

**WATER USE OF TROPICAL VEGETATION
IN BELIZE, CENTRAL AMERICA:
(1) A COFFEE PLANTATION AND A NATURAL UPLAND FOREST;
AND (2) TWO NEARBY SWAMP FORESTS**

by

Sharon Billings

Nicholas School of the Environment

Date: March 5, 1996

Approved:

Daniel D. Richter

Daniel D. Richter, Supervisor

W.D. Beech

Reiner Fimromann

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science
in the Nicholas School of the Environment
in the Graduate School of
Duke University

1996

Acknowledgments

Many people have helped me through this project. I could not have completed the thesis without the help of Dr. Reiner Zimmermann, whose great enthusiasm for ecology and technical assistance provided me with the support needed to finish the manuscript. I would like to thank my adviser, Dr. Dan Richter, who provided me with much-appreciated support and valuable critiques of the manuscript. The project began under the auspices of Jet Propulsion Laboratories of Pasadena, California, and I am indebted to those who worked to create such an extensive collection of data. Funding for travel to the site was obtained from Jet Propulsion Laboratories, the Duke University Chapter of Sigma Xi Scientific Research Society, the Center for International Studies at Duke, and the Mellon Travel Grant of the Duke/University of North Carolina-Chapel Hill Program in Latin American Studies. I thank Dr. Dwight Billings for his valuable insights for improving the manuscript during my thesis defense. Dr. Ram Oren, Nathan Phillips, Dan Markewitz, Diane Pataki, Peter Jipp, Wendy Weiher, and Huang Ce all gave time and great ideas. And, of course, I thank my friends and family for their unquestioning support of me and my endeavors.

M.S.
B598W
1996

ABSTRACT

An understanding of the patterns and quantities of water consumption and water balance of various vegetation types is necessary for agricultural and ecological applications. Clearing forested land for agricultural use alters regional water balance (Luvall et al. 1985, Wiersum 1985, Pereira 1989, Bruijnzeel 1990, Anderson and Spencer 1991, Roberts et al. 1993, Zimmermann et al. 1993), and on a large scale may affect global hydrologic cycles. The dry and wet season water use of various forest types can alter the phenology of vegetation and vegetation/soil water relations (Becker et al. 1988, Borchert 1994, Reich and Bochert 1982, 1984, Fanjul and Barradas 1985); water use may also seasonally affect global water cycles.

This paper describes two studies in Belize, Central America. One study examines the potential effects of forest conversion to a coffee/cacao plantation. The second study analyzes the water uptake patterns of two seasonally dry swamp forests and their soil characteristics. Both studies indicate the complexities of estimating stand water use in tropical areas, as well as how differences in vegetational land cover, soil type, and soil structure can affect the long term and seasonal water use of an area.

CHAPTER 1

Tropical Coffee Plantation Water Use Compared to a Natural Forest

Abstract

Perennial tree crops may consume sufficient water to prevent the increased runoff, erosion, and downstream flooding often associated with replacement of forests with row crops. To examine the potential consequences for the regional hydrologic balance of tropical forest conversion to agroforestry crops, water uptake by vegetation and micrometeorologic variables were measured continuously for more than one year at two sites in a semi-deciduous, subtropical rain forest in Belize, Central America. One site is a coffee/cacao plantation, which replaced a portion of a forest similar in composition to the other site, a broadleaf natural forest. We analyzed transpiration and conductance of water in trees at various spatial and temporal scales to compare the behavior of the plantation with that of the natural site.

Daily averaged transpiration over one year for the coffee/cacao plantation was more than twice that of the broadleaf forest site at the stand level. Coffee and cacao trees were responsible for 84.3% of the plot transpiration due to their high sapwood area per unit of ground area. In the dry season, coffee and cacao trees showed a water uptake response opposite to that of native overstory tree species. Coffee and cacao trees showed increasing water uptake with increased driving force for transpiration, as indicated by the saturation vapor pressure deficit (VPD). In contrast, native overstory tree species developed greater resistance to water flux, reflected in decreased water uptake with the onset of the dry season and its associated higher atmospheric demand for water vapor. Water flux and stand sapwood area data indicate that the plantation altered the hydrologic balance and water uptake behavior of the natural overstory remaining in the plantation.

The study identifies potential consequences for land use changes where perennial crops with high stem densities replace natural forests in tropical areas.

Introduction

The conversion of tropical forests for agricultural use replaces structurally complex, perennial vegetation with seasonal crops of simpler architecture and floristics. Converting forest to cropland may also reduce vegetation water consumption, canopy interception, and soil pore space from roots and soil fauna, which lowers soil water retention during precipitation events; it may also alter the seasonal pattern of soil moisture storage. Especially in the tropics, the large amounts and high kinetic energy of rainfall can quickly erode soils cleared for agriculture (Kinnell 1985). Thus, the replacement of forests with a large leaf surface area that transpires year-round, and their replacement with crop species that are only seasonally present can result in significantly increased runoff, erosion, and downstream flooding (Lundgren and Nair 1985, Luvall et al. 1985, Wiersum 1985, Pereira 1989, Bruijnzeel 1990, Anderson and Spencer 1991, Roberts et al. 1993, Zimmermann et al. 1993). While information is available on the effects of various tropical crops on soil, microclimate, and hydrology (Binsack 1984, Barradas and Fanjul 1986, O'Kting'Ati and Mongi 1986, Jackson 1989), relatively few attempts have been made to measure, directly and continuously, the water use of crops compared to the natural forest they replace.

The hydrologic function of tropical regions after cultivation may be preserved best by perennial species such as tree crops, both because of their year-round water consumption and their promotion of water infiltration with their root systems. Coffee and cacao both occur naturally in the understory in this and other tropical forest regions, and hydrologically may be an adequate replacement for a natural forest understory. If so, replacing certain portions of the mid- and lower-canopy trees and shrubs by coffee and

cacao may adequately preserve the hydrologic characteristics of the manipulated area, as well as those of downstream ecosystems. We measured vegetational water use in a natural sub-tropical forest site and a coffee/cacao plantation continuously for one and two years, respectively, in order to determine the effects of land use change in a tropical broadleaf forest on the seasonal water balance.

Methods

The study area is in northwestern Belize, Central America (17°32 N, 89°08 W) and lies in the "subtropical moist" life zone (Holdridge et al., 1971), at the transition from evergreen to semideciduous broadleaf forests of the Yucatan Peninsula. The region experiences large year to year variation of precipitation, averaging 1500 mm yearly with an often pronounced dry season extending from February through May. Rainy season precipitation can be as high as 250 mm per month from June through December and typically tapers off in January; in most years, occasional light rain showers interrupt weeks of dry weather during the dry season (Brokaw and Mallory 1993).

The study area is separated into several limestone plateaus, divided by three steep escarpments of 50-100 meters. Spatial variation in escarpment slumping, erosion, and soil development result in a wide range of physical soil properties. The soils are generally shallow and formed over porous Eocene limestone bedrock (Wright et al., 1959). At lower elevations, soils are calcareous clay or loam and tend to become compacted and hard when drying out. Upland areas are well-drained and have lower concentrations of clay (Brokaw and Mallory 1993). There are four major vegetation types in the region: tall upland broadleaf forest (63%); swamp and bajo (seasonally flooded areas with stout shrub and tree cover) vegetation (22%); palm forests (9%); and marshes (6%) (Brokaw and Mallory 1989).

We studied two upland sites: a broadleaf upland forest, labeled Punta de Cacao 1 (PC1); and a thinned forest with a understory of coffee/cacao plantation (CC). The broadleaf natural forest supports a species mix including *Brosimum alicastrum*, *Drypetes brownei*, and *Aspidosperma megalocarpon*. The plantation is a thinned, moderately tall (20 m) overstory with natural broadleaf forest species such as *Matayba oppositifolia*, *Bursera simaruba*, and *Calophyllum brasiliense* on level ground with good drainage. The middle- and understory was completely removed in 1989 and replaced by rows of coffee and cacao trees, *Coffea arabica* and *Theobroma cacao*, respectively. Naturally occurring species at both sites are commonly found in the region's upland forests (Brokaw et al. 1990).

Water uptake by trees was measured continuously for two years at the natural forest and for one year at the plantation using a thermal constant energy input method (Granier 1985). Sap flux density (SFD) was measured in six to nine trees at each site with a 2 mm diameter probe inserted 20 mm into each tree's bole sapwood (10 mm on coffee and cacao trees due to their smaller diameter). Measurements of SFD were taken every 30 seconds and averaged every half hour (DL-2 datalogger, Delta-T Devices LTD, Burwell, England).

We calculated transpiration using Granier's (1985) formula for transforming temperature difference measurements into sap flux density (SFD) and by multiplying the SFD measurements ($\text{gH}_2\text{O m}^{-2}\text{sapwood s}^{-1}$) by the hydroactive tree xylem area. Hydroactive xylem depth for trees was determined visually by taking tree cores near the sensor and measuring the color-differentiated xylem area. Xylem depth was also compared to dielectric profiles, gathered with a handheld single channel dielectric probe (Brownfeld Devices, USA). The stems of coffee and cacao trees were assumed to be all active xylem within the cambium; this assumption is based on the plantation trees' young

age (< 5 years) (Zimmermann 1971, Romberger et al. 1993). Diurnal transpiration values per unit of cross-sectional sapwood area then were summed and extrapolated to the stand level using stand sapwood area per unit of ground area.

Mid-canopy air temperature and relative humidity were recorded (Delta-T Devices LTD, England) and used to calculate the mid-canopy vapor pressure deficit (VPD). Photosynthetically active radiation (400-700 nm) was measured 0.3 m above the forest floor with two spherical quantum sensors (LICOR, USA). These data were averaged and recorded at the same time intervals as the xylem flux data.

Stem density data were recorded at the natural forest in a 26 x 26 m and a 40 x 40 m sub-plot for under- and overstory, respectively. In the plantation, a 15-m radius circle was sampled to determine the density of the plantation trees. Diameter at breast height (dbh) was measured for all overstory trees. For coffee and cacao, crown area and height data revealed no significant size differences between individuals, so we assumed the diameter of the trees with sensors in them to be representative of all in the plantation.

Results:

The mean daily water use of the coffee-cacao plantation (0.82 mm day^{-1} , s.d. = 0.23) is more than twice that of the naturally forested site (0.32 mm day^{-1} , s.d. = 0.08, Table 1). The SFDs of individual coffee trees were lower than the cacao, and both species had SFDs lower than those of the natural overstory; mean values over one year were 5.1, s.d. = 2.6, 7.0, s.d. = 2.3, and 9.7, s.d. = 2.5 $\text{g}_{\text{water}}\text{m}^{-2}\text{sapwood area sec}^{-1}$, respectively. At the natural forest, the average SFD was 8.46, s.d. = 2.99. The higher readings of sub-canopy photosynthetically active radiation at the plantation result from the partial canopy clearing, which contributes to the generally higher VPD values at the plantation.

Leaf area index measurements were higher at the natural forest than at the plantation (Table 1). The residual canopy at the plantation had a leaf area of $3.1 \text{ m}^2 \text{ m}^{-2}$

(s.d. 0.35), and the coffee trees had a slightly lower LAI of $2.3 \text{ m}^2 \text{ m}^{-2}$ (s.d. 0.30). The total LAI for the plantation thus was lower than at the natural forest, with a LAI of $7.4 \text{ m}^2 \text{ m}^{-2}$ (s.d. 0.25). Tree density and sapwood area at the plantation were larger than at the natural forest, however (Table 1). The high number of stems at the plantation compared to the natural forest (5035 vs. 2940 stems/ha) is a result of the high density of coffee trees. Because the basal area of the young coffee and cacao trees has sapwood that is entirely hydroactive, total sapwood area at the plantation is high compared to the natural forest. Thus, in spite of the generally low coffee SFDs compared to overstory trees, plantation water use was dominated by the coffee trees, due to their abundance and resulting large sapwood area. Coffee trees were responsible for 77.5% of the water transpired from the plantation, and the few cacao trees transpired an additional 6.8% of the plantation transpiration over the year. Natural overstory trees, in spite of their higher SFDs, transpired only 15.7% of the water because of their small sapwood per unit of ground area.

The primary reason for the greater transpiration rate in the plantation relative to the natural forest is the difference in stand sapwood area (4.78 and $11.68 \text{ m}^2 \text{ ha}^{-1}$ for the natural forest and the plantation, respectively). We measured the sapwood areas of broadleaf forest plots surrounding the plantation to infer sapwood area in the pre-existing forest. The sapwood areas of these similar non-palm dominated forests ranged from 4.70 to $5.22 \text{ m}^2 \text{ ha}^{-1}$, similar to the value at the natural forest of $4.78 \text{ m}^2 \text{ ha}^{-1}$. The forest replaced by the plantation thus likely had a sapwood area similar to these measured plots.

We calculated a more conservative estimate of water use at the plantation by assuming only 75% of the basal area is hydroactive instead of 100%; this may better reflect the fraction of each stem in which sap flux was actually measured. This assumption produces an estimated active sapwood area of $8.835 \text{ m}^2 \text{ ha}^{-1}$, resulting in an average

mean daily water use at the plantation of 0.62 mm d^{-1} , s.d. = 0.17. Thus even assuming the least possible active sapwood area at the plantation, water use at the plantation is twice that of the natural forest.

SFD values strongly responded to microclimatic conditions (Figures 1 and 2). Air temperature and relative humidity can be used to calculate the VPD of the air, which was consistently higher at the plantation than at the natural forest, probably due to the partial clearing. The VPD can be considered a surrogate for the transpiration driving force if leaf temperatures are close to the canopy air temperature, as can be the case in large, closed canopies where only a small fraction of the upper canopy is exposed to direct solar radiation (Kostner et al. 1992, Oren et al. 1995). Ten days after the dry season rain, the original VPD data are missing for the plantation on 27 March due to sensor malfunction (Figure 2). We assume the VPD at the plantation is slightly higher than the VPD shown for the natural forest, due to the slightly higher temperatures.

The relationship between stand transpiration and VPD was analyzed using standardized daytime VPD values (DVDP). To obtain DVDP values, the half-hourly VPD data during daylight were summed and standardized for sea-level atmospheric pressure and for the number of daylight half-hours divided by 48. The resulting DVDP values are comparable for any date or location. Whole site responses to water availability and climatic conditions varied seasonally (Figure 3). During the wet season, approximately from June through December 1991, transpiration and conductance (transpiration divided by atmospheric driving force) respond positively to VPD. Dry season responses are more muted, reflecting increasing resistance to water uptake under limited soil water availability.

Discussion

We used the cross-sectional sapwood areas found at the natural forest and forest plots surrounding the plantation to estimate whether converting the forest to a coffee and

cacao plantation under a remnant upper canopy has altered the water balance, or changed the seasonal water dynamics. Because of the well-drained status of the plantation site and the species composition of the natural overstory, we assume that the replaced forest was similar in sapwood area to those at the upland sites. Given this, and the similarity of the SFDs of the natural forest and the natural trees at the plantation, we assume that the pre-plantation forest at the plantation site was similar in water uptake rates as surrounding upland forest sites. The average transpiration rates of the plantation, twice those of the natural forest with even the most conservative estimate of active sapwood area (0.62 mm d^{-1} , s.d. = 0.17 vs. 0.32 mm d^{-1} , s.d. = 0.08), thus represent a significant departure from the water consumption of the previous forest.

During the wet season, diurnal patterns demonstrate the effects of VPD on vegetation water uptake in the absence of soil water limitation (Figure 1). As VPD increases over the ten-day drying cycle, the water consumption of individual coffee and cacao trees increases. The cacao trees respond dramatically to only a small increase in VPD (e.g. after midday on 31 October), demonstrating a high tree canopy conductance and water loss during the wet season, even after ten days with no precipitation (Figure 1b).

The averaged SFDs of the natural forest trees, the plantation natural overstory, and plantation understory coffee and cacao trees each reveal different behavior of these components. Higher VPD after ten days of a drought during the wet season does not elicit a proportional increase in natural forest whole-site transpiration (Figure 1c). In contrast, the plantation natural overstory trees actually have a reduced water uptake rate. This plantation natural overstory thus shows a greater development of resistance to water flux than the natural forest. In contrast to the natural overstory component at the plantation, understory water uptake increases with VPD even at the end of the drying

cycle. This implies that the increased transpiration of the coffee and cacao results in a depletion of soil moisture so much that the interspersed upper canopy trees find it increasingly difficult to take up water.

Individual trees responded differently to increases in VPD in the dry season than in the wet season (compare Figures 2b, b' and 1b, b'). At this dry season stage of low soil water availability and high VPDs, water uptake is reduced in the coffee trees and in one cacao tree. The other cacao tree, however, shows a higher water uptake probably because of spatial variability in available soil moisture supply (Figure 2b'). Nighttime water uptake is usually considered to be recharge of a tree's capacitance.

One day after rain in the dry season, stand water use at the natural forest is very similar to that one day after rain in the wet season (compare Figure 2c with 1c). In contrast, the plantation overstory has a lower water flux rate in the dry season just after rain compared to the wet season. Ten days after rain in the dry season, the natural forest behaves similarly as in the wet season, with a very slight increase in water use with high VPD, while the plantation overstory shows a continuous decrease in water use with time between rain events. The mean uptake of the plantation understory trees increases, largely as a result of the recharging of the cacao tree.

The observation that the SFDs of trees parallel the daily changes in DVDP is reflected on a larger temporal and spatial scale in Figure 3. Generally, tree transpiration responds to DVDP throughout the year, but to a lesser extent during the dry season. This effect can be seen for the natural forest in the dry season, from December to late May 1992 (Figure 3). The DVDP values during these days do not result in a concomitant increase in water use of matching amplitude. This reflects seasonal changes in water availability and the development of resistance to water uptake and/or stomatal resistance to water vapor release. This pattern in the coffee/cacao plantation is visible during the dry

season, from February through June 1992. As at the natural forest, transpiration at the plantation did not increase with DVPD to the extent that it did during wetter months. The plantation trees as a whole, however, used more water than did the naturally forested site.

Stand canopy conductance values (transpiration divided by standardized DVPD) are similar between the sites, in spite of the much higher DVPDs at the plantation (Figure 3), because the water use at the natural forest was low. Transpiration thus increased approximately proportionately to the differences in driving force between the two sites.

This effect is predictable given the lower resistances to water flux of the predominant coffee trees at the plantation. It is also congruent with Jarvis' canopy coupling coefficient, the Ω factor (Jarvis 1985), which describes the degree of coupling between a canopy and the atmosphere. Ω , the coupling coefficient, ranges in value from 0 to 1, and can be included as a coefficient in the Penman-Monteith equation (Monteith and Unsworth 1990) for estimating transpiration. Greater resistance developed at each site during the dry season, showing decreased soil moisture availability to vegetation (Figure 4). Thus, the higher transpiration at the plantation (Figure 3) may be partially the result of better turbulent mixing in the canopy (smaller Ω), due to greater canopy roughness than at the natural forest. This is confirmed by the generally higher VPD at the plantation. This tighter coupling of the canopy with the atmosphere at the plantation implies that the Ω factor at the plantation is small, which parallels measured Ω values of other tree crops, which range from 0.1 to 0.3 (Jarvis 1985).

The slopes of the curves in Figure 4 indicate the differences of each site's sensitivity to reduced water availability, and the resulting different conductances. A site that transpires more at a given DVPD demonstrates a lower resistance to water uptake or release. The higher transpiration for each DVPD value during the wet season at each site represents concurrent increases in soil water availability and movement, and conductance.

The development of resistance to water uptake and release at higher DVDPs is smaller at the plantation than at the natural forest. This lower resistance at the plantation is highly dependent on the behavior of the understory (Figure 5). Regression curves of conductance at the natural forest and the plantation have similar shapes, but the plantation curve is the average of the natural overstory and the coffee and cacao understory. These two components' curves are dramatically different, and emphasize the different behavior of these forest layers.

Our study shows that an agroforestry plantation of mixed coffee-cacao in the understory of a forest canopy can alter the seasonal dynamics and hydrologic balance in a tropical broadleaf forest. Forest conversion to an understory plantation of perennial tree crops increased vegetation water consumption compared to a natural forest. The higher water consumption at the plantation was due to both the increased understory sapwood area of coffee and cacao and the increased mid-canopy VPDs.

The plantation acted as a more effective hydrologic pump than the natural forest and may dampen the effects of precipitation events, a characteristic typically cited as an important function of forests. The plantation trees also altered the behavior of the natural overstory component. In both wet and dry seasons, the plantation overstory showed decreased water uptake at the end of a drying cycle, in comparison to the trees at the natural forest site, which showed more consistent responses to microclimatic variables. The plantation understory was the most responsive to atmospheric demand and may have used enough water to restrict water uptake and, in turn, the conductance of the natural overstory trees. High-density agroforestry plantations thus can decrease the amount of water leaving a system as streamflow, a system response that is contrary to conventional concerns of increased runoff and watershed degradation due to clearing for crops. Effects on downstream ecosystems may include decreased water availability.

CHAPTER 2

Tropical Forest Water Relations in Areas with Seasonal Inundation and Drought

Chapter 2 Abstract

Vegetation water use is governed by soil water availability, microclimate, and species' ability to control stomatal conductance. In a study separate from the one described above, we measured the water uptake of two lowland swamp forests in Belize, Central America, continuously for one year and analyzed their soil profiles to determine these sites' water use. One site is a seasonal flooded swamp (bajo) at the lower edge of a limestone plateau with small-stature trees and bushes for vegetation on fine, mixed, isohyperthermic Endoaquerts. The other site is a mixed deciduous swamp forest with dense understory on fine, mixed, isohyperthermic Fluvaquentic Vertic Endoaquolls. Analysis of tree water uptake at different spatial and temporal scales reveals different responses to atmospheric demand for water vapor between the two sites. This can be explained by the contrasting soil properties at each site and the corresponding different rooting volumes exploited by each forest.

The bajo site had generally higher sap flux densities than the swamp forest ($12.44 \text{ gH}_2\text{O m}^2_{\text{sapwood s}^{-1}}$, s.d. = 3.6 vs. $7.88 \text{ gH}_2\text{O m}^2_{\text{sapwood s}^{-1}}$, s.d. = 2.45, respectively). Our calculations show the mixed deciduous swamp forest transpiring 20% more than the bajo site due to the presence of palms at the swamp forest, which we considered to be 100% hydroactive sapwood (Zimmermann 1971).

Estimates of transpiration per unit of leaf area were approximately the same between the two sites. This, in conjunction with the higher transpiration estimates at the swamp forest compared to the bajo site, indicates that resistances to water flux were higher at bajo. Both sites possess firm, sticky, plastic clay subsoils in the A and C

horizons (no B horizons are present), but the swamp forest soils' prismatic blocky structure and higher organic matter content created less resistance to water flow. The study demonstrates the potential consequences of differences in soil properties on site vegetation water use.

Introduction

Soil structure can dramatically affect the ability of vegetation to maintain water uptake rates in response to increases in atmospheric demand. Soil structure is particularly important in areas with large seasonal fluctuations in rainfall because soils differ in their water storage capacity. The regular occurrence of seasonal dry periods in tropical areas produces dramatic changes in vegetation, leaf phenology, and vegetation/soil water relations while episodic, more severe drought events may determine forest species composition and vegetation cover type (Becker et al. 1988, Borchert 1994, Reich and Borchert 1982, 1984, Fanjul and Barradas 1985). Water resources during the dry seasons can be partitioned among different species types in lowland tropical forests (Jackson et al. 1995). Vegetation water use, governed by soil water holding capacity, micro-climatic conditions, and species' ability to regulate water release by transpiration, has been largely unexplored in tropical swamps that experience dramatic changes in water availability due to seasonal drought and inundation.

This study shows that soil structure can strongly influence vegetation/soil water relations by examining the development of resistance to vegetation water uptake with decreasing water availability. We examined the water uptake and canopy conductance at two sites with slightly different soil properties supporting different swamp vegetation. The swamp vegetation types of northwestern Belize provide a unique environment to examine factors that govern transpiration because of their extreme seasonal changes from inundations to drought. We measured water uptake continuously at two swamp forest

sites and analyzed their soil profiles in order to identify site differences that may govern vegetation water dynamics.

Methods

The study was conducted at two seasonally inundated forested sites in northwestern Belize, Central America (17°32 N, 89°08 W). Both sites are within 1 km of the coffee/cacao plantation and upland forest described above. We studied two lowland sites: a seasonal swamp on a flat valley floor supporting small trees, brush, and sedges in the understory (bajo); and a swamp in a slight depression of a limestone plateau supporting a mixed, deciduous, broadleaf swamp forest. Bajo supports species such as *Metopium brownei*, *Manilkara zapota*, *Coccoloba reflexiflora*, *Byrsonima bucidifolia*, and *Hemiangium excelsum*. Many of the species at bajo are xeromorphic scrub vegetation with sclerophyllous leaves. The taller broadleaf swamp forest has a tree species mix including *Spondias mombin*, *Swietenia macrophylla*, *Coccoloba belizensis*, *Lonchocarpus castilloi*, and *Acosimum panamense*. These species comprise taller, more mesomorphic broadleaf vegetation than the bajo site, although both sites are considered swamp forests due to the seasonal flooding. Soils at bajo are classified as fine, mixed, isohyperthermic Endoaquerts. Standing water is often present during the wet season, from July through November. The broadleaf swamp has fine, mixed, isohyperthermic Fluvaquentic Vertic Endoaquolls. Both sites are rarely completely covered with an above-ground closed water table. Water drainage is especially slow at the bajo site. The soil moisture decreases abruptly after evaporation of any standing water at the beginning of the dry season. The deciduous swamp, in contrast, maintains a smooth transition of soil moisture throughout the year with only the topsoil drying.

Water use by trees was measured continuously for one year at both the broadleaf and bajo sites using a thermal constant energy method. Xylem sap flux density (SFD) was

monitored in six to seven trees at each site with a 2-mm diameter probe inserted 20 mm into each tree's bole sapwood. Measurements of SFD were taken every 30 seconds and averaged every half hour (DL-2 datalogger, Delta-T Devices LTD, Burwell, England).

We calculated transpiration by multiplying the SFD ($\text{g m}^{-2}_{\text{sapwood s}^{-1}}$) by the hydroactive tree xylem area. Hydroactive xylem depth for trees was determined visually by taking tree cores at the sensor and measuring the color-differentiated xylem area. Daily transpiration values were then summed and extrapolated to the stand level using water use/hydroactive sapwood ratios.

Mid-canopy air temperature and relative humidity were recorded (Delta-T Devices LTD, England) and used to calculate the mid-canopy vapor pressure deficit (VPD). Photosynthetically active radiation (400-700 nm) was measured 0.3 m above the forest floor with two spherical quantum sensors (LICOR, USA). These data were averaged and recorded at the same time intervals as the xylem flux data. Canopy density data were recorded at each site in a 26 x 26 m and a 40 x 40 m sub-plot for under-and overstory, respectively and leaf area index measurements were taken at each site (LICOR, USA).

One soil profiles was analyzed at each site, to 110 cm at bajo and to 230 cm at the broadleaf site (Schoenberger unpublished data). One pit was dug at each site. Soil taxonomy and each horizon's texture, color, ped structure, and root content were assessed according to Soil Taxonomy guidelines (Soil Survey Staff 1994).

Results

Daily water use estimates, averaged over one year for each site, show that the broadleaf swamp forest transpires 20% more than the bajo site (Table 2). The mid-canopy VPD values at the broadleaf site were slightly lower at bajo than at the broadleaf site. Mean sap flux of bajo trees was considerably higher than at the broadleaf swamp, but the larger active sapwood area measurements at the broadleaf site (corresponding to its larger

LAI measurements) resulted in a higher tree water consumption. Transpiration estimates per unit of leaf area were approximately the same for each site (Table 2).

The SFD values show marked responses to alterations in microclimatic conditions (Figures 6 and 7). As described in the previous study at the coffee plantation, the mid-canopy VPD can be considered a surrogate for the driving force of transpiration. We performed an analysis of site transpiration and VPD using daytime VPD values standardized (DVPD) according to the methods outlined in the previous study. Each site responded seasonally to the water availability and the climatic conditions (Figures 8 and 9). Responses of transpiration to DVPD in the wet season are very pronounced; during the dry season the responses of both water uptake and canopy conductance are more muted, reflecting increasing resistance to water uptake when soil water becomes less available.

While plastic clay is present at both sites, each soil possesses different soil properties. Bajo has an organic layer of slightly decomposed, small sclerophyllous leaves which is sparsely covered by small sedge tussocks. Very firm, sticky, plastic clay makes up the A horizon. The C horizon at bajo has gleyed, firm, sticky, plastic clay with a blocky structure down to 110 cm. Few fine roots were found down to 110 cm. At the broadleaf site, the A horizon also has very firm, sticky, plastic clay but with a strong blocky structure. Coarse roots were still found down to 110 cm at the broadleaf site amidst common very fine, fine, and medium roots throughout the entire horizon, in contrast to bajo's few fine roots at this depth. Clay in the C horizon at the broadleaf site down to 130 cm was also gleyed, but only slightly sticky and plastic. Very fine and fine roots were found at the broadleaf site to 230 cm, the maximum depth analyzed.

Discussion

The effects of soil water availability on vegetation water uptake are seen in both diurnal patterns (Figures 6 and 7) and in seasonal patterns (Figures 8 and 9). At both sites in the wet season, an increase in VPD over an eleven-day drying cycle results in a concomitant increase in water uptake. Similar increases in VPD in the dry season over an eleven-day drying cycle do not elicit increased water uptake to the same extent; this reflects the increased resistance to soil water flow as soil water availability decreases (Figures 6 and 7). The sites' water uptake responses to microclimatic conditions and soil water availability is also evident on a larger temporal scale (Figures 8 and 9).

Both sites show diminished dry season (January to June 1992) water uptake responses to changes in DVPD compared to those during the wet season (June to December 1991; Figures 10 and 11). This phenomenon of constant or even decreased water uptake responses in spite of higher DVPD values, evident at both temporal scales during the dry season, reflects changes in seasonal water availability. The bajo site had higher resistance to water flux with increasing DVPD than the broadleaf site, which is indicated by transpiration rising only slightly with increases in DVPD in both the wet and dry seasons at bajo. Dry season data at bajo show strong increases in resistance to water flow. The lowest dry season canopy conductance value at the broadleaf site represents a ten-day period of drought.

The potential transpiration, estimated by extrapolating the relationship between transpiration and VPD, under the assumption that soil water is not limiting, also reveals site water use differences when compared with actual transpiration (Figures 10 and 11). Even during the wet season, transpiration at bajo does not keep pace with increases in VPD as would occur with unlimited water supply, while at the broadleaf forest the differences between the potential and actual regression lines are less dramatic.

The hysteresis in water flux rates vs. DVPD that develops each day also shows this increased resistance at each site over a drying cycle (Figures 12 and 13). It also indicates possible capacitance effects of the tree trunk and canopy biomass where water depletion occurs. The top part of each curve represents the first half of each day, when soil water is available to allow vegetation response to atmospheric demand. Equivalent DVPD values during the afternoon result in lower water flux rates as soil water in the rooting zone becomes more depleted and stomata may close due to transpirational loss. The slopes of these curves reveal distinct behavioral differences between the sites during wet and dry season drying cycles (Figures 14 and 15). At both bajo and the broadleaf site during the dry season, slopes of SFD curves are lower at the end of a drying cycle. During the wet season at the broadleaf site, site water uptake just after a rain event is nearly identical to that after 11 days of drought, indicating that soil water storage is being tapped by the root system. Water uptake at bajo is lower at the end of the wet season drying cycle, however. Water availability is limiting the vegetation at this site with more limited rooting volume after eleven days of drought even during the wet season.

The lower water uptake at bajo during the wet season might be due to limited oxygen in the soil, so that standing water cannot be used even if plentiful during the wet season. Only the vegetation at the broadleaf site during the wet season showed increased canopy conductance for water in response to atmospheric demand (Figure 16). The bajo site, in contrast, was unable to maintain water uptake rates over the drying cycle. This again indicates that vegetation at the broadleaf site has access to a larger water supply, or to a water supply that can travel faster towards the root system than that at bajo.

The similar values of transpiration per unit of leaf area at bajo and the broadleaf site show that a factor other than vegetation density is affecting the ability of each site to respond to atmospheric demand. The different physical properties and soil structure,

which determine water availability and uptake by roots, are more restrictive to root growth and water flow at bajo than at the broadleaf site.

The firm and sticky plastic clays in the Vertisols found at bajo shrink and swell with drought and rain, respectively. This massive structure limits plant available water by becoming an impenetrable hard clay when dry, and by inhibiting water availability with the clay particle binding forces when soil moisture is higher. At the broadleaf site, however, the blockier structure of the clays and its higher humus content result in a higher available water content and larger available rooting zone. These Mollisols permit percolation of precipitation and root penetration. This structure, with well-defined vertical faces in the A horizon at the broadleaf site, also allows growth for all root diameters throughout the top 12 cm of the soil profile. Very fine to and medium roots are common, and coarse roots are still present down to 130 cm at the broadleaf site, which explains the ability of the broadleaf site to increase conductance during the wet season even as soil water is exiting the system. At bajo, with its heavy clay structure, no coarse roots are found below 14 cm, and below 96 cm only a few fine roots are present. This structural difference between the sites' soils leads to the differences in root growth and water conductance, thus limiting water uptake and release to a larger extent at bajo than at the broadleaf site.

This study shows that soil property differences can govern large differences in water relations of tropical swamp forests. It also illustrates that we can predict and then measure any differences we may expect from site edaphic properties. Two seasonal swamp forests with almost identical precipitation and microclimatic conditions and plastic clay soils showed different water uptake and release patterns based on the structural differences of their soils. The less sticky clays and blockier soil structure at the deciduous broadleaf swamp, compared to those at the bajo site, allow for more extensive rooting through the soil profile and thus for a more productive forest; the more massive clays at

the scrub bajo forest restrict water availability and limit the growth potential of the vegetation. The water fluxes of seasonally inundated, sub-tropical areas thus can be governed to a large extent by the differences in soil properties that can be found within small areas. This emphasizes the need for analyzing the physical properties of site soil profiles in addition to vegetation and general soil composition to evaluate how forested areas may respond to climatic and soil hydraulic conditions.

Figure 1: Mid-canopy temperature and vapor pressure deficit (VPD, top), and sap flux densities (SFDs) during the wet season. Plots on left are one day after significant rainfall; right-hand plots are after eleven days without precipitation. The top plots are for CC (open symbols) and PC1 (closed symbols), respectively. The behavior of individual coffee and cacao trees is shown in 1b. Averages of CC plantation overstory (open circles), CC coffee and cacao understory (closed circles), and the natural forest at PC1 (triangles) are in 1c.

Figure 2: SFDs and corresponding micro-climatic data for ten day drying cycle in the wet season. Left-hand plots are one day after a significant rainfall; right-hand plots are twelve dry days later. Original VPD data are missing for the plantation for one day; we assume it is slightly higher than that at PC1 due to the higher temperatures and the relationship between VPD at the two sites on other days.

Figure 3: Precipitation (a), standardized daytime VPDs (b), stand transpiration (c), and stand conductance (d) over one year for CC (left) and PC1 (right). The dry season is from December 1991 through June 1992. Asterisks indicate missing data.

Figure 4: Canopy conductances at each site in wet and dry seasons. The inverse of the slopes of water uptake vs. driving force curves is the resistance to flux.

Figure 5: Second-order regression curves of conductance trends over one year for each site, and the overstory natural and understory components at the plantation. Plantation curve is the average of the two CF component curves from the natural and understory trees.

Figure 6. Bajo site diurnal curves for temperature, VPD, individual measurement trees' sap flux densities, and averaged measurement trees' fluxes on four days, at the beginning and end of drying cycles in both wet and dry seasons. Each curve on the SFD plot represents an individual tree.

Figure 7. Swamp site diurnal curves for temperature, VPD, individual measurement trees' sap flux densities, and averaged measurement trees' fluxes on four days, at the beginning and end of drying cycles in both wet and dry seasons. Each curve on the SFD plot represents an individual tree.

Figure 8. Ten-day averages over one year (marked in Julian dates) at Bajo site for conductance, transpiration, standardized vapor pressure deficit (DVPD), and precipitation. Dry season begins at Julian day 730.

Figure 9. Ten-day averages over one year (marked in Julian dates) at Swamp for conductance, transpiration, standardized vapor pressure deficit (DVPD), and precipitation. Dry season begins at Julian day 730.

Figure 10. Bajo site dry and wet season responses in water flux to standardized vapor pressure deficit (DVPD). Second-order regression curves indicate actual responses; linear regression is extrapolation of water flux responses when soil water is not limiting. The difference between potential and actual response indicates the development of resistance to water flux at the site, as soil water availability decreases. Note the different y-axis scale from Figure 6.

Figure 11. Swamp site dry and wet season responses in water flux to standardized vapor pressure deficit (DVPD). Second-order regression curves indicate actual responses; linear regression is extrapolation of water flux responses when soil water is not limiting. The difference between potential and actual response indicates the development of resistance to water flux at the site, as soil water availability decreases. Note the different y-axis scale from Figure 5.

Figure 12. Development of hysteresis on four different days at Bajo, at the beginning and end of drying cycles in the wet and dry seasons. Morning water fluxes are represented at the top of the curves, when soil water is more available than in the afternoon, when similar DVPD values result in lower water uptake rates.

Figure 13. Development of hysteresis on four different days at Swamp, at the beginning and end of drying cycles in the wet and dry seasons. Morning water fluxes are represented at the top of the curves, when soil water is more available than in the afternoon, when similar DVPD values result in lower water uptake rates.

Figure 14. Regression slopes of hysteresis curves in Figure 7, for Bajo site. Resistance develops in both wet and dry season over 11 days.

Figure 15. Regression slopes of hysteresis curves in Figure 8, for Swamp site. Wet season response of water uptake is similar both at beginning and end of a drying cycle, while dry season water uptake shows development of resistance.

Figure 16. Relationship between conductance and soil water lost via transpiration in wet and dry season for both sites. The Swamp site is able to increase conductance with increased soil moisture loss in the wet season, in contrast to the Bajo site.

Table 1

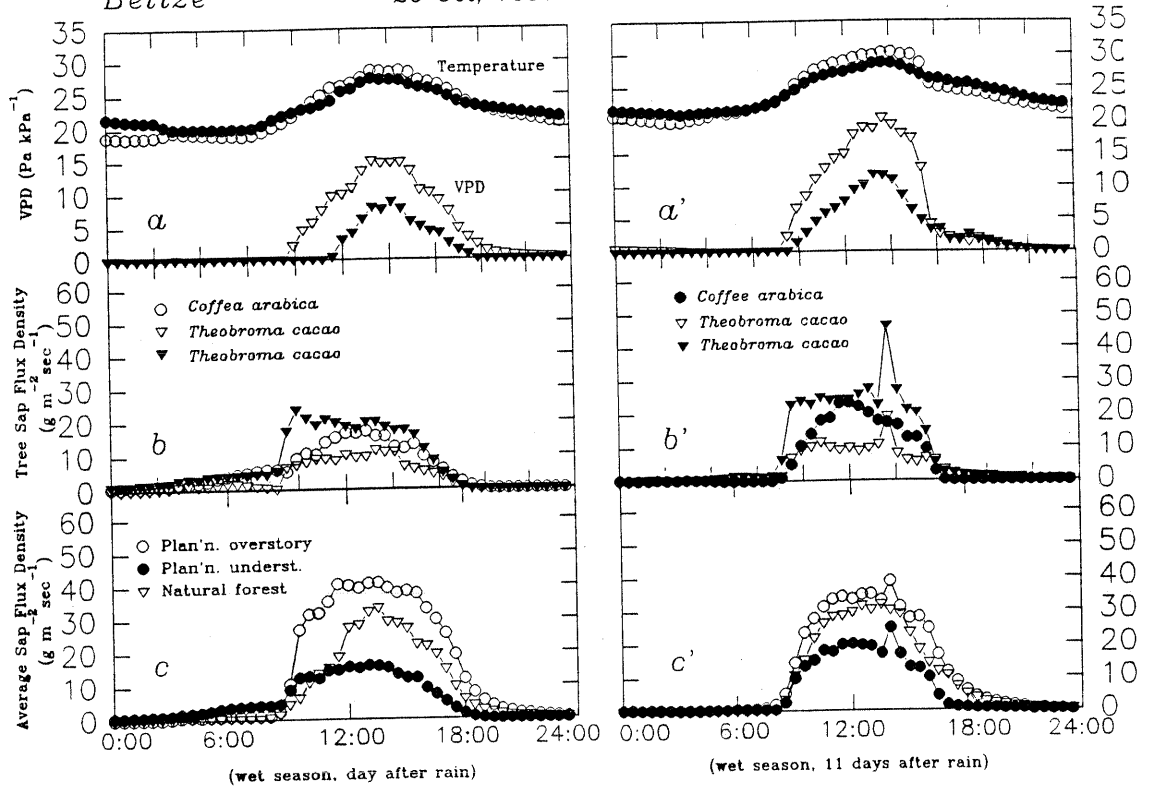
<u>Site</u>	<u>Tree Density</u> Stems/ha	<u>Sapwood Area</u> m ² ha ⁻¹	<u>E_t</u> mm day ⁻¹	<u>PAR</u> μmol m ⁻² s ⁻¹	<u>DVPD</u> kPa kPa ⁻¹	<u>LAI</u> m ² m ⁻²
Natural forest (1991)	2940	4.78	0.32, s.d. (0.08)	1.81, s.d. (0.82)	0.33, s.d. (0.17)	7.4, s.d. (0.25)
Natural forest (1992)			0.32, s.d. (0.08)	1.41, s.d. (0.65)	0.25, s.d. (0.12)	
Plantation (1992)				3.20, s.d. (1.68)	0.42, s.d. (0.17)	
Residual overstory	141	2.82	0.14, s.d. (0.07)			3.1, s.d. (0.35)
Coffee and cacao	4894	8.86	0.68, s.d. (0.20)			2.3, s.d. (0.30)
Total	5035	11.68	0.82, s.d. (0.23)			5.4, s.d. (0.30)

Table 1: Annual mean of tree densities and sapwood area, daily water use for the plantation (CC) and a natural forest (PC1), total photosynthetic irradiation, standardized daytime vapor pressure deficit (DVPD), and leaf area index (LAI).

Gallon Jug,
Belize

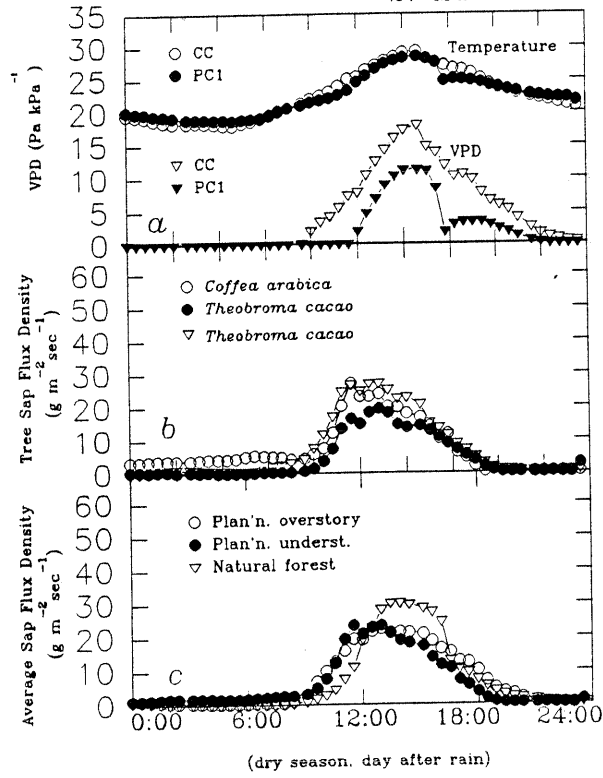
20 Oct, 1991

31 Oct, 1991

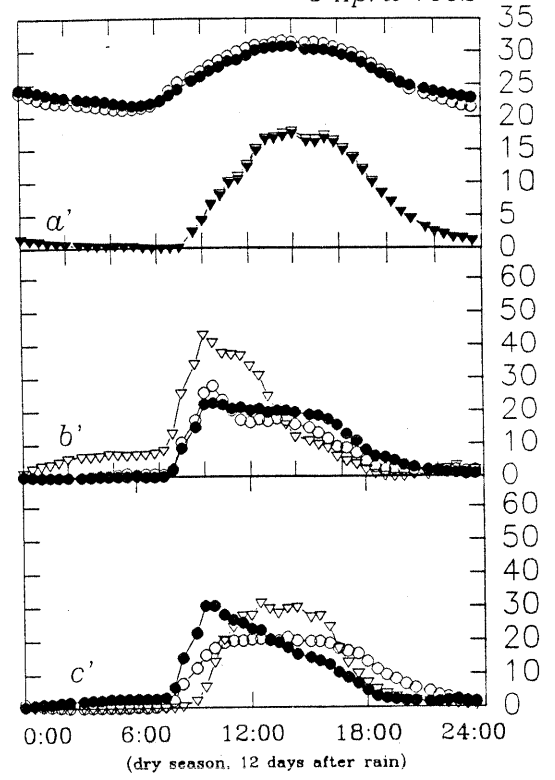


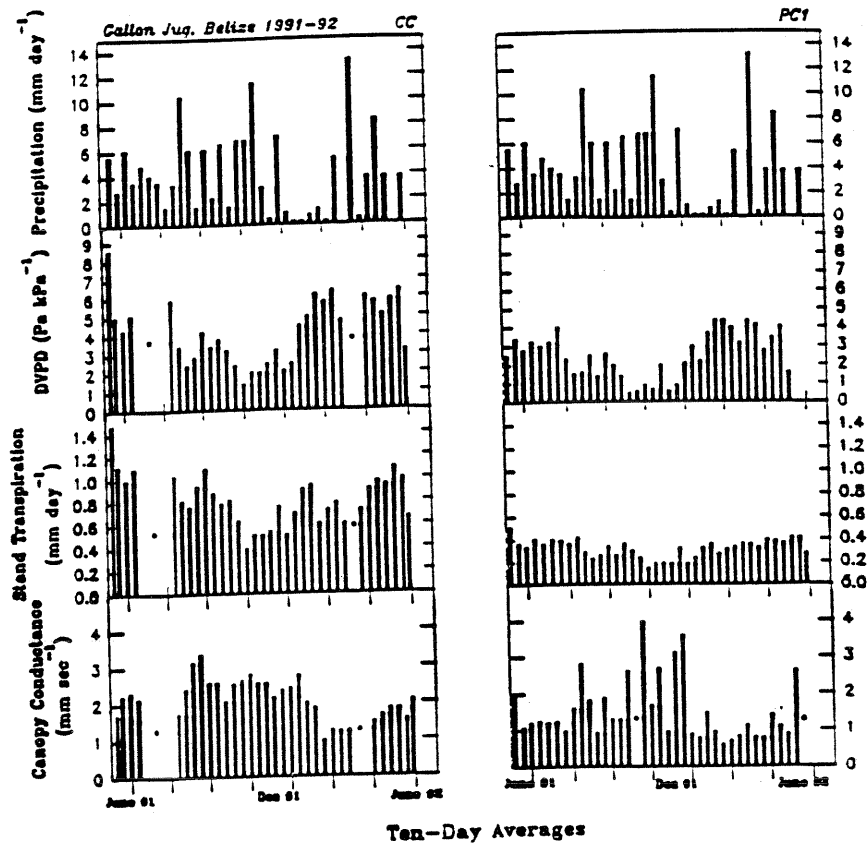
Gallon Jug,
Belize

27 March 1991



8 April 1992

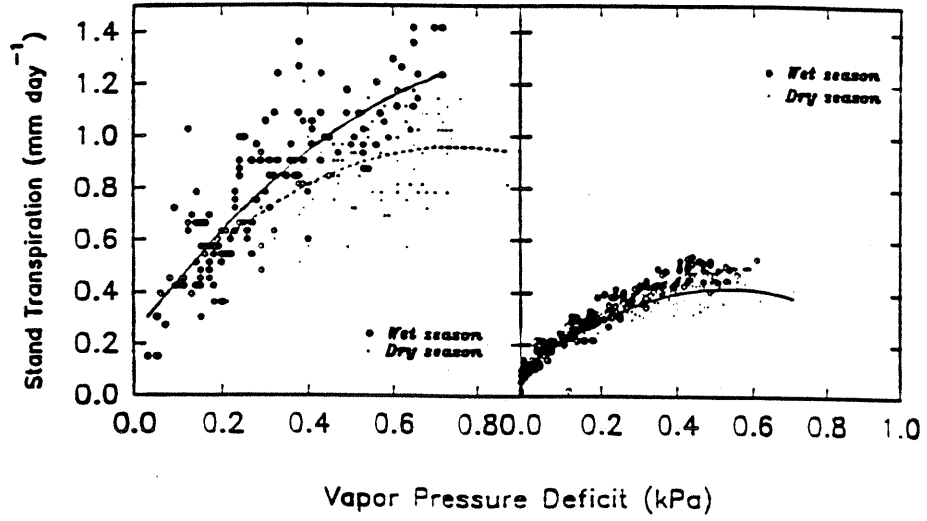




Gallon Jug, Belize
1991-92

CC

PC1



Gallon Jug, Belize

1991-92

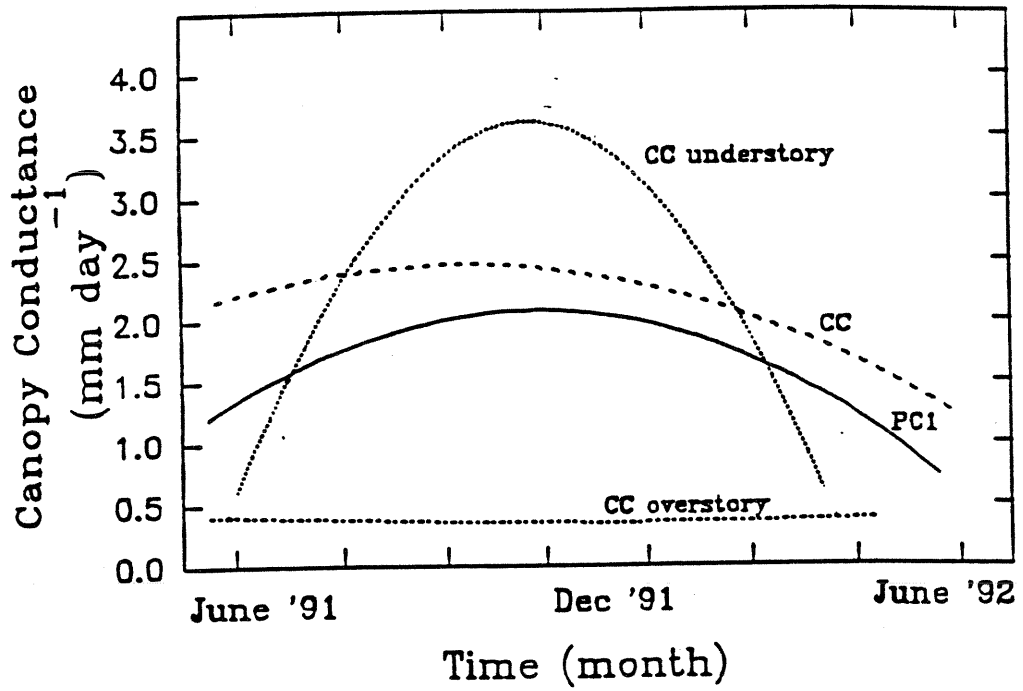
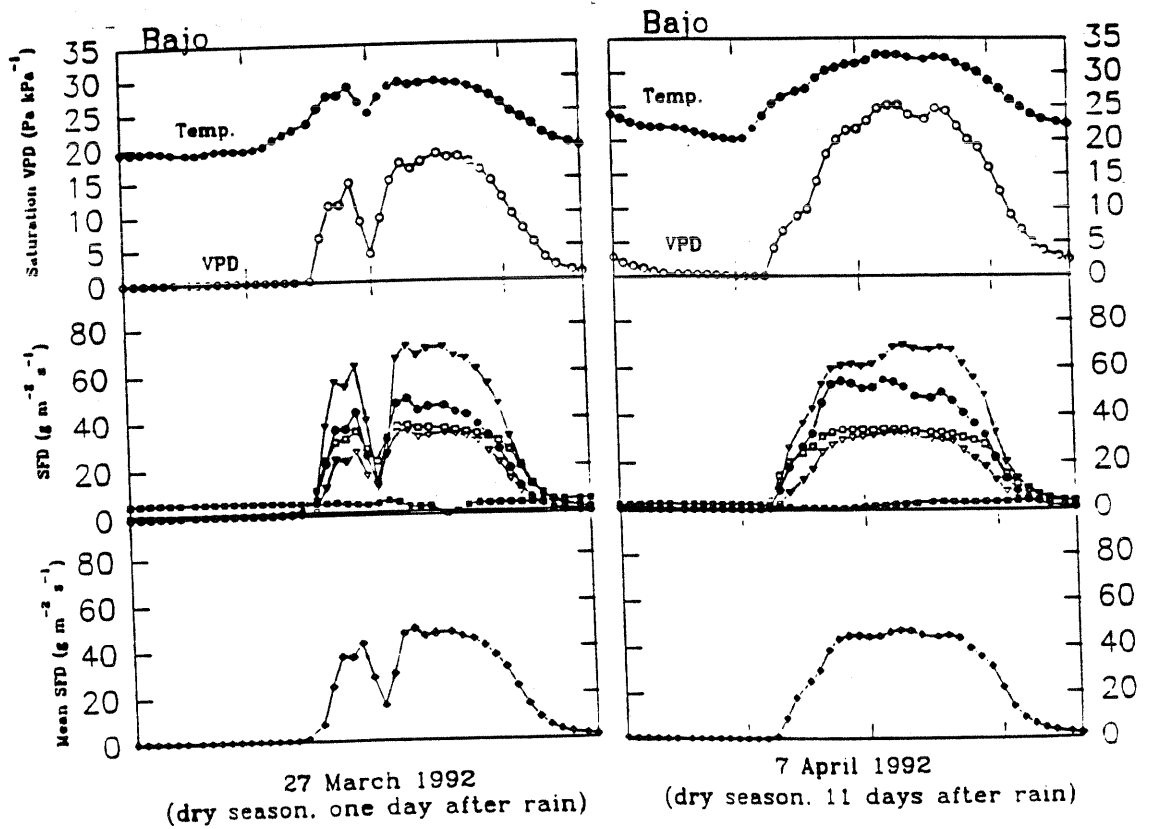
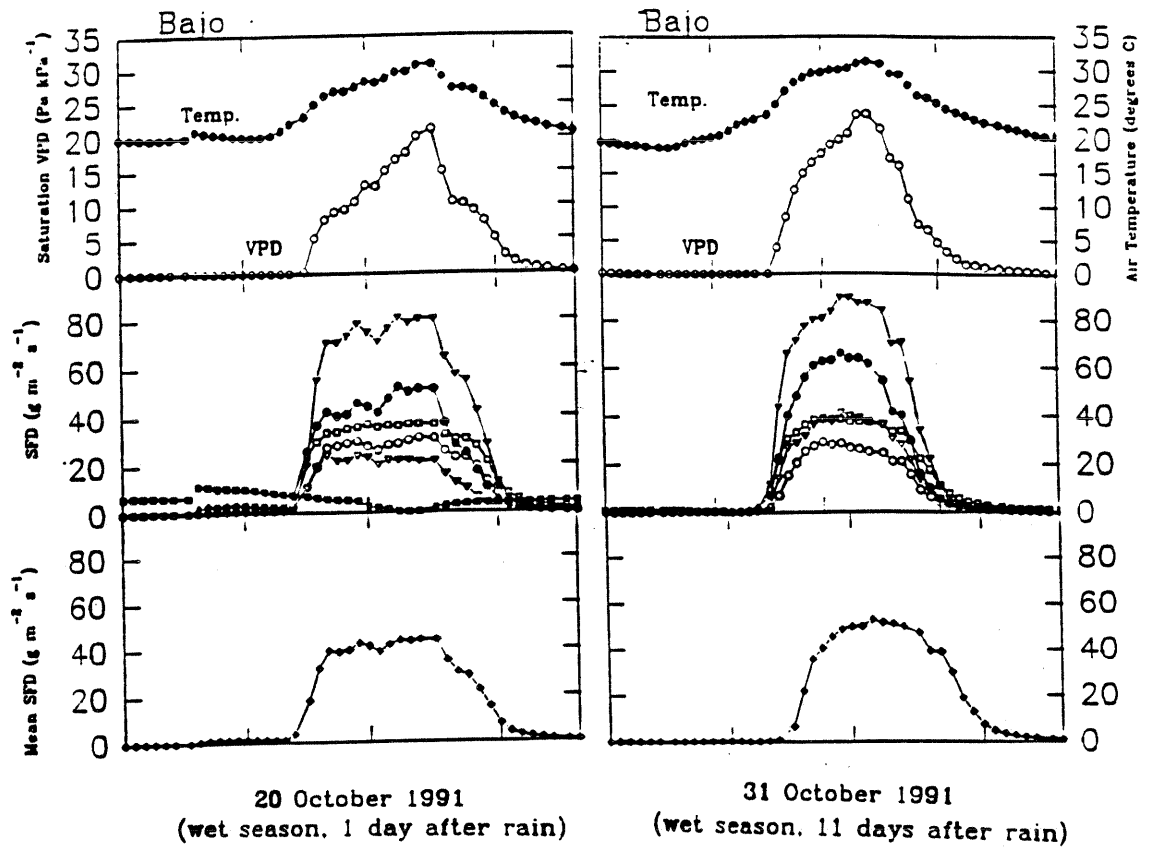
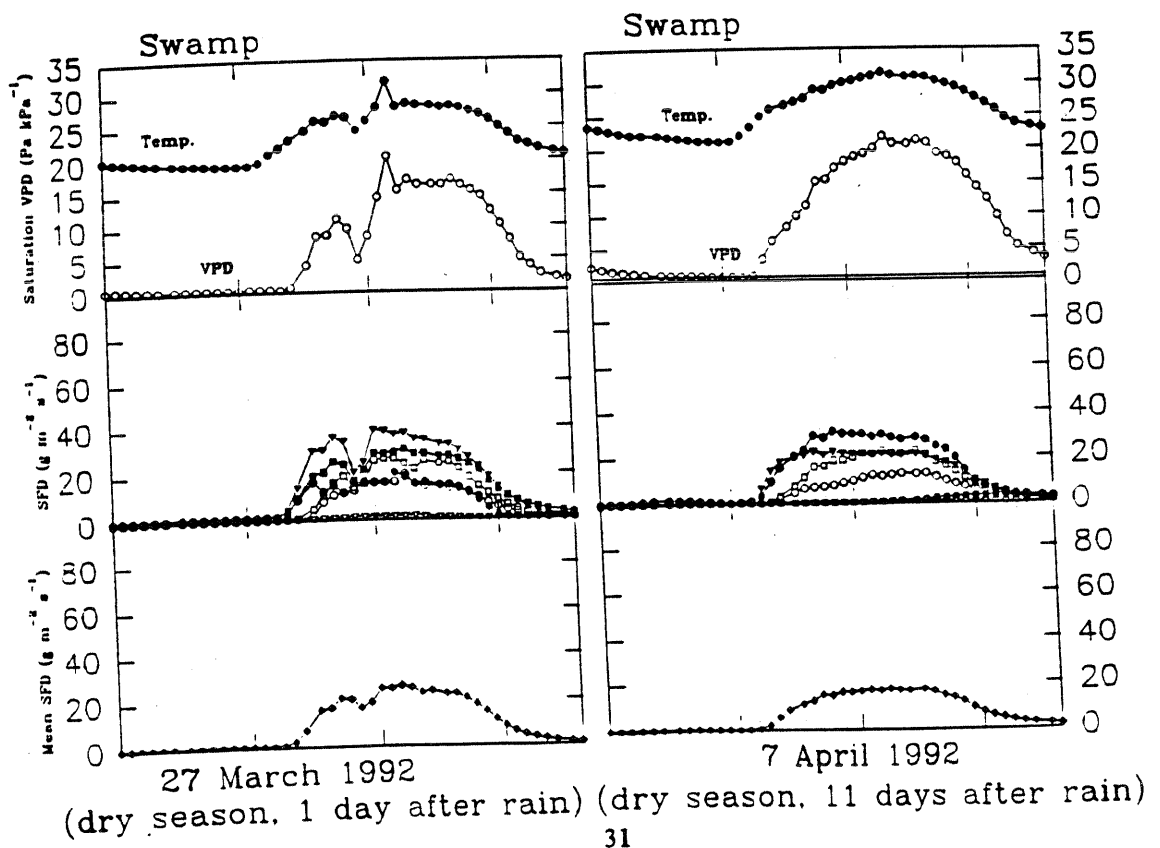
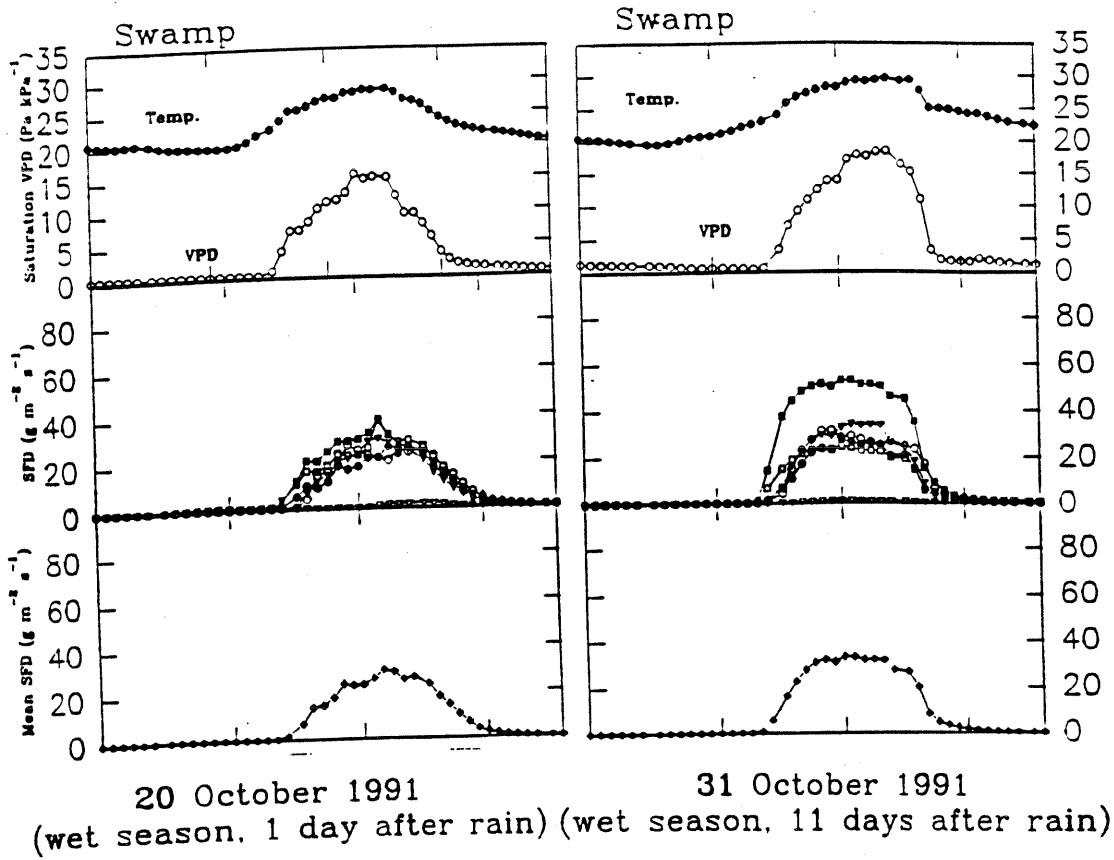


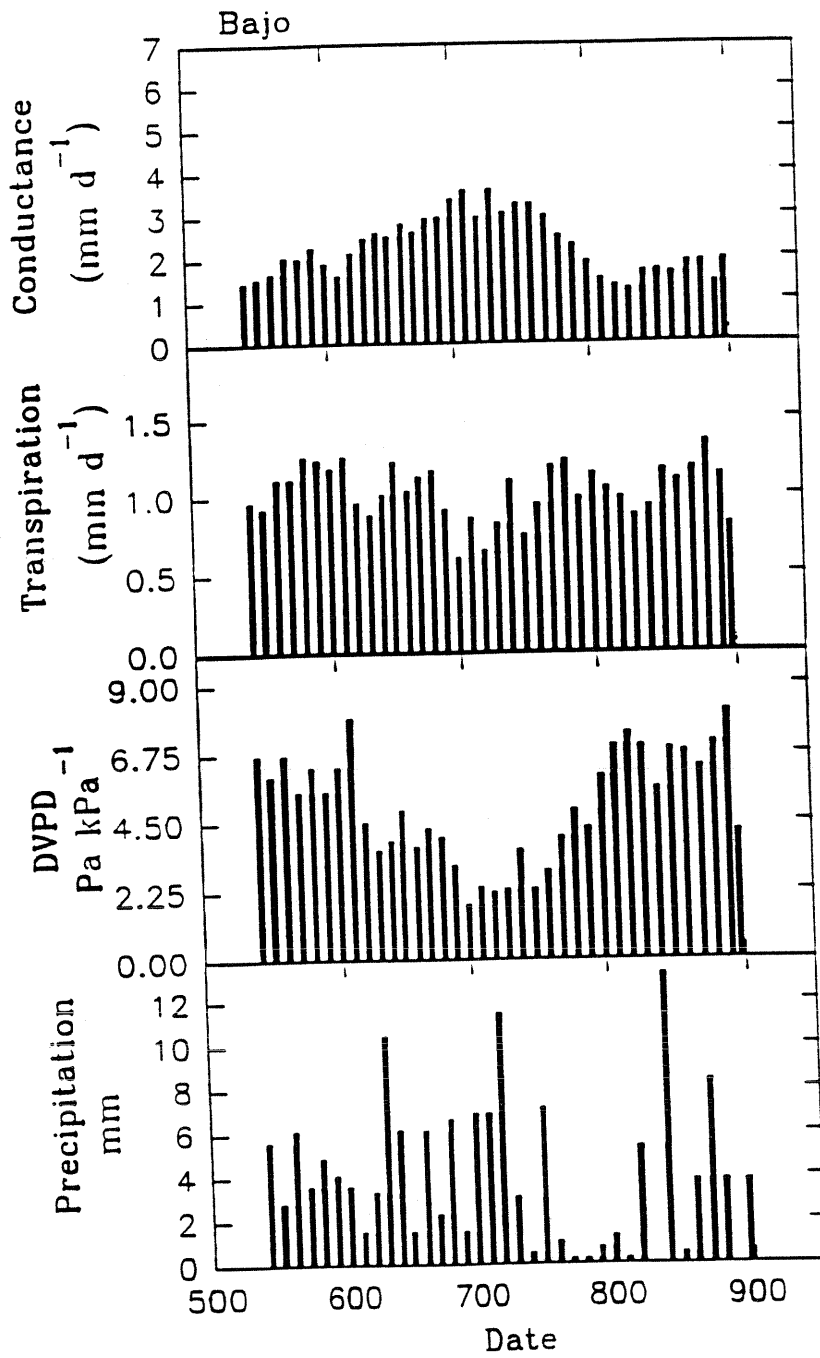
Table 2.

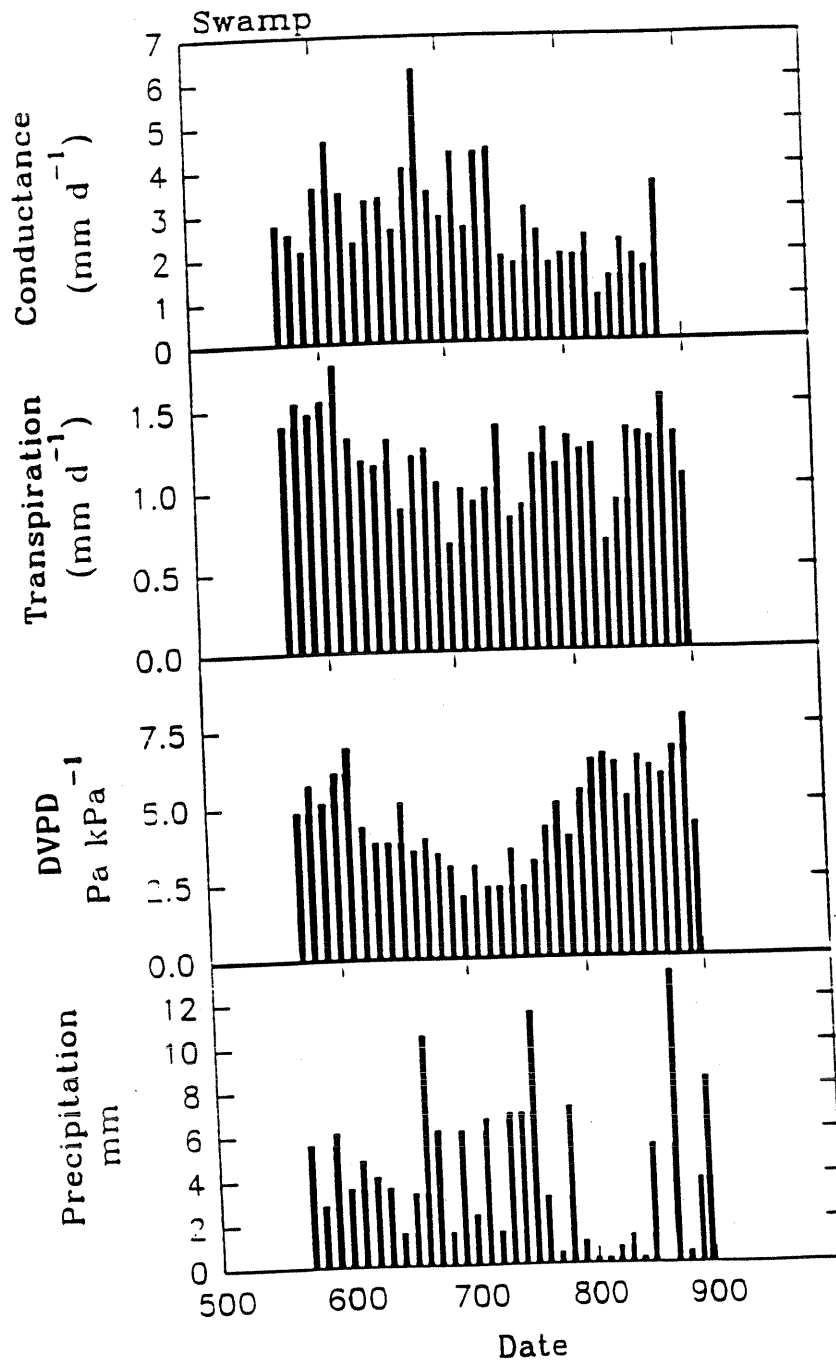
	<u>E</u> (mm d ⁻¹)	<u>VPD</u> (kPa)	<u>SFD</u> (gm ⁻² s ⁻¹)
<u>Swamp</u>	1.20 (0.25)	0.47 (0.16)	7.88 (2.45)
<u>Bajo</u>	1.03 (0.18)	0.50 (0.18)	12.44 (3.60)
<hr/>			
	<u>Q</u> (μmolm ⁻² s ⁻¹)	<u>LAI</u> (m ² m ⁻²)	<u>E/LAI</u> (mm d ⁻¹)
<u>Swamp</u>	5.02 (3.42)	5.4 (0.2)	0.22 (0.25)
<u>Bajo</u>	4.51 (1.43)	4.1 (0.1)	0.25 (0.18)
<hr/>			

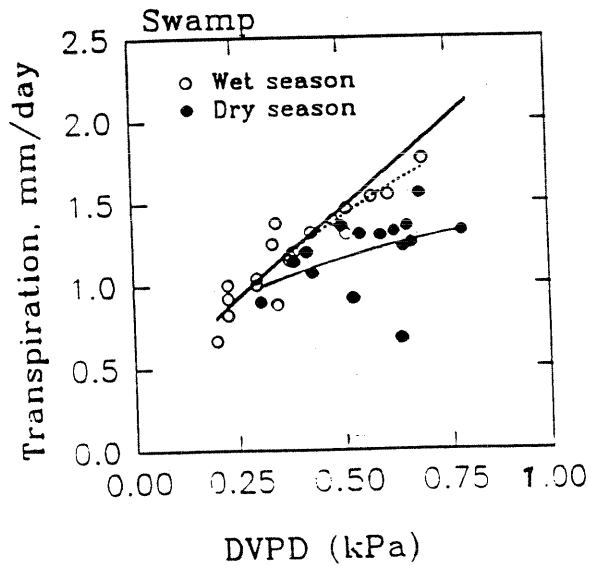
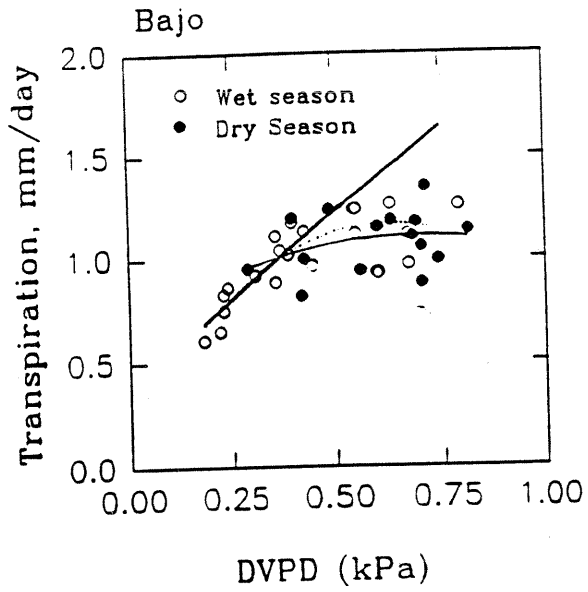
Table 2. Daily averages of parameters measured at Swamp and Bajo sites in Gallon Jug, Belize with standard deviations in parentheses. E: estimates of transpiration; VPD: vapor pressure deficit; SFD: sap flux density; Q: spherical quantum sensor (μmols of photons); LAI: leaf area index.

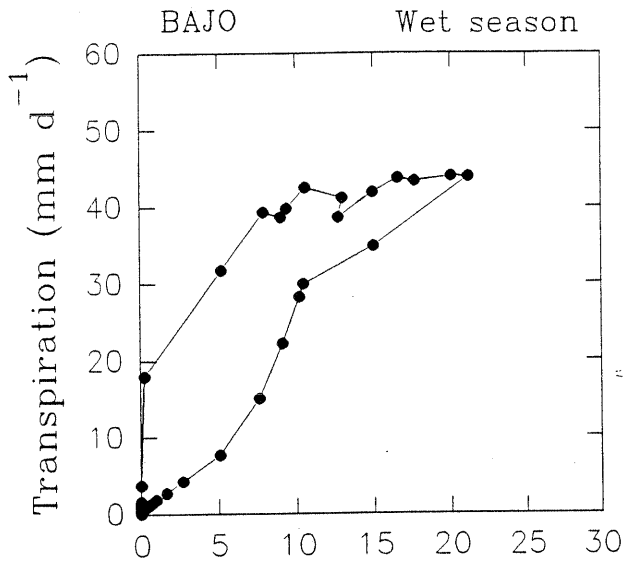




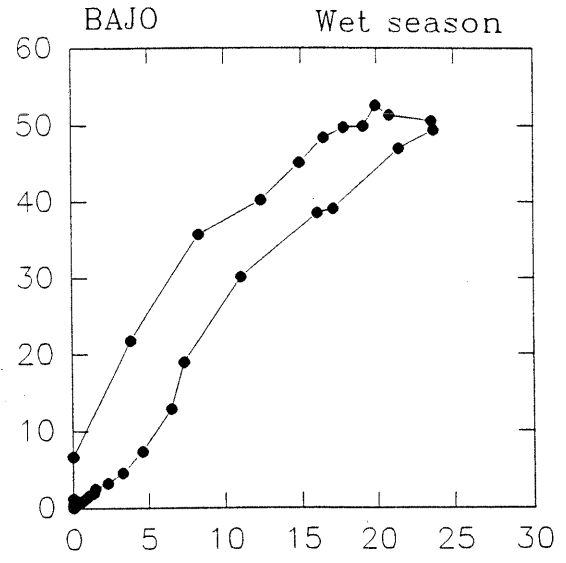




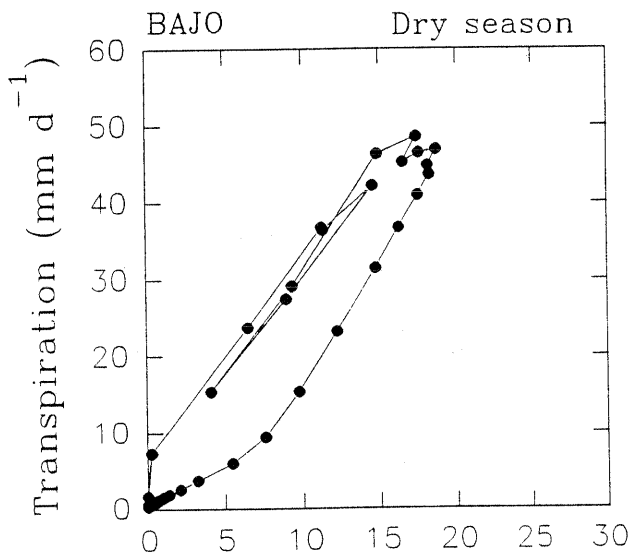




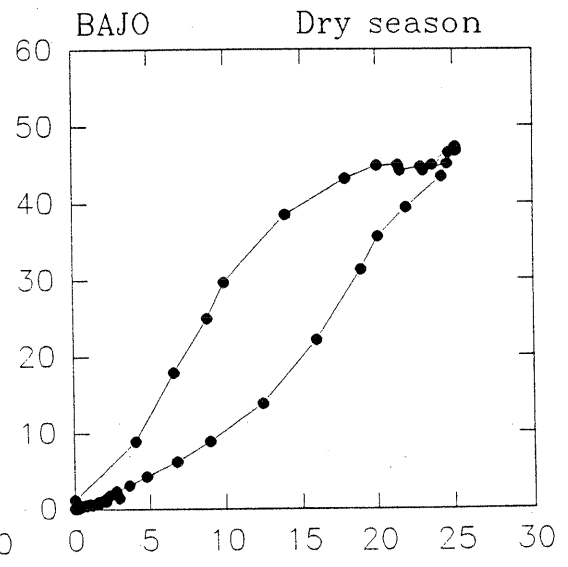
DVPD (Pa kPa^{-1})
20 October 1991
(1 day after rain)



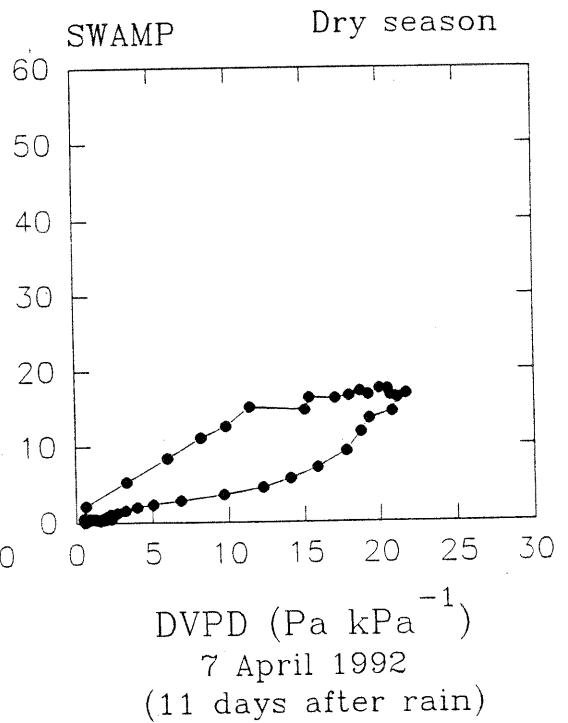
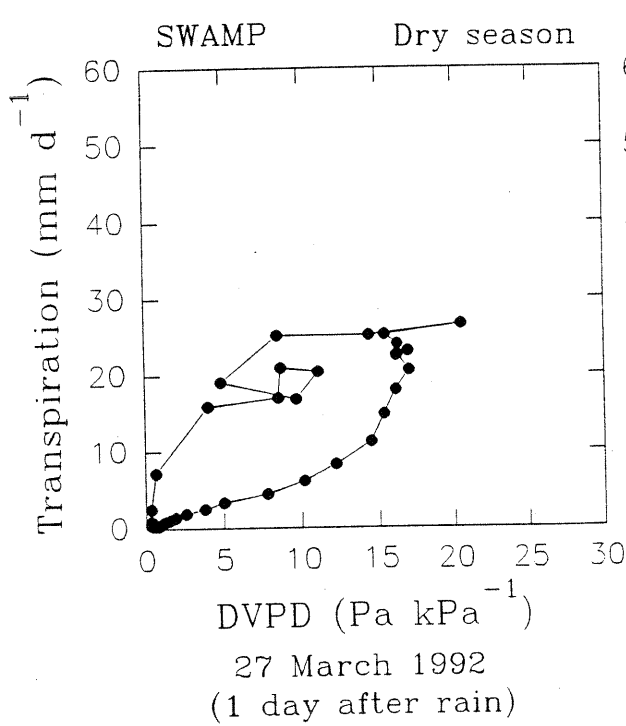
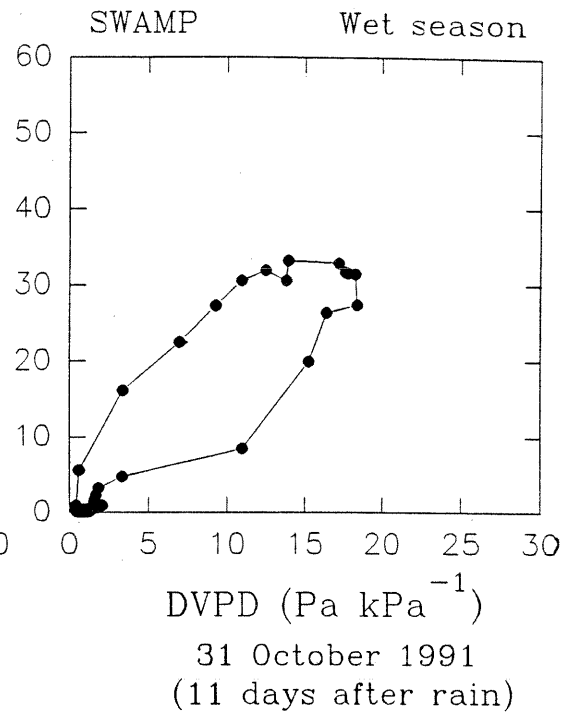
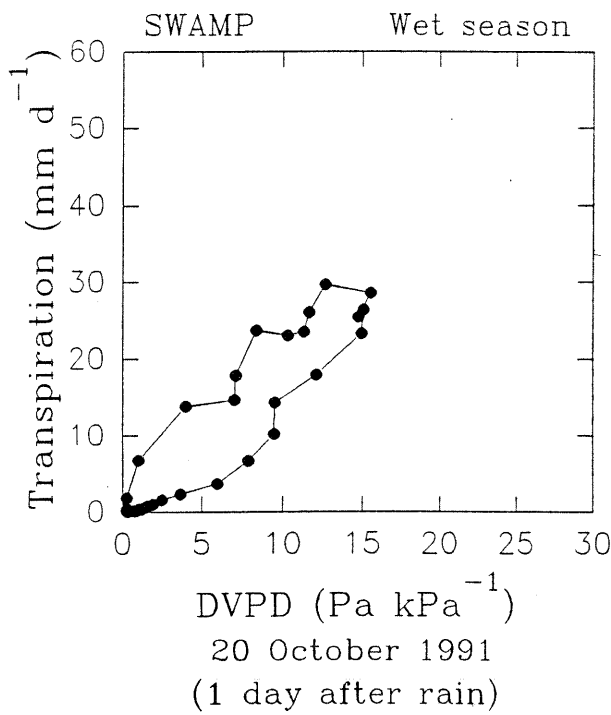
DVPD (Pa kPa^{-1})
31 October 1991
(11 days after rain)

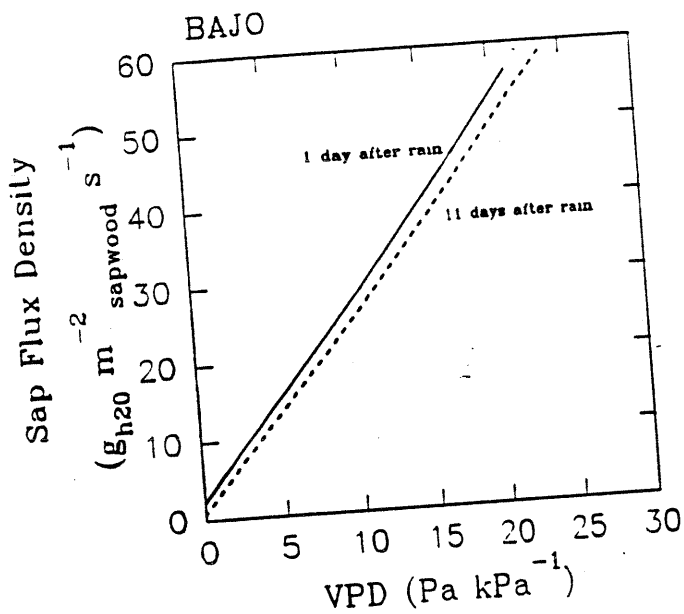


DVPD (Pa kPa^{-1})
27 March 1991
(1 day after rain)

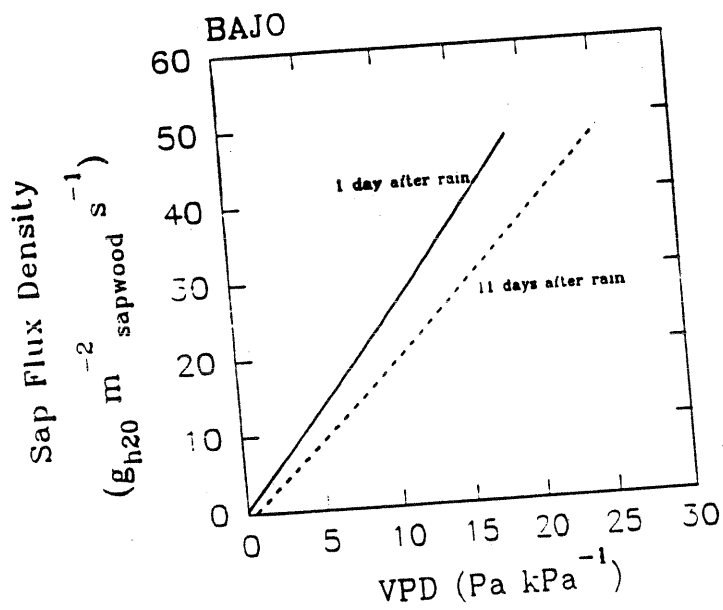


DVPD (Pa kPa^{-1})
7 April 1991
(11 days after rain)

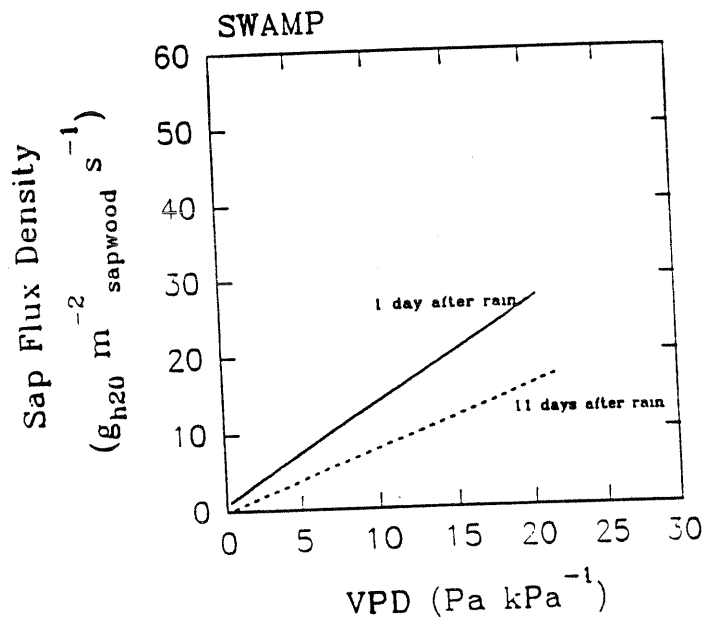
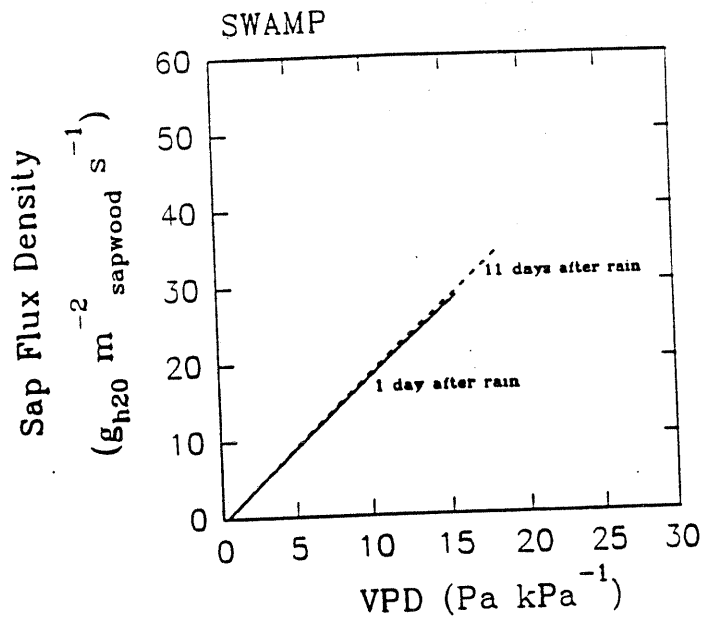


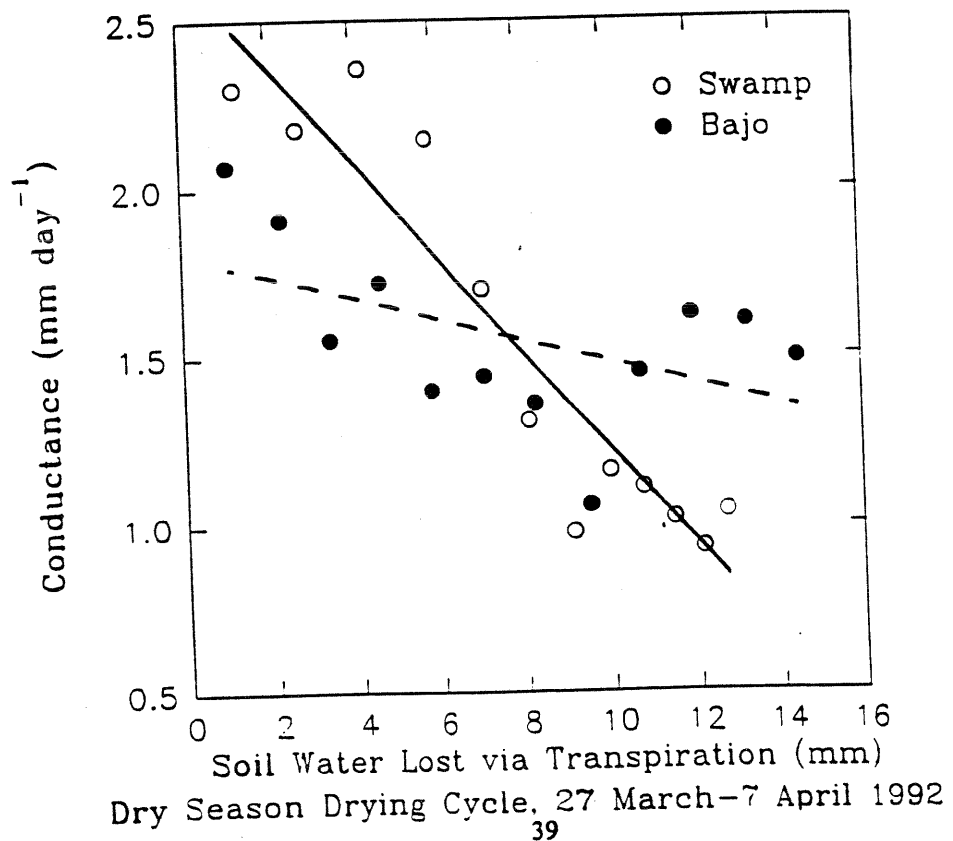
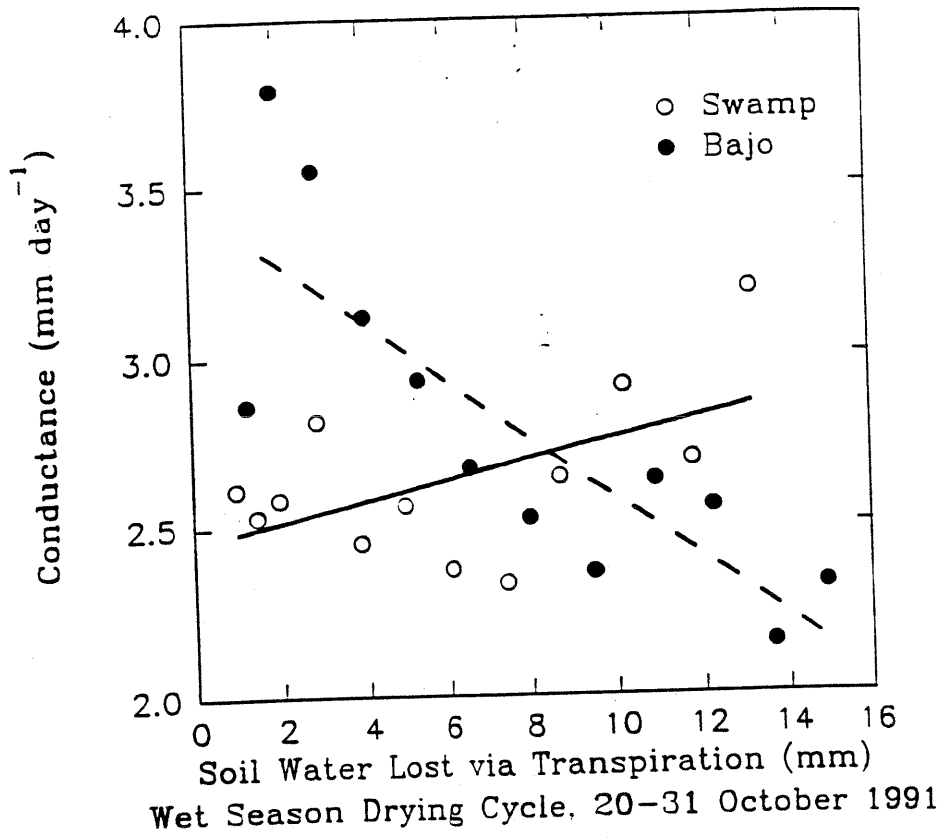


20 and 31 October 1991
(wet season)



27 March and 7 April 1991
(dry season)





Literature Cited:

- Anderson JM and Spencer T (1991) Carbon, nutrient and water balances of tropical rain forest ecosystems subject to disturbance: management implications and research proposals. MAB Digest 7. UNESCO, Paris.
- Barradas VL, Fanjul L (1986) Microclimatic characterization of shaded and open-grown coffee (*Coffea arabica*) plantations in Mexico. Agricultural and Forest Meteorology **38**: 101-112.
- Becker P, Rabenold PE, Idol JR, Smith AP (1988) Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. Journal of Tropical Ecology **4**: 173-184.
- Binsack R (1984) Problems and consequences of agriculture and cattle breeding in tropical rain forests. Spixiana Supplement **9**: 85-96 (abstract).
- Borchert R (1994) Water status and development of tropical trees during seasonal drought. Trees **8**: 115-125.
- Brokaw NVL, Mallory EP (1989) Natural history of the Rio Bravo resource management and conservation area. Report for the Programme for Belize, Belize City.
- Brokaw NVL, Mallory EP (1993) Vegetation of the Rio Bravo conservation and management area, Belize. Manomet Bird Observatory, Manomet, Massachusetts.
- Brokaw NVL, Mallory EP, Alcorn PW (1990) Trees of Rio Bravo: A guide to trees of the Rio Bravo Conservation and Management Area, Belize. Manomet Bird Observatory, Manomet, Massachusetts.
- Bruijnzeel LA (1990) Hydrology of moist tropical forests and effects of conversion: a state of knowledge review. UNESCO International Hydrological Programme, Humid Tropics Programme, Free University, Amsterdam.
- Fanjul L, Barradas VL (1985) Stomatal behavior of two heliophile understory species of a tropical deciduous forest in Mexico. Journal of Applied Ecology **22**: 943-954.
- Granier A (1985) Une nouvelle methode pour la mesure du flux de seve brute dans le tronc des arbres. Annales Sciences Forestiers **42**: 193-200.
- Holdridge LR, Grenke WC, Hathaway WH, Liang T, Tosi JA (1971) Forest environments in tropical life zones. Pergamon, New York.

- Jackson IJ (1989) Climate, water and agriculture in the tropics. Longman Scientific and Technical, New York.
- Jackson PC, Cavelier J, Goldstein G, Meinzer FC, Holbrook NM (1995) Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* **101**: 197-203.
- Jarvis, PG (1985) Coupling of transpiration to the atmosphere in horticultural crops: the Omega factor. *Acta Horticulturae* **171**: 187-205.
- Kinnell PIA (1985) Runoff effects on the efficiency of raindrop kinetic energy in sheet erosion. In: Soil erosion and conservation, SA El-Swaify, WC Moldenhauer, A Lo, eds. Soil Conservation Society of America, Iowa, pp. 399-405.
- Kostner BMM, Schulze ED, Kelliher FM, Hollinger DY, Beyers JN, Hunt JE, McSeveny TM, Meserth R, Weri PL (1992) Transpiration and canopy conductance in a pristine broadleaf forest of *Nothofagus*: An analysis of xylem sap flow and eddy correlation measurements. *Oecologia* **91**: 350-359.
- Lundgren B and Nair PKR (1985) Agroforestry for soil conservation. In: Soil erosion and conservation, SA El-Swaify, WC Moldenhauer, A Lo, eds. Soil Conservation Society of America, Iowa, pp. 703-717.
- Luvall JC, Parker GG, Jordan CC (1985) Tropical deforestation and evapotranspiration. In: Symposium on tropical hydrology, Quinones F and Sanchez AV, eds. American Water Resources Association, Maryland, pp. 7-10.
- Monteith JL, Unsworth MH (1990) Principles of Environmental Physics. Edward Arnold Publishing, London.
- O'Kting'Ati A, Mongi HO (1986) Agroforestry and the small farmer: a case study of Kilema and Kirua Vunjo in Kilimanjaro (Tanzania). *International Tree Crops Journal* **3**: 257-266 (abstract).
- Oren R, Zimmermann R, Terborgh J (1995) Transpiration in upper Amazonia flood plain and upland forests in response to drought-breaking rains. *Ecology* (submitted).
- Pereira HC (1989) Policy and practice in the management of tropical watersheds. Westview Press, Boulder, Colorado.

- Reich PB, Borchert R (1982) Phenology and ecophysiology of the tropical trees, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology* **63**: 294-299.
- Reich PB, Borchert R (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* **72**: 61-74.
- Roberts J, Cabral OMR, Fisch G, Molion LCB, Moore CJ, Shuttleworth WJ (1993) Transpiration from an Amazonian rain forest calculated from stomatal conductance measurement. *Agricultural and Forest Meteorology* **65**: 175-196.
- Romberger JA, Hajnowicz Z, Hill JF (1993) Plant structure: function and development, a treatise on anatomy and vegetative development, with special reference to woody plants. Springer-Verlag, New York.
- Schoenberger P (1991-1992) Unpublished data from analyses of soil samples collected during project.
- Soil Survey Laboratory Staff (1992) Soil Survey Laboratory Methods Manual. Soil Survey Investigations Report No. 42, Version 2.0. USDA Soil Conservation Service National Soil Survey Center, Washington D.C.
- Soil Survey Staff (1994) Keys to soil taxonomy, sixth edition. USDA Soil Conservation Service, Washington D.C.
- Wiersum KF (1985) Effects of various vegetation layers in an *Acacia auriculiformis* forest plantation on surface erosion in Java, Indonesia. In: Soil erosion and conservation, SA El-Swaify, WC Moldenhauer, A Lo, eds. Soil Conservation Society of America, Iowa, pp. 79-89.
- Wright ACS, Romney DH, Arbuckle RH, Vial VE (1959) Land in British Honduras: report of the British Honduras land use survey team. Her Majesty's Stationery Office, London.
- Zimmermann M (1983) Xylem structure and the ascent of sap. Springer-Verlag, New York.
- Zimmermann M, Brown C (1971) Trees: structure and function. Springer-Verlag, New York.
- Zimmermann R, Oren R, Mueller-Ezards C, Schaaff C, Strohmeier P, Obermaier E, Klein S, Stumpf B, and Granier A (1993) Diurnal and seasonal changes of tree transpiration in a semideciduous neotropical rain forest in Belize, Central

America. Poster presentation at the Sixth Annual Meeting of the German Society of Tropical ecology, 18-20 February 1993, Berlin, FRG.