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Contribution of transpiration to forest ambient vapour based on isotopic measurements

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Abstract

Using a simple isotope mixing model, we evaluated the relative proportion of water vapour generated by plant transpiration and by soil evaporation at two sites in the Amazon basin. Sampling was carried out at two different soil covers (forest and pasture), in a seasonal tropical rainforest at eastern Amazon where major deforestation is the result of land-use change, and compared to a less seasonal central Amazon forest. In both forests, vapour from transpiration was responsible for most, if not all, of the water vapour generated in the forest, while it could not be detected above the grassy pastures. Thus the canopy transpiration may be a major source of water vapour to the forest and perhaps to the atmosphere during the dry season. The results are discussed in relation to predictive models based on net radiation that usually are not able to distinguish between transpiration and evaporation.

Keywords: Amazon tropical forest, evaporation, stable isotopes, transpiration, water cycle, water vapour

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Introduction

The Amazon basin is the world's largest dense stand of natural tropical rain forest, spread over an estimated area of 6.4 million km^2. The annual precipitation at the basin averages 2200 mm per year (Salati 1986). The Atlantic Ocean provides the main external influx of water vapour for the Amazon basin, which is channeled to the southwestern part of the basin. Movement of vapour to the north and west is blocked by the Andes mountains, and there is few evidence of moisture exchange with other regions (Salati & Nobre 1991). At the site of this blockage, precipitation as high as 5000 mm y^{-1} can be measured (Salati & Vose 1984). The main sink for this large amount of precipitation in the Amazon basin is the Amazon river. Measurements of the mainstream discharge (estimated to be 6×10^{12} m^3 y^{-1}, Richey *et al*. 1986), indicate that the river channel only discharges $\top$ 40% of the yearly precipitation (Victoria *et al*. 1991; Salati & Marques 1984; Salati *et al*. 1979). One question that immediately comes to mind is the destiny of the other 60% of the precipitation. Previous studies have shown that a significant part of this water is returned to the atmosphere by evapotranspiration (Molion 1976; Villa Nova *et al*. 1976; Marques *et al*. 1977; Salati *et al*. 1979). Salati *et al*. (1979) concluded that much of the rain water in the Amazon is recycled following a cycle of: precipitation–soil–atmosphere–re-precipitation. Thus evapotranspiration plays a crucial part in this cycle. The relative importance of evaporation and transpiration on the recycling of water in the Amazon has been the subject of recent investigations (Gat & Matsui 1991; Victoria *et al*. 1991; Martinelli *et al*. 1996; Ribeiro *et al*. 1996). The answer to this question is useful, since any realistic model predicting the effect of deforestation on the water cycle should be sensitive to the relative contribution of different sources of water vapour.

Many of the conclusions on recycling of rainfall in the Amazon have been based on isotopic measurement of rainfall across a longitudinal gradient (east to west),

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where previous investigators reasoned that because of Rayleigh distillation effects, there should be a progressive isotopic depletion of water in precipitation towards westerly longitudes (Dall'Olio 1976; Salati *et al.* 1979). This phenomenon is commonly observed in temperate regions and known as the continental effect (Gat 1980). Because this depletion was not observed in the dry season for the Amazon basin, Salati *et al.* (1979) postulated that there must be a source of isotopically enriched vapour compensating for the Rayleigh distillation effect. This source could be pools of water undergoing evaporation as well as plant transpiration (Gat & Matsui 1991; Victoria *et al.* 1991). In a recent evaluation, Martinelli *et al.* (1996) could not find an evaporative source for this enriched vapour based on the available isotopic data of the following water pools: rainfall, stemflow and throughfall, lakes, soil and river water.

In this study, with the use of stable isotopes, we attempt to determine the relative contribution of soil evaporation and plant transpiration to the forest ambient vapour. This question is important because, presumably much of the water recycling in the Amazon occurs through the mixing of ambient forest vapour with the troposphere. The use of stable isotopes to decipher the relative contribution of evaporation and transpiration to ambient forest vapour is possible, because vapour from evaporation processes should be isotopically depleted relative to that derived from transpiration (Gat & Matsui 1991).

Utilization of stable isotopes to interpret the source of vapour in the forest

There are naturally occurring stable isotopes of the elements found in water: hydrogen and oxygen. These are deuterium (D), the heavier stable isotope of hydrogen, and oxygen-17 and – 18 (^{17}O and ^{18}O), the heavier stable isotopes of the oxygen–16. For oxygen, only ^{18}O and ^{16}O will be measured and discussed in this paper. Abundance of these isotopes is expressed as deviation from a standard in parts per thousands (‰), as expressed by the following equation:

$$\delta\ (‰) = [(R_s/R_{st}) - 1] \cdot 1000, \qquad (1)$$

where R_s and R_{st} are the molar ratio between the heavier and lighter isotope of the sample and standard, respectively. The Vienna-Standard Mean Ocean Water (V-SMOW) is used as the international standard to refer to isotope measurements reported here.

Water molecules containing any of the stable isotope having a heavier mass will have a lower vapour pressure. Thus, processes such as evaporation and condensation will lead to differences in isotopic composition between the different phases of water. The process that causes differences in isotopic composition between different water phases is called isotopic fractionation. For example, isotopic fractionation between vapour and liquid water at equilibrium with each other is mathematically expressed as:

$$R_l/R_v = \alpha^*, \qquad (2)$$

where R_l and R_v are the isotopic ratio of the liquid and vapour phases, respectively.

Fractionation during evaporation and condensation of water can be caused by two major processes. First, by the isotopic equilibrium between the liquid and vapour phase. In a closed system where saturation is reached and both phases are at the same temperature, this is the only process causing isotopic differences between the vapour and liquid phase, and the vapour phase will be depleted in heavy isotopes with respect to the liquid phase by the factor α^*. Second, in opened systems, where part of water vapour is removed from the equilibrium situation, a differential diffusion of heavy to light isotopes through air increases the differences in isotopic ratios between phases. The isotopic fractionation of this kinetic effect is expressed here as α_k, a constant which describes the relative ability of different molecules to diffuse through air and the boundary layer (Flanagan *et al.* 1991). Thus, these two quantifiable processes together will make the vapour generated by evaporation depleted in heavy isotopes relative to its liquid source. In large forest patches lacking lakes and rivers during dry season, the soil surface will provide the major flux of evaporated vapor. Another major source of vapour to forest ambient would be the vapour generated by plant transpiration. The source of water for plant transpiration is essentially the soil water. If vapour from plant transpiration is isotopically distinct from vapour generated by evaporation, the proportion of these two major vapour sources to the ambient forest vapour could be established.

Soil water uptake and transport to the leaves inside the plants was first shown to be isotopically non-fractionating by Wershaw *et al.* (1970). In other words, the isotopic composition of water arriving at the leaf is identical to that of the soil. Water in the leaf however, will become isotopically enriched because of equilibrium and kinetic isotopic fractionation effects (Allison *et al.* 1985; Yakir *et al.* 1989, 1990; Flanagan & Ehleringer 1991; Flanagan *et al.* 1991). As discrepancies arose between experimental and modelled isotopic values it has been hypothesized that water undergoing evaporation in the leaf is compartmentalized (Yakir 1992a;b). However, it has been demonstrated that at steady-state transpiration, when the rate of water uptake is the same as that of the transpiring flux, the vapour leaving the leaf from the compartment undergoing evaporation has the same isotopic composition as that of water entering the leaf (Flanagan *et al.* 1991; Yakir 1992a; Fig. 1). Even for different conditions

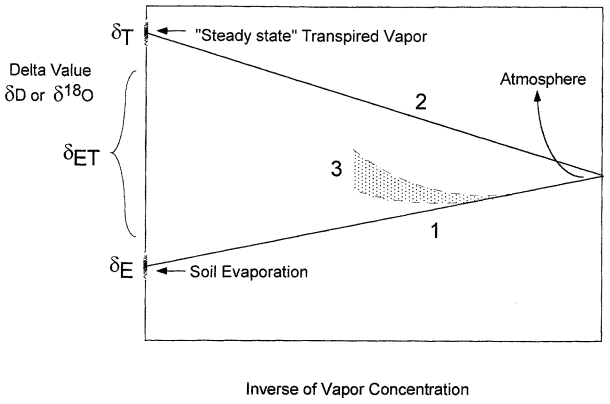

Fig. 1 Hypothetical graph showing the relationship between ambient isotopic composition of vapour in the forest vs. inverse concentration and the isotopic composition of vapour from evaporation and transpiration. Three scenarios as discussed in the text are shown: (1) Soil evaporation as the major source of vapor; (2) plant transpiration as the major source, and (3) both evaporation and transpiration as the major sources of vapour to the forest.

and pre-treatments in chamber experiments the isotopic value of transpired vapour was the same as the stem water in a couple of hours (Flanagan *et al.* 1991; tables I and II). Therefore, it is likely that the major sources of water vapour (evaporation and transpiration) to the forest ambient air would have different isotopic composition. We expect that vapour from transpiration is isotopically enriched relative to vapour from soil evaporation.

Isotopic identification of potential sources of vapour in the forest in Amazon

Equation (5) of Flanagan *et al.* (1991) can be used to describe the water evaporation process through a boundary layer if the isotopic composition of liquid water at the evaporating surface is known, by:

$$R_e \top (1/\alpha_k)\ \{[(R_s/\alpha^*)\ e_s - R_a\ e_a]/(e_s - e_a)\}, \qquad (3)$$

where R_e is the molar ratio of heavy to light isotopes of the vapour generated at the evaporating surface, R_s is the molar ratio from the liquid water at the surface, and R_a is the atmospheric vapour molar ratio above the surface. α_k and α^* are the kinetic isotope fractionation factor across the boundary layer and the equilibrium fractionation factor between vapour and liquid water, respectively. For the kinetic isotope fractionation factor (α_k) we used the value of 1.017 and 1.0189 for hydrogen and oxygen as calculated in Kays & Crawford (1980) and Merlivat (1978). For the equilibrium fractionation factor we used Majoube's equation for deriving the value α^* as a function of temperature (Majoube 1971); e_s and e_a are the partial vapour pressure at the immediate vicinity of the evaporating surface and of the atmosphere, respectively. If the temperature at the surface and atmosphere are the same, then the above equation can be simplified to:

$$R_e = (1/\alpha_k)\ [(R_s/\alpha^*) - R_a\ h]/(1 - h), \qquad (4)$$

where h is the air relative humidity. Thus, the vapour generated by evaporation from soil surface can be calculated using isotopic values for the soil surface water and eqn (4).

Isotope values of vapour from plant transpiration can be derived by measuring the isotope ratio of stem water. This is possible because previous observations (Flanagan *et al.* 1991; Yakir 1992a) indicate that, although the isotopic composition of leaf water does not agree with the modelled evaporative steady state value, the water vapour leaving the leaf at steady state transpiration has the same isotopic composition of the stem water (see fig. 1 in both articles).

Another natural source of water vapour to the forest air is the external atmospheric vapour. Atmospheric vapour is mainly generated by Atlantic Ocean evaporation and moves into the Amazon basin toward the West with the equatorial Atlantic winds (Salati & Vose 1984; Salati & Nobre 1991). We were not able to measure the isotope composition of this pool. Previous measurements of atmospheric vapour collected during November and December in 1989 at coastal sites (Alcântara, Belém and Clevelândia do Norte) showed δ^{18}O and δD average values in the vapour of – 10 and – 67‰, respectively, indicating that the vapour is close to the equilibrium with the ocean water.

Mixing model for vapour in ambient forest air

There are three major vapour sources in the forest: atmospheric vapour from the troposphere, evaporation from soil surface and other wet surfaces, and plant transpiration. Determining the relative proportion of vapour generated by plant transpiration and soil evaporation in forest ambient air is the goal of this study. At a qualitative level, if a significant amount of water vapour comes from plant transpiration, one could expect to find a daily variation in the isotope ratios and absolute concentration of forest ambient vapour.

To develop a mixing equation we will consider that ambient vapour in the forest is a mixture of two major components: (i) forest derived vapour – such as soil evaporation and/or plant transpiration – and (ii) atmospheric vapour. The mixture of these two vapour sources can be expressed by the equation below similar to the one used to interpret the carbon dioxide concentration in other studies (Keeling 1961; Sternberg 1989).

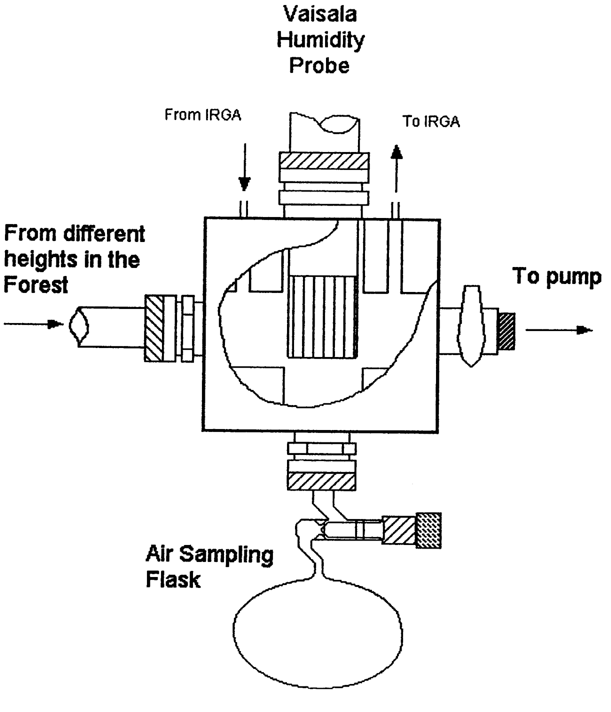

Fig. 2 Aluminium manifold used to collect ambient forest air vapour from different heights.

$$\delta_F = [AH_{atm}(\delta_{atm} - \delta_{ET})] * (1/AH_F) + \delta_{ET}. \quad (5)$$

This equation relates the isotope composition of the ambient forest vapour (δ_F) to the independent variable which is the inverse of the air absolute humidity inside the forest, ($1/AH_F$), multiplied by the term in the brackets composed of the atmospheric absolute vapour concentration (AH_{atm}), and the isotopic ratios of two sources of vapour in the forest: atmospheric (δ_{atm}) and forest derived vapour (δ_{ET}), and added to isotope ratio for the forest derived vapour (δ_{ET}). There are three possible scenarios with respect to change in isotopic composition and concentration of ambient forest vapour throughout the day and location in the forest. These scenarios will plot differently in Fig. 1. First, if soil evaporation is the principal source of vapour to the forest, and its contribution changes diurnal or spatially, a plot of variation in isotopic composition of forest vapour (δ_F) on the inverse of the vapour concentration ($1/AH_F$) will fit well to line 1 in the Fig. 1. Second, if plant transpiration is the major source of vapour to the forest, a plot of the variation of δ_F vs. ($1/AH_F$) will fit line 2 in the Fig. 1. Finally, on the third scenario, if both evaporation and transpiration contribute significant amount of vapour to the forest and the relative contribution by these two processes varies diurnal and spatially, the relationship between δ_F and ($1/AH_F$) would differ between day and night, and between different heights leading to a low correlation. At night, the data would fit closer to the scenario one indicating a mixture of mostly evaporated and atmospheric vapour while during the day the data would spread in the shaded area 3 in the Fig. 1. The samples taken closer to the soil would plot on the bottom of the shaded area whereas the closest to the canopy would be at the top of that area. The latter scenario is probably the situation expected in the rainy season. This model is applicable only to situations where there is no condensation and there are only transpiration and evaporation of a homogeneous body of water as the major sources of vapour within the forest canopy.

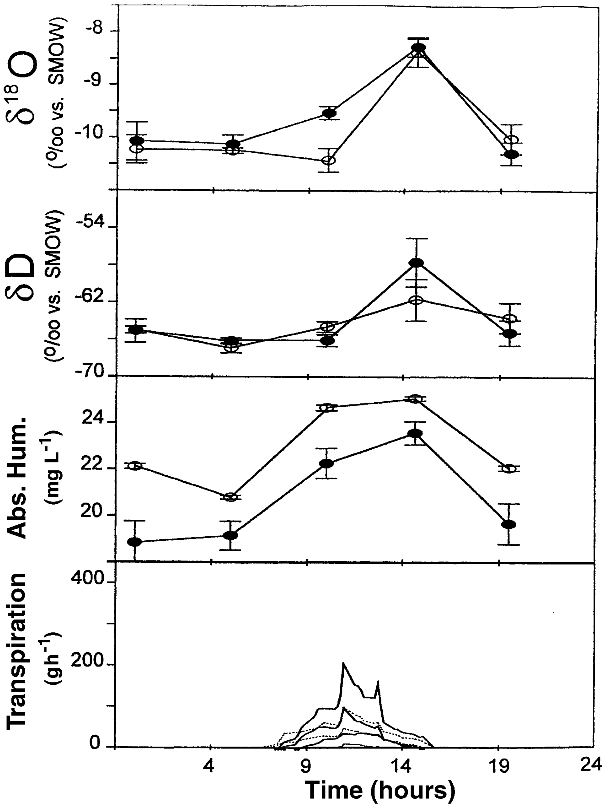

Fig. 3 Daily variation of $\delta^{18}O$ and δD (± SEM) in air water vapour at different levels above the ground (open symbols: 0 and 0.5 m average; full symbols: 18 and 45 m average), absolute humidity, and transpiration for six plants in the understorey of the forest at Ducke Reserve, Manaus.

The data obtained in this study will be used to determine which of the previous mentioned scenarios best illustrate the generation of vapour in the forest. This is done by measuring (i) the isotopic composition of water in the soil surface, to derive the isotopic composition of the vapour from evaporation; (ii) stem water, to derive the isotopic composition of the transpired water; and (iii) forest vapour concentration and isotopic composition to determine whether there is a relationship between δ_F and ($1/AH_F$) closely fitting: (i) line 1, indicative of soil evaporation as a major source of vapour, (ii) line 2,

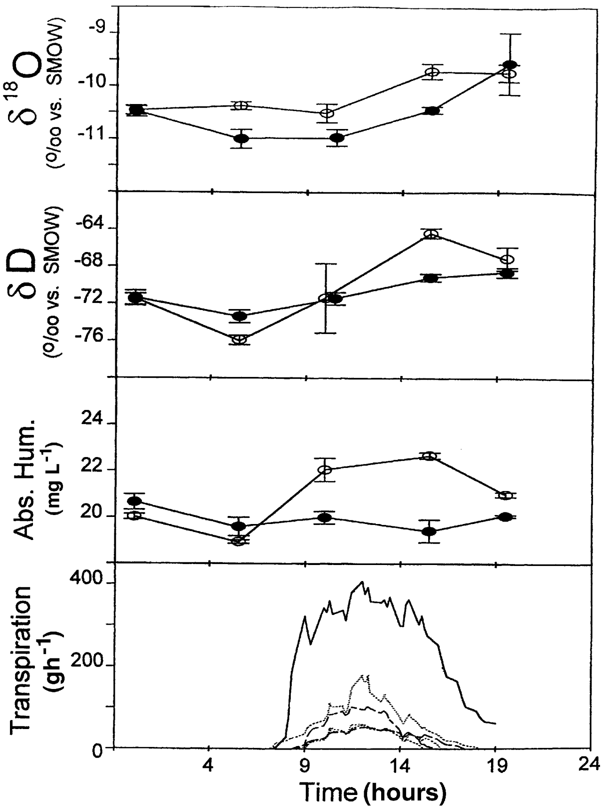

Fig. 4 Daily variation of $\delta^{18}O$ and δD (± SEM) in the air water vapour at different levels above the ground (open symbols: 0 and 0.5 m average; full symbols: 16 m and above canopy average), absolute humidity, and transpiration for six plants in the understorey of the forest at Vitoria farm, Paragominas.

indicative of plant transpiration as major contributor to the forest vapor, or (iii) a low correlation and scatter indicating of both evaporation and transpiration as important contributors to the forest ambient vapor.

Material and methods

Sites

Two sites were selected to reflect the climate gradient encountered from eastern to western latitudes; in the eastern latitudes of the Amazon basin, dryer conditions and seasonality is more prevalent than in western Amazon. Different forest structures are associated with these climatic differences. At the eastern limit, we used a site established by the Woods Hole Research Centre, in cooperation with the Universidade Federal do Pará (UFPA) and the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) called Vitoria farm. This 250 ha site is located in Paragominas (state of Pará, 2°59′S, 47°31′W), where the major economic activities are ranching and logging. It is characterized by drier conditions during the 6-month summer season with a marked drought from June/July to November/December (< 250 mm), compared to the annual average rainfall of 1750 mm (Nepstad *et al.* 1994). An important feature of this site is the ability of the trees to continue photosynthesis and transpiration during the long dry summer. The forest structure in this site is best described as an open tropical rain forest (LAI = 5–5.5 and 300 t ha^{-1}), with an average height of 30 m in the undisturbed lots. Additionally we also gathered samples in an adjacent pasture to compare with the native forest.

The second site was chosen in collaboration with the Instituto Nacional de Pesquisa da Amazônia (INPA), in Manaus (state of Amazonas, 3°8′S, 60°1′W). This is an undisturbed site at the Ducke Reserve (10,000 ha), about 30 km north of Manaus reflecting more humid conditions of western Amazon. Unlike Vitoria farm, this site has an annual average rainfall close to 2000 mm and little seasonality. The forest in this site is characterized by a closed canopy forest (LAI = 6.1 and 730 t ha^{-1}) with a permanently wet and well-developed understorey, and a 35 m-tall canopy. The experiment was set up next to a 45 m-high tower for meteorological data collection previously used for other studies (Shuttleworth *et al.* 1984), where a vertical profile of the forest could be sampled from ground up to 10 m above to canopy. Sampling at the Ducke Reserve site was carried out on 25 October and at Vitoria farm site on 4 November at the end of the 1994 summer season, when the rain is less abundant. The pasture sampling was done on 5 November 1994.

Collection of samples

Air Water Vapour. The apparatus used to collect air samples at various heights in the forest is shown in Fig. 2. It consists of a metallic manifold with: an outlet where polypropylene hoses leading to different heights in the forest were attached; an outlet with a stopcock where a 12 V pneumatic pump pulls the air through a Vaisala humidity probe inserted through another outlet; two ports for CO_2 analysis; and an outlet to attach the gas collection flasks. All attachments to the manifold were of Cajon type and airtight.

Collection at any particular height consisted of pumping air through the manifold for several seconds until the humidity probe read a constant relative humidity and temperature after which the stopcock leading to the suction pump was closed. The stopcock to the gas collection flask was then opened and the air allowed to equilibrate for 10 s whereupon the relative humidity and temperature were read and stopcock of the collection flask was closed. Samples in the collection flasks were taken to University of Miami for isotopic analysis. This

Table 1 δ^{18}O and δD (± SD) for soil surface water, estimated values of δ^{18}O and δD (± SD) for vapour from soil evaporation and averages δ^{18}O and δD (± SD) for plant stem water in each site. The values of vapour generated by evaporation were calculated with eqn (4) using the soil surface water isotopic values as the liquid source. The plant averages were done over three replicates for each of six species listed in the methods in the forest. The average for *P. maximum* was used in the pasture (n = 5).

Site	Soil surface	Vapour generated by Soil evaporation δ^{18}O/δD (± SD)	Vapour generated by* Steady state transpiration δ^{18}O/δD (± SD)
Ducke Forest	–1.9 ± 0.1/–14.0 ± 0.4	–36 ± 1/–227 ± 3	–3.1 ± 0.3/–20 ± 3
Vitoria Forest	–0.3 ± 0.1/–3.2 ± 0.7	–22.8 ± 0.7/–126 ± 5	–3.2 ± 0.5/–27 ± 2
Vitoria Pasture	1.0 ± 1.0/–3.5 ± 1.4	–20 ± 7/–140 ± 46	–3.4 ± 1.0/–21 ± 6

*The same value of plant stem water under steady-state transpiration.

type of procedure was used to collect samples at a few mm above the forest floor, 0.5 and 16 (Vitoria farm) and 18 (Ducke Reserve) m above the ground. Collection of samples above the canopy was done manually on top of a 45 m-tower at Ducke Reserve and on a 14 m-wooden tower in the pasture, and by a tethered balloon in the pasture and forest at the Vitoria farm. The heights for the tethered balloon samples were variable according to the wind speed and site: from 10 to 35 m above ground in the pasture and, from 20 to 50 m in the forest. The latter method involved a styrofoam box with a gas collection flask connected to a solenoid valve activated by a timer. This styrofoam box was attached to a helium-filled balloon which was raised to the desired altitude. The timer was programmed to open 5 min after activation, remaining open for one minute and closing after that. For balloon samples HOBO micro-dataloggers (Onset Computers Inc.) recorded the air temperature and relative humidity in the styrofoam box during the air sampling. A portable humidity/temperature Vaisala probe was used on the top of the tower, in the Ducke Reserve. In addition, a simple anemometer attached to a data logger was also used to record the wind speed variation at both sites about 10 m above the canopy. Sampling was scheduled at approximately midnight, 05:00, 10:00, 14:00 and 19:00 hours. In the pasture we only collected samples at 14:00 and 19:00 hours.

Plant tissue and soil. Wood stems from six species – three individuals per species – were cut to extract their water for isotopic analysis. The following species were sampled in the Ducke Reserve: Cipó de Fogo (*Davilla* sp.), Cipó Titica (*Heteropsis* aff. *spruceana* Schott), Castanha Jacaré (*Corithophora rimosa* Rodr.), Cardeiro (*Scleronema micrantum* Ducke), Breu (*Protium* sp.), and Acariquara Roxa (*Minquartia guianensis* Aubl.). At the Vitoria farm, the following species were taken from the primary forest: Escada de Jaboti (*Bauhinia guianensis*), Vine (*Memora* sp.), Taxi Preto (*Tachigalia paniculata* Aubl.), Tacacazeiro (*Sterculia pruriens* (Aubl.) K.Schum), Jatereu (*Lecythis idatimon* Aubl.), and Quariquarana (*Rinorea guianensis* Aubl.); and five replicates of main pasture species (*Panicum maximum* Jacq. and *Solanun crinitum* Lamb.) were also taken. Three replicates of surface soil samples were collected at both sites. Plant and soil samples were stored in screw-cap culture tubes and further sealed with Parafilm to prevent water loss during air transport. These samples were taken to the University of Miami Biology Department where water was extracted by vacuum distillation.

Laboratory analysis

We determined the δ^{18}O values of the water vapour by a modification of the micro-equilibration method developed by Kishima & Sakai (1980). Water vapour from flasks was quantitatively transferred to small break-seal glass vessels together with a known amount (30 ⊤ 60 μmols) of carbon dioxide (CO_2) with a known isotopic composition. The vessel volumes average 0.4 cm^3 so that the average internal pressure is 1.5–2 ATM. After sealing of the vessels, equilibrium was established in three days at a constant temperature (25 °C). Equilibration vessels were broken under vacuum, where CO_2 was cryogenically separated from the water and sealed in ampoules for mass spectrometry. The water from the vapour sample was then reduced to gaseous hydrogen over hot uranium in the same line, and the gas sealed for mass spectrometry (Bigeleisen *et al.* 1952).

Plant tissue and soil water samples were analysed by the same indirect process of CO_2 equilibration using the method developed by Epstein & Mayeda (1953). After two days in equilibrium with 1 mL of sample, the CO_2 is separated and analysed in the mass spectrometer. Hydrogen isotopic analysis of plant and soil water samples were done as in Bigeleisen *et al.* (1952). All isotope ratios were determined in a Prism mass spectrometer (Phison Ind) with a precision of ± 0.1‰ for oxygen and ± 1‰ for hydrogen isotope ratios.

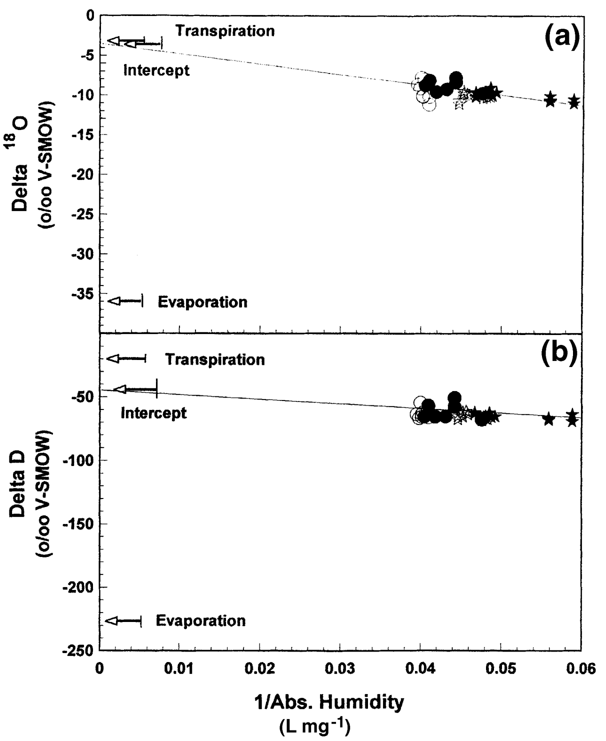

Fig. 5 Relationship between $\delta^{18}O$ (a) and δD (b) of ambient vapour at different levels above the ground and the inverse of the absolute humidity at Ducke Reserve, Manaus. The slope and intercept of the regression equations are shown in Table 2; open symbols represent samples collected at 0 and 0.5 m above the ground; full symbols represent samples collected at 18 and 45 m above the ground. Samples collected during the day are represented by circles and those collected at night are represented by stars. Correlations for upper elevation (full symbols) are significant and the theoretical regression lines are shown. Correlations for lower elevation (open symbols) are not significant. The arrow's vertical bars represent the standard error of the means of the isotopic values.

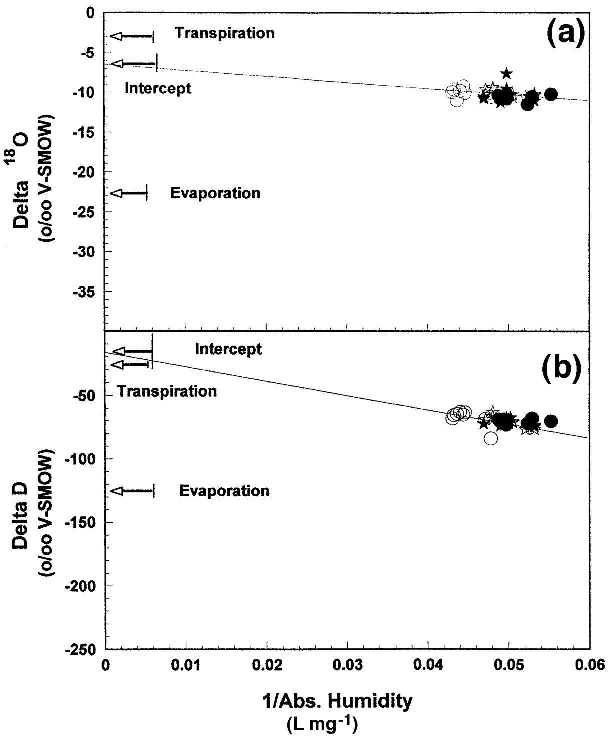

Fig. 6 Relationship between $\delta^{18}O$ (a) and δD (b) of ambient vapour at different levels above the ground and the inverse of the absolute humidity at Vitoria farm, Paragominas. The slope and intercept of the regression equations are shown in Table 2; open symbols represent samples collected at 0 and 0.5 m above the ground; full symbols represent samples collected at 16 m above the ground and above canopy using the tethered balloon. Samples collected during the day are represented by circles and those collected at night are represented by stars. Correlations for lower elevation (open symbols) are significant and the theoretical regression lines are shown. Correlations for upper elevation (full symbols) are not significant. The arrow's vertical bars represent the standard error of the means of the isotopic values.

Plant sap flow

Sap flow for some of the subcanopy plants was measured with the Dynamax Flow32 (Baker & Nieber 1989). Transpiration rates were recorded during the entire sampling day for six plants. The species selected for transpiration measurements at the Ducke Reserve site were: *Protium apiculatum* Swartz, *Heteropsis* aff. *spruceana* Schott, an unidentified species of the Anonaceae family and also one of the Violaceae, *Sterculia pruriens* (Aubl.) K. Schum., and *Siparuna* sp. At the Vitoria farm site the six plants were: two individuals of *Tachigalia paniculata* Aubl., *Memora* sp., and two other not yet identified species (known by the common name of Capoteiro and Arataciurana). Sap flow was measured to determine whether change in isotopic composition of vapour was correlated with the period of transpiration.

Results

The average (± SEM) $\delta^{18}O$ and δD values of forest vapour close to the ground (1 and 50 cm above ground), referred to hereafter as lower level, and at canopy level (16 m and the balloon height at Vitoria farm; 18 and 45 m at Ducke Reserve), hereafter referred to as upper level, their absolute humidity, and transpiration rate throughout the sampling period for Ducke Reserve and Vitoria farm are shown in Fig. 3 and Fig. 4, respectively. There was an increase in the isotopic composition of vapour concomitant with an increase in absolute humidity and transpiration for the samples taken at the Ducke Reserve at both lower and upper levels of the forest. A concomitant increase in vapour isotopic composition and absolute humidity with transpiration was observed only at the lower level of the forest at the Vitoria farm site. Isotopic

Table 2 Location, slope and intercept of the regression lines between δD or δ^{18}O values of ambient water vapour and the inverse of its concentration at upper and lower elevations at each site, significance of correlation, calculated isotopic composition of vapour derived from soil evaporation, and isotopic composition of vapour derived from steady state (ss) transpiration.

Location/Level/ Isotope	Slope ± SEM	Intercept ± SEM	*P*	Vapour from soil evaporation ± SD	Vapour from ss transpiration ± SD
Ducke Reserve					
Upper					
D	–395 ± 155	–44.6 ± 7.7	< 0.05	–227 ± 3	–20 ± 3
^{18}O	–124 ± 21	–3.6 ± 1.0	< 0.01	–36 ± 1	–3.1 ± 0.3
Lower					
D	–395 ± 210	–47.1 ± 9.2	> 0.10	–227 ± 3	–20 ± 3
^{18}O	–124 ± 60	–4.4 ± 2.3	> 0.10	–36 ± 1	–3.1 ± 0.3
Vitoria farm					
Forest					
Upper					
D	–73 ± 244	–67.1 ± 12.2	> 0.10	–126 ± 5	–27 ± 2
^{18}O	–6 ± 88	–10.2 ± 4.4	> 0.10	–22.8 ± 0.7	–3.2 ± 0.5
Lower					
D	–1110 ± 305	–16.8 ± 14.8	< 0.01	–126 ± 5	–27 ± 2
^{18}O	–72 ± 26	–6.6 ± 1.3	< 0.05	–22.8 ± 0.7	–3.2 ± 0.5
Pasture					
Upper					
D	2628 ± 555	–207 ± 29	< 0.01	–140 ± 46	–21 ± 6
^{18}O	40 ± 36	–12 ± 2	> 0.25	–20 ± 7	–3.4 ± 1.0
Lower					
D	–781 ± 84	–28 ± 4	< 0.01	–140 ± 46	–21 ± 6
^{18}O	12 ± 33	–10 ± 2	> 0.25	–20 ± 7	–3.4 ± 1.0

composition and absolute humidity stayed relatively constant throughout the day at the upper levels of the forest in that site. All transpiration measurements were taken on saplings below the canopy level and thus we probably underestimated the amount of transpiration taking place in the forest. At Vitoria farm one of the sensors was in a vine which showed relatively high transpiration values, probably because much of the vine evaporative surface was exposed to direct solar radiation at the canopy level.

The isotope values for water at the soil surface, vapour generated by evaporation of soil surface water as calculated in eqn (4), and plant stem water at the Ducke Reserve site and at both forest and pasture at the Vitoria farm site are shown in Table 1. Note that average δ^{18}O values of plant water collected at Ducke Reserve and at Vitoria farm do not differ, but the isotopic compositions of their soil surfaces do, suggesting that plant water uptake is deeper than the surface level. The average δ^{18}O and δD values for soil surface water are lower at Ducke Reserve than at both locations at the Vitoria farm site. At the Vitoria farm site soil surface moisture was more enriched in heavy isotopes in the pasture than in the forest. This pattern could be consistent with the longer drought season in the eastern Amazon. The isotopic values of the surface soil water are progressively enriched as the soil moisture decreases by water loss through evaporation, making R_s higher in eqn (4). Thus vapour generated by evaporation in the pastures should be isotopically enriched relative to that generated in the forest. δ*D* values of stem water from forest plants at Vitoria farm were significantly lower from pasture plants at Vitoria farm and from forest plants at Ducke Reserve.

Figures 5, 6, and 7 show the relationship between δ*D* and δ^{18}O values of ambient vapour and the inverse of its absolute humidity at Ducke Reserve, Vitoria farm forest, and Vitoria farm pasture, respectively. Only significant regression lines are shown in figures.

Table 2 shows the mathematical treatment for data shown on Figs 5, 6, and 7 including the slope and intercept of the regression equations between δD and δ^{18}O values of vapour and the inverse of absolute humidity at all sites studied here. Table 2 also shows the significance of the regression equations, and calculated δD and δ^{18}O values of vapour generated from evaporation and transpiration.

Discussion

Table 1 shows the isotopic values for the two likely major sources for the forest vapour during the dry season. No direct evaporation was expected from any wet surface in

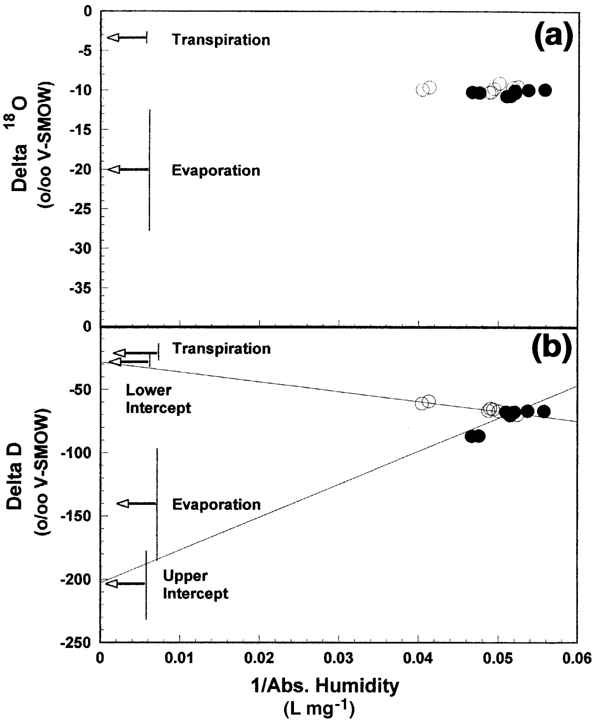

Fig. 7 Relationship between $\delta^{18}O$ (a) and δD (b) at different levels above the ground and the inverse of the air absolute humidity in the pasture at Vitoria farm, Paragominas. The slope and intercept of the regression equations are shown in Table 2; open symbols represent samples collected at 0 and 0.5 m above the ground; full symbols represent samples collected above the canopy using the tethered balloon and the 14 m high tower. Correlations for δD values are significant and the theoretical regression lines are shown. The arrow's vertical bars represent the standard error of the means of the isotopic values.

the canopy at that time. The closest open water body that could generate water vapour by evaporation is a creek which is at least 1 km away. Thus, the two sources for the water vapour would be direct soil evaporation and plant transpiration. The isotopic values of vapour generated by soil evaporation were calculated using the isotopic values of soil surface water (eqn 4). The isotopic values of plant stem water, which were taken after two hours of steady-state transpiration, were used as isotopic values of vapour generated via plant transpiration.

Vapour generated by plant transpiration is isotopically enriched relative to that generated by soil evaporation; the data in Table 1 corroborate this idea. The diurnal isotopic enrichment of water vapour in the forest vapour concomitant with the increase in transpiration (Figs 3 and 4) is evidence that transpiration contributes a significant amount of vapour to the forest ambient air. There was, however, a slight lag period between isotopic enrichment and transpiration in both sites. Peak isotopic values were encountered when transpiration began to decrease. Two explanations are possible regarding this lag period. The first relates to the fact that transpiration rates were measured at an instantaneous basis, whereas isotopic measurements of forest ambient vapour will, to some extent, record the accumulation of vapour generated by plant transpiration throughout the day. The second explanation is that isotopic composition of transpired vapour may take some time to reach steady-state values (Flanagan *et al.* 1991), and before this time the vapour added to the forest ambient will be isotopically depleted relative to the steady state, being isotopically closer to the soil evaporation.

The relationship between isotopic values of vapour samples (δ_F) vs. the inverse of the vapour concentration ($1/AH_F$), and isotopic composition of transpired (δ_T) and evaporated vapour (δ_E) for Ducke Reserve, and forest and pasture at the Vitoria farm site are shown in Figs 5, 6, and 7, respectively. The regression line parameters for the relationship between δ_F vs. $1/AH_F$, according to the previously discussed mixing model, are shown on Table 2 for both sites. Significant correlation between isotopic values and inverse of vapour concentration was only observed for upper elevation samples in the Ducke Reserve and lower elevation samples from the Vitoria farm forests. With the exception of the pasture samples, it can be seen that these regressions extrapolate to intercepts that are very close to that expected if transpiration was the sole source of vapour input to the forest ambient air. Even the samples that did not give a significant regression are very close to the regression lines (Figs 5 and 6). Thus, generation of vapour in forests most closely fits the second scenario: transpiration is the major source of vapour for the forest ambient vapour. Lack of a significant correlation between δ_F and $1/AH_F$ at the lower level for samples from the Ducke Reserve was probably caused by some evaporation from moist surfaces found throughout the year at this site (compare absolute humidity in Fig. 3 and 4). At the Vitoria farm site, where the forest floor was relatively dry, a significant correlation between isotopic composition and inverse of vapour concentration was observed. At the upper level of the Vitoria farm site, however, no correlation was observed. This lack of correlation may be due to the high winds present at this site (on average 2.2 vs. 1.2 m s^{-1} at Ducke Reserve, with peaks of 3.3 and 1.6 m s^{-1}, respectively), causing a low range in isotopic and vapour concentration values. The relatively strong turbulence in this open forest rapidly mixed forest-generated vapour with the tropospheric pool and prevented any build up of vapour in the forest canopy.

No significant correlation was observed between $\delta^{18}O$ values and inverse vapour concentration for pasture samples, but significant regressions were observed for both upper and lower elevations between δD values and inverse vapour concentration. Although the number of samples taken at the pasture was low, it indicates that transpiration contributes little to the ambient vapour at upper elevation in the pasture. During the dry season the conditions at pasture were so dry that two scenarios were found according to different heights: at lower level plant transpiration seems to determine the isotopic variation of the vapour while at upper level this effect has vanished. The third scenario would indeed be the situation during the rainy season in the pasture as the data should fit the shaded area 3. Nepstad *et al.* (1994) have shown that pasture leaf area promptly recovers from the dry season as the rain returns, quickly transporting water from the shallower soil layer to the atmosphere. Under the forest canopy, however, it is likely that transpiration will increase more than evaporation during the rainy season, moving up the data in area 3, and eventually becaming closer to scenario 2.

Our observations on diel isotopic variation of ambient forest vapour are similar to Ribeiro *et al.* (1996) in that during the day, when transpiration was occurring the δD and $\delta^{18}O$ values of ambient vapour and absolute humidity increased. Ribeiro *et al.* (1996) found that δD and $\delta^{18}O$ of vapour, and absolute humidity decreased during the night and ascribed this decrease to condensation processes. Our results differ in that we did not find a decrease in δD and $\delta^{18}O$ values and absolute humidity of ambient vapour throughout the night. A possible reason for the differences in results is that our sampling period was at the end of the dry season, while for Ribeiro *et al.* (1996), the sampling was done during the wet season.

The intercepts of the regression lines at Ducke Reserve and Vitoria farm show a high transpiration contribution for the forest vapour, suggesting that this source plays an important role in the water cycle of both regions throughout the dry season. Furthermore, the measurements in the pasture, where much of the compact plant cover is removed, show that transpiration plays a minor role in contributing to the ambient vapour at upper levels, although more samples will be necessary to confirm this observation. These results should serve to emphasize the importance of plant cover in the water cycling at these sites, as predicted by Salati *et al.* (1979) and Victoria *et al.* (1991) based on isotopic behaviour of water from precipitation throughout the basin. On the other hand, Gat & Matsui (1991) predicted the existence of an evaporative water source contributing up to 20–40% of the evapotranspirative flux. There is a need to find such a source, but this study could not find ambient forest vapour derived by evaporation of pools such as soil surface or other wet surface, and thus this pool is not likely to be found in the forest. Early attempts to find this evaporative pool by using stable isotope measurements of lakes, rivers, etc. were also unsuccessful (Martinelli *et al.* 1996). Previous models which attempt to predict the effects of deforestation did not distinguish between evaporation and transpiration and thus used a single equation to predict evapotranspiration (Pereira 1973). Our results indicate that these models are not applicable. Transpiration is the major source of vapour leaving the forest and thus, as several models predict (Dickinson & Henderson-Sellers 1988; Shukla *et al.* 1990; Nobre *et al.* 1991), deforestation will lead to reduced precipitation throughout the basin.

Conclusions

Isotopic analysis of water vapour and its concentration allowed this first comparison between vapour in the ambient forest air and isotopic ratios of potential vapour sources. The mixing model developed here was utilized to qualitatively access the proportion of vapour generated by transpiration and that generated by evaporation. Our findings indicate that ambient forest vapour is mostly, if not completely, generated by plant transpiration. This high proportion of vapour generated by transpiration occurs both in an aseasonal wet forest, represented by the Ducke Reserve site, and in a seasonal dry forest, represented by the Vitoria farm during the dry season. The implication of these findings is important because, presumably much of the water recycling in the Amazon occurs by the input of forest vapour to the troposphere. At Vitoria pasture it was observed that transpiration may not be a major source of input above the canopy. Although more sampling will be necessary for a better understanding of the processes responsible for the formation of forest and pasture vapour, our preliminary findings are consistent with the biological water pump suggested by several previous authors (Araguás-Araguás *et al.* 1995). Thus, it indicates that deforestation could cause a dryness of the system by removing this biological water pump. This preliminary collection was made at the end of the dry season to evaluate extreme conditions. A more extensive sampling is underway to study these processes from the end of the rainy season throughout the following dry season.

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