasing shade tolerance is supported previous work (Kubiske and Pregitzer 1996, Strauss-Debenedetti and Bazzaz 1991, Mooney *et al.* 1980, Koyama 1981).

We observed certain other significant physiological trends among functional groups. Pioneer species tend to have high photosynthetic rates and high leaf % N contents, whereas shade tolerant species have low rates of photosynthesis and % N content. These results are consistent with other tropical studies that were conducted with species along successional gradients (Ellsworth and Reich 1996, Reich *et al.* 1995) and with plants of contrasting shade tolerance (Chazdon 1987, Walters 1987). Temperate studies have also shown that pioneer species have higher photosynthetic rates (Kubiske and Pregitzer 1996). Their comparative study in Michigan of a shade intolerant, a moderately shade tolerant, and a shade tolerant species showed the same clear organization of group photosynthetic rates, with pioneer species leading intermediates both of which had higher photosynthetic rates than shade tolerants. A second temperate study links % N content to other physiological aspects of the plant. A higher photosynthetic nitrogen use efficiency (PNUE) and leaf nitrogen content are found in the faster growing species (Lambers and Poorter 1992, Poorter *et al.*, 1990, Poorter and Bergkotte 1992). A similar finding for trees, also from the temperate zone, shows that shade-intolerant pioneer *Betula* seedlings had a higher percent leaf nitrogen content than either of the more shade tolerant *Quercus* or *Acer* seedlings (Kubiske and Pregitzer 1996). A possible explanation for these observations is that there is a lower average leaf age in faster-growing trees due to faster leaf production and senescence. Also, younger leaves have a higher N content than older leaves, which are no longer engaged in such high rates of protein synthesis. So a faster growing species with more recently produced leaves could be expected to have more nitrogen available to it for photosynthesis.

However, our data shows no overall relationship between P_{max} and N content. Although the lack of a significant correlation between the two is surprising given the work of Evans (1989), an identical finding, also for tropical trees, was reported by Strauss-Debenedetti and Bazzaz (1991). They too found relationships among successional classes but none overall. We believe, as they do, that despite the lack of an overall correlation, the group trends indicate different nutrient allocation patterns.

In addition, Reich *et al.* (1992) suggest that this relationship holds true only when photosynthesis is expressed on a per unit mass basis. However, clearly, other field studies studying nitrogen and photosynthesis among different types of functional groups are needed.

Overall, our cohort of tropical trees had a higher leaf nitrogen content compared to temperate species (Abrams and Mostoller 1995) while our values are consistent with reported foliar N contents from other tropical studies (Ellsworth and Reich 1996, Huante *et al.* 1995). These differences did not arise as a result of sampling uniquely within gap environments. Vitousek and Denslow (1986) report no difference in soil N content between mature forest sites and treefall gaps in the tropics. This seems to indicate that the differences observed in leaf nitrogen content among species and between tropical and temperate areas is not the result of sampling location but rather natural variance among species and habitats.

Only WUE_{ave} and % N differed significantly among seasons, though several traits showed significant interactions. WUE_{ave} was higher in the wet season than in the dry season for all functional groups which is not surprising given the higher ambient relative humidity during the wet season (Windsor 1990). The finding of a much lower WUE_{ave} in the dry season is interesting given that our data for pioneer species also show a photosynthetic interaction between species and season, a result of an increase in species' photosynthetic rate during the dry season (Table 2). Other studies have shown that photosynthesis declines in the dry season due to evapotranspirative losses (Hogan *et al.* 1995). Our data for intermediates and shade tolerant species support this idea, but we offer two possible explanations for the observed behavior of pioneers. First, the mean light environment was higher in the dry season than the wet due to the more frequent cloud cover during the wet season months. It is evident from the species light-response curves that although most intermediate and shade tolerant species reach their P_{max} by 200-300 $\mu E\ m^{-2}\ s^{-1}$, pioneers continue to increase their photosynthetic rate, often not reaching their P_{max} until 600-700 $\mu E\ m^{-2}\ s^{-1}$. With a higher mean light level in the dry season, pioneers are able to increase their photosynthetic rate while the more shade tolerant species have already reached their plateau. This would also explain differences in nitrogen content among groups. A second possible explanation is that the higher temperatures of the dry season brought about lower humidity and consequently stomatal closure. Pioneer species, being better adapted for high-light conditions, may also be better

adapted to higher leaf temperatures. While shade tolerant species appear to close their stomates more readily in the dry season, pioneer species seem to be able to continue photosynthesizing. The demonstrated fluctuations in physiological traits resulting from seasonal shifts from this experiment and others (Hogan *et al.* 1995) underscore the need to characterize the physiology of a tree throughout a growing season.

Growth, Photosynthesis, and Functional Groups

So far, we have chiefly examined physiological traits. Yet the original grouping of species was based on ecological traits. To examine whether A_{ave}, is a reliable predictor of functional group status based on diameter growth, we computed a linear regression between traits. We found that 55% of the variance among species in growth rate was explained by photosynthesis. This strong relationship confirms that faster growing species have higher photosynthetic rates. Other studies have also observed that faster growing species exhibit higher rates of photosynthesis (Poorter *et al.* 1990, Reich *et al.* 1992), but correlations between growth and photosynthesis have not always been detected (Zelitch 1982, Lambers and Poorter 1992, Huante *et al.* 1995). Poorter *et al.* (1990) speculated that these correlations will only be detected when gas exchange and growth measurements are conducted on several plant species under ambient environmental conditions. This conclusion is supported by Zelich (1982) who found that a growth/photosynthesis relationship only becomes apparent if photosynthesis is measured under non-standardized or controlled conditions that use environmental variability. Studies that incorporated multiple seasons and species tended to produce a high correlation whereas measuring growth and photosynthesis on a single plant or in a single season found no relationship (Zelich 1982). However, Lambers and Poorter (1992) also point out that although differences in photosynthesis will explain differences in growth among dissimilar species, the correlation breaks down within a group of ecologically similar species. Our results support these view. Although a strong overall correlation was found, it is only evident when all the functional groups or both seasons are included. We also believe that this correlation between photosynthesis and growth demonstrate the versatility of our field methodology.

By combining all of the measured physiological traits with a discriminant function analysis, we were able to evaluate the reliability of using ecological criteria to group species with similar physiologies. Classifications based on the eight

physiological traits grouped species identically to ecological data in 18 out of 21 cases or 86% of the time. It is notable that Factor 1, which explains over 89% of the variance, separates pioneer species from the intermediates and shade tolerants on the basis of photosynthesis and growth. Species with higher photosynthetic and growth rates also tend to be early colonizers of gaps and intolerant of shade whereas those with more shade tolerance have lower rates of photosynthesis. This addresses an important point, that of whether this technique and these results are sufficiently generalized so as to be applicable elsewhere. We feel that this, coupled with the robustness of the group means, indicates that you can use other species for which the ecological data is less well established and classify them on the basis of a suite of physiological traits. A discriminant analysis can characterize functional groups (and the membership of a given species) at least as well if not better than univariate traits.

Conclusion

Our work has shown a strong linkage between the ecology and physiology of species and successional groups in a tropical forest community. For many physiological traits, species-specific differences are detectable under heterogeneous environmental conditions. Furthermore, functional groups defined in an ecological context have a physiological basis, and group means are robust— not dependent on one or even half of the component species. Two physiological traits (A_{ave} and % N), when measured under natural conditions, reliably separate species into ecological groups. We believe that grand mean photosynthesis and leaf % N are sufficiently different among groups to act as reliable group membership predictors for other species and that the functional group means are robust and not greatly affected by one or a few species. Both these facts indicate that future sampling of these traits will help quantify life-history traits and augment both the physiological and ecological data available for tropical forests.

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FIGURE LEGENDS

FIGURE 1: Variation in grand mean photosynthetic rate (A_{ave}) among species measured under natural conditions. For each species, A_{ave} represents the mean of the ~280 steady-state, leaf-level photosynthetic measurements taken throughout the growing year. Means include daily (AM and PM) and seasonal (Dry and Wet) replicates from 8 individuals per species. Shading represents functional group membership. Error bars indicate ± 1 SE.

FIGURE 2: Grand mean photosynthetic rate (A_{ave}) from both seasons among the three functional groups. All species differ significantly from one another in mean photosynthetic rate and these differences are robust, remaining significant even after the removal of one or half the constituent species. Data shown represent the yearly photosynthetic mean of all seven constituent species per group. Each species is comprised of 8 invididuals measured in the AM and PM during both seasons. Means are shown with ± 1 SE, and for each group, $n > 1850$. Letters represent significant differences between groups at the 0.05 level. Shading indicates functional group status as in Figure 1.

FIGURE 3: Variance in grand mean water use efficiency (WUE_{ave}) across species. For each species, values represent the mean of the approximately ~140 measurements taken in the AM and PM for both the wet and dry seasons. Species-level differences in WUE_{ave} are significant but functional groups do not differ significantly, though species were significantly organized into their functional groups. Shading indicates functional group status and error bars show ± 1 SE.

FIGURE 4 (a-c): A/PAR response curves for the 21 species, divided into the three functional groups. In all graphs, photosynthetically active radiation (PAR) is measured in $\mu E\ m^{-2}\ s^{-1}$ and photosynthesis in $\mu mol\ m^{-2}\ s^{-1}$. Pioneer species (a) are characterized by a slower rate of increase of photosynthesis to light (slope) but a higher maximal photosynthetic rate (P_{max}). Shade tolerant species (c) show the reverse trend, a sharp increase in photosynthesis at low light but a lower overall P_{max}. Intermediate species (b) do not show a characteristic trend for either parameter. Curves follow the hyperbolic model of Thornley (1976) and were constructed with a minimum of seven measurements per species.

FIGURE 5: Interspecific variation in maximal photosynthetic rate (a) and in rate of photosynthetic response to light or slope of the light response curve (b) for each of the 21 species.

FIGURE 6: Relationship between leaf-level grand mean photosynthesis and the relative growth rate among 18 tropical tree species. Each point represents a species mean. Functional group classification is denoted by typestyle: pioneers are underlined, intermediates are outlined, and shade tolerants are *italicized*. The overall linear relationship for the species was significant ($r^2 = 0.55$) and is defines as [GROWTH] = - 8.66 + 1.74 [PHOTOSYNTHESIS]. Individual relationships for each functional group were not significant (data not shown). Species whose photosynthetic rate was primarily measured in a different location from their growth rate (*Hura*, *Dipteryx*, and *Swietenia*) were not included in this regression.

FIGURE 7: Interspecific differences in leaf nitrogen (% dry weight) are displayed with shading to denote functional group membership. Bars represent the mean of wet and dry season samples with ± 1 SE; n = 8 leaves per species.

FIGURE 8: Plot of factor scores from the discriminant function analysis. This analysis provides an evaluation of group differences and indicates which variables are most responsible for the similarities or differences. The analysis categorizes the species on the basis of eight dependent variables: photosynthesis at ambient CO_2 (PS), water use efficiency (WUE), percent leaf nitrogen (%N), percent leaf carbon (%C), specific leaf area (SLA), maximal photosynthetic rate (PMAX), slope of the light response curve (SLOPE), and growth rate (GR). The canonical coefficients given with each variable represent the degree to which that variable contributes to the factor in that direction; larger coefficients indicate a greater influence of that variable. Species are identified with four-letter codes listed in Table 1. *A priori* functional group classification is indicated by different type styles as in Figure 6.

TABLE 1: The 21 study species, listed in their ecologically-defined functional groups. These groups were defined on the basis of the BCI 50-ha plot data. Species are listed with their six-letter abbreviation code, botanical family as recorded by Croat (1978), and Spanish common name. The growth form for all species is classified as either canopy tree or understory treelet.

SPECIES	CODE	FAMILY	COMMON NAME
Pioneer			
Cecropia insignis	CECRIN	MORACEAE	Guarumo blanco
Croton billbergianus	CROTBI	EUPHORBICEAE	Vaquero
Luehea seemannii	LUEHSE	TILIACEAE	Guácimo colorado
Miconia argentea	MICOAR	MELASTOMATACEAE	Dos caras
Ochroma pyramidale	OCHRPY	BOMBACACEAE	Balsa
Trema micrantha	TREMMI	ULMACEAE	Capulín macho
Zanthoxylum belizense	ZANTBE	RUTACEAE	Arcabú o Tachuelo
Intermediate			
Anacardium excelsum	ANACEX	ANACARDIACEAE	Espavé
Cordia bicolor	CORDBI	BORAGINACEAE	Laurel
Dipteryx panamensis	DIPTPA	LEGUMINOSEAE: PAPIL.	Almendro
Gustavia superba	GUSTSU	LECYTHIDACEAE	Membrillo
Hura crepitans	HURACR	EUPHORBIACEAE	Hura, Javillo
Palicourea guianensis	PALIGU	RUBIACEAE	Café de monte
Swietenia macrophylla	SWIEMA	MELIACEAE	Mahogany, Caoba
Shade Tolerant			
Alseis blackiana	ALSEBL	RUBIACEAE	Mameicillo
Beilschmiedia pendula	BEILPE	LAURACEAE	Añushi rumo
Faramea occidentalis	FARAOC	RUBIACEAE	Huesito
Poulsenia armata	POULAR	MORACEAE	Cucúa
Protium tenuifolium	PROTTE	BURSERACEAE	Copá
Simarouba amara	SIMAAM	SIMAROUBACEAE	Aceituno
Trichilia tuberculata	TRICTU	MELIACEAE	Alfajía

TABLE 2: ANOVA table and significance levels for main effects and interactions of leaf-level anverage photosynthetic rate and water use efficiency. Main effects in the model are functional group (Pioneer, Intermediate, or Shade Tolerant), species nested under functional group, and season (Wet or Dry). Stars indicate degree of significance (* < 0.05, ** < 0.001).

Source of Variation	PHOTOSYNTHESIS					WATER USE EFFICIENCY				
	df	MS	F	*p*		df	MS	F	*p*	
FUNCTIONAL GROUP	2	25.7	15.8	0.0001	**	2	0.87	1.3	0.2968	ns
SPECIES (FG)	18	1.6	24.3	0.0001	**	18	0.67	11.7	0.0001	**
SEASON	1	0.05	0.7	0.4190	ns	1	15.2	263.7	0.0001	**
SEASON * FG	2	1.5	1.6	0.2338	ns	2	1.1	1.2	0.3124	ns
SEASON * SPECIES (FG)	18	0.9	13.8	0.0001	**	18	0.9	14.9	0.0001	**

TABLE 3: Summary of results of jackknife analysis testing group mean stability. *Aave* is the grand group mean including all species. In the test, one and three species per group respectively were removed to test the sensitivity of group means to one or a few species. With respect to *Aave* no significant differences are noted when one species ($p = 0.774$) or when three species are removed ($p = 0.331$). All means are shown with ± 1 SE.

		Number of Species Removed per Group	
	Aave	One Species	Three Species
Pioneer	15.7 ± 0.2	15.3 ± 0.2	16.9 ± 0.3
Intermediate	12.5 ± 0.2	12.8 ± 0.2	12.6 ± 0.2
Shade Tolerant	8.9 ± 0.1	8.8 ± 0.0	9.0 ± 0.2

TABLE 4: ANOVA table and significance levels for the analysis of the leaf elemental characteristics data. Data was analyzed from eight total leaves per species (four leaves per season). All the main effects of the model are shown, but none of the interactions were significant and are not listed. Significance symbols as in Table 2.

Source of Variation	% NITROGEN					% CARBON					SPECIFIC LEAF AREA				
	df	MS	F	*p*		df	MS	F	*p*		df	MS	F	*p*	
FUNCTIONAL GROUP	2	2.4	11.1	0.0001	**	2	90.7	6.9	0.0015	*	2	4887	1.9	0.1559	ns
SPECIES (FG)	18	3.4	15.7	0.0001	**	18	79.7	6.0	0.0001	**	18	28127	10.9	0.0001	**
SEASON	1	0.9	4.1	0.0447	*	1	8.9	0.67	0.4142	ns	1	41	0.02	0.9000	ns

TABLE 5: Summary of the results of the discriminant function analysis. A comparison of the *a priori* functional group classifications and the classifications produced by the discriminant analysis. On the basis of physiological traits, 18 out of 21 species are classified the same way as they were ecologically. Those species that are classified differently by the discriminant analysis are listed below.

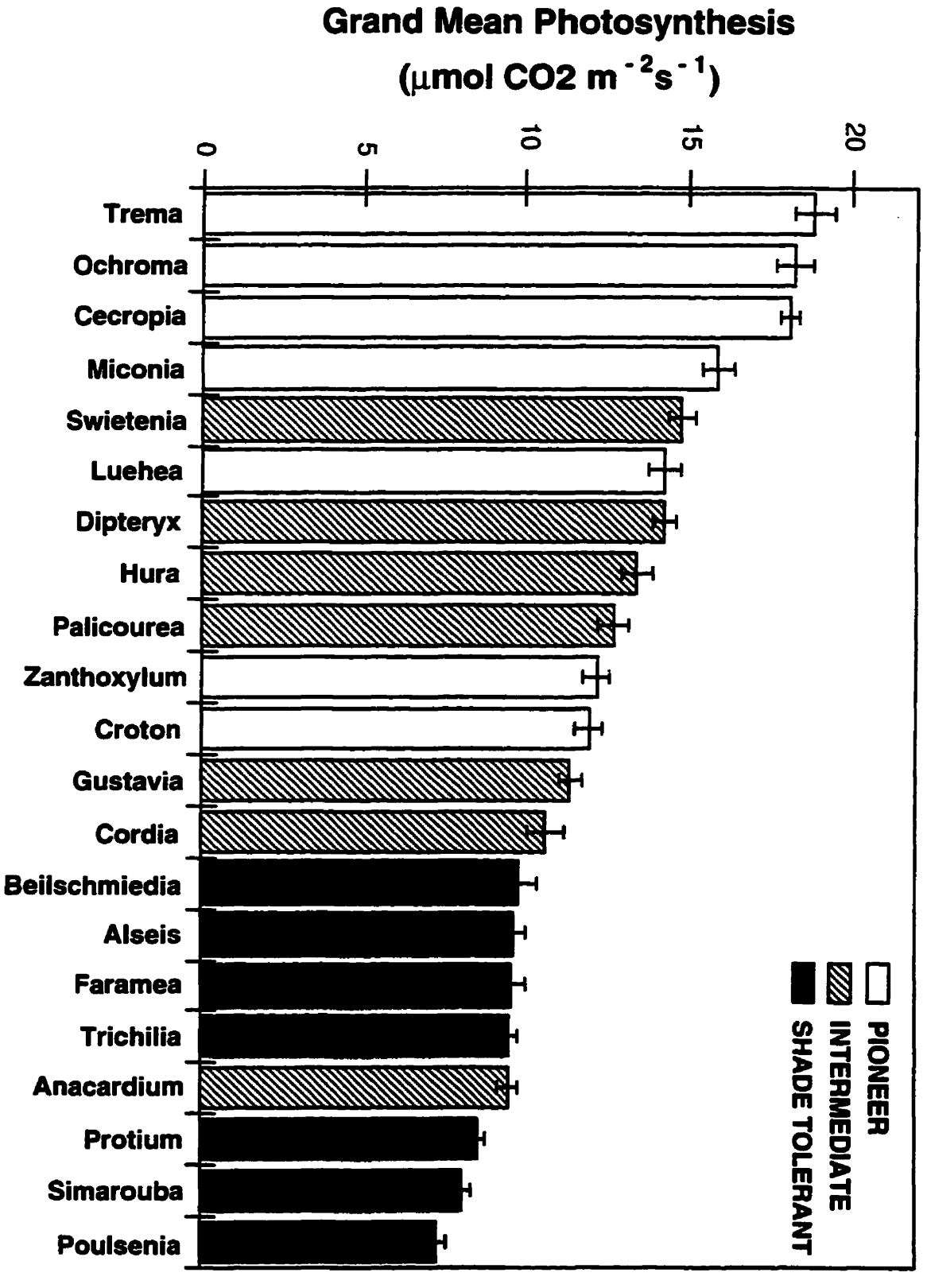
	DISCRIMINANT ANALYSIS PREDICTIONS			
***A PRIORI* PREDICTIONS**	**Pioneer**	**Intermediate**	**Shade Tolerant**	**Total**
Pioneer	6	1	0	7
Intermediate	0	5	2	7
Shade Tolerant	0	0	7	7
Total	6	6	9	21

SPECIES	**PREDICTIONS OF GROUP MEMBERSHIP**	
	A PRIORI	**ANALYSIS**
Croton	Pioneer	Intermediate
Anacardium	Intermediate	Shade Tolerant
Cordia	Intermediate	Shade Tolerant

APPENDIX 1: Leaf-level gas exchange and water use efficiencies for 21 tropical trees. Average photosynthesis per unit leaf area (A_{ave} , µmol CO_2 m^{-2} s^{-1}) represents the mean of the daily (AM/PM) and seasonal (dry/wet) replicates of 8 individuals per species. Pmax is the maximal photosynthetic rate for each species over a wide range of incident light radiation (0-1200 µE m^{-2} s^{-1}) in a gap. Average Water Use Efficiency (WUE_{ave} ; in µmol CO_2 / mmol H_2O) is also the mean of daily and seasonal replicates. It was measured simultaneously with photosynthesis but varied strongly between seasons and is therefore reported for both of them. Values are shown with ± 1 SE.

SPECIES	PHOTOSYNTHESIS	P_{max}	WUE	
			Dry	Wet
Alseis blackiana	9.7 ± 0.4	28.1	2.7 ± 0.2	5.3 ± 0.4
Anacardium excelsum	9.5 ± 0.3	22.1	2.7 ± 0.1	3.5 ± 0.3
Beilschmiedia pendula	9.8 ± 0.3	22.1	3.3 ± 0.2	4.7 ± 0.2
Cecropia insignis	18.1 ± 0.6	39.8	2.5 ± 0.1	5.0 ± 0.4
Cordia bicolor	10.7 ± 0.4	23.3	3.2 ± 0.2	4.1 ± 0.2
Croton billbergianus	12.0 ± 0.4	27.3	3.6 ± 0.3	4.3 ± 0.2
Dipteryx panamensis	14.2 ± 0.5	30.5	2.7 ± 0.1	3.1 ± 0.1
Faramea occidentale	9.6 ± 0.4	29.4	4.0 ± 0.2	4.1 ± 0.2
Gustavia superba	11.4 ± 0.5	26.9	2.7 ± 0.1	4.7 ± 0.3
Hura crepitans	13.4 ± 0.5	33.7	3.0 ± 0.1	3.1 ± 0.2
Luehea seemannii	14.3 ± 0.5	33.2	2.9 ± 0.1	3.8 ± 0.2
Miconia argentea	15.9 ± 0.6	44.9	2.8 ± 0.1	4.3 ± 0.2
Ochroma pyramidale	18.3 ± 0.6	44.3	2.5 ± 0.1	4.5 ± 0.2
Palicourea guianensis	12.7 ± 0.5	31.2	3.2 ± 0.1	5.3 ± 0.3
Poulsenia armata	7.3 ± 0.3	15.7	3.5 ± 0.2	3.9 ± 0.2
Protium tenuifolium	8.6 ± 0.2	16.8	2.7 ± 0.1	4.7 ± 0.2
Simarouba amara	8.0 ± 0.3	26.5	5.1 ± 0.3	3.4 ± 0.2
Swietenia macrophylla	15.8 ± 0.4	30.6	3.2 ± 0.1	2.9 ± 0.1
Trema micrantha	18.9 ± 0.6	39.5	2.7 ± 0.1	4.3 ± 0.3
Trichilia tuberculata	9.6 ± 0.3	22.3	2.4 ± 0.1	3.4 ± 0.2
Zanthoxylum belizense	12.2 ± 0.4	28.3	2.4 ± 0.1	2.8 ± 0.2

FIGURE 1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(μmol CO2 m -2s -1)
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5
10
15
20
Trema
Ochroma
Cecropia
Miconia
Swietenia
Luehea
Dipteryx
Hura
Palicourea
Zanthoxylum
Croton
Gustavia
Cordia
Beilschmiedia
Alseis
Faramea
Trichilia
Anacardium
Protium
Simarouba
Poulsenia
PIONEER
INTERMEDIATE
SHADE TOLERANT

FIGURE 2

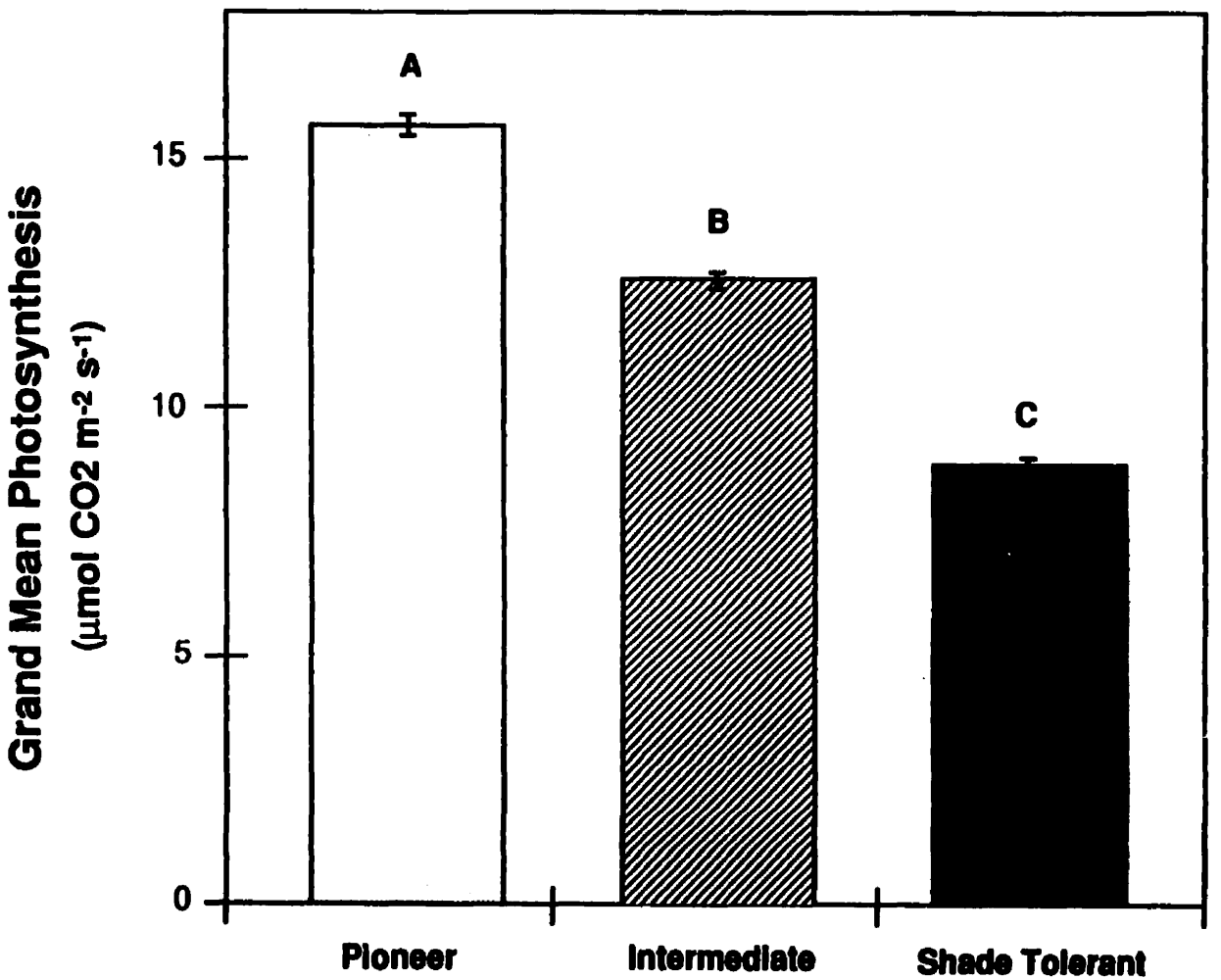
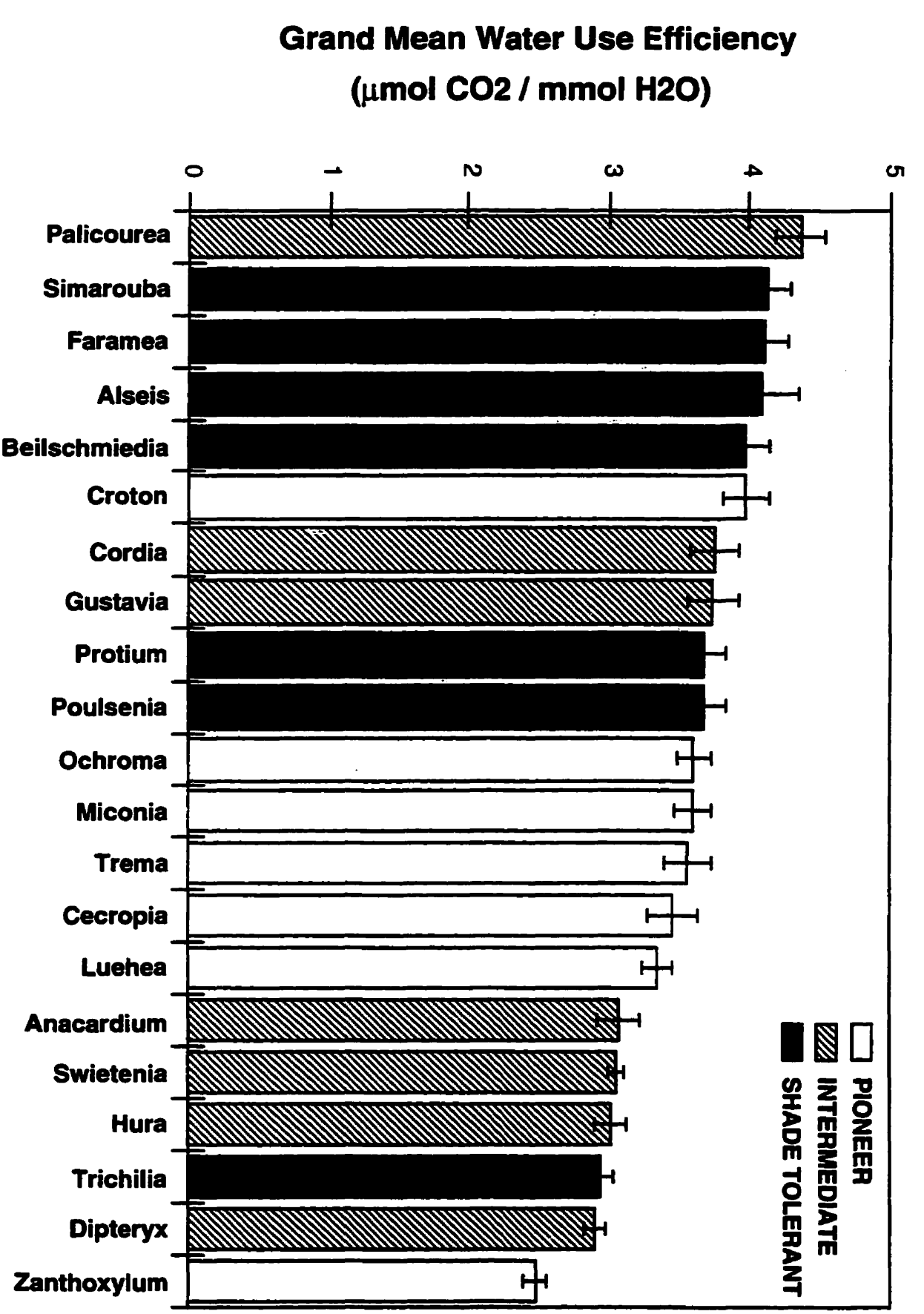

Grand Mean Photosynthesis
(µmol CO2 m-2 s-1)
15
10
5
0
A
B
C
Pioneer
Intermediate
Shade Tolerant

FIGURE 3


Grand Mean Water Use Efficiency
(μmol CO2 / mmol H2O)
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1
2
3
4
5
Palicourea
Simarouba
Faramea
Alseis
Beilschmiedia
Croton
Cordia
Gustavia
Protium
Poulsenia
Ochroma
Miconia
Trema
Cecropia
Luehea
Anacardium
Swietenia
Hura
Trichilia
Dipteryx
Zanthoxylum
PIONEER
INTERMEDIATE
SHADE TOLERANT

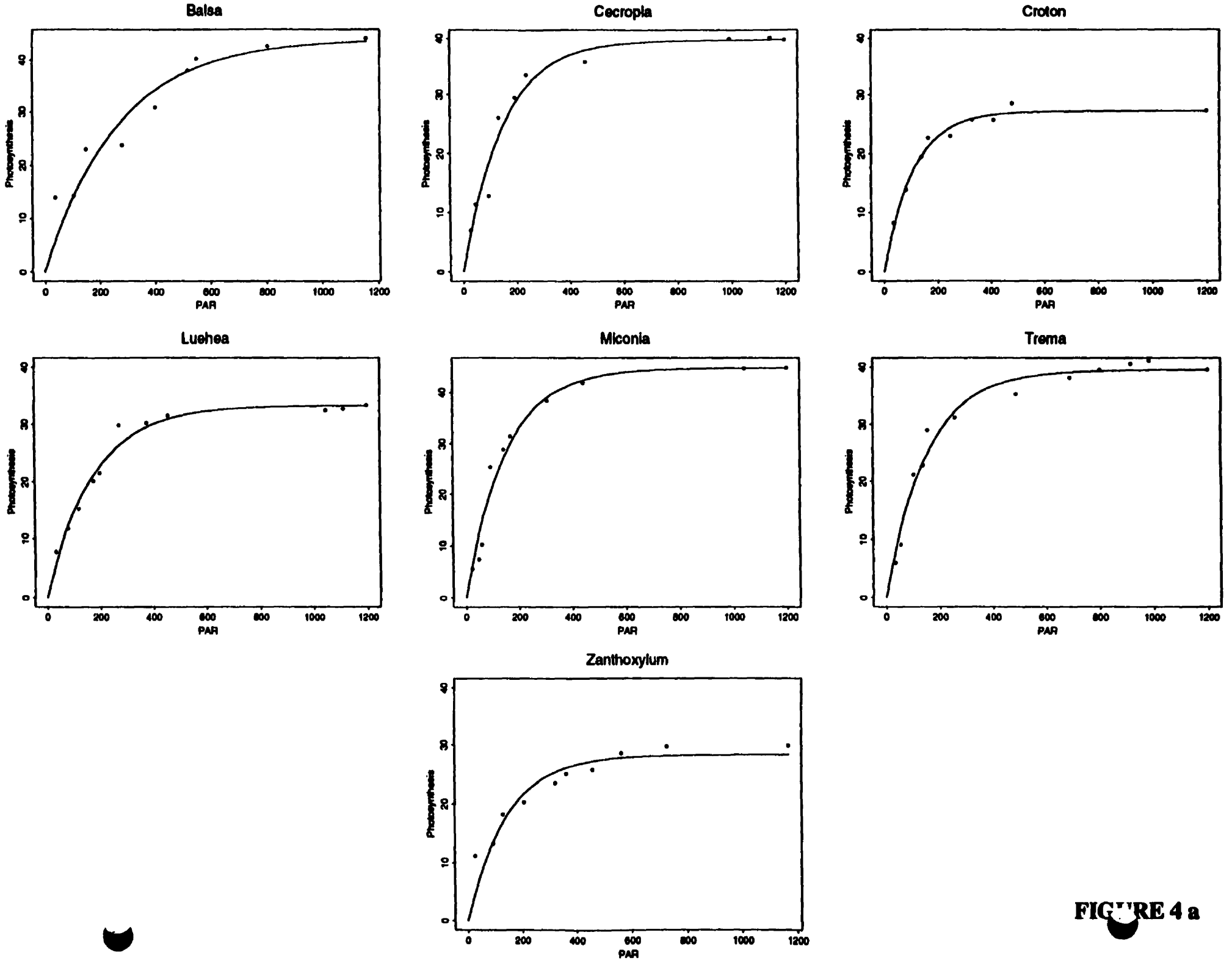
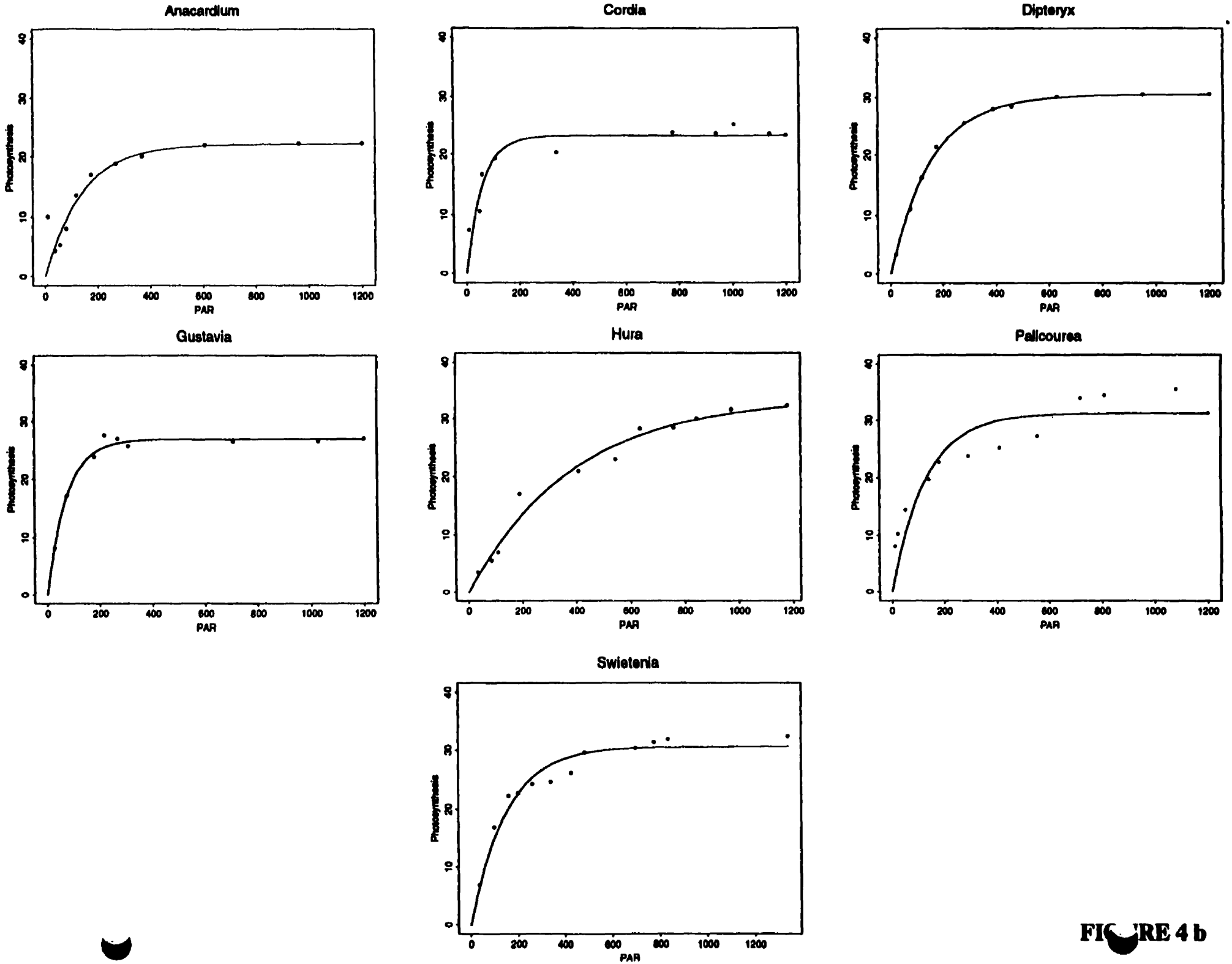

Balsa
Cecropia
Croton
Luehea
Miconia
Trema
Zanthoxylum
Photosynthesis
PAR
0
10
20
30
40
0
200
400
600
800
1000
1200

FIGURE 4 a


Anacardium
Cordia
Dipteryx
Gustavia
Hura
Pallcourea
Swietenia
Photosynthesis
PAR
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10
20
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40
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200
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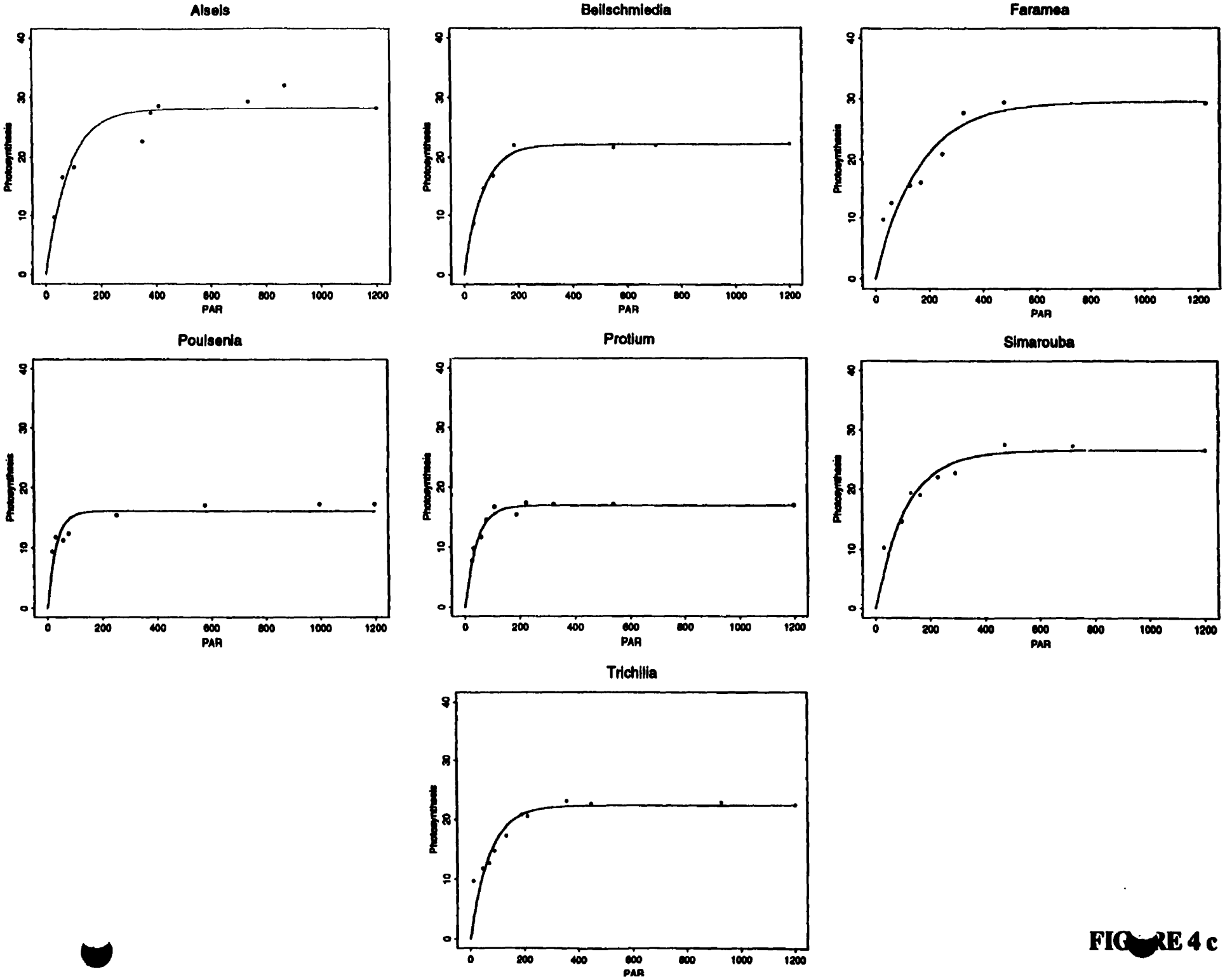
800
1000
1200

FIGURE 4 b


Alseis
Beilschmiedia
Faramea
Poulsenia
Protium
Simarouba
Trichilia
Photosynthesis
PAR
0
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20
30
40
0
200
400
600
800
1000
1200

FIGURE 4 c

FIGURE 5 (a-b)

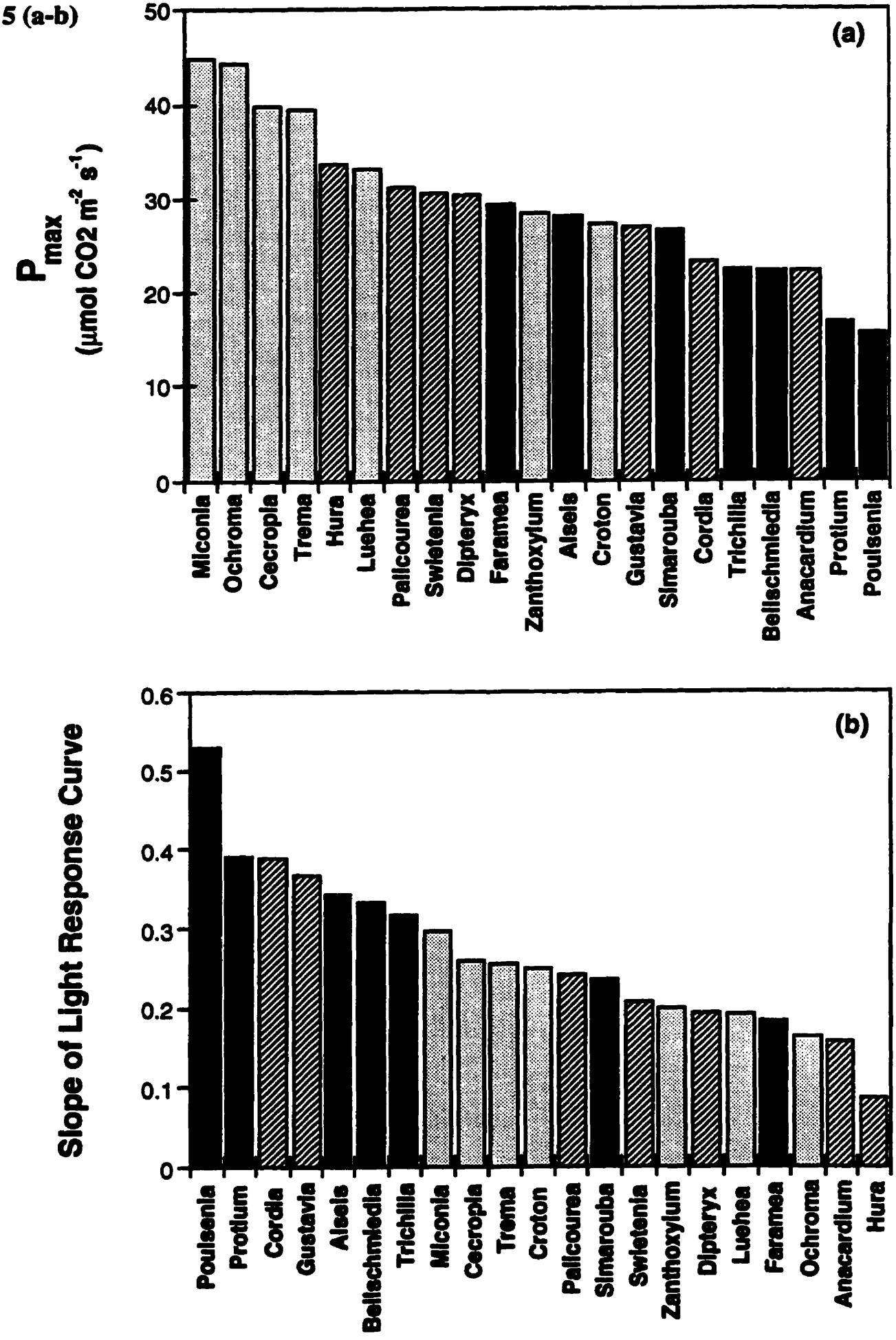

(a)
P_{max} (µmol CO2 m^{-2} s^{-1})
50
40
30
20
10
0
Miconia
Ochroma
Cecropia
Trema
Hura
Luehea
Pallcourea
Swietenia
Dipteryx
Faramea
Zanthoxylum
Alseis
Croton
Gustavia
Simarouba
Cordia
Trichilia
Bellschmiedia
Anacardium
Protium
Poulsenia
(b)
Slope of Light Response Curve
0.6
0.5
0.4
0.3
0.2
0.1
0
Poulsenia
Protium
Cordia
Gustavia
Alseis
Bellschmiedia
Trichilia
Miconia
Cecropia
Trema
Croton
Pallcourea
Simarouba
Swietenia
Zanthoxylum
Dipteryx
Luehea
Faramea
Ochroma
Anacardium
Hura

FIGURE 6

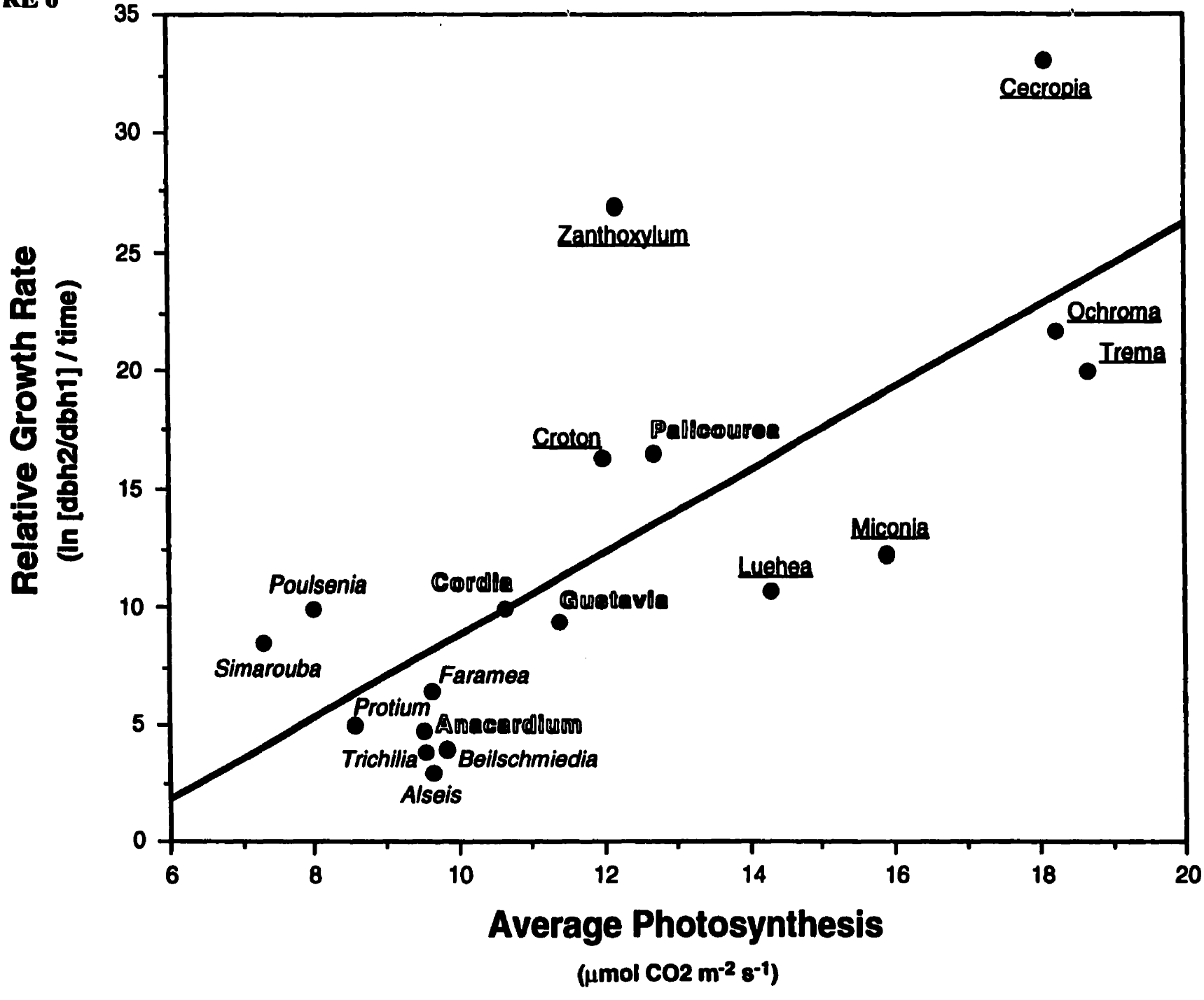

Relative Growth Rate
(ln [dbh2/dbh1] / time)
35
30
25
20
15
10
5
0
6
8
10
12
14
16
18
20
Average Photosynthesis
(μmol CO2 m-2 s-1)
Cecropia
Zanthoxylum
Ochroma
Trema
Croton
Pallcourea
Miconia
Luehea
Poulsenia
Cordia
Guatavia
Simarouba
Faramea
Protium
Anacardium
Trichilia
Beilschmiedia
Alseis

FIGURE 7

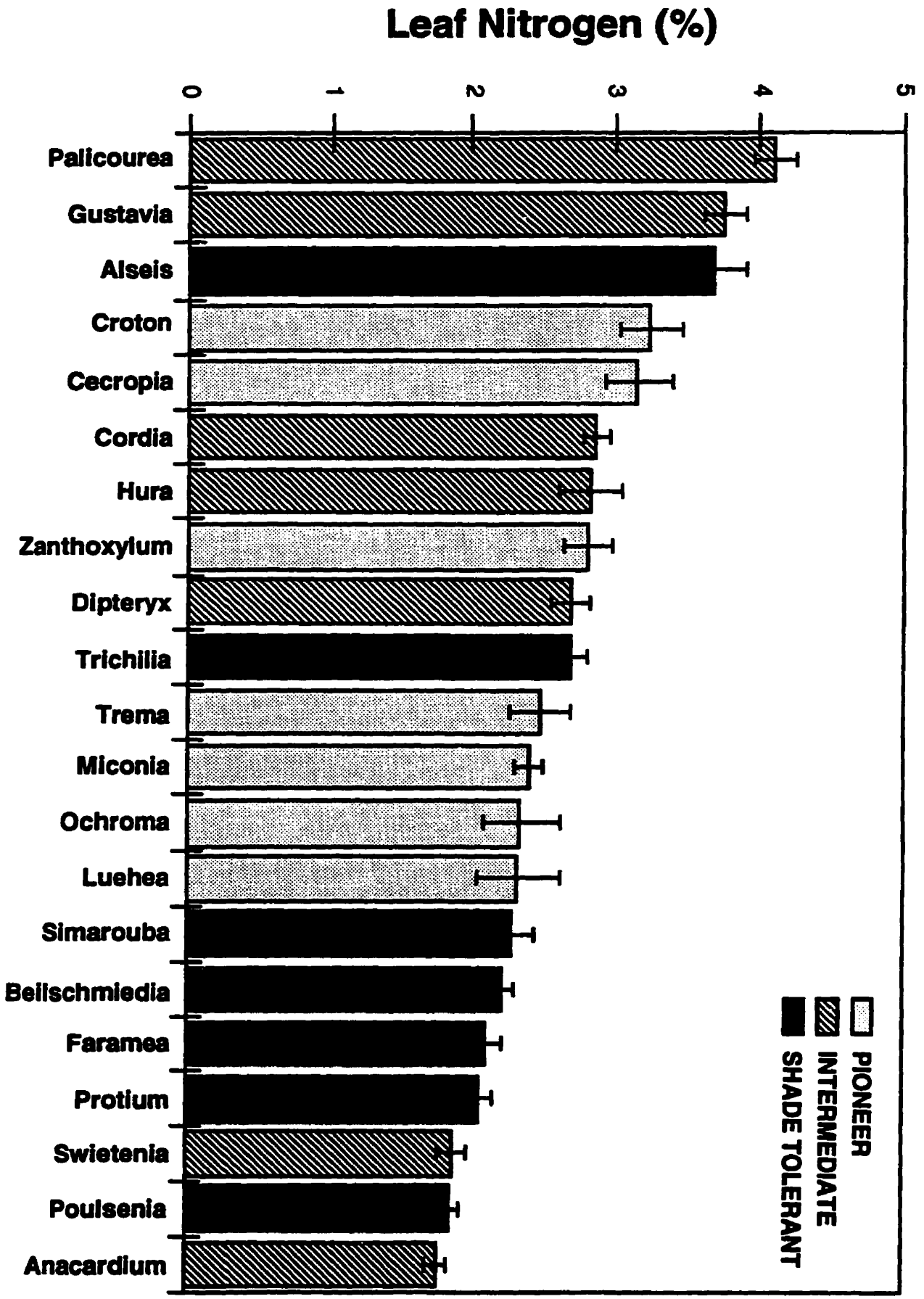
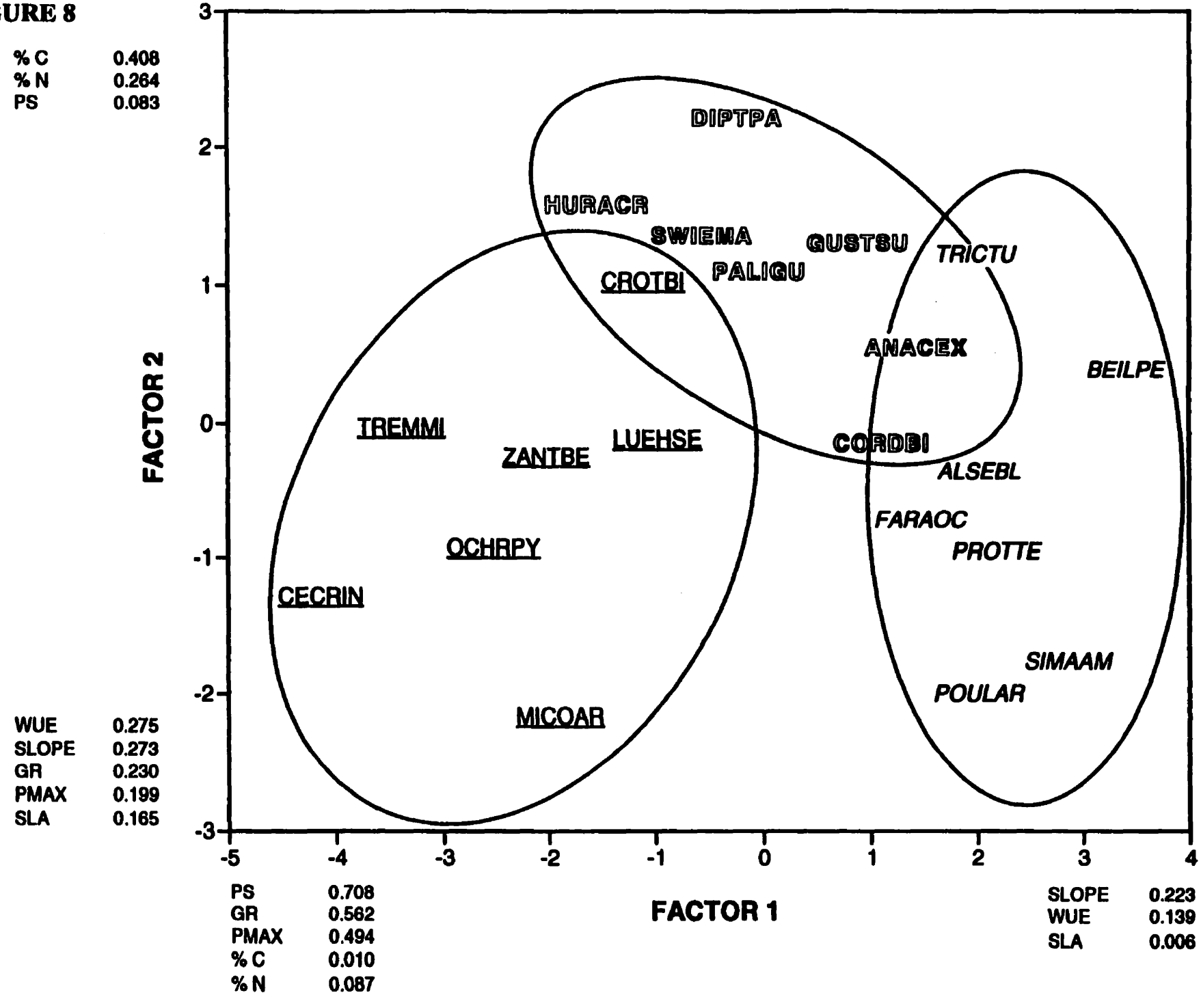

Leaf Nitrogen (%)
0
1
2
3
4
5
Palicourea
Gustavia
Alseis
Croton
Cecropia
Cordia
Hura
Zanthoxylum
Dipteryx
Trichilia
Trema
Miconia
Ochroma
Luehea
Simarouba
Beilschmiedia
Faramea
Protium
Swietenia
Pouisenia
Anacardium
PIONEER
INTERMEDIATE
SHADE TOLERANT

FIGURE 8


% C 0.408
% N 0.264
PS 0.083
WUE 0.275
SLOPE 0.273
GR 0.230
PMAX 0.199
SLA 0.165
PS 0.708
GR 0.562
PMAX 0.494
% C 0.010
% N 0.087
SLOPE 0.223
WUE 0.139
SLA 0.006
FACTOR 1
FACTOR 2
DIPTPA
HURACR
SWIEMA
GUSTSU
TRICTU
PALIGU
CROTBI
ANACEX
BEILPE
IREMMI
ZANTBE
LUEHSE
CORDBI
ALSEBL
FARAOC
PROTTE
OCHRPY
CECRIN
SIMAAM
POULAR
MICOAR

The Effect of Elevated CO_2 on the Photosynthetic Rate of Species and Functional Groups of Tropical Trees

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Running header: Tropical Tree Photosynthesis and Elevated CO_2

Key Words: tropical trees, functional groups, physiology, photosynthesis, water use efficiency, CO_2, fertilization effect, community dynamics, forest models.

ABSTRACT

The effects of elevated levels of atmospheric carbon dioxide on tropical forest species and ecosystems remains poorly understood. This work examines *in situ* photosynthetic and water use responses of 21 tropical tree species from Barro Colorado Island, Panamá to CO_2 enrichment. The study species differ in ecology and successional class and were categorized into one of three functional groups: pioneer, intermediate, or shade tolerant. Leaf-level photosynthetic rates of these species were measured on 8 forest-growing trees per species at ambient (~360 $\mu L\ L^{-1}$) and elevated (~750 $\mu L\ L^{-1}$) CO_2 in both the wet and dry seasons. A short-term doubling of the CO_2 level resulted in a significant increase in grand mean photosynthesis (A_{ave}) and water use efficiency (WUE_{ave}) for all species. Overall, A_{ave} increased 200% and WUE_{ave} rose 204% when exposed to elevated CO_2. Response to CO_2 was strongest at the species level, with *Swietenia macrophylla* and *Anacardium occidentale* experiencing the largest CO_2-induced photosynthesis and WUE increases. Photosynthetic enhancements differed significantly between seasons under elevated CO_2, with a greater response to CO_2 occurring during the dry season. At the functional group level, however, no significant differences in either photosynthesis or WUE were observed as a result of the CO_2 increase. This experiment suggests that: (1) physiological responses to elevated CO_2 are detectable under heterogeneous environmental conditions and (2) that the effects on photosynthesis and WUE are strongest at the species level but not detectable at the group level. These results contraindicate the use of functional groups as a means of simplifying the forest community for global carbon models. Seasonal effects on photosynthetic enhancements and implications for "scaling up" from the species to the community level are discussed.

INTRODUCTION

Long-term atmospheric sampling has shown that the global CO_2 concentration has risen dramatically since the Industrial Revolution, beginning in the 1850's (Keeling *et al.* 1995, Bacastow *et al.* 1985). At the current rate of increase, the atmospheric CO_2 concentration is expected to double from the current level of 360 μL L^{-1} to ~700 μL L^{-1} by the middle of the next century (IPCC 1990). In addition to changes in atmospheric chemistry, environmental effects such as alterations in temperature and precipitation patterns have already been recorded and more are predicted (Schneider 1993). To date, efforts to assess the impact of these changes on terrestrial ecosystems have been conducted principally in temperate regions. It has been established that, in general, trees experience an increase in photosynthetic rate when exposed to elevated CO_2, a so-called fertilization effect (*see* Ceulemans and Mousseau 1994, Ziska *et al.* 1991, Kubiske and Pregitzer 1996, Reekie and Bazzaz 1989). In growth studies, some tropical trees have been reported to increase their stem biomass from 11 - 31% relative to growth under ambient conditions (Körner and Arnone 1992, Ziska *et al.* 1991). However, most of these research efforts have been limited to single, isolated seedlings or conducted under controlled light, water, and nutrient conditions (Ceulemans and Mousseau 1994, Körner 1993b, Woodward *et al.* 1991). While "single-species-in-pot" studies allow for a more precise determination of individual stem response, there is a growing concern that these type of studies are sub-optimal for "scaling up" to predict community responses to global change under naturally heterogeneous conditions (Pitelka 1994, Körner 1993b). A method for reliably estimating community-level enhancement effects is needed.

Although the effects of this CO_2 increase on temperate vegetation are coming into sharper focus, much less is known about tropical biotas (Bawa and Markham 1995, Körner and Arnone 1992, Pitelka 1994). The importance of tropical biotas in the global carbon cycle is underscored by estimates that conclude that tropical forests represent 46% of the terrestrial living carbon on the planet (Brown and Lugo 1982). Not only are they enormous carbon stores, but the forests also cover 2.2×10^9 ha or 17% of the earth's land surface (Melillo *et al.* 1993). However, due primarily to human activity, the world's tropical forests are declining in number and size, chiefly as a result of slash-and-burn agriculture. Combustion of tropical forest trees releases sequestered carbon back into the atmosphere at an amount equal to 35-50% of the CO_2 produced from worldwide petroleum use every year (Houghton 1989). Yet,

despite its importance to in the global carbon cycle and the long-standing call for a better understanding of tropical forest physiology (Mooney *et al.* 1980), no study prior to 1989 had assessed the potential consequences of elevated CO_2 on plants under tropical conditions (Ziska *et al.* 1991). In addition, few *in situ* photosynthetic studies have examined the community level responses to increases in CO_2, none of them yet in the tropics. Certainly, the importance of the tropics in terms of both biological wealth and importance to the carbon cycle merit a more in-depth understanding of the ramifications resulting from this atmospheric change. This study is the first multi-species CO_2 study on tropical trees to be undertaken under the natural environmental conditions of a neotropical rainforest.

Global change simulation models have been developed which examine potential effects of elevated CO_2 on species diversity and ecosystem processes (e.g. Bolker *et al.* 1995). However, to accurately calibrate these models, an estimate of species or community response to elevated CO_2 is required (Pitelka 1994, IGBP 1992, Bolker *et al.* 1995). For some temperate or boreal forests, this can be accomplished by measuring every constituent tree species within the community. Yet, the sheer number of species within a tropical forest makes sampling each species impossible, even for models whose scope only encompasses trees. However, an ecological technique of combining species into functionally-related groups may provide a reliable alternative by simplifying community structure (Körner 1993a). This would shift the focus from the species-level to the group-level. Functional groups of trees have been shown to share certain physiological traits (Ellis *et al. submitted*), and thus for these purposes may be able to characterize entire strata of species (Körner 1993a). If this is the case and the response of groups can be shown to accurately reflect the responses of the constituent species, perhaps groups, rather than species can be used to parameterize these models.

This study begins by examining the degree to which physiological responses to elevated CO_2 are detectable under natural conditions. In doing so, it documents changes in the photosynthetic rate and water use efficiency of tropical trees in response to short-term elevated CO_2 exposure. The expectation is that species-specific physiological responses to increased CO_2 should be detectable under the heterogeneous environmental conditions of the forest. Next, it examines group-level effects and asks whether cohorts of ecologically-similar species collectively differ in their photosynthetic rate or water use efficiency when exposed to higher levels of

CO_2. Based on work showing growth and light-response differences among successional classes (*e.g.* Fetcher *et al.* 1987, Ellsworth and Reich 1996, Ellis *et al. submitted*), the early successional pioneer group was expected to derive a disproportionate benefit from the enhanced levels of CO_2 compared to the later successional intermediate and shade tolerant groups. Since pioneer species process carbon at a higher rate, it is reasonable to predict that they would benefit from a larger supply of available carbon.

MATERIALS AND METHODS

Study site, species, and functional groups

The study was conducted on and around Barro Colorado Island (BCI) in the Republic of Panamá. BCI is a 15.6-km^2 reserve of tropical moist forest (Holdridge Life-Zone System) ranging in age from 80 to 500 years old (Foster and Brokaw 1982) and is managed by the Smithsonian Tropical Research Institute. This forest receives a mean annual rainfall of ~2700 mm, concentrated during the eight month wet season (May through December). Only 88 mm of rain falls during the pronounced dry season (January through April; Windsor 1990). Monthly average rainfall data for our sampling period was provided by the Environmental Sciences Program at the Smithsonian Tropical Research Institute (Figure 1). Field physiological measurements were also conducted in large reforestation plots in Las Pavas, a small village located several miles from the island. A full description of the flora and fauna of BCI and the Panama Canal area are provided by Croat (1978), Leigh, *et al.* (1982) and Gentry (1990).

This study focused on saplings of 21 neotropical understory treelets and canopy tree species representing sixteen tropical plant families (Table 1). The selected species, with the exception of SWIEMA, all naturally co-occur on BCI in both gaps and later-successional forest. SWIEMA ("mahogany") is a locally cultivated species and was included because of its significant economic interest. Specific morphological and taxonomic characteristics for each species can be found in Croat (1978) and Gentry (1993). The 21 species were classified into one of three successional guilds or functional groups (pioneer, intermediate, or shade tolerant) on the basis of recruitment and successional data obtained from the BCI 50-ha plot (Welden *et al.* 1991, Hubbell *et al. in prep*, Ellis *et al. submitted*). The ecological criteria for

categorizing species into these groups is detailed in Ellis *et al.* (submitted). Because SWIEMA does not occur in the 50-ha plot, it was classified as an intermediate species on the basis of what is known from the preliminary reforestation data and a previous study from a different forest (Gullison *et al. in press*).

Forest gaps and sampling

Physiological measurements were taken exclusively in forest treefall gaps. It has been determined that interspecific competition in gaps determines future canopy composition, making gaps the epicenters of forest regeneration (Whitmore 1989, Hubbell *et al.* in prep). Furthermore, gap environments were selected because they experience a wide range of light, humidity, and temperature conditions and provide a common environment in which to census many co-existing species. A total of eight gaps were selected on BCI, each containing at least six co-existing species. Due to difficulties in locating juveniles in sufficient quantities on BCI, the majority of measurements for HURACR, DIPTPA and SWIEMA were conducted in the Las Pavas plots. These trees were 2.5 year old saplings planted in two principal reforestation plots surrounded by patches of secondary growth forest.

Gas exchange measurements in gaps were conducted under naturally heterogeneous temperature, humidity, and light conditions. With extensive sampling, it was possible to record both the environmental variables and the plant's response across a range of inherent natural variation. Using solar irradiance as an example, sampling during sunny and cloudy days yielded readings from very low light (< 20 $\mu E\ m^{-2}\ s^{-1}$) to very high light (1200 - 1500 $\mu E\ m^{-2}\ s^{-1}$) for every species. Measurements were made without any preference given to light conditions. This allowed us to assess photosynthesis and water use efficiency on each species in the range of natural conditions they likely experience over the course of their growth, not just under sub-saturated or light-saturated conditions. For the purposes of this study, we report both grand mean photosynthesis (A_{ave}, *in* $\mu mol\ m^{-2}\ s^{-1}$) and water use efficiency (WUE_{ave}, *in* $\mu mol\ CO_2$ / $mmol\ H_20$) for each species on the basis of these measurements taken under randomly selected meteorological conditions over the course of one year. Calculation of these means is subsequently defined.

Gas exchange measurements

Leaf-level photosynthetic rate and water use efficiency were measured using a leaf-enclosing cuvette and a portable open-system infrared gas analyzer (ADC model LCA-2 IRGA, Hoddesdon, England). Air flow at both ambient and elevated CO_2 was controlled by a mass flow pump (ADC model A-SUM II). Ambient air was drawn into the mixing chamber from the within forest at approximately the same height as the leaf being measured and was measured at 360 ± 40 μL L^{-1}. Elevated CO_2 air was supplied by mixing ambient air with CO_2-rich exhaled air in a large inflatable air bladder. The concentration produced was 750 ± 50 μL L^{-1}. Fine adjustments to the CO_2 level were made using the intake controls on the mass flow pump. Air of both CO_2 concentrations was allowed to circulate in an external air mixing chamber before entering the IRGA to help prevent large fluctuations in CO_2. This system of air bladder, mixing chamber and pump controls produced remarkably stable CO_2 concentrations in the forest such that during the sampling period per individual, there was no more than ± 20 μL L^{-1} variation in reference CO_2 at either concentration.

Relative humidity and temperature of both the leaf and the air were also recorded by the IRGA at the time of the CO_2 differential measurements. Light, reported as photosynthetically active radiation (PAR, in μE m^{-2} s^{-1}), was measured using a cuvette-mounted filtered selenium quantum sensor (ADC, sensitivity over 400-700 nm) and temperature was measured with both a leaf thermocouple and a cuvette-mounted thermistor (ADC, ± 0.3°C over 0° - 45°C). To be accurate in the tropics, the span of the cuvette humidity sensor was adjusted for maximum sensitivity in the range of 65 - 95% humidity rather than the default setting of 35 - 85% (A. Brady, Nortech, *pers. comm.*). Readings above or below this range were not considered in the analyses. Consequently, WUE analyses were conducted using a reduced dataset. Both the gas analyzer and the cuvette sensors were calibrated weekly. Photosynthesis and water use efficiency were calculated according to the equations found in von Caemmerer and Farquhar (1981) and are reported on a per unit leaf area basis.

Forest trees selected for study were all < 10 cm diameter at breast height (DBH). Leaves were chosen to be fully-expanded and mature with a minimum of herbivory damage. Measurements were taken on 8 individuals per species (n = 168

total trees sampled per season). For each tree, once the leaf had been inserted into the cuvette, the gas exchange system was allowed to stabilize for at least three minutes or until it reached steady-state. Then, a series of 8-10 minute readings were taken, at either ambient or elevated CO_2. Immediately following the first series of readings, the leaf was removed from the cuvette and the CO_2 level switched. Subsequently, the leaf was re-inserted, and a second series of gas exchange readings were taken in an identical fashion. The choice of whether the first set of readings on a tree were made at ambient or elevated CO_2 was made at random. Together, the ambient/elevated CO_2 paired readings comprise a set. Sets of readings on a given individual were repeated both daily and seasonally. Daily replicates were taken in the morning between 0830 and 1200h and again in the afternoon from 1230 to 1530h, to account for diurnal plant and environmental variation (*i.e.* light and temperature fluxes, stomatal closure). This procedure was repeated for all 8 individuals per species. The daily replication was complemented with seasonal replicates; responses were measured from every individual in both the dry season (January - April 1995) and the wet season (September - December 1995).

To calculate grand mean annual photosynthesis (A_{ave}) and water use efficiency (WUE_{ave}), the gas exchange measurements over the 8-10 minute sampling periods were averaged for both the morning and afternoon. Subsequently, these daily mean photosynthetic rates for all the eight individuals per species from both the wet and dry seasons were averaged to create the grand mean A_{ave} for the species. In all, approximately 260 measurements were made per species or nearly 2000 individual gas exchange readings per functional group. Enhancement ratios are defined as the elevated rate divided by the ambient rate of a measured parameter.

Statistical Analyses

Photosynthetic and water use efficiency data were analyzed with a repeated measures ANOVA using the General Linear Models (GLM) procedure in SAS (SAS Institute 1988). Photosynthetic and water use data were log-transformed prior to analysis following the results of normality tests. The main effects of the analysis are season, functional group (FG), and species nested under functional group, with the repeated effect being CO_2 concentration. The nested design necessitated use of specific error terms; for the FG and SEASON * FG effects, the appropriate error terms were SPECIES (FG) and SPECIES (FG) * SEASON. Rank order correlations were

calculated using Kendall's tau tests for paired samples and Kruskal-Wallis analyses were used to test for significant clustering of species within functional groups.

RESULTS

Photosynthesis

Doubling the CO_2 concentration resulted in a 200% higher grand mean photosynthetic rate compared to the ambient rate (Figure 2 a). This increase A_{ave} across species due to high CO_2 is highly significant (Table 2). At the group level, the photosynthetic effects of increasing the CO_2 this response was not significant (Table 2), indicating that there are no significant differences in response to CO_2 among the ecologically-defined groups. This is further illustrated by the lack of a significant functional group pattern among photosynthetic enhancement ratios of species (Figure 3; Kruskal-Wallis, H = 0.386, p = 0.825). No functional group had a characteristic photosynthetic enhancement response to CO_2.

Although increasing the CO_2 did not have a significant effect on A_{ave} at the group level, grand mean photosynthetic rate did vary significantly among species (Table 2). This is illustrated in Figure 2 which shows that the degree of photosynthetic enhancement in response to CO_2 varies widely across all species examined. An increase in carbon dioxide level greatly increased the photosynthetic rates for all species (Table 3). The A_{ave} among species ranged from 7 - 19 $\mu mol\ m^{-2}\ s^{-1}$ under ambient conditions while elevated CO_2 rates ranged from 15 - 40 $\mu mol\ m^{-2}\ s^{-1}$ (Table 3). Certain species such as SWIEMA and ZANTBE greatly increased their photosynthetic rates at elevated CO_2 relative to ambient conditions. In contrast, although species such as PROTTE and PALIGU did photosynthesize at a higher rate when exposed to higher CO_2 concentrations, the amount of increase over their ambient rates was comparatively small relative to the other study species (Figure 3).

Species were ranked on the basis of their A_{ave} under both ambient and elevated CO_2. Rankings are depicted as both absolute increases in photosynthetic rate (Figure 4 a) and relative changes in photosynthetic rank order (Figure 4 b). Changes in the photosynthetic rank order of species indicate the degree to which a species increases its photosynthetic rate relative to the others in the cohort. For these species, the rank order of species is significantly altered by the increase in CO_2 concentration (Kendall's tau = 0.714, $p < 0.0001$). Certain species such as ANACEX and

SWIEMA drastically increase their photosynthetic rate relative to the other study species (2.4 - 2.7 times) while some species such as PALIGU and LUEHSE showed little increase in photosynthetic rate (1.6 - 1.8 times; Figure 4 b). Interestingly, changes in the rank order of species occur throughout the range of photosynthetic capacities; CO_2-induced enhancements are not limited to only slow or rapidly photosynthesizing species but rather affect all classes of species, though to varying degrees.

Seasonality also significantly affected the photosynthetic response to CO_2 (Table 2). At ambient CO_2, the grand mean photosynthetic rate across species did not differ from the wet to the dry season (Figure 1 c). But, under elevated CO_2, the grand mean photosynthetic rate for all species in the dry season was found to be significantly higher than the average of wet season rates ($p < 0.0001$). In addition, seasonal effects on photosynthetic rate were significant at the species level ($p < 0.0001$) but not at the group level ($p = 0.2230$). This indicates that although species shift their photosynthetic response to CO_2 depending on the season, these changes are not apparent at the group level.

Water Use Efficiency

Grand mean water use efficiency (WUE_{ave}) is significantly affected by the CO_2 level (Table 2). When exposed to higher concentrations of CO_2, species lose less water per time on average than under ambient CO_2 levels (Figure 2 b). This increase in efficiency under elevated CO_2 (204%) is of the same magnitude as the observed increase in grand mean photosynthetic rates across all species. Under ambient CO_2, WUE_{ave} rates range from 2.6 - 4.4 μmol CO_2 / mmol H_2O while under elevated CO_2, they occur from 6.1 - 9.5 μmol CO_2 / mmol H_2O.

Changes in WUE in response to CO_2 are not related to their functional group classification (Table 2). Similarly, no significant clustering of species into functional groups is noted at either ambient (Kruskal-Wallis; $H = 3.50$, $p = 0.174$) or elevated CO_2 (Kruskal-Wallis; $H = 1.81$, $p = 0.404$). Taken together, these findings indicate that changes in water use efficiency in response to a higher CO_2 level are not apparent at the group level. However, a CO_2 effect is evident at the species level. The responses of WUE to an augmentation of the CO_2 level varies significantly among species (Table 2). As with photosynthesis, all species experience an increase in WUE

in a more carbon-rich environment. However, the amount of WUE_{ave} fertilization is not the same for all species. SWIEMA and ANACEX experience the largest enhancement ratio in response to elevated CO_2 (enhancement ratio = 2.6) while the same increase in CO_2 level resulted in a smaller increase in WUE_{ave} for SIMAAM and PALIGU (enhancement ratios = 1.6 and 1.7 respectively).

Species-specific changes in WUE are also apparent through rank order analyses. The rank order for species' WUE_{ave} significantly changes with an increase in CO_2 (Kendall's tau = 0.371, $p = 0.0185$). This change is most visibly noted in species such as ANACEX and SWIEMA which experience a large increase in WUE under elevated CO_2 compared to the other species in the study. On the other hand, SIMAAM and POULAR both exhibit a relatively large decline in WUE with respect to the others.

Furthermore, the effect of CO_2 on water use efficiency differs significantly depending on the season (Table 2). Among the study species, wet season water use efficiencies were consistently higher than the dry season rates, regardless of the CO_2 level. (Figure 2 d). This is consistent with higher relative humidities in the forest understory during the wet season (Windsor 1990).

Environmental Conditions

In addition to differing humidities, tropical seasons are characterized by marked variations in precipitation (Figure 1). During the 1995 dry season, rainfall averaged 55 mm per month while the average precipitation in the eight month wet season was 302 mm per month (S. Paton, *pers. comm.*). Seasonally, differences in light levels were also apparent. The distributions of recorded light levels at both CO_2 levels and in both seasons are shown in Figure 4 a. Dry season light levels (490 $\mu E\ m^{-2}\ s^{-1}$) were found to be higher than in the wet season (327 $\mu E\ m^{-2}\ s^{-1}$), though there was no significant difference between CO_2 levels (wet: $p = 0.1300$; dry: $p = 0.783$).

Across seasons, the overall light environment was similar during both ambient and elevated CO_2 measurements. The mean PAR reading for ambient photosynthesis and WUE measurements was 396 $\mu E\ m^{-2}\ s^{-1}$ while, at elevated CO_2, the light level averaged 408 $\mu E\ m^{-2}\ s^{-1}$. Light has been shown to be a significant

covariate with photosynthesis at both ambient ($F = 1269$, $p < 0.0001$) and elevated ($F = 2250$, $p < 0.0001$) CO_2 levels.

DISCUSSION

Seasonal Effects on Photosynthetic Enhancement

We were interested in the differential photosynthetic and WUE enhancements resulting from exposure to elevated CO_2. Measurements for this experiment were taken throughout an entire year which, for this tropical forest, consists of both a wet and a dry season. Under ambient CO_2, we noted no overall difference in grand mean photosynthetic rate (A_{ave}) between seasons despite observing striking variation among species' A_{ave} between the seasons. Such seasonal photosynthetic effects for species have been previously described under ambient CO_2 (Hogan *et al.* 1995). Working in the tropical canopy, they too found that the seasonal responses of photosynthetic rates were species-specific and that the grand photosynthetic mean was equivalent between seasons.

When the CO_2 level was increased, however, overall seasonal differences in response became statistically significant. A larger photosynthetic enhancement in response to CO_2 was observed during the dry season. The interaction of CO_2 with water and light factors has been discussed by Bazzaz (1990) but, to our knowledge, this result is the first indication that photosynthetic enhancements differ seasonally under enhanced CO_2. The paucity of previous relevant work is not surprising given that these conditions are uniquely tropical, as temperate or boreal deciduous forests do not photosynthesize throughout all seasons of the year.

One possible explanation for seasonal differences in enhancement relates to environmental factors. Conditions during the dry season are markedly different from those in the wet season both in terms of water and light conditions. Although water is less plentiful, our observed enhancement effects are not believed to be water-driven given that no relationship was found between A_{ave} and WUE_{ave} in either season or at either CO_2 level ($r^2 \leq 0.168$ in each case). Stomatal effects were therefore considered to be independent of photosynthetic responses.

On the other hand, light was found to be a significant seasonal covariate for both CO_2 levels. Trees in the dry season experienced a greater mean light level than in the wet season, regardless of the CO_2 level. This is particularly evident from the skewed distribution of dry season light levels. Peaks of high light readings (800 - 1300 $\mu E\ m^{-2}\ s^{-1}$) were observed for both CO_2 levels in the dry season, yet are absent in the wet season data (Figure 5a). Rather, the wet season is characterized by a larger number of lower-light readings (< 250 $\mu E\ m^{-2}\ s^{-1}$).

As a covariate under both CO_2 levels, light is expected to have a strong relationship with photosynthesis. Even so, light explained 63% more of the variance in photosynthesis under elevated CO_2 than it did under ambient CO_2. Dependence on light is therefore presumed to be stronger at elevated CO_2. The distribution of photosynthetic rates varies noticeably from ambient to elevated CO_2 (Figure 5b). A higher frequency of low rates were observed under ambient CO_2 regardless of season while, under elevated CO_2, the distribution becomes skewed towards the higher rates. Clearly, under elevated CO_2, there are more photosynthetic measurements > 40 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$. Also, while no seasonal differences in distribution are apparent under ambient CO_2, they are evident in the elevated CO_2 photosynthetic distributions (Figure 5b). The right-hand tail of the photosynthetic distribution is longer in the dry season than in the wet. We believe that the increase in CO_2 level may be responsible for the appearance of seasonal differences. It has been observed that, for crop species, an increase in CO_2 can offset low light levels (Acock and Allen 1985). We believe that the phenomenon that we observed for trees was the same. Low light levels are much more common in the wet season as evidenced by Figure 5a, yet while elevated CO_2 increases the number of high photosynthetic rates, it is not sufficient to fully compensate for the reduction in light. Consequently, at elevated CO_2, photosynthetic distributions differ between seasons, though only at the very high photosynthetic values (Figure 5b).

We observe a larger number of high photosynthetic values over the range of light. Specifically, the number of photosynthetic readings > 70 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ is greater in the dry season than in the wet season (Figure 5b). However, this increase in frequency of high photosynthetic measurements during the dry season cannot be uniquely attributed to light. When photosynthesis/light curves were constructed for all elevated CO_2 measurements and fitted by a hyperbolic curve (*see* Ellis *et al. submitted*), no difference in photosynthetic response to light was noted between the

dry and wet seasons (slopes: 0.683 and 0.657 respectively). Furthermore, maximal photosynthetic rates did not differ between seasons. Under elevated CO_2, the maximal photosynthetic rate in the dry season was 71.8 μmol CO_2 m^{-2} s^{-1} while the maximal rate in the wet season was only slightly lower at 70.1 μmol CO_2 m^{-2} s^{-1}. Consequently, although differences in both the light environment and CO_2 level appear to have the net effect of increasing the enhancement due to elevated CO_2, this explanation is clearly not sufficient or complete. Further research is clearly warranted given the implications of this differential seasonal enhancement, especially in light of global climate models which predict longer dry seasons for many of the remaining Central American and African forests (Schneider 1993). Furthermore, this interaction between CO_2 and season may complicates predictive efforts. Overall, we believe these results indicate that seasonal effects, both climatic and physiologic, may play an important role in the photosynthesis and productivity of trees in the future and thus warrant detailed future investigation.

Functional groups and community impacts of CO_2

Previous studies involving a single species, rather than a multiple species or a habitat subset, have speculated about the effects of enhanced CO_2 on future forest responses or global carbon storage (Idso 1991). However, such extrapolations are not particularly meaningful or accurate at the community level. Consequently, to accurately assess CO_2 effects on a system, multi-species enhancement experiments are needed. Yet, although it might be possible to sample all constituent species from certain forests, the richness of species precludes this for tropical forests.

Previously, it has been demonstrated that ecological groups of species remain coherent and closely related when examined physiologically (Ellis *et al. submitted*). Thus, we had hoped these grouping trends would hold up when the CO_2 level was increased. Given that sampling all constituent species within a speciose tropical community is virtually impossible, the ability to use groups as a tool to simplify the forest diversity is appealing. The advantage to this tool is that estimating system responses to elevated CO_2 consists of evaluating several groups rather than hundreds of species. At present, quantifying the ecological niche of species to group it seems to be easier than measuring their response to CO_2. In general, the current understanding of the life-history of many tropical trees is adequate to categorize a tree in a given ecological niche (e.g. *Cecropia* and *Ficus* are two well described pioneer genera).

Thus, we felt that if the response to CO_2 were consistent within a niche group, estimations of system-level responses could be made at the group rather than the species level.

For tropical forests, the use of functional groups in this manner would have been an ideal approach. In fact, such a technique is in keeping with the recommendations of the International Geosphere-Biosphere Programme, which advocates both *in-situ* measurements and the development of techniques for scaling up from the species level to the community (IGBP 1992). Consequently, our analyses were focused around ecological groupings of species. However, our results clearly indicate that the resolution of functional groups defined on the basis of ecological data is insufficient to accurately describe species-level differences in response. Although, as previously noted, species lumped together in the same functional group do respond similarly under ambient CO_2 (Ellis *et al. in review*), when exposed to elevated CO_2, the ecological groupings cease to be informative regarding the physiology or response of the species. Therefore, this approach to simplifying the structure of a system is not likely to be appropriate when parameterizing global carbon models because they do not accurately reflect constituent species behavior. This is a surprising result given that we observed a strong CO_2 effect at the species level.

Species-specific physiological responses to elevated CO_2

Gas exchange and water use measurements were taken from 168 individual trees growing in the BCI forest throughout 1995 to measure the strength of the response to elevated CO_2 as well as its variability among species. One important conclusion is that elevated CO_2 effects are detectable in a heterogeneous environment from a large cohort of species. *A priori*, it was not clear that photosynthetic enhancements would be identifiable in the presence of variable light, water, and temperature conditions. Furthermore, Bazzaz (1990) notes that under nitrogen or phosphorus-poor soils, the effects of CO_2 could vanish and tropical soils are known to be phosphorus deficient (Vitousek and Denslow 1986). Although we cannot comment on the relative impacts of these environmental factors, we can conclude that species-specific responses to elevated CO_2 are neither hidden nor homogenized by the environmental conditions on BCI.

An instantaneous rise in the CO_2 concentration around the leaves of *in-situ* trees resulted in photosynthetic and WUE increases. These enhancement effects varied in magnitude among species, though all substantially increased their photosynthetic rates and WUE when exposed to elevated CO_2. Previous results provide equivocal support for this finding. One study for tropical seedlings did not find any effect of elevated CO_2 on leaf-level photosynthesis (Reekie and Bazzaz 1989) while another found a growth increase but a photosynthesis decrease (Oberbauer *et al.* 1985). Yet, some previous work has demonstrated the existence of such species-specific responses to elevated CO_2. Studies that examined both temperate and tropical trees have recorded significant CO_2-induced photosynthetic enhancements among species (Ziska *et al.* 1991, Idso and Kimball 1992, El-Kohen *et al.* 1993, Gunderson *et al.* 1993). The majority of these works, though, have been conducted in growing chambers or have involved a small number of species. To the best of our knowledge, this study represents the first examination of the effects of elevated CO_2 on a large cohort of tropical tree species measured under their natural growing conditions.

Unequal photosynthetic enhancement among species resulting from higher levels of CO_2 represents an important finding since it indicates some species within a community will benefit disproportionately, perhaps resulting in a growth or reproductive gain for them. Caution is however warranted before such an extrapolation. It is possible that the short-term responses of trees to elevated CO_2 will differ on the long-term. Evidence indicates that many plants in tropical forests (except understory species) may be close to carbohydrate saturation at present. Still, this may not preclude further enhancement (Bawa and Markham 1995) and studies from other biomes indicate that, in fact, photosynthetic enhancement may not diminish with time (Gunderson et al. 1993, Norby *et al.* 1992, Potvin and Kraenzel *in prep.*). Although we still are uncertain as to the persistence of photosynthetic enhancements over long time periods, much more evidence exists today compared to just five years ago (*see* Ceulemans and Mousseau 1994). If such long-term photosynthetic enhancements *do* translate into growth, defense, or reproductive benefits, the increase in CO_2 we are experiencing could potentially bring about a competitive shift within a community, benefiting the species with higher fertilization effects. Such individual life-history shifts would have obvious implications for species' population biology.

Previous studies for grassland ecosystems have indicated that changes in competitive interactions and dominance could arise as a result of global atmospheric change (Stewart and Potvin *in press*, Potvin and Vasseur *in press*). Likewise, in a simulated tropical ecosystem, shifts in abundance of groups of species were observed, though only a small increase in productivity was noted when the CO_2 level was increased (Arnone and Körner 1995). Yet, as noted by Ceulemans and Mousseau (1994), trees experience the 'compound interest' effect by which the effects of small changes in tree physiology can accumulate and have significant long-term impacts. Consequently, although further work is required to establish the link between an observed short-term physiological change and a long-term ecological one, small changes in physiology resulting from global change could lead to larger ecological ramifications.

One method of getting at these questions is with Free Air CO_2 Enrichment (FACE) rings. They hold the promise of yielding representative enhancement results under natural conditions despite certain drawbacks including cost, lengthy duration, and limited practicality in remote locations. Therefore, given our current technological abilities and resources, it is impractical to consider using FACE rings to assess responses on the entire suite of species from a tropical tree community. Yet, parameterization of global carbon models increasingly requires reliable estimates of photosynthesis and water relations at the community level rather than from single species. Although an alternative, functional groups, proved not to represent fully the response of a suite of species to an increase in CO_2, this approach does address questions regarding global change impacts on diversity raised by Mooney and Chapin (1994). It shows that the ecosystem processes of species-rich biomes such as tropical forests are not effectively dominated by a few species but rather receive significant contributions, albeit varying in magnitude, from all constituent species. This is important in light of the result that functional groups defined ecologically do not reliably convey inherent species-level variation and are thus inappropriate to estimate future carbon fixation under elevated CO_2. However, an understanding of the leaf-level response of trees and the ability to detect CO_2 enhancement effects on in-situ trees are important advances towards an understanding of the biological repercussions of elevated CO_2.

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FIGURE LEGENDS

FIGURE 1: Rainfall data for Barro Colorado Island, Panamá. Average monthly rainfall for 1995, the period during which the experiment was conducted, is shown with the closed circles while the 65 year running average is displayed with the open circles. Dry and wet seasons are denoted by shading in the bar running beneath the graph. The open area identifies the dry months and the dark area shows the wet months. Data courtesy of the Smithsonian Environmental Sciences Program.

FIGURE 2 (a-d): Grand mean photosynthesis (A_{ave}) and water use efficiency (WUE_{ave}) for all species at ambient (~350 μL L^{-1}) and elevated (~750 μL L^{-1}) CO_2. Grand means for A_{ave} (**a**) and WUE_{ave} (**b**) across all species are displayed at ambient and elevated CO_2. These means for A_{ave} (**c**) and WUE_{ave} (**d**) at both CO2 levels are subdivided into seasonal components to display the interaction of season and CO_2. Letters indicate significant differences between treatments at the 0.05 level within a given graph. Error bars are ± 1 SE.

FIGURE 3: Distribution of photosynthetic enhancement ratios for 21 tropical tree species. For each species, the enhancement ratio is defined as the grand mean photosynthetic rate at elevated CO_2 divided by the grand mean photosynthetic rate at ambient CO_2. Each species A_{ave} value represents the mean of the measurements for all 8 individuals sampled. Higher ratios indicate a larger fertilization effect in response to increased CO_2. Shading denotes functional group membership. Species codes are shown in Table 1.

FIGURE 4 (a-b): Schematic representation of the species-specific effect of elevated CO_2 on the annual photosynthetic rate of 21 tropical trees. (**a**) Diagram of A_{ave} values for all species at ambient CO_2 (left) compared to their A_{ave} rates at elevated CO_2 (right). (**b**) Changes in photosynthetic rank order under elevated CO_2 also show the different responses of species to the same stimulus. Photosynthetic rank order at ambient is displayed on the left hand side of the chart while the rank order at elevated CO_2 is shown on the right. Sharply increasing or decreasing lines signify large changes in photosynthetic rank between CO_2 levels. Lines with low slopes indicate a small change in rank relative to the other study species. Species codes are defined in Table 1.

FIGURE 5 (a-b): Histograms displaying the distribution of recorded photosynthetic rates (a) and light levels (b) under ambient and elevated CO2 for both the wet and dry seasons. For each graph, counts include measurements from all individuals sampled within a season at a CO2 level.

TABLE 1: The 21 study species, listed in their ecologically-defined functional groups. These groups were defined on the basis of the BCI 50-ha plot data. Species are listed with their six-letter abbreviation code, botanical family as recorded by Croat (1978), and Spanish common name. The growth form for all species is classified as either canopy tree or understory treelet.

SPECIES	CODE	FAMILY	COMMON NAME
Pioneer			
Cecropia insignis	CECRIN	MORACEAE	Guarumo blanco
Croton billbergianus	CROTBI	EUPHORBICEAE	Vaquero
Luehea seemannii	LUEHSE	TILIACEAE	Guácimo colorado
Miconia argentea	MICOAR	MELASTOMATACEAE	Dos caras
Ochroma pyramidale	OCHRPY	BOMBACACEAE	Balsa
Trema micrantha	TREMMI	ULMACEAE	Capulín macho
Zanthoxylum belizense	ZANTBE	RUTACEAE	Arcabú o Tachuelo
Intermediate			
Anacardium excelsum	ANACEX	ANACARDIACEAE	Espavé
Cordia bicolor	CORDBI	BORAGINACEAE	Laurel
Dipteryx panamensis	DIPTPA	LEGUMINOSEAE: PAPIL.	Almendro
Gustavia superba	GUSTSU	LECYTHIDACEAE	Membrillo
Hura crepitans	HURACR	EUPHORBIACEAE	Hura, Javillo
Palicourea guianensis	PALIGU	RUBIACEAE	Café de monte
Swietenia macrophylla	SWIEMA	MELIACEAE	Mahogany, Caoba
Shade Tolerant			
Alseis blackiana	ALSEBL	RUBIACEAE	Mameicillo
Beilschmiedia pendula	BEILPE	LAURACEAE	Añushi rumo
Faramea occidentalis	FARAOC	RUBIACEAE	Huesito
Poulsenia armata	POULAR	MORACEAE	Cucúa
Protium tenuifolium	PROTTE	BURSERACEAE	Copá
Simarouba amara	SIMAAM	SIMAROUBACEAE	Aceituno
Trichilia tuberculata	TRICTU	MELIACEAE	Alfajía

TABLE 2: ANOVA table and significance levels for within subject effects of short-term, leaf-level grand mean photosynthesis (*Aave*) and water use efficiency (WUE*ave*). Main effects of the model are the CO2 level, (ambient or elevated), functional group (Pioneer, Intermediate, Shade Tolerant), species nested under functional group (FG), and season (Wet or Dry). Stars indicate degree of significance (* < 0.05, ** < 0.001, ns = not significant).

Source of Variation	PHOTOSYNTHESIS					WATER USE EFFICIENCY				
	df	MS	F	*p*		df	MS	F	*p*	
CO2	1	264.40	8730	0.0001	**	1	284.44	9648.0	0.0001	**
CO2 * FG	2	0.26	0.62	0.5487	ns	2	0.52	1.12	0.3472	ns
CO2 * Species (FG)	18	0.42	13.6	0.0001	**	18	0.5	15.6	0.0001	**
CO2 * Species (FG) * Season	18	0.14	4.6	0.0001	**	18	0.12	4.0	0.0001	**
CO2 * Season	1	1.46	48.3	0.0001	**	1	0.89	30.01	0.0001	**
CO2 * Season * FG	2	0.19	1.36	0.2812	ns	2	0.17	1.46	0.2579	ns

TABLE 3: Leaf-level grand mean photosynthesis (A_{ave} , in µmol CO_2 m^{-2} s^{-1}) and water use efficiency (WUE_{ave} , in µmol CO_2 / mmol H_2O) on a leaf-area basis for 21 tropical trees. A_{ave} and WUE_{ave} represent the grand mean of the daily (AM/PM) and seasonal (dry/wet) replicates of 8 individuals per species. The enhancement ratio of a trait compares the rate at ambient conditions to the rate at elevated conditions. For each CO_2 level, the n per species is ≥ 260 for A_{ave} and ≥ 240 for WUE_{ave} . Means shown with ± 1 SE. Ambient measurements from Ellis *et al.* (submitted).

SPECIES	PHOTOSYNTHESIS			WATER USE EFFICIENCY		
	Ambient CO_2	Elevated CO_2	Enhan. Ratio	Ambient CO_2	Elevated CO_2	Enhan. Ratio
Alseis blackiana	9.7 ± 0.4	19.8 ± 0.7	2.05	4.00 ± 0.2	7.99 ± 0.3	1.99
Anacardium excelsum	9.5 ± 0.3	22.6 ± 0.8	2.38	3.09 ± 0.2	7.86 ± 0.2	2.55
Beilschmiedia pendula	9.8 ± 0.3	20.4 ± 0.6	1.85	4.01 ± 0.2	9.54 ± 0.4	2.38
Cecropia insignis	18.1 ± 0.5	33.4 ± 1.0	1.86	3.70 ± 0.2	6.34 ± 0.2	1.71
Cordia bicolor	10.7 ± 0.4	19.8 ± 0.7	1.77	3.71 ± 0.2	6.96 ± 0.2	1.88
Croton billbergianus	11.9 ± 0.4	21.1 ± 0.8	2.25	4.00 ± 0.1	7.18 ± 0.2	1.80
Dipteryx panamensis	14.2 ± 0.5	32.1 ± 1.1	2.00	2.91 ± 0.1	6.48 ± 0.2	2.23
Faramea occidentale	9.6 ± 0.4	19.3 ± 0.7	2.05	4.08 ± 0.2	8.76 ± 0.4	2.15
Gustavia superba	11.4 ± 0.5	23.3 ± 0.9	2.01	3.82 ± 0.2	7.57 ± 0.3	1.98
Hura crepitans	13.4 ± 0.5	27.0 ± 0.9	1.80	3.03 ± 0.1	6.45 ± 0.1	2.13
Luehea seemannii	14.3 ± 0.5	25.7 ± 0.8	2.10	3.36 ± 0.1	6.73 ± 0.2	2.00
Miconia argentea	15.9 ± 0.6	33.4 ± 1.3	2.08	3.59 ± 0.1	7.20 ± 0.2	2.01
Ochroma pyramidale	18.3 ± 0.6	38.0 ± 1.1	2.07	3.63 ± 0.1	7.46 ± 0.2	2.06
Palicourea guianensis	12.7 ± 0.5	19.8 ± 0.7	1.56	4.37 ± 0.2	7.58 ± 0.3	1.73
Poulsenia armata	7.3 ± 0.3	15.3 ± 0.6	2.10	3.68 ± 0.2	6.14 ± 0.2	1.67
Protium tenuifolium	8.6 ± 0.2	14.9 ± 0.4	1.74	3.74 ± 0.1	7.42 ± 0.2	1.98
Simarouba amara	8.0 ± 0.3	14.7 ± 0.7	1.84	4.13 ± 0.2	6.48 ± 0.3	1.57
Swietenia macrophylla	14.8 ± 0.4	40.3 ± 0.8	2.72	3.06 ± 0.1	8.07 ± 0.2	2.63
Trema micrantha	18.9 ± 0.6	38.7 ± 1.2	2.05	3.54 ± 0.2	6.97 ± 0.2	1.97
Trichilia tuberculata	9.6 ± 0.3	21.0 ± 0.7	2.20	2.91 ± 0.1	6.72 ± 0.2	2.31
Zanthoxylum belizense	12.2 ± 0.4	30.0 ± 0.9	2.46	2.60 ± 0.1	6.11 ± 0.2	2.35

FIGURE 1

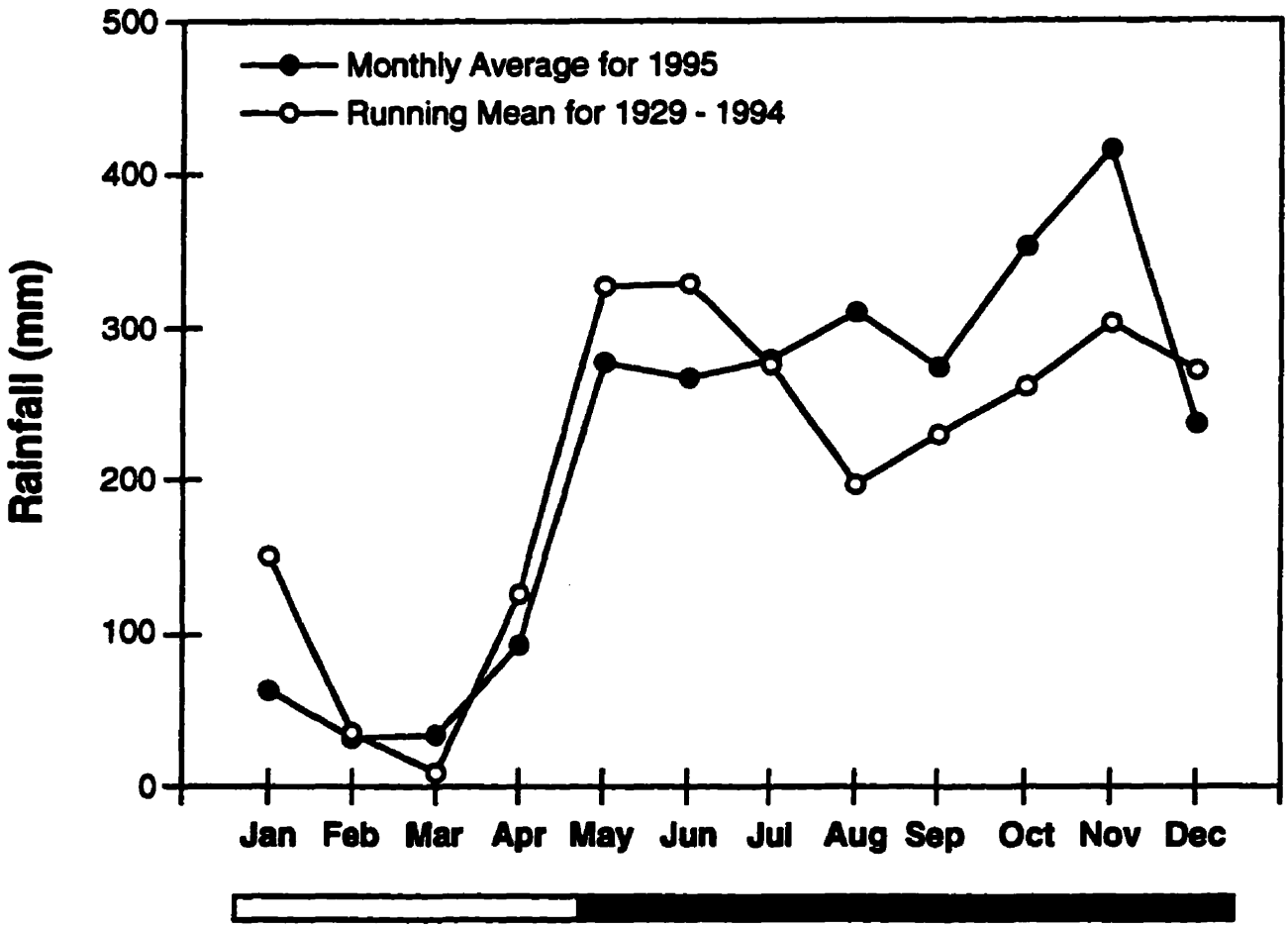

Monthly Average for 1995
Running Mean for 1929 - 1994
Rainfall (mm)
500
400
300
200
100
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

FIGURE 2 (a-d)

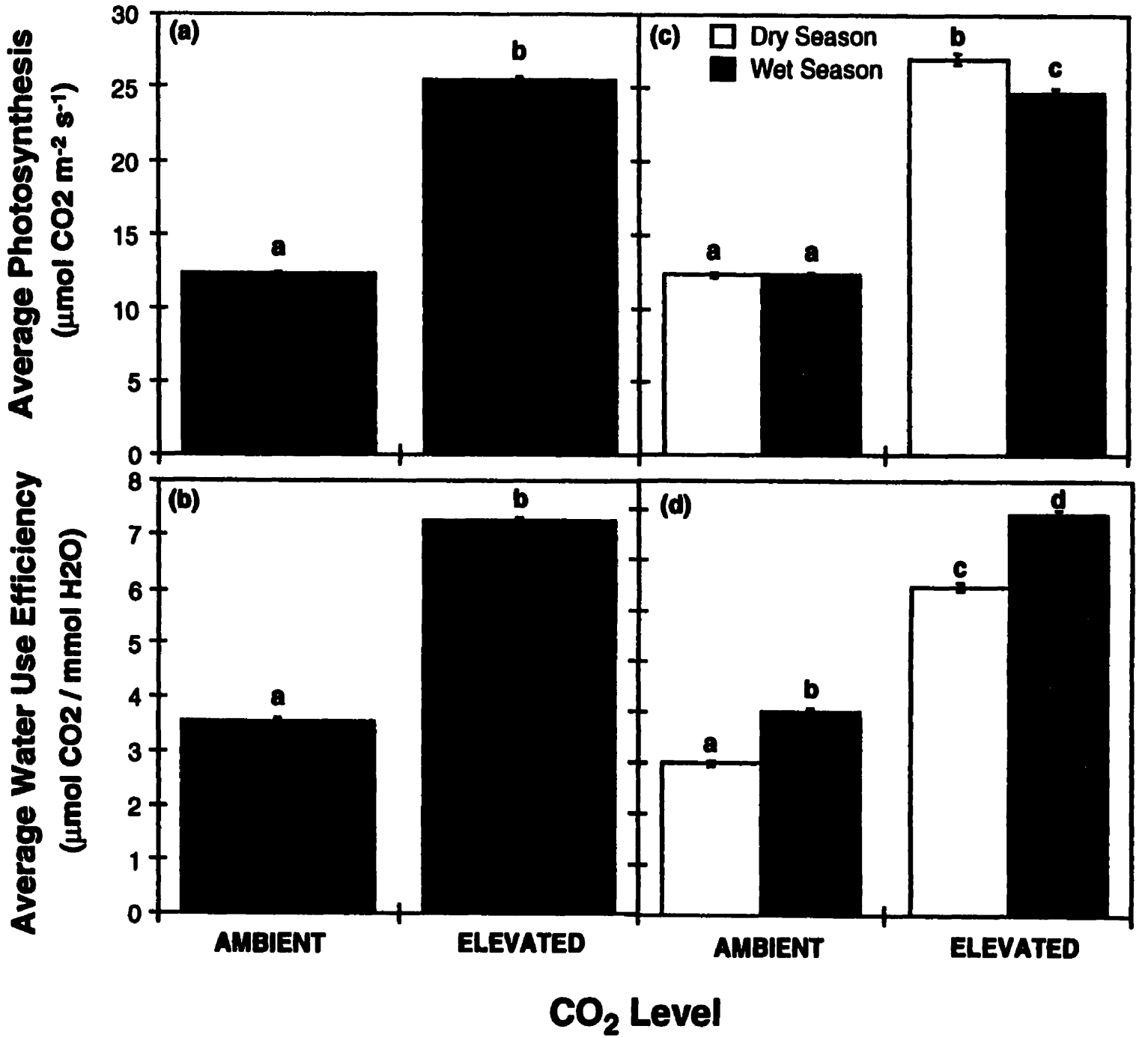

(a)
(b)
(c)
(d)
Dry Season
Wet Season
Average Photosynthesis (µmol CO2 m-2 s-1)
Average Water Use Efficiency (µmol CO2 / mmol H2O)
AMBIENT
ELEVATED
AMBIENT
ELEVATED
CO2 Level

FIGURE 3

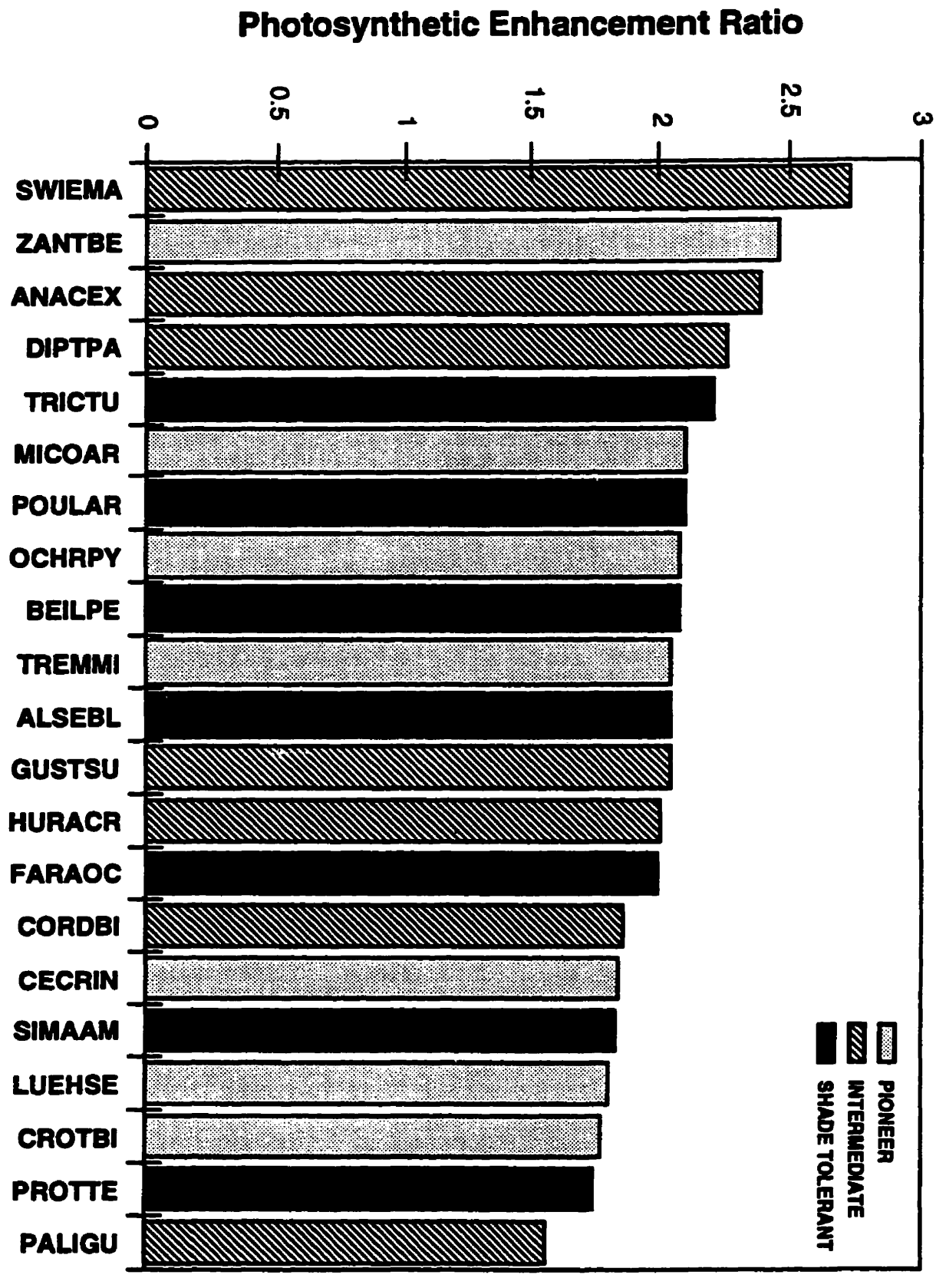
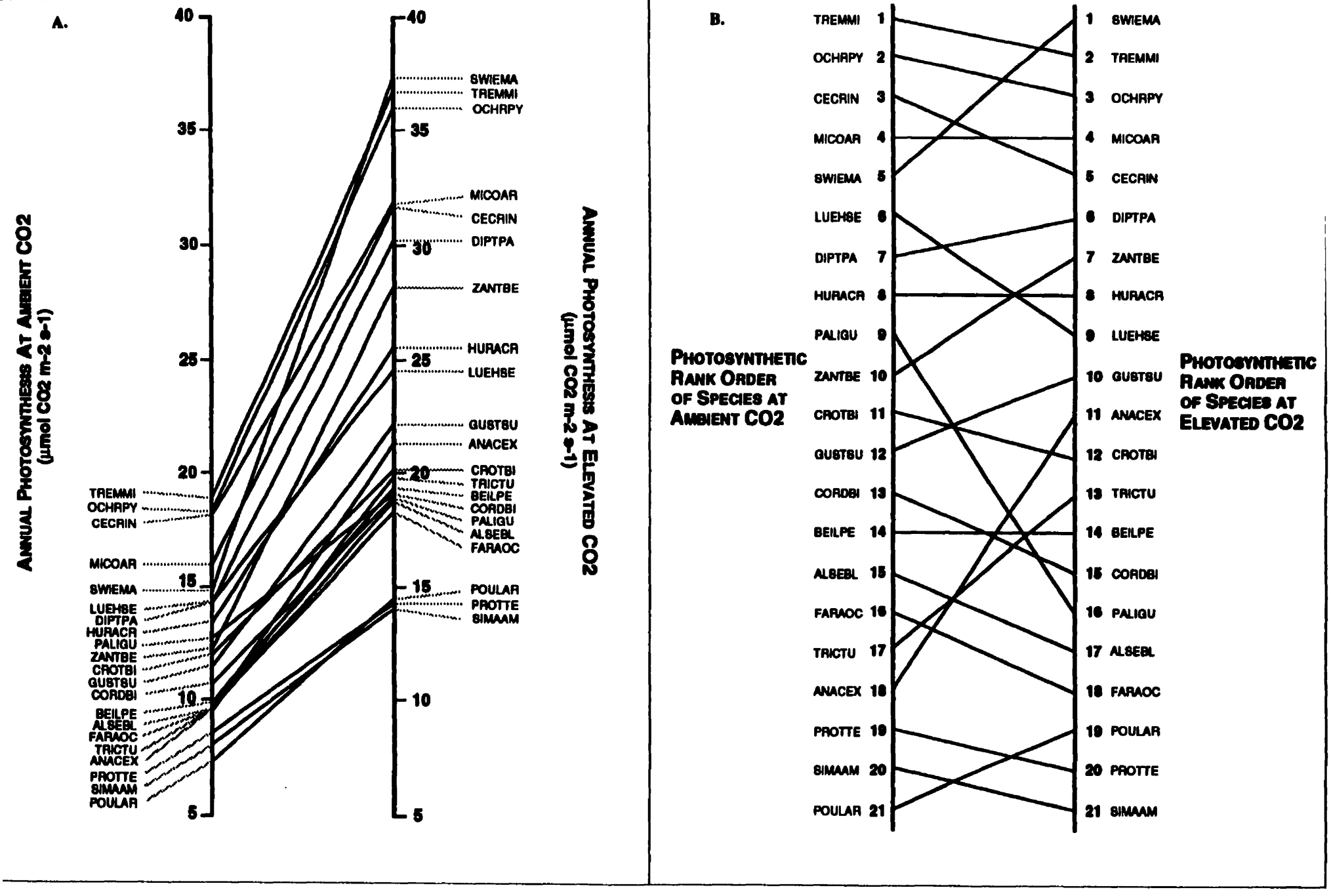

Photosynthetic Enhancement Ratio
0
0.5
1
1.5
2
2.5
3
SWIEMA
ZANTBE
ANACEX
DIPTPA
TRICTU
MICOAR
POULAR
OCHRPY
BEILPE
TREMMI
ALSEBL
GUSTSU
HURACR
FARAOC
CORDBI
CECRIN
SIMAAM
LUEHSE
CROTBI
PROTTE
PALIGU
PIONEER
INTERMEDIATE
SHADE TOLERANT

FIGURE 4


A.
ANNUAL PHOTOSYNTHESIS AT AMBIENT CO2
(µmol CO2 m-2 s-1)
ANNUAL PHOTOSYNTHESIS AT ELEVATED CO2
(µmol CO2 m-2 s-1)
40
35
30
25
20
15
10
5
TREMMI
OCHRPY
CECRIN
MICOAR
SWIEMA
LUEHSE
DIPTPA
HURACR
PALIGU
ZANTBE
CROTBI
GUSTSU
CORDBI
BEILPE
ALSEBL
FARAOC
TRICTU
ANACEX
PROTTE
SIMAAM
POULAR
SWIEMA
TREMMI
OCHRPY
MICOAR
CECRIN
DIPTPA
ZANTBE
HURACR
LUEHSE
GUSTSU
ANACEX
CROTBI
TRICTU
BEILPE
CORDBI
PALIGU
ALSEBL
FARAOC
POULAR
PROTTE
SIMAAM
B.
PHOTOSYNTHETIC RANK ORDER OF SPECIES AT AMBIENT CO2
TREMMI 1
OCHRPY 2
CECRIN 3
MICOAR 4
SWIEMA 5
LUEHSE 6
DIPTPA 7
HURACR 8
PALIGU 9
ZANTBE 10
CROTBI 11
GUSTSU 12
CORDBI 13
BEILPE 14
ALSEBL 15
FARAOC 16
TRICTU 17
ANACEX 18
PROTTE 19
SIMAAM 20
POULAR 21
1 SWIEMA
2 TREMMI
3 OCHRPY
4 MICOAR
5 CECRIN
6 DIPTPA
7 ZANTBE
8 HURACR
9 LUEHSE
10 GUSTSU
11 ANACEX
12 CROTBI
13 TRICTU
14 BEILPE
15 CORDBI
16 PALIGU
17 ALSEBL
18 FARAOC
19 POULAR
20 PROTTE
21 SIMAAM
PHOTOSYNTHETIC RANK ORDER OF SPECIES AT ELEVATED CO2

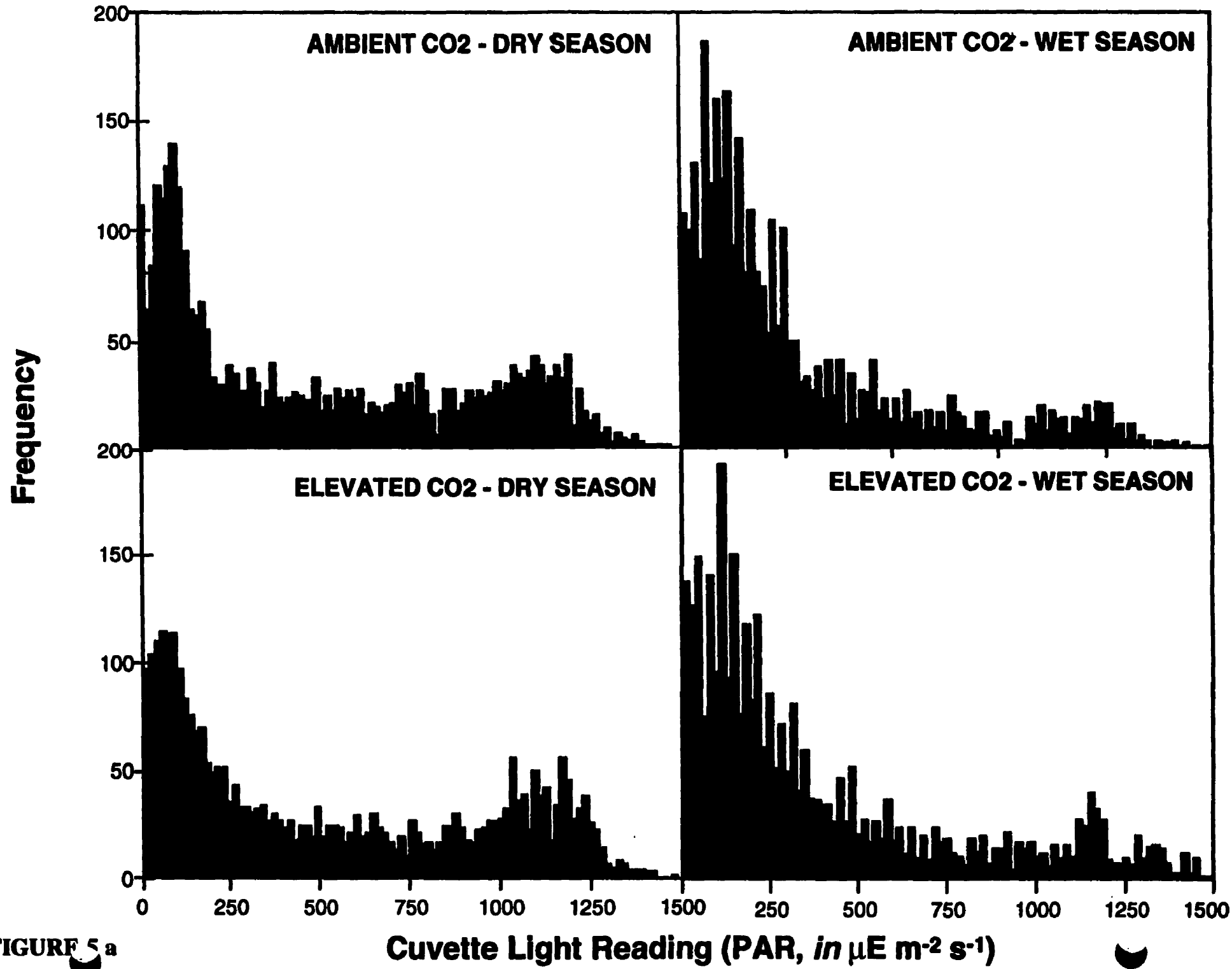

AMBIENT CO2 - DRY SEASON
AMBIENT CO2 - WET SEASON
ELEVATED CO2 - DRY SEASON
ELEVATED CO2 - WET SEASON
Frequency
200
150
100
50
0
0
250
500
750
1000
1250
1500
Cuvette Light Reading (PAR, in µE m-2 s-1)

FIGURE 5 a

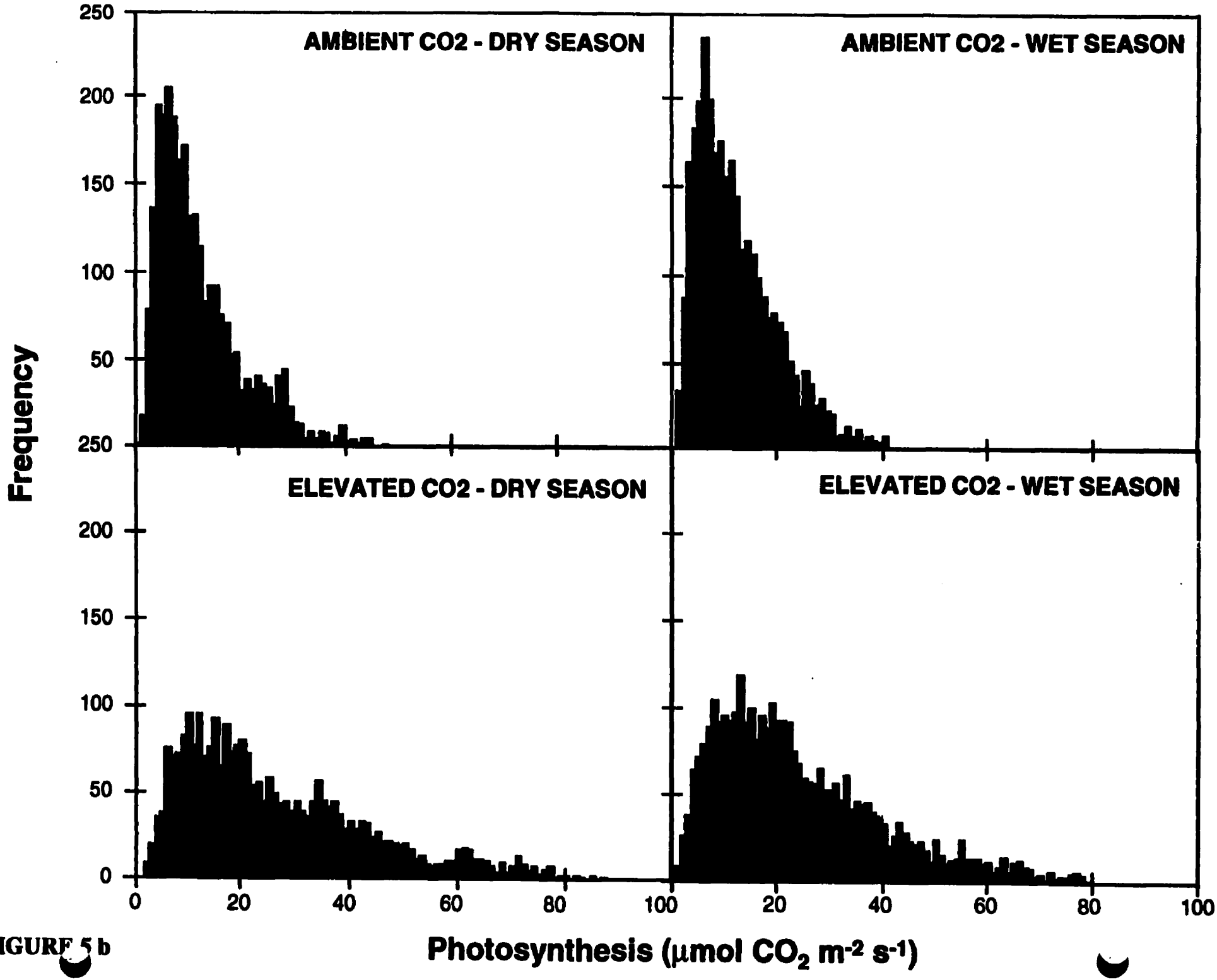

AMBIENT CO2 - DRY SEASON
AMBIENT CO2 - WET SEASON
ELEVATED CO2 - DRY SEASON
ELEVATED CO2 - WET SEASON
Frequency
250
200
150
100
50
0
0
20
40
60
80
100
Photosynthesis (µmol CO2 m-2 s-1)

FIGURE 5 b

CONCLUSION

In researching and writing this thesis, I had two primary objectives. First, I was interested in whether interspecific differences in photosynthesis could be detected under heterogeneous environmental conditions such as in the forest. If so, I was further interested in whether ecologically-similar species also share physiological traits. Since most previous work has been conducted in greenhouses or open-top chambers, the extent to which species differences were detectable in the forest was unknown. Furthermore, few studies — especially for highly diverse systems — have described a link between a documented ecological trait and a measured underlying physiological mechanism. The first paper addresses these issues, concluding that indeed species differences can be recorded above the environmental background variation. It further resolved that groups assembled on the basis of related ecological traits have some physiological traits in common. Pioneer, intermediate, and shade tolerant trees have long been known to share similar ecological traits like abundances, recruitment, and growth rate. However, as this work demonstrates, groups that behave similarly in the forest in terms of recruitment or growth likewise share related underlying mechanisms such as photosynthesis and leaf elemental composition. Specifically, groups of ecologically-similar species do share comparable photosynthetic rates and leaf nitrogen contents. Trends in light response and water use efficiency among groups are also clear.

The second portion of this work had the proximate goal of examining the impact of elevated CO_2 on a large cohort of tropical trees to ascertain whether the functional groups continue to behave correspondingly under altered atmospheric conditions. But the ultimate goal was to assess whether the CO_2 fertilization effect on tropical communities could be modeled at the group level. In contrast to the results obtained under ambient CO_2, groups were not found to represent species-level variation adequately. At elevated CO_2, differences in response that were clearly visible at the species-level ceased to be apparent when viewed as groups. Functional groups no longer summarized species-level performance but instead masked the contrasting responses of species. Ecologically-defined groups are therefore not sufficiently accurate to summarize species variation and from which to estimate community response to elevated CO_2.

APPLICATIONS

I believe this thesis contributes to three significant aspects of tropical biology. First, it confirms that ecophysiological measurements can be conducted in the forest, under natural conditions, and still detect species differences. Above the environmental noise of light differences, seasonal patterns, relative humidity, or temperature, strong, consistent photosynthetic contrasts were observed among all species. Second, it demonstrates that collections of species, such as successional classes, are also related physiologically. Both of these results establish fundamental relationships between two seemingly distinct realms in biology. In selecting rapidly-photosynthesizing species for a carbon-sequestration project or reforestation effort, an investigator need not take costly and lengthy physiological measurements from all the species in question but may instead use growth rate or another known ecological trait as an indicator of the physiological performance. However, if understanding how certain species perform under contrasting environmental conditions (e.g. wet/dry conditions or good/poor soil) is crucial to which tree species is selected for a plantation or reforestation project, this project shows that if differences in physiological traits like photosynthesis and water use efficiency exist, they will be detectable above the remaining environmental variation, allowing the work to be conducted in the area in question.

Third and perhaps the most important in terms of future research directions, this thesis argues that the impact of CO_2 on neotropical forests cannot be reliably estimated on the basis of group-level response. Although ecologically-defined functional groups of species closely resemble one another physiologically at ambient CO_2, this relationship no longer holds true when the atmospheric CO_2 level is increased. Thus, the impact of CO_2 must be evaluated at the species level, and cannot be extrapolated up from the group level to the forest. Forest and global climate models should not estimate fertilization benefits to tropical forests on the basis of data for collections of species but rather must continue to parameterize models using species level data. This poses a significant problem for models of tropical forests whose diversity makes measuring every species impossible. Therefore, I suggest that a new direction in tropical global change research should emerge to develop an approach that would reduce the number of measurements required yet still produce a reliable estimate of the increase in carbon assimilation.

I believe that the most important direction for future global change research is investigating the impact of elevated CO_2 on biodiversity. We are now altering the living conditions of one of the largest treasure troves of genetic and biological richness. Yet, we are investing little effort in learning what our impacts will be. Furthermore, we also must not lose sight of the fact that we depend on the forest for many products (i.e. food, wood, medicine, water and carbon cycling, etc.) and any change in the health of the forest will have repercussions for us as well as the trees. To accomplish this, further development of models and the tools for assessing ecosystems enhancement effects are necessary. Although the CO_2 increase seems unavoidable to some degree, by learning more about its effects, we might be able to mediate some of the more harmful impacts.

As the world's output of CO_2 continues relatively unabated, it is becoming increasingly important to ascertain the potential impact of elevated CO_2 on diverse ecosystems such as tropical forests. I hope that this work has contributed to furthering our understanding of the effects of global change on tropical forests and how to gauge them. Perhaps, in its own small way, this work will also act as a reveille for mankind, reminding us of our impact on the world around us and urging us to not just understand our impacts but to change our acts.

APPENDIX A: Percent N, percent C and specific leaf area (SLA) for the leaves of 21 tropical tree species. Values represent means from four leaves per species in both the wet and dry seasons (n = 8 total). All three traits were strongly species-specific, though only nitrogen content differed significantly among groups.

Species	Nitrogen (% dry wt.)	Carbon (% dry wt.)	SLA (cm2/g)
Alseis blackiana	3.696 ± 0.218	47.508 ± 0.772	351.95 ± 29.0
Anacardium excelsum	1.771 ± 0.079	48.786 ± 0.616	173.79 ± 21.9
Beilschmiedia pendula	2.364 ± 0.271	50.670 ± 0.567	190.53 ± 30.1
Cecropia insignis	2.238 ± 0.090	45.780 ± 0.640	166.16 ± 8.60
Cordia bicolor	3.164 ± 0.233	46.362 ± 0.656	284.03 ± 31.9
Croton billbergianus	2.876 ± 0.099	40.725 ± 0.787	242.91 ± 21.6
Dipteryx panamensis	3.251 ± 0.208	51.881 ± 0.536	231.58 ± 17.2
Faramea occidentale	2.696 ± 0.130	44.181 ± 1.165	159.10 ± 10.9
Gustavia superba	2.123 ± 0.122	46.785 ± 1.031	206.17 ± 18.4
Hura crepitans	3.761 ± 0.144	47.123 ± 1.022	237.23 ± 24.0
Luehea seemannii	2.832 ± 0.223	48.288 ± 1.229	189.82 ± 16.3
Miconia argentea	2.340 ± 0.284	50.476 ± 0.917	220.89 ± 28.3
Ochroma pyramidale	2.423 ± 0.093	44.256 ± 1.320	191.79 ± 14.9
Palicourea guianensis	4.100 ± 0.144	47.228 ± 0.810	315.24 ± 17.2
Poulsenia armata	1.857 ± 0.067	38.249 ± 0.891	181.49 ± 12.7
Protium tenuifolium	2.065 ± 0.097	44.115 ± 0.990	235.11 ± 18.9
Simarouba amara	2.297 ± 0.162	46.524 ± 3.055	237.50 ± 31.1
Swietenia macrophylla	1.879 ± 0.103	49.996 ± 0.860	97.77 ± 5.3
Trema micrantha	2.495 ± 0.208	46.413 ± 3.504	172.52 ± 19.0
Trichilia tuberculata	2.695 ± 0.114	50.223 ± 0.677	161.81 ± 9.9
Zanthoxylum belizense	2.819 ± 0.171	47.265 ± 0.397	232.57 ± 15.4

APPENDIX B

Calculating Gas Exchange Parameters

Version 5

The following equations are used in the calculation of plant carbon assimilation rate and water relations. The required input parameters are the raw output of a typical infra-red gas analyzer. They are: C_{ref}, C_{ana}, RH_{in}, RH_{out}, $Temp_{leaf}$, $Temp_{air}$, and PAR. The equations were derived and cross-checked from three primary sources:

1. Von Caemmerer and Farquhar (1981) *Planta* **153**:376-387.
2. Dewpoint Hygrometer manual, General Eastern Instruments (1988).
3. LCA-4 IRGA Manual, Analytic Development Corporation (1993).

I. Saturation Vapor Pressure

e_{ws} = saturation vapor pressure, in bars (1 bar = 10^5 Pa).
e_i = vapor pressure with respect to water going to the leaf, in bars.
e_o = vapor pressure with respect to water coming from the leaf, in bars.

$$e_{ws} = \frac{1.0007 + \left(\frac{3.46}{1\times10^6} \times P_{mBar}\right) \times 6.1121 \times e^{\left(\frac{17.502 \times Temp°C}{240.9 + Temp°C}\right)}}{1000\frac{mBar}{bar}}$$

$$e_i = \frac{(e_{ws} \times RH_{in})}{100}$$

$$e_o = \frac{(e_{ws} \times RH_{out})}{100}$$

* Note: In the e_{ws} expression, the exponential is "e" or 2.718. In Excel, the function is written EXP(x).

II. Volume Flow → Molar Flow

u = molar air flow, in mol air s^{-1}
u_s = molar flow per m^2 of leaf area, in mol m^{-2} s^{-1}

$$u = \frac{\text{VolFlow(mL/min)}}{Vm20 \times \left(\frac{273K + \text{Temp°C}}{293K}\right) \times P_{bar} \times 60\,\text{sec/min}}$$

$$u_s = \frac{u}{\text{LeafArea}(m^2)}$$

where V_{m20} is the volume of 1 mole of an ideal gas at 1 atm (1.013×10^5 Pa) and 20°C
$V_{m20} = 2.405 \times 10^{-2}$ m^3 or 24.04 L, and $m^2 = cm^2 \times 10^{-5}$.

III. Water Vapor Concentration

w_{ref} = water vapor concentration entering cuvette, in mol mol^{-1}
w_{an} = water vapor concentration leaving cuvette, in mol mol^{-1}
w'_{an} = correction of analysis H_2O for transpiration dilution or water picked up in leaf chamber, in mol mol^{-1}
w_{leaf} = saturated water vapor concentration at leaf temperature, in mol mol^{-1}

NOTE: Convert e_i and e_o from bars into mbars (multiply by 1000) for proper units

$$w_{ref} = \frac{e_i}{P_{mBar}}$$

$$w_{an} = \frac{e_o}{P_{mBar}}$$

$$w'_{an} = w_{an} \times \left(\frac{1 - w_{ref}}{1 - w_{an}} \right)$$

$$w_{leaf} = \frac{e_{ws}}{P_{mBar}}$$

$$\Delta w = w'_{ana} - w_{ref}$$

IV. Transpiration and Water Use Efficiency

E = Transpiration rate, in mol H_2O m^{-2} s^{-1}
WUE = Water Use Efficiency, in µmol CO_2 / mmol H_2O

$$E = u_s \times \Delta w \qquad\qquad WUE = \left(\frac{A}{E} \right)$$

NOTE: Multiply E by 1000 to convert from mol to mmol, the commonly reported units.

V. Stomatal Conductance

r_s = stomatal resistance to water vapor, in m^2 s mol^{-1}
r_b = boundary layer resistance, in m^2 s mol^{-1} (I used 0.3)
g_c = total conductance, in mol m^{-2} s^{-1}
g_s = stomatal conductance, in mmol H_2O m^{-2} s^{-1}

$$r_s = \frac{\left(w_{leaf} - w_{an} \right)}{\Delta w \times u_s} - r_b \qquad g_c = \frac{1}{1.6 r_s + 1.37 r_b} \qquad g_s = \frac{1}{r_s} \times 1000 \frac{\text{mmol}}{\text{mol}}$$

VI. Carbon Assimilation

A = photosynthetic rate of CO_2 exchange in the cuvette, in µmol CO_2 m^{-2} s^{-1}
C_{ref} = ambient (REF) CO_2 concentration
C_{ana} = CO_2 concentration after passing over leaf (ANA)
C'_{ana} = correction of ANA for dilution by water vapor, in vpm

$$\Delta c = c_{ref} - c'_{ana}$$

$$c'_{ana} = c_{ana} \times \left(\frac{1 - w_{ref}}{1 - w_{ana}} \right)$$

$$A = u_s \times \Delta c$$

VII. Sub-Stomatal Cavity CO_2 Concentration

C_i = sub-stomatal cavity CO_2 concentration, in µmol CO_2 m^{-2} s^{-1}
E = transpiration, *NOTE: in mol*

$$C_i = \frac{\left(\left(g_c - \frac{E}{2} \right) C_{ref} \right) - A}{\left(g_c + \frac{E}{2} \right)}$$

$$C_i / C_{ref} = \frac{C_i}{C_{ref}}$$

APPENDIX C

A / PAR Curve Fitting Program

Written in the statistical language S-Plus for UNIX
with Dr. James O. Ramsay, McGill University

Note: Italizized sections are those that are changed by the user with each iteration.

```
#  Splus code for the analysis of Alexander Ellis's
photosynthesis dataset

#  Estimates the model  y = a[1 - exp (-x*exp(b))] by least
squares
#   parameters a and b are estimated by numerical
minimization of the error SS

#  set up graphics window on IRIX

motif()

# set up graphics window on Sun OpenWindows

openlook()

#  bring in the numerical minimization routine "brent"

source("brent.s")

#  input a set of data

temp <- scan("SPP_NAME.dat",0)

n <- length(temp)/2

temp <- matrix(temp,n,2,byrow=T)

x <- temp[,2]

y <- temp[,1]

# plot the data and define x ranges

plot(x,y)

xval <- seq(0,x[n],length=101)

#  define the function for estimating a and b

#  this first function just computes an estimate of a given b
and returns the error sum of squares
```

```
bfnval <- function(bval) {
      xtran <- 1 - exp(-x*exp(bval))
      aval <- sum(y*xtran)/sum(xtran^2)
      yhat <- aval*xtran
      res  <- y - yhat
      sse <- sum(res^2)
      return(sse)
}

# This is the second function that funds the up and down
distances.
#    b0     ... initial estimate of b
#    bstep  ... step size for finding values of b bracketing
the solution
#    TOL    ... convergence criterion for estimate

abest <- function(x, y, b0, cstep, tol=1e-3) {

n <- length(x)

      #  find bdn and bup

  bfn0  <- bfnval(b0)
  bdn   <- b0
      #  step down to find lower bound
  bfndn <- bfn0
  while (bfndn <= bfn0) {
    bdn   <- bdn - bstep
    bfndn <- bfnval(bdn)
  }
      #  step up to find upper bound
  bup <- b0
  bfnup <- bfn0
  while (bfnup <= bfn0) {
    bup <- bup + bstep
    bfnup <- bfnval(bup)
  }
      #  optimize error sum of squares with respect to b using
Brent's method
  result <- brent(bdn, b0, bup, bfnval, tol)
  bval <- result[[1]]
  return(bval)
}

#  Set up arguments for function abest. Defines precision and
initial starting point. Remains constant across all species.

b0 <- 0

bstep <- 0.1

tol <- 1e-3
```

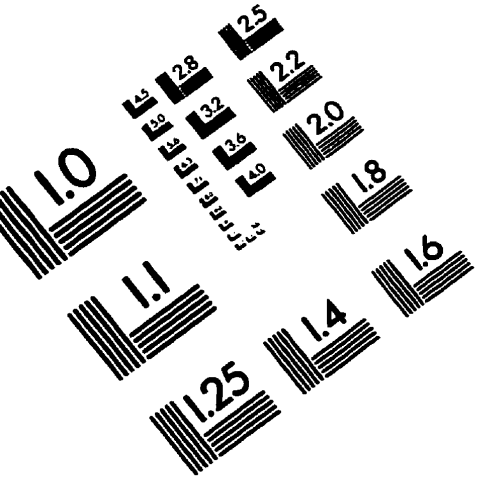
```
#  call abest to estimate optimum value of bval. Unlike the
above two functions, this changes for each new species.

bval <- abest(x, y, b0, bstep, tol)

#  compute aval

xtran <- 1 - exp(-x*exp(bval))
aval <- sum(y*xtran)/sum(xtran^2)

#  re-express aval and bval in form used in paper

Pmax <- aval

alpha <- exp(bval + log(Pmax))

#  plot the data and the model values. To make scales equal,
you can change the xlim and ylim values.

yhat <- Pmax*(1 - exp(-xval*alpha/Pmax))

plot(x,y,xlim=c(0,x[n]),ylim=c(0,y[n]),xlabel=("PAR"),
     ylabel=("Photosynthesis"))

lines(xval,yhat)

title(main="SPP_NAME")

# output as PostScript file

printgraph(file="FILE_NAME.ps", hor=F)

# to print final estimates of a and b parameters

print(Pmax)

print(alpha)
```

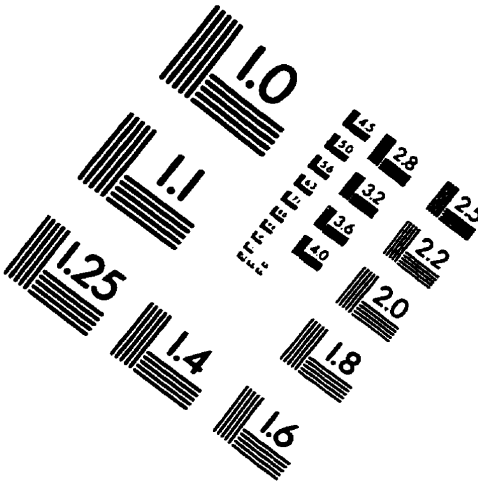
BRENT Numerical Estimation Routine

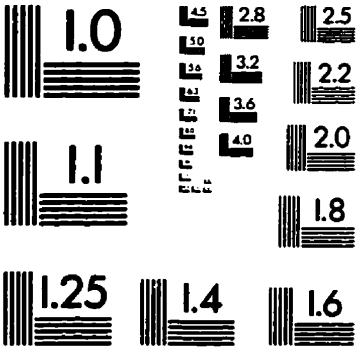
```
brent <- function(ax, bx, cx, f, step, tol=1e-7)
{

#  AX < BX < CX  and  F(BX) < F(AX) and F(BX) < F(CX)
#  F  ...  function of a single argument to be minimized
#  TOL  ...  desired precision (> sqrt(dmach))

      itmax <- 100
      cgold <- .3819660
      zeps  <- 1.0e-10
      a  <- min(c(ax,cx))
      b  <- max(c(ax,cx))
      v  <- bx
      w  <- v
      x  <- v
      e  <- 0.
      fx <- f(x)
      fv <- fx
      fw <- fx
      for (iter in 1:itmax)
      {
        xm   <- 0.5*(a+b)
        tol1 <- tol*abs(x)+zeps
        tol2 <- 2.*tol1
        if (abs(x-xm) <= (tol2-.5*(b-a))) return( list(x, fx)
)
        noparab <- T
        if (abs(e) > tol1) {
          r <- (x-w)*(fx-fv)
          q <- (x-v)*(fx-fw)
          p <- (x-v)*q - (x-w)*r
          q <- 2.0*(q-r)
          if (q > 0.) p <- -p
          q     <- abs(q)
          etemp <- e
          e     <- d
          noparab <- abs(p) >= abs(0.5*q*etemp) | p <= q*(a-
x) | p >= q*(b-x)
          if (!noparab)  {
            d <- p/q
            u <- x + d
            if (u-a < tol2  |  b-u < tol2) {
              if (xm-x > 0) d <- tol1 else  d <- -tol1
            }
          }
        }
        if (noparab) {
          if (x >= xm) e <- a-x else e <- b-x
          d <- cgold*e
        }
        if(abs(d) >= tol1)  u <- x + d else {
```

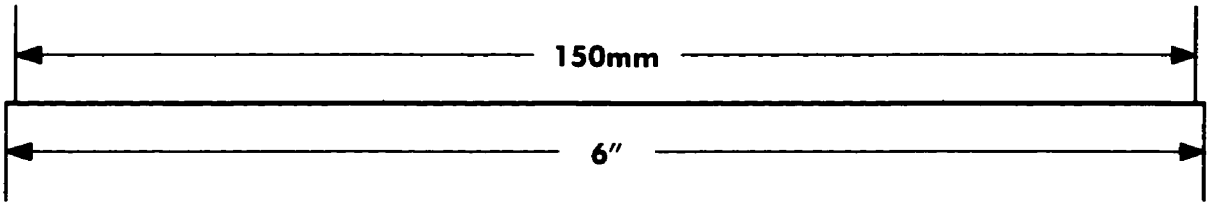
```
            if (d >= 0) u <- x + tol1 else u <- x - tol1
          }
          fu <- f(u)
          if (fu <= fx) {
            if (u >= x)  a <- x else b <- x
            v  <- w
            fv <- fw
            w  <- x
            fw <- fx
            x  <- u
            fx <- fu
          } else {
            if (u < x) a <- u else b <- u
            if (fu <= fw  |  w == x) {
              v  <- w
              fv <- fw
              w  <- u
              fw <- fu
            } else {
              if (fu <= fv  |  v == x  |  v == w) {
                v  <- u
                fv <- fu
              }
            }
          }
        }
        warning ("BRENT exceeded maximum iterations")
        return ( list(x, fx) )
}
```

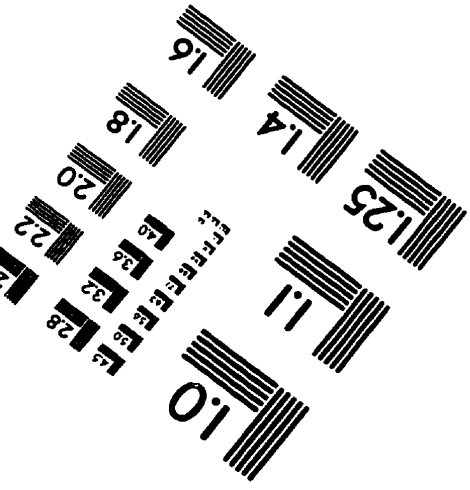
IMAGE EVALUATION TEST TARGET (QA-3)

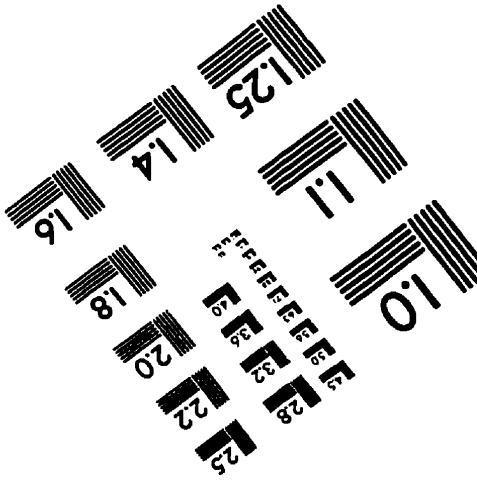












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