Computing the Net Primary Productivity for a Savanna-Dominated Ecosystem Using Stable Isotopes: A Case Study of the Volta River Basin

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Abstract

The hydrologic systems and the terrestrial ecosystem of the Volta river basin in West Africa, play important role in the carbon cycle. This is so because of the coupling of water vapour release and CO_2 uptake during photosynthesis, expressed as water use efficiency or transpiration ratio. Hydrologic and land-cover data, together with stable isotope ratio measurements of $\delta^{18}O$ and δD, and data from the global network of isotopes in precipitation (GNIP) are used to determine the net primary productivity (NPP) of the savanna-dominated ecosystem. The $\delta^{18}O$ and δD values in the Volta rivers range from -4.72 to 2.37 mm^{-1} and from -35.28 to 9.30 mm^{-1} SMOW, respectively. The results indicate that the vegetation is supported by 380 km^3 of rainfall, out of which 50% is returned to the atmosphere *via* plant transpiration. Associated with annual transpiration is the NPP of $0.170 \times 10^{15} gCyr^{-1}$ or 428 gCm^{-2} from the terrestrial ecosystem. Modelled estimates of heterotrophic soil respiration in this study slightly exceeded the NPP estimates, implying a small source of CO_2 to the atmosphere. This condition does not favour the postulated existence of a major sink of atmospheric CO_2 in the Volta basin.

Introduction

The terrestrial biosphere is a significant, but poorly constrained component of the global carbon cycle. Despite its importance, quantitative assessments of terrestrial net primary productivity and respiration are rare. Indeed, only a few studies on carbon fluxes are available world wide. Given the failure of current global carbon budgets to account for nearly one-quarter of the anthropogenic CO_2 emission (Prentice *et al.*, 2001), the distribution and magnitude of potential carbon sinks is an important question yet to be properly addressed. Indications are that if the present increase in productivity of CO_2 (between 1–2% per year) continues, a doubling of the CO_2 concentration will be reached towards the end of the century (Bolin *et al.*, 1986). Similarly, the evaluation of results from climate models lead to the conclusion that an increase in global temperature due to increases in CO_2 is likely to be in the range of 1.5-5.5 ^{o}C. Based on these models it is evident that future climate changes could have profound effect on global ecosystems.

The Volta river basin has an ecosystem dominated by savanna woodland, with more than 50% cropland concentrated in the north of the watershed. Cropland and open woody vegetation are found in northern Ghana and Burkina Faso; deciduous shrub-land with sparse trees in northern Ghana, eastern Burkina Faso and northern Togo; deciduous woodland in central and southern Ghana; and degraded lowland evergreen forest in south-eastern Ghana and Togo. The vegetation can be put into two distinct plant groups; C_3 and C_4 plants. In most ecosystems of the world, C_3 plants with broad leaves dominate.

However, under conditions which promote closure of stomata; including high temperature, drought, high salinity, and low humidity, C_4 plants tend to perform better than C_3 plants (Saga *et al.*, 1999). Due to these environmental factors, grass floras tend to dominate C_4 plants of West Africa, and represent the only significant source of C_4 vegetation in the Volta river watershed. In this ecosystem, transpiration, evaporation, precipitation and river discharge constitute the hydrologic cycle.

Through photosynthesis, plants sequester CO_2 from the atmosphere and, subsequently, recycle precipitation into the atmosphere through transpiration and evaporation. During this process, water and carbon cycling occur at specific water and carbon dioxide ratio, known as the water use efficiency (WUE). In this WUE, carbon fixation by a plant is accompanied by simultaneous transpiration of water that exceeds the quantity of carbon fixed, by a factor of $n \times 10^2$, where n is an integer. It describes the moles of H_2O that must be transpired to enable the uptake of one mole CO_2. Telmer & Veizer (2000) used the WUE method to estimate CO_2 sequestration and so the NPP for the Ottawa river watershed. Lee & Veizer (2003) tested this concept on the Mississippi watershed and obtained NPP fluxes that were in good agreement with empirical model estimates of heterotrophic soil respiration. The use of this method was further tested on the Saskatchewan, Great Lakes-St Lawrence and Ottawa river (Freitag *et al.*, 2006) and on the Danube river, the second largest river in Europe, (Pawelek *et al.*, 2002) with excellent results.

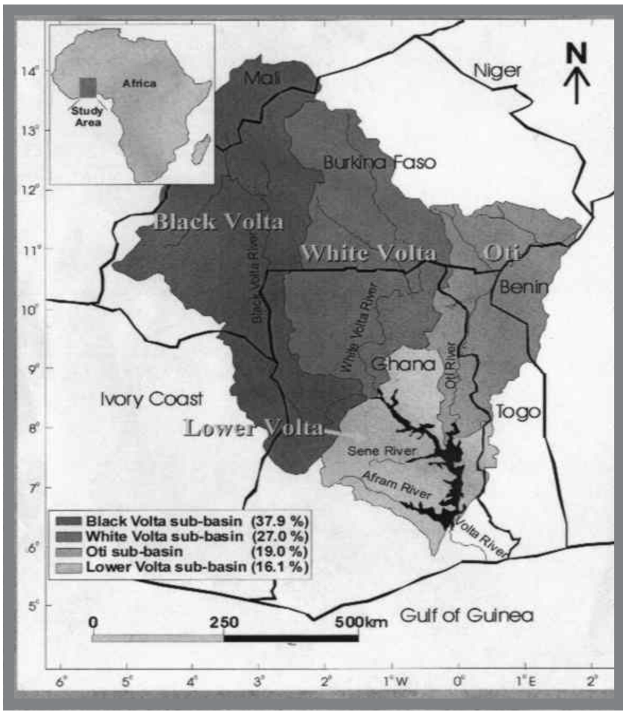
The above approach, which involves the use of stable isotopes, enables the determination of photosynthetic CO_2 fluxes for river basins at a fraction of the cost compared to the old laborious approach that include eddy covariance and lysimeter measurements and estimates. The work presented here seeks to quantify water fluxes in transpiration using stable isotopes ($\delta^{18}O$ and δD) and to determine whether the Volta river watershed is a source or sink of CO_2. Data from GNIP center for Africa indicates that this is the first African catchments study that applies stable isotope approach to determine transpiration and CO_2 intake.

Materials and methods

Study area

The Volta river basin located in West Africa has an area of approximately 406,000 km^2 (Freitag *et al.*, 2006) and stretches from the Gulf of Guinea to the southern boundary of the Sahel zone (longitude 0–3‘W). It lies between latitude 6°–14° N in the Sudan and Guinea-Congolian zones, and so most of the natural vegetation is woodland savanna, with tall grasses forming the ground cover beneath a discontinuous canopy of deciduous trees (Mistry, 2000; Breckle, 2002).

Politically, the watershed is shared by six countries (Fig.1). The greater portion of the watershed, however, lies in Burkina Faso (42.1%) and Ghana (40.2%), with the remaining area in Côte d’Ivoire, Mali, Togo and Benin. Collectively, the three sub-basins comprise about 84% of the total drainage area. They are Black Volta river sub-basins (156,900 km^2), White Volta river sub-basins (111,800 km^2), and Oti river sub-basins (78,800 km^2) (Fig. 1) (Dickson & Benneh, 1995; Andreini *et al.*, 2000; Hayford *et al.*, 2006). Each of these major tributaries, plus several small rivers located in the Lower



The Volta Basin (West-Africa)

– Black Volta sub-basin	156900 km^2
– White Volta sub-basin	111800 km^2
– Oti sub-basin	78800 km^2
– Lower Volta sub-basin without Lake Volta	58200 km^2
– Lake Volta	8500 km^2
Total	414200 km^2

Fig. 1. The Volta river watershed, showing the positions of the sub-basins and the political controls shared by six neighbouring countries: Ghana, Burkina Faso, Ivory Coast, Mali, Togo and Benin (modified from Dickson & Benneh, 1995; Freitag *et al.*, 2006).

Volta drainage area, discharge into the Volta lake with the three largest rivers accounting for about 80% of total discharge (Hayford *et al.*, 2006).

The climate of West Africa is characterized by high year-round temperature (> 25 °C) and strong rainfall seasonality (Scholes & Hall, 1996). Dry, continental airmasses from the Sahara are typical of the dry season (November–April) and rainfall is usually brought only by the African monsoon (May–October). Spatial variability in rainfall is observed within the watershed, with mean annual rainfall decreasing with increasing distance from the Gulf of Guinea. The mean annual rainfall for the entire watershed is 935 mm (Freitag *et al*., 2006).

Theoretical background

On the chart of the nuclides, hydrogen has two stable isotopes (^{1}H and D), while oxygen has three stable isotopes (^{16}O,^{17}O, and ^{18}O). These have nine isotopic configurations ($H_2{}^{16}O$, $H_2{}^{17}O$, $H_2{}^{18}O$, $HD^{16}O$, $HD^{17}O$, $HD^{18}O$, $D_2{}^{16}O$, $D_2{}^{17}O$, $D_2{}^{18}O$), whose atomic masses are approximately given by their mass numbers. The vapour pressure of the different isotopic molecules of water are inversely proportional to their masses. Therefore, $H_2{}^{16}O$ has a significantly higher vapour pressure than $D_2{}^{18}O$ (Hoefs, 1980). For this reason, water vapour formed by evaporation of liquid water, is enriched in ^{16}O and H while the remaining water is enriched in ^{18}O and D. (Faure, 1986). These stable isotopic composition of

TABLE 1

Values of stable isotope analysis ($\delta^{18}O$ and δD). Values represent mean of daily samples collected over the individual rivers. Samples which showed some contamination was ignored.

Rivers	*White Volta river*		*Black Volta river*		*Oti river*		*Sene river*		*Afram river*	
Date	$d^{18}O$	*dD*	$d^{18}O$	*dD*	$d^{18}O$	*dD*	$d^{18}O$	*dD*	$d^{18}O$	*dD*
19 May 03	1.20	2.18	0.90	4.42	2.13	7.00	–	–	–	–
31 May 03	1.24	4.09	0.88	5.84	2.21	9.30	-0.54	-12.6	-2.24	-10.03
14 Jun 03	-3.48	-20.29	-2.72	-13.36	-3.82	-28.57	-3.78	-25.12	-4.04	-27.24
28 Jun 03	-2.82	-16.41	-4.00	-25.64	-3.57	-22.53	-3.55	-19.34	-3.16	-17.58
12 Jul 03	-2.19	-17.00	-3.14	-20.76	-3.00	-19.31	-2.66	-9.93	-2.58	-12.74
26 Jul 03	–	–	-3.29	-22.26	–	–	-2.28	-13.22	-2.41	-12.76
09 Aug 03	-2.89	-13.39	-3.40	-23.23	-3.22	-18.12	-1.50	-10.28	-2.28	-10.3
23 Aug 03	-4.20	-27.43	-4.88	-35.28	-3.98	-21.96	-2.00	-8.44	-2.22	-9.59
06 Sep 03	-4.52	-30.81	-4.37	-28.51	-4.57	-30.32	-2.24	-9.68	-2.47	-12.58
20 Sep 03	-4.72	-30.73	-4.80	-33.23	–	–	-2.24	-14.22	-3.83	-22.39
04 Oct 03	-3.71	-25.86	-4.27	-30.50	-3.73	-23.31	-3.72	-21.44	-3.13	-17.08
18 Oct 03	-3.07	-17.21	-3.94	-25.21	-2.98	-18.69	-3.04	-10.94	-2.62	-12.98
01 Nov 03	-2.32	-17.30	-3.08	-17.94	-2.68	-17.26	-2.31	-11.93	-2.24	-11.81
15 Nov 03	-2.28	-17.99	-2.57	-17.20	-2.32	-17.94	-1.84	-6.21	-2.23	-10.7
29 Nov 03	-2.33	-17.09	-1.98	-10.30	-2.01	-21.61	-1.78	-8.9	-1.73	-8.02
13 Dec 03	-1.68	-13.13	-1.53	-13.54	-2.01	-21.82	-1.08	-7.9	-2.28	-15.24
27 Dec 03	-1.61	-10.24	-0.85	-11.51	-1.59	-19.33	0.06	-2.43	-2.26	-13.38
10 Jan 04	-1.20	-12.87	-0.60	-11.28	-1.37	-7.45	0.02	-5.16	-2.15	-14.32
24 Jan 04	-1.19	-12.73	-0.34	-10.46	–	–	0.00	-1.46	-2.12	-13.53
07 Feb 04	-1.34	-14.75	-0.18	-12.99	-0.76	-11.93	-1.77	1.59	-1.85	-10.32
21 Feb 04	-0.47	-14.70	0.24	-11.38	-0.19	-6.82	1.00	2.59	-1.65	-8.56
07 Mar 04	–	–	0.88	-8.78	0.39	-4.83	2.19	8.4	–	–
21 Mar 04	–	–	2.21	-1.23	1.30	-2.47	1.48	6.47	-1.05	-4.46
04 Apr 04	-0.41	-13.35	–	-0.86	0.75	-7.34	2.37	6.58	-0.9	-3.18
18 Apr 04	–	–	3.04	3.44	-1.56	–	-0.68	7.02	-1.19	-3.72
02 May 04	–	–	0.14	-3.53	-0.26	-6.64	-0.60	1.92	-2.00	-7.02
10 May 04	-0.63	-11.43	0.26	-4.14	-0.24	-7.12	-2.41	-5.86	-2.48	-9.59

hydrogen and oxygen are reported in terms of D/H and $^{18}O/^{16}O$ ratios and related to a standard called standard mean ocean water (SMOW) proposed by Craig (1961a).

Numerous isotope mass balance equations are proposed to quantify the proportion of annual evaporation relative to total rainfall (Gonfiantini, 1986; Gat & Bowser, 1991; Gat &Matsui, 1991; Wang & Veizer, 2000). Utilizing the coupling of transpiration and CO_2 flux during photosynthesis, annual transpiration is converted to NPP:

$$\frac{\text{NPP (mol C yr}^{-1}\text{)} = \text{Transpiration (mol H}_2\text{O yr}^{-1}\text{)}}{\text{WUE (mol H}_2\text{O per mol C)}}$$

yielding a *first order* estimate of annual photosynthetic carbon flux.

The loss of water by transpiration may, therefore, be a defining parameter of the ecosystem's capacity to sequester CO_2, and can be calculated using the water balance equation. The general water balance equation is expressed (Leopoldet *et al.*, 1995) as:

$ET = P – (Q_{DS} + Q_{BF}) – \Delta S = P- Q_T - \Delta S$ ....(1) where ET is water loss to evaporation, P is precipitation, Q_{DS} is surface runoff , Q_{BF} is base flow, Q_T is total runoff and ΔS is change in groundwater storage.

The water balance equation is further simplified by averaging water fluxes for multi-year time scale, in which case ΔS approximates zero. ET is, thus, easily obtained since P and Q_T can be measured directly. By this simplification,

$ET = P-Q_T$ .... (2) Evapotranspiration (ET) component in the evapo-transpiration flux can, thus, be extracted by using isotope mass balance equations, such as those proposed by Gonfiantini (1986), leading to:

$x = E/I = (\delta_S – \delta_I)(I – h + \Delta\in)/(\delta_S + 1)$
$(\Delta\in + \in/\alpha) +h(\delta a – \delta_S)$ .... (3)

where x is the percentage of evaporation (E) with respect to the total water input into the area (I), which mostly equals the total precipitation (P). δ_S is the weighed mean δD (or $\delta^{18}O$) value measured at the mouth of the river. δ_I is the mean isotopic composition of precipitation in the basin (Table 2).

For the more or less closed-systems, such as lakes, it is given by the intersection between the meteoric water line (MWL) (either global or local) and the regression line for the measured δD and $\delta^{18}O$ values of the waters (Gat & Matsui, 1991). Given a through flowing rivers, the intersect may be less well constrained, but the evaporative trend will still deviate from the slope of the MWL, permitting a first order estimate of the evaporative flux (Telmer & Veizer, 2000).

TABLE 2

Variables used in the isotope mass balance equation are obtained from standard values from Gonfiantini, 1986

	White Volta River	*Black Volta River*	*Oti River*
δ_S	-0.00262	-0.00245	-0.00209
δ_I	-0.005	-0.005	-0.005
δ_a	-0.01534	-0.01548	-0.01540
α	1.010344	1.010483	1.010403
$\in$	0.010344	0.010483	0.010403
$\Delta\in$	0.003124	0.002414	0.002414
T (°K)	301.6	300.0	300.9
Humidity (%)	78	83	83
Evaporation*(%)	15.6	22.6	30.7

δa is the mean δD (or $\delta^{18}O$) value of water vapour calculated assuming an isotopic equilibrium with a local precipitation ($\delta a = \delta_I – \in *$).

Although δa can be reasonably estimated by assuming an isotopic equilibrium between atmospheric moisture and mean annual precipitation (Gat & Matsui, 1991), Gibson (2002) pointed out that the seasonality of evaporation flux needs to be considered for accurate constrained values. h is the mean relative humidity, α is the equilibrium fractionation factor for oxygen ($\ln\alpha = 1137 T^{-2} – 0.4156 T^{-1} – 0.00207$) and hydrogen isotopes ($\ln\alpha = 24844 T^{-2} – 76.248 T^{-1} +0.05261$) (Friedman & O'Neil, 1977), $\Delta\in$ is the kinetic energy enrichment factor for oxygen (14.2 (1-h)) and hydrogen isotopes (12.5 (1-h)), and $\in = \alpha -1$. Similarly, according to Gibson *et al.* (1993), $x = E/I = (\delta_S - \delta_I) / (h/1 – h)(\delta* -\delta_S)$ ....(4) where $\delta* = (h.\delta a + \in)/(h-)$ is the limiting isotopic composition under local climate conditions, ε is the isotopic separation between liquid and vapour such that $\in = \in* + \in_K$ and $\in* = (\alpha-1). 1000$, $\in_K \cong C_K (1-h)$. This gives C_K values for oxygen and hydrogen as 14.3‰ and 12.5‰, respectively

(Gonfiantini, 1986). The other variables are the same as in the Gonfiantini equation (1986). These are standard model equations used in calculating the per mil values of oxygen and hydrogen isotopes.

Field sampling

The main stem of the Volta river and its largest tributaries were sampled during low water stand in the dry season and high water stand in the rainy season in 2003 and 2004. This was done in order to capture the system at its hydrologic extremes. Samples of river discharge (for isotopic analysis, reported relative to SMOW) were collected on the Black Volta, White Volta, Oti river, Sene river, Afram river and the Lower Volta river. Samples were taken from the north-ends of the six rivers directed towards the south, and brought to sample stations which were set up at the north-ends of the rivers. With the help of canoes, samples were taken at intervals of 5 km towards the south every 2 weeks. Collected samples were stored in unused white plastic bottles, filtered through a 0.45-μ millipore membrane and stored at a temperature of 4 ^{o}C. For the isotopic analysis, samples were acidified with strong HNO_3.

Isotope analyses

For deuterium and hydrogen ratios, 0.3 ml of river water was injected into an evacuated 6-mm Pyrex tube containing 100 mg of Zn and sealed. The water was subsequently oxidized with zinc at 500 ^{o}C for 30 min to release H_2 gas (Coleman *et al.*, 1982). The H_2 gas, thus, released was introduced into a VG 602D mass spectrometer through a tube cracker port. The reproducibility of hydrogen isotope analysis is less than ± 2‰.

For the $^{18}O/^{16}O$ ratio of water, 1 ml of water sample was equilibrated with a small amount of CO_2 gas at 25 ^{o}C for 6 h in a specially designed online shaker/equilibrator. After equilibration, the CO_2 gas was extracted and purified cryogenically and introduced into a VG Isogas SIRA-12 triple collector mass spectrometer. Reproducibility of oxygen isotope analyses is less than α 0.1‰. Both hydrogen and oxygen isotope ratios are reported in δ values relative to SMOW. All stable isotope measurements were conducted at the G.G. Hatch Isotope Laboratory of the University of Ottawa, Canada.

Vegetation in the Volta river watershed

The spatial distribution of vegetation types for the Volta watershed was based primarily on the 1 km^2-resolution global land cover (GLC2000) map for Africa, derived from daily measurements collected during the year 2000 by the Vegetation sensor on-board the Spot-4 satellite (Mayaux *et al.*, 2004). Through a combination of remote-sensing data and expert knowledge, Mayaux *et al.* (2004) classify the entire continent of Africa into 27 land-cover categories. Four GLC2000 land-cover classes constitute greater than 95% of the total vegetation in the Volta watershed although the proportions vary between sub-basins (Fig. 2). According to data from GLC2000 land-cover classes, deciduous woodlands and deciduous shrublands with sparse trees predominate in the Ghana and southern Burkina Faso portions of the Volta watershed. It is associated with higher mean annual rainfall and often referred to as Guinean savanna (Mistry, 2000).

Using the vegetation continuous fields product (Hansen *et al.*, 2003), Mayaux *et* *al.* (2004) estimated percentages of tree cover, shrub/grass cover, and bare soil for each GLC2000 vegetation class. Further refinements of vegetation distribution within each class were made in this study by incorporating additional information regarding the proportion of croplands in each class from a global distribution of agricultural vegetation (Wang & Veizer , 2000) and from biome-specific data (Olson *et al*., 2001). Using the methods of water and carbon cycles proposed by Telmer & Veizer (2000, 2001) photosynthetic NPP for terrestrial ecosystem can be computed (Table 5).

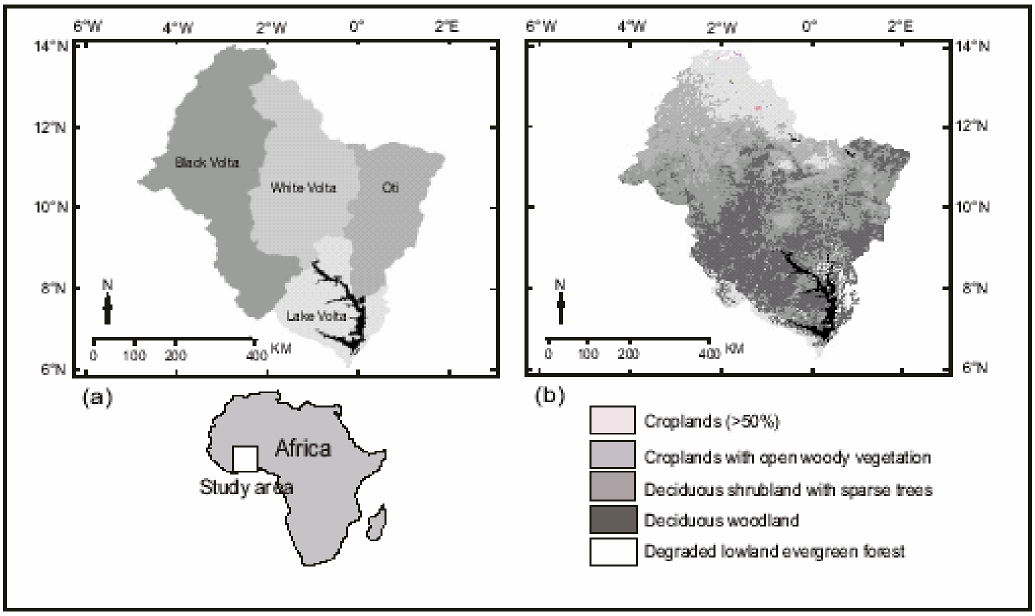


Fig. 2. (a) Location of Volta River Watershed in West Africa (b) Distribution of vegetation in the Volta River Watershed from the Vegetation sensor on-board the SPOT-4 satellite (Modified from Mayaux et al., 2004).

Results

The calculated proportions of trees, shrubs, grasses, and crops in the Volta watershed are presented in Table 3. The results of this study show that about 36% of woody and herbaceous plants in the Volta river watershed are estimated to utilize the C_4 photosynthetic pathway. Significant variation in C_4 percentage is observed within individual land-cover classes, reaching a maximum of 52% in GLC2000 land-cover class croplands with open woody vegetation. Influence of classes with higher proportions of C_4, however, is diminished by their overall contribution to total vegetation area. Long-term WUE values from Jones (1992) are: 1 mole of CO_2 per 500 to 1500 moles H_2O for C_3 plants and 350 to 550 moles for C_4 plants. These values are similar to estimates from Molles (2002): 1 mole of CO_2 per 500 to 1200 moles H_2O for C_3 plants and 1 mole of CO_2 per 350 to 450 moles H_2O for C_4 plants. Thus, long-term WUE is considered to be in the range of 1 mole of CO_2 per 925 ± 506 moles H_2O and 1 mole of CO_2 per 425 ± 96 moles H_2O for C_3 and C_4 plants, respectively.

TABLE 3

Vegetation characteristic of the Volta river watershed and its tributaries calculated from daily measurements collected by the vegetation sensor on-board the SPOT-4 satellite during the year 2000

Sub-basin	*Trees(%)*	*Shrubs(%)*	*Grass(%)*	*Crops(%)*	*C_4(%)*	*WUE (mol H_2O per mol CO_2)*
Black Volta	18.0	16.7	44.0	21.3	39	730
White Volta	18.8	17.6	40.0	23.6	35	750
Oti River	22.3	21.4	42.5	13.7	37	740
Lower Volta	25.9	23.6	40.4	14.4	35	750
Average	21.5	19.85	41.7	18.2	36.5	742.5

The proportions of C_3 and C_4 plants in each respective sub-basin of the Volta river watershed and WUE for each sub-basin are listed in Table 3. In general, if evaporation is a significant factor, then the isotope data of river water plot on a local evaporation line in the $\delta D - \delta^{18}O$ should cross plot, with the slope less steep than that of the meteoric water line (MWL) (Fig. 3). Similarly, the $\delta^{18}O$ and δD values in the Volta rivers range from -4.72 to 2.37 per mil and from -35.28 to 9.30 per mil SMOW, respectively. In almost all cases, the difference in values within the rivers is very minimal, since the rates of flow are very similar. However, the Sene river invariably has one of the highest $\delta^{18}O$ and δD (9.39 and 2.37 per mil, respectively) values much heavier than the

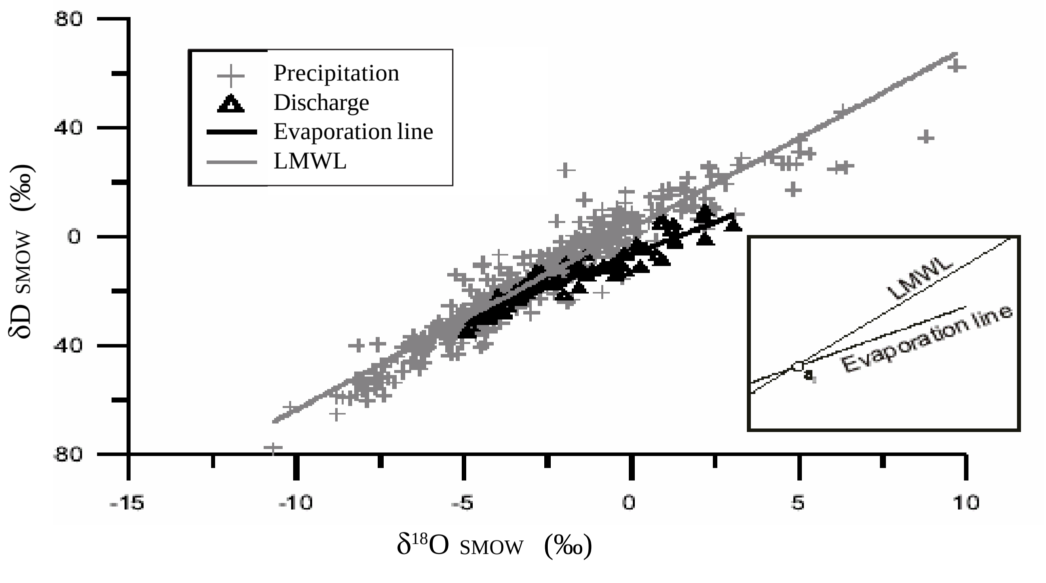


Fig. 3. Isotopic composition of ($\delta^{18}O$ and δD) of precipitation (local meteoritic water line) and river discharge (evaporation regression line). The diagram shows precipitation record for the last 30 years (recorded by the Meteorological Department, Accra) which plots around the LMWL. The recorded discharge concentrates on the evaporation regression line.

comparative values measured for the White and the Black Volta rivers. This possibly can be due to anthropogenic influences.

Discussion

Annual rainfall in the Volta river watershed is apportioned between numerous components of the water cycle, several of which are readily-available from historical records, and some which require alternative methods to be constrained. In alternative method, stable isotopes are used to separate evaporation and transpiration. Separating evaporation and transpiration is important because transpiration is the only water flux associated with carbon sequestration. Transpiration and interception are both non-fractionating processes and do not alter the isotopic composition ($\delta^{18}O$-δD) of surface water as it moves through the hydrologic system. However, due to isotopic fractionation during evaporation, river discharge (surface water leaving the hydrologic system) is enriched in the heavier isotopes, ^{18}O and D, relative to precipitation (water entering the hydrologic system). If evaporation is a significant component of the annual water balance, then a plot of the isotopic composition ($\delta^{18}O$-δD) of river discharge should define a regression line with a shallower slope than that of regional precipitation (Fig. 3). The difference in slopes is proportional to the degree of evaporation in the watershed.

Using the isotope mass balance equations proposed by Gonfiantini (1986) to quantify the proportion of annual evaporation relative to total rainfall, it is found that the Volta river watershed sequester 0.170×10^{15} g C or 428 g C m^{-2} yr^{-1} from the atmosphere each year. The WUE component of the equation is principally estimated using the vegetation distribution in the watershed. The significant aspects, therefore, are vegetation where proportions of C_3 and C_4 plants can be distinguished.

Using floral inventories and agricultural statistics from UNEP/GEF (2002), 85% of the grasses and 6% of the crops in the Volta watershed utilize the C_4 photosynthetic pathway. Overall, grasses represent an average of 41.7% of total vegetation (Table 3). This is considered a reasonable proportion given the predominance of woodland savanna vegetation which is significantly influenced by C_3 crops. Modelled estimates of heterotrophic soil respiration from Raich & Potter (1995) exceed NPP estimates from this study, implying that the Volta river watershed is a minor source of CO_2 to the atmosphere. However, the error associated with the water-use efficiency values for C_3 and C_4 plants in this study is 55% and 23%, respectively, implying that watershed NPP could be significantly higher if different WUE values were used.

According to Raich & Potter (1995) and the calculations in this study, heterotrophic soil respiration for the Volta river watershed is estimated to be 0.199×10^{15} g C or 501 g C m^{-2} yr^{-1}, a 15% difference from the NPP estimates. Using the existing water balance, the associated water-use efficiency needed to reach this rate of productivity is 625 moles H_2O per mole of carbon. This water-use efficiency corresponds to 60% C_4 vegetation in the Volta river watershed. Intuitively, this situation seems improbable, given the significance of croplands and woody vegetation in the watershed. The only ecosystems that may sustain such high water-use efficiency are C_4-dominated grasslands, which may occur in the Sahel

TABLE 4

Components of the water balance for the Volta river watershed from data collected from the Meteorological Department, Accra and the Department of Botany, University of Ghana

Sub-Basin	*Precipitation (km^3)*	*Discharge (km^3)*	*ET (km^3)*	*Interception (km^3)*	*Evaporation (km^3)*	*Transpiration (km^3)*
Black Volta	140	7	133	34	24	75
White Volta	101	7	94	24	12	58
Oti River	84	11	73	19	20	34
Lower Volta	47	6	41	10	8	23
Total	372	31	341	87	64	190

TABLE 5

Annual carbon flux estimates and net ecosystem productivity calculated from the model calculations of Gonfiantini, 1986

Sub-basin	*Transpiration (km^3)*	*NPP (10^{15} g C yr^{-1})*	*NPP (g C $m^{-2}yr^{-1}$)*	*Heterotrophic soil respiration (10^{15} g C yr^{-1})*	*Net ecosystem productivity (10^{15} g C yr^{-1})*
Black Volta	75	0.069	437	0.077	+0.008
White Volta	58	0.052	461	0.053	+0.001
Oti River	34	0.031	389	0.040	+0.009
Lower Volta	23	0.020	400	0.029	+0.009
Total	190	0.172	1687	0.199	+0.027

region of West Africa. Some of the vegetation in the Volta river watershed, however (especially the Lower Volta) is woodland savanna and, therefore, a mixture of woody and grassy vegetation and unlikely to contain such high proportions of C_4 vegetation.

Recognizing that NPP estimates from this study were considered first order and the soil respiration estimate is global in scale, the 15% discrepancy was relatively small given the dissimilarity of methods used for determination of each. Overall, the similarity of productivity and soil respiration fluxes suggests that carbon fluxes to and from the Volta river watershed are close to being in balance or that respiration slightly exceeds terrestrial productivity. For the Volta river watershed, the difference between NPP and heterotrophic soil respiration was estimated as 0.029×10^{15} g C yr^{-1}, implying a source of carbon to the atmosphere. Incorporating the additional 0.026×10^{15} g C (estimated as 15% of annual NPP; Scholes & Walker, 1993) to be lost each year possibly due to the burning of vegetation, the flux to the atmosphere could increase to 0.052×10^{15} g C yr^{-1}.

Conclusion

Differences in NPP between the Black Volta river, White Volta river and Oti river sub-basins appear to be solely related to the annual water cycle as carbon dioxide pressure ($pCO_{2)}$, temperature, and vegetation characteristics are similar for all three of the basins. Importantly, NPP estimates for the Volta watershed highlight the strong coupling of water and carbon cycles in terrestrial ecosystems and demonstrate the value of watershed-scale estimates of NPP in constraining the terrestrial carbon cycle.

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