

Differences in transpiration between a forest and an agroforestry tree species in the Sudanian belt

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Abstract Average population growth in the African Sudanian belt is 3 % per year. This leads to a significant increase in cultivated areas at the expense of fallows and forests. For centuries, rural populations have been practicing agroforestry dominated by *Vitellaria paradoxa* parklands. We wanted to know whether agroforestry can improve local rainfall recycling as well as forest. We compared transpiration and its seasonal variations between *Vitellaria paradoxa*, the dominant species in fallows, and *Isoberlinia doka*, the dominant

species in dry forests in the Sudanian belt. The fallow and dry forest we studied are located in northwestern Benin, where average annual rainfall is 1200 mm. Sap flow density (SFD) was measured by transient thermal dissipation, from which tree transpiration was deduced. Transpiration of five trees per species was estimated by taking into account the radial profile of SFD. The effect of the species and of the season on transpiration was tested with a generalized linear mixed model. Over the three-year study period, daily transpiration of the agroforestry trees, *V. paradoxa* (diameters 8–38 cm) ranged between 4.4 and 26.8 L day⁻¹ while that of the forest trees, *I. doka*, (diameters 20–38 cm) ranged from 9.8 to 92.6 L day⁻¹. Daily transpiration of *V. paradoxa* was significantly lower (15 %) in the dry season than in the rainy season, whereas daily transpiration by *I. doka* was significantly higher (13 %) in the dry season than in the rainy season. Our results indicate that the woody cover of agroforestry systems is less efficient in recycling local rainfall than forest cover, not only due to lower tree density but also to species composition.

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Introduction

To understand the impact of changes in the composition of the woody cover on local rainwater recycling

to the atmosphere in the case of land use changes, the transpiration rate of each species needs to be quantified. Quantification is necessary both to compare the dynamics of water transfer between stands and to understand the hydric functioning of the species that make up the stands (Granier 1985).

Between 1990 and 2000, 0.25 % of the total tree cover (dense and open) in the Sudanian belt was lost every year (Bodart et al. 2013). In 2000, only 2.8 % of the total area still had a dense tree cover, 8 % had an open tree cover and 50 % of the land was covered with shrubs and forest regrowth (Bodart et al. 2013). Land use changes were also observed in the Djougou district in northwestern Benin due to population growth, which has exceeded 3 % a year since 1972 (INSAE-Bénin 2013). In this district, open woodland cover decreased from 60 % to less than 40 % of total land area in favor of cropland (+12.5 %) and fallows (+6 %) between 1973 and 2000 (Leroux 2012). There was a decrease in tree density and changes in the species composition of the woody cover, the latter leading to changes in the hydric functioning of the woody tree cover, which can be quantified via transpiration (Aussenac 2000). In the forest-cropland-fallow secondary succession that dominates the Sudanian belt (Djossa et al. 2008; Seghieri et al. 2009), *Isoblerlinia doka* dominates in dry forests, and *Vitellaria paradoxa* dominates in successive rotations comprising agroforestry parklands and fallows. To date, there has been no quantification of transpiration of *I. doka* making ours the first report. Little research has been done on the functional traits of *V. paradoxa*, despite the importance of its non-timber products (shea nuts and butter) for rural households and for the economies of shea producer countries (Glèlè Kakai et al. 2011; Gwali et al. 2012). Only Compaoré (2006) and Bayala et al. (2008) quantified transpiration by *V. paradoxa*, Compaoré (2006) in a fallow in northeastern Ghana (average annual precipitation: 700–1100 mm) and Bayala et al. (2008) in an agroforestry parkland in Burkina Faso (average annual precipitation: 730 mm). This is the first estimation of transpiration of *V. paradoxa* trees in northern Benin.

In this study, we compared transpiration and its seasonal variations in *I. doka* and *V. paradoxa*. The forest species, *I. doka* would be expected to transpire less intensely than the agroforestry species *V. paradoxa*. This hypothesis is based on the fact that agroforestry trees benefit from less competition than

forest trees as they grow in a less dense cover and benefit from the care given to the crops (soil tillage, possible fertilization, etc.) (Dupraz and Liagre 2008). In addition, the species used in agroforestry are generally light-demanding species and have a higher transpiration rate than the less light-demanding species in forests (Fernandez et al. 2009; Gyenge et al. 2011). The second hypothesis is that the tree transpiration is higher during the rainy season than during the dry season, since the canopies of the two species shed at least 50 % of their leaves—but never 100 %—between November and February (Seghieri et al. 2012).

Materials and methods

Study site, types of cover, and species studied

The two study sites are located 540 km northwest of Cotonou (9°40′–9°54′N, 1°34′–1°58′E). The rainy season lasts from April to October, with an average annual rainfall of 1200 mm (1950–2005) (Lawin 2007). The soils are mainly ferruginous according to the French soil classification (Faure and Volkoff 1998). Croplands are composed of a patchwork of crops (manioc, groundnuts, yams, maize, millet, sorghum, cotton), grown under the cover of *V. paradoxa* and *Parkia biglobosa* (Locust bean) trees. Not only has cropland area increased by at least 20 % between 1973 and 2000, but cropping has also intensified in the last decade, with new pioneer deforestation fronts since the building of an asphalt road between Cotonou and Djougou (Seghieri et al. 2009).

The first study site is located in the protected Béléfoungou forest, an open forest resulting from the degradation of a Leguminosae forest (Aubreville 1950). A previous study (Blanchard et al. 2007) of the structure of the woody stand reported that *I. doka* (Caesalpiniaceae) accounted for 43 % of the density in the stratum over 12 m in height and for 28 % in the stratum less than 6 m in height. *I. doka* has semi-persistent foliage (Seghieri et al. 2012). It occupies open woodlands in West and Central Africa (Aubreville 1950). Its taproots and oblique deep roots enable the tree to exploit groundwater, thereby drawing up nutrients that are favorable to crops, which explains why soils covered with *I. doka* are highly prized by farmers (Dourma et al. 2009).

The second study site is located in a young fallow (5–10 years old) near Bira village. Vegetation is composed of perennial and annual grasses and young trees. Analysis of the woody stand structure showed that *V. paradoxa* (Sapotaceae) accounted for up to 55 % of the density of the stratum over 6 m in height (Blanchard et al. 2007). *V. paradoxa* also has semi-persistent foliage (Seghieri et al. 2012). It grows in Sudano-Guinean savannas and in all types of soil except water-saturated soils (Hall et al. 1996).

For each study year and for each study site (forest and fallow), seasons were defined using an ombrothermic diagram, the dry season being the period when $2T > P$ (T = temperature, P = rainfall). From this definition, at the two study sites, the rainy season lasted from mid-April to mid-October 2011 and from early April to late October in 2012 and 2013. Annual rainfall was 1148 mm (2011), 1708 mm (2012), and 1017 mm (2013) at Béléfoungou and 1173 mm (2011), 1532 mm (2012), and 1127 mm (2013) at Bira.

Tree sampling and measurement device per tree

At each site, five trees were chosen that were representative of the dominant class sizes (diameter and height) within the population of each species. Each tree was identified by the initials of its scientific name and a number (Table 1). Their diameter at breast height (DBH) was measured in November 2010 (Table 1). We extracted one wood core from each trunk at breast height using a Pressler's increment borer. Sapwood was distinguished from heartwood because it was lighter and wetter. Sapwood thickness was measured and its area was calculated as the difference between the total area of the trunk section and the surface area of the heartwood section, disregarding the thickness of the bark and approximating the shape of the trunk as a circle.

Five trees per species were equipped with sensors that differed depending on the diameter of the tree concerned (Table 1). In half the small- and medium-diameter trees (*I.d3*, *I.d4*, and *V.p8*), two sensors were inserted in the outer sapwood, one on the north side (5–30 mm in depth) and one on the south side (10–20 mm in depth) of the trunk. In the others (*I.d5*, *V.p2* and *V.p10*), only one sensor was inserted (5–30 mm in depth) on the north side of the trunk. In

large-diameter trees (*I.d2*, *I.d7*, *V.p1*, and *V.p3*), five sensors were inserted at five depths: 10–20 mm depth on the south side, and at depths of 5–30, 30–55, 60–85, and 90–115 mm on the north side of the trunk. The sensors were protected from direct radiation, dust, and rain with aluminum shield. Data were recorded with a Campbell CR1000 data logger.

Estimation of transpiration at tree scale

Automatic measurements of sap flow density (SFD)

SFD was measured using the transient thermal dissipation (TTD) method (Do and Rocheteau 2002). Intermittent 10-min periods of heating were followed by 20 min of natural cooling in order to limit errors due to thermal interference (natural thermal gradient, heat storage). SFD J was measured by sensors consisting of two temperature probes inserted radially in the sapwood of the tree at breast height, separated vertically by about 8 cm. Each probe contained a copper–constantan (Cu–Cn) thermocouple 2 mm in diameter. The higher probe, located downstream with respect to sap flow, was equipped with a resistance that heated at a power of 0.1 W/cm. The lower probe was not heated and showed the temperature of the tree. Temperature signals were recorded at 10 min intervals. The transient or alternate signal ΔT_a was defined as follows:

$$\Delta T_a = \Delta T_{on} - \Delta T_{off}, \quad (1)$$

where ΔT_{on} is the temperature difference measured at the end of the heating period and ΔT_{off} is the temperature difference measured at the end of the cooling period. By analogy with the continuous heating method (Granier 1985), Do and Rocheteau (2002) defined a flow index K_a from the temperature differences between the two probes:

$$K_a = (\Delta T_{0a} - \Delta T_{ua}) / \Delta T_{ua}, \quad (2)$$

where ΔT_{0a} is the transient signal when there is no flow and ΔT_{ua} the transient signal in the presence of flow.

Isarangkool Na Ayutthaya et al. (2010) defined SFD J ($L \, dm^{-2} \, h^{-1}$) estimated every 30 min as follows: (the formula is assumed to be valid for all woody species).

$$J = 12.95 * K_a. \quad (3)$$

Table 1 Species and trees studied. Structural characteristics of the trees studied, number of sensors per tree, average SFD, and tree transpiration in *Vitellaria paradoxa* and *Isoberlinia doka*

in Bira fallow site and Belefoungou forest site, respectively, in the North Benin

Species	Tree sampled	DBH (cm)	Sapwood depth (cm)	Sapwood area (cm ²)	Number of probes	Daily SFD (L dm ² day ⁻¹)		Average daily transpiration (L day ⁻¹)	
						Mean	SD	Mean	SD
<i>Isoberlinia doka</i>	<i>I.d2</i>	37.7	5	518.40	5	8.1	4.3	42.1	22.5
	<i>I.d3</i>	20.7	4.5	316.52	2	3.1	2.2	9.8	6.8
	<i>I.d4</i>	22.7	3.5	214.41	2	9.5	4.7	20.4	10.0
	<i>I.d5</i>	26.5	6.0	395.84	1	4.7	4.1	18.6	16.1
	<i>I.d7</i>	37.6	5.5	561.56	5	16.5	5.3	92.6	29.7
<i>Vitellaria paradoxa</i>	<i>V.p1</i>	32.5	4.0	351.86	5	7.6	3.4	26.8	12.1
	<i>V.p2</i>	14.7	3.0	113.10	1	6.2	3.3	7.0	3.7
	<i>V.p3</i>	38.2	4.5	473.60	5	4.6	2.7	21.7	12.8
	<i>V.p8</i>	15	3.0	103.67	2	8.69	4.26	9.3	4.4
	<i>V.p10</i>	8.3	3.5	71.47	1	6.15	4.17	4.4	3.0

Calculation of tree transpiration

Sap flow was computed as half the cumulated semi-hourly flows over a period of 24 h. Average daily sap flow over 24 h is the mean of the 24-h flows for a number of days that varied with the species and the season (573 days in the rainy season and 433 days in dry season for *I. doka*; 562 days in the rainy season and 495 days in dry season for *V. paradoxa*). Daily flow was an estimate of daily tree transpiration, ignoring any changes in tree water storage.

To quantify sap flow at the scale of an entire tree, flow densities can be measured over the entire cross-section of sapwood, from periphery to center (Hatton et al. 1990). Another method is based on extrapolation from a single “reference” probe using the shape of the radial profile (Delzon et al. 2004). The second method is based on calculation of a specific correction factor c that accounts for both the equation of the SFD radial profile and the portion of the sapwood cross-sectional area sampled by the “reference” probe.

The four large-diameter trees in which the flows were measured by four sensors covering the entire cross-section of sapwood were used to determine the radial profile of a given tree. The radial profile is defined based on the values of the ratio $J_i:J_1$, where J_i is SFD measured by the sensor installed at a given depth i ($i = 1-4$) and J_1 is SFD measured at the “reference” depth (here, 5–30 mm). The radial profile was determined by computing the mean of the ratios

$J_i:J_1$ over 298 days for *V. p1*, 86 days for *V. p3*, 264 days for *I.d7*, and 146 days for *I.d2*. For each species, the radial profile determined was fitted by a regression line (Fig. 2) to determine the specific correction coefficient c . The equation of this regression line was determined using the R software package (version 3.1.1). The best fit was selected based on the residual standard error and the adjusted R -squared (R^2). The correction coefficient c was calculated as follows (Delzon et al. 2004):

$$c = \sum_{i=1}^n R_i \left(\frac{A_i}{A} \right), \quad (4)$$

where R_i is the ratio $J_i:J_1$ estimated from the regression line illustrated in Fig. 2. A and A_i are, respectively, the total area of sapwood and area of the ring containing the sensor inserted to depth i .

For trees whose sapwood depth was more than 30 mm (Table 1), the sap flow F (in L h⁻¹) was calculated as follows:

$$F = J_{\text{ext}} * A * c, \quad (5)$$

where J_{ext} is SFD in L dm² h⁻¹, measured in the outer sapwood.

For trees that had two sensors in the outer sapwood (5–30 and 10–20 mm), J_{ext} is the mean of the values measured by the two sensors to account for part of the azimuthal variation.

c is the correction factor (0.54 for *V. paradoxa* et 0.60 for *I. doka*).

A is the sapwood area calculated as follows:

$$A = \pi(r_{\text{tot}}^2 - r_{\text{heartwood}}^2), \quad (6)$$

where r_{tot} and $r_{\text{heartwood}}$ are, respectively, the total radius of the tree trunk and the heartwood radius in dm.

For trees whose sapwood depth was less than 30 mm (Table 1), the sensors covered the entire cross-section of their sapwood and a correction factor was consequently not required for extrapolation. Tree sap flow F (in L h^{-1}) at the tree scale was then deduced from the following equation (Granier 1985):

$$F = J_{\text{ext}} * A. \quad (7)$$

Assessment of transpiration variability

Analysis of variance (ANOVA) using the generalized linear mixed model (GLMM) in the Minitab 14.1 software package with year as random factor was performed to evaluate the effects of species, season, year, and individual (sampled tree) on the SFD and on transpiration. Generalized linear mixed models (GLMMs) represent a more flexible way of analyzing non-normal data when random effects are present (Bolker et al. 2009). This method makes it possible to obtain an adequate estimate of the error that accounts for the hierarchical structure and the autocorrelation of data due to the repeated measurements over time in the same individual (Dupéré et al. 2007).

The relationships between transpiration and vapor pressure deficit VPD and between transpiration and the diameter of the tree were tested with linear regressions using the R software package (version 3.1.1).

Results

Diurnal patterns of SFD and daily SFD at the tree scale

Figure 1a and b shows an example of the diurnal courses of SFD at different depths of sapwood in one tree per species (*V.p3* and in *I.d7*) over two bright days. The diurnal dynamics of SFD measured by the five sensors were almost identical. SFD was maximum from 11 am to 3 pm. It dropped to zero from 6 pm to 6

am (UT+1) at all depths. In the middle of the rainy season, small intra-daily decreases (Fig. 1a and b) were probably due to cloudy periods that reduced incident radiation and probably caused partial closure of the stomata.

Over the three study years, the average daily SFD varied from 5 to 9 $\text{L dm}^{-2} \text{ day}^{-1}$ for *V. paradoxa* trees (diameters 8.3–38.2 cm) while that of *I. doka* trees (diameters 20.7–37.7 cm) varied from 3 to 16 $\text{L dm}^{-2} \text{ day}^{-1}$ (Table 1). The effect of the individual tree and of the season on the SFD were significant ($p < 0.05$; Table 2) at tree scale. Second-order interactions between season and year or species were significant ($p < 0.05$; Table 2) indicating that differences between seasons vary significantly between years and between species.

Figure 1a and b also illustrates the azimuthal variation in SFD in the outer sapwood (sensors inserted to depths of 10–20 and 5–30 mm). Over the 3 years, this variation reached an average of 73 % in *I. doka* and of 63 % in *V. paradoxa*, underlining the need to take them into account when estimating sap flow at the tree scale.

Radial profile of SFD

Figure 2 shows the shape of the radial profiles of SFD in the two species studied. For four trees (*V.p1*, *V.p3*, *I.d2*, and *I.d7*), the ratio $J_i:J_1$ decreased from the periphery to the center of the sapwood, with maximum values recorded at the periphery (5–30 mm). The decrease was more abrupt in *V.p1*, *V.p3*, and *I.d2* than that in *I.d7*, illustrating the variability of the radial profile between individuals in a given species. The minimum flow was reached at depths of 30–55 or 60–85 mm in *V. paradoxa* (10 % average of reference SFD J_1 , Fig. 2a). In this species, SFD measured at a depth of 90–115 mm reached 15 % of the reference SFD. Combined with measurements of sapwood thickness using Pressler's increment borer (4 and 4.5 cm for *V.p1* and *V.p3*, respectively), leads us to suppose that the probes probably protruded into the heartwood section. In *I. doka*, the minimum flow was reached at a depth of 90–115 mm (an average of 5 % of reference SFD J_1). In this species, the $J_i:J_1$ ratio was close to zero for the deepest sensor (depth of 90–115 mm; Fig. 2b), confirming that the measurement probe accounted for most of the transpiring section of the sapwood.

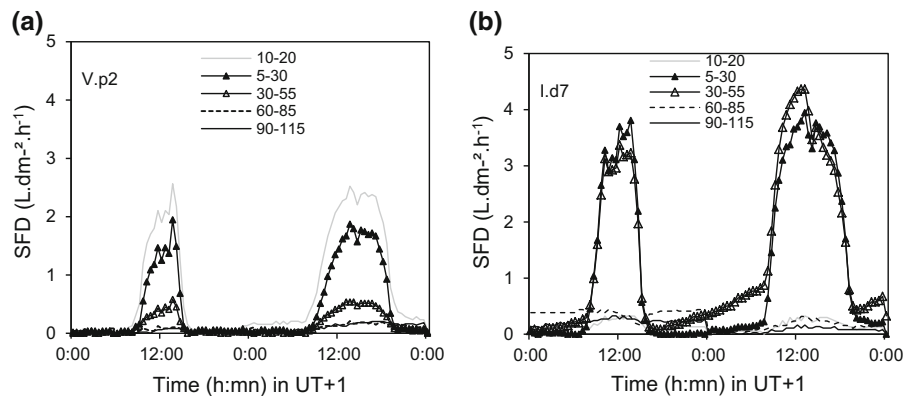


Fig. 1 Variation in SFD over 24 h at different depths in the sapwood during the rainy season in one tree of *Vitellaria paradoxa* (V.p2 **a**) in Bira fallow, and one tree of *Isoberlinia doka* (I.d7, **b**) in Belefungou forest both in the North Benin. Gray solid line 10–20 mm depth; solid triangle

5–30 mm depth, empty triangle 30–55 mm depth, dotted line 60–85 mm depth, and black solid line 90–115 mm depth. Days selected as representative for both species: 26–27 May 2011. The time of day is in UT+1 (local time in Benin)

Table 2 Analysis of variance (ANOVA) using generalized linear mixed effects model (GLMM): effect of the year, season, species, and individual trees and their interactions on the SFD

Source	DF	SFD		Transpiration	
		<i>F</i> value	<i>p</i>	<i>F</i> value	<i>p</i>
Year	2	5.46	0.133 ^{ns}	6.48	0.174 ^{ns}
Season	1	21.43	0.044*	25.71	0.037*
Species	1	0.16	0.725 ^{ns}	70.62	0.014*
Individual (species)	8	19.29	0.000***	50.72	0.000***
Year*individual (species)	16	41.11	0.000***	41.19	0.000***
Season*individual (species)	8	73.75	0.000***	73.90	0.000***
Year*season	2	6.53	0.001***	0.45	0.689 ^{ns}
Year*species	2	1.71	0.212 ^{ns}	1.36	0.286 ^{ns}
Season*species	1	85.23	0.000***	6.34	0.128 ^{ns}

DF degree of freedom, *F* Fisher's exact test, *P* *p* value, *ns* not significant

* Significant, ** Highly significant, *** Very highly significant

Daily transpiration at the tree scale

Over the 3 years, average daily transpiration was significantly lower in *V. paradoxa* trees than in *I. doka* trees. It varied between 4.4 and 26.8 L day⁻¹ in *V. paradoxa* trees, while it varied from 9.8 to 92.6 L day⁻¹ in *I. doka* trees (Table 1). Analysis of variance showed that species significantly affected transpiration ($p < 0.05$; Table 2), whereas there was no significant interaction between species and year or season ($p > 0.05$, Table 2).

and transpiration in *Vitellaria paradoxa* and *Isoberlinia doka* in Bira fallow site and Belefungou forest site, respectively, in the North Benin

Average daily transpiration over the study period varied highly significantly between individuals whatever the species, the year, and the season ($p < 0.0001$, Table 2). In each species, the highest transpiration rates were measured in large-diameter trees (*V.p1* and *V.p3* for *V. paradoxa*; *I.d2* and *I.d7* for *I. doka* (Table 1). In general, transpiration increased with tree diameter regardless of the species. It became almost constant above 32 cm diameter in *V. paradoxa*, whereas in *I. doka*, *I.d7* transpired twice as much as *I.d2* although these trees had the same diameter (DBH = 38 cm; Fig. 3).

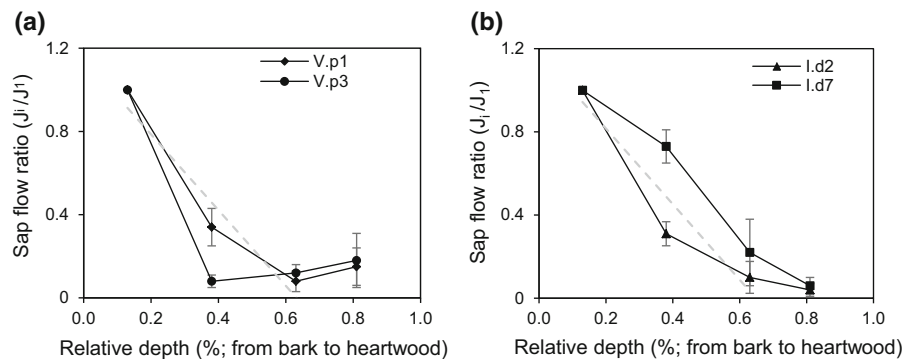


Fig. 2 Ratio of SFD measured at depth i to SFD at the reference depth (5–30 mm) as a function of the insertion depth of the sensors in *Vitellaria paradoxa* trees in Bira fallow (a) and in *Isoberlinia doka* trees in Belefoungou forest (b) both in the North Benin. Solid diamond for *V.p1*, filled circle for *V.p3*, solid

triangle for *I.d2*, solid square for *I.d7*. The dots indicate the mean ratio per sensor inserted at the different depths for periods of 298, 86, 264, and 146 days in *V.p1*, *V.p2*, *I.d2*, and *I.d7* in 2011. The vertical bars represent standard deviations. The dotted line is the regression line ($p < 0.0001$)

Nevertheless, in both species, there was a significant relationship between average daily transpiration and the diameter of the tree ($p < 0.0001$; $R^2 = 0.46$ for *I. doka*, 0.54 for *V. paradoxa* and 0.49 for the two species).

Analysis of variance revealed a significant effect of season on transpiration ($p < 0.05$; Table 2), whereas the interactions between season and year or species were not significant ($p > 0.05$; Table 2), suggesting that the differences between seasons do not vary significantly between years or between species. In *V. paradoxa*, transpiration was lower during the dry season than during the rainy season, whereas in *I. doka*, transpiration was slightly higher in the dry season than in the rainy season in three trees out of five. The decrease ranged from 0 to 31 % in *V. paradoxa* and from 0 to 75 % in *I. doka*. During the rainy season, transpiration first increased with VPD and then reached a plateau at higher VPD values (0.8–1.0 kPa) suggesting that stomata probably limited transpiration (Fig. 4). During the dry season, whatever the species, no correlation was found between daily transpiration and VPD.

Whatever the species, the year did not affect transpiration ($p > 0.05$, Table 2) and there was no significant interaction between years and species or season ($p > 0.05$, Table 2).

Discussion

In our study conditions, our findings lead us to reject the hypothesis that agroforestry tree species have a higher transpiration rate than forest tree species. This

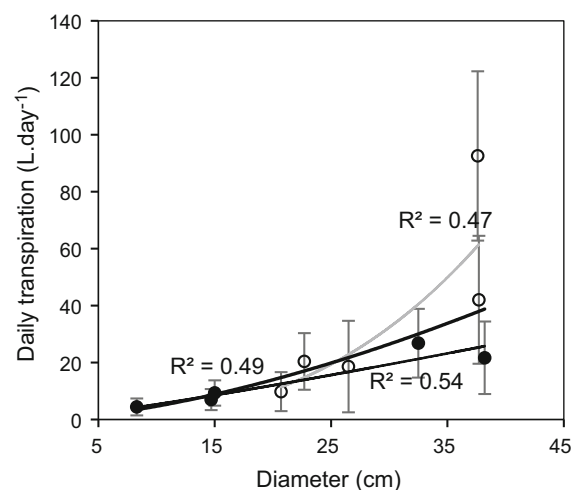
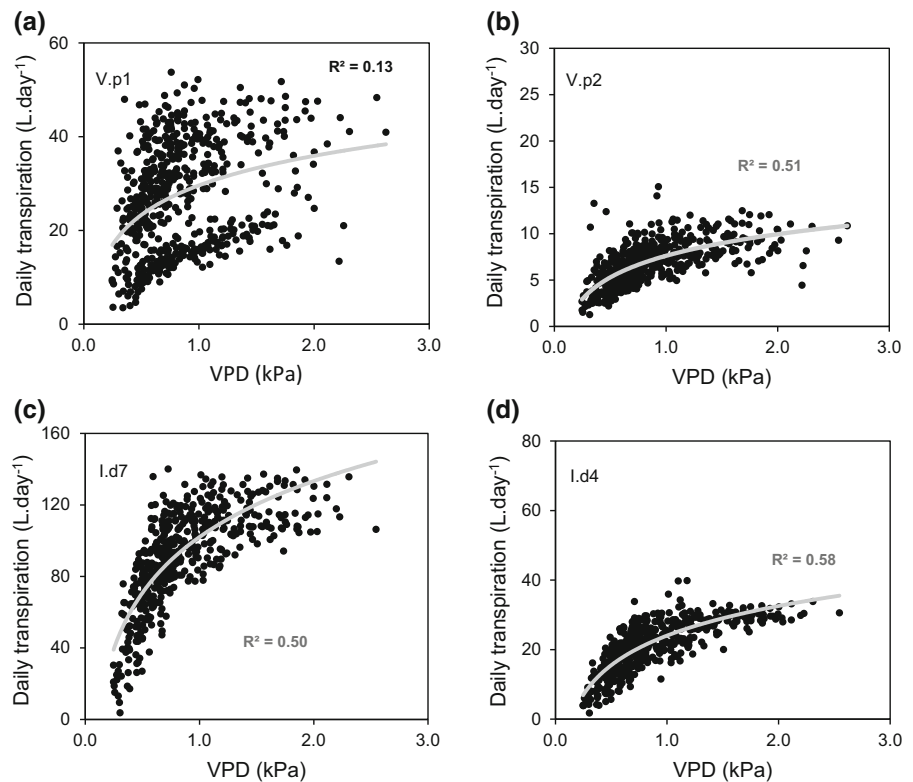


Fig. 3 Relationships between daily transpiration and tree diameter in *Vitellaria paradoxa* in Bira fallow (filled circle) and *Isoberlinia doka* in Belefoungou forest (open circle) both in the North Benin. Each dot represents the mean calculated for 573 and 433 days, respectively, in the rainy and dry seasons for *I. doka*; 562 and 495 days, respectively, in the rainy and dry seasons for *V. paradoxa*. The vertical bars represent standard deviations. The gray line represents the regression line for *I. doka*, the black solid line for *V. paradoxa*, and the fat solid line for the two species. R^2 is the adjusted R -square of each relationship. These non-linear relationships are significant ($p < 0.0001$)

could have several possible causes, probably combined. The relatively smaller diameter of *V. paradoxa* trees in our study is one, since we found that tree diameter is a good predictor of transpiration in both species although it is not the only one (low R^2). The

Fig. 4 Relationship between daily transpiration and VPD in *Vitellaria paradoxa* trees (V.p1 **a**, V.p2 **b**), *Isoberlinia doka* trees (I.d7 **c** and I.d4 **d**) during the rainy season in Bira fallow, and in Belefoungou forest, respectively, both in the North Benin. The solid line is the regression line of the relationship. R^2 is the adjusted R -square of each relationship



difference from what we expected could also be explained by the larger cross-sectional area of the sapwood in *I. doka* compared to *V. paradoxa*. These results confirm the importance of the surface area of sapwood in tree transpiration (Meinzer et al. 2001; Köhler et al. 2009). In addition, the radial profiles of SFD we observed indicate that SFD is higher in the internal part of the sapwood in *I. doka* than in *V. paradoxa*. The ratio of the cross-sectional area of sapwood to that of the tree trunk is now recognized to be governed by the tree hydraulic architecture, which operates at different scales, and defines the efficiency of transport within the plant (West et al. 1999; Meinzer et al. 2005). Specific anatomical and physiological properties such as the structure and density of the sapwood, leaf water content and leaf mass per area (LMA) (Poorter et al. 2009), root structure, and the ratio of leaf area to the cross-sectional area of the stem (West et al. 1999; Issoufou et al. 2015) also control plant hydraulic conductivity, and hence transpiration. We are currently continuing the research presented here by studying water regulation mechanisms in *I. doka* and *V. paradoxa* in order to understand the processes at work.

Bayala et al. (2008) estimated the average annual transpiration in *V. paradoxa* taking into account the azimuthal variations (120-degree intervals around the stem) of the sap flow at 121 L day^{-1} for trees with $\text{DBH} = 64 \text{ cm}$, that is 78 % more than the DBH of the largest trees we studied in Benin ($\text{DBH} = 38.2 \text{ cm}$). This confirms our results showing that the diameter of the stem is a good predictor of transpiration in *V. paradoxa*. In addition, the trees in Bayala's study were probably subject to less competition for water and nutrients, in addition to benefiting from soil improvements by farmers because they were growing in a crop field (Dupraz and Liagre 2008). For the smaller DBH trees, equipped with only one sensor in our study, azimuthal variation of the sap flow is not accounted for, which may lead to bias in transpiration estimation even larger than bias due to ignoring radial variation (Shinozaki et al. 2013).

Research has already been conducted on sap flow over the whole sapwood radius, but in other species and other tropical ecosystems than in our study. The values we obtained for daily transpiration in *V. paradoxa* and *I. doka* in Benin are, respectively, lower and higher than those found by Meinzer et al. (2003) in

Panama in a more humid tropical forest (1800 mm of annual rainfall) in *Cordia alliodora* trees (46 L day⁻¹) with a similar diameter (34 cm) with probes inserted at four depths (17–110 mm). Similarly, the daily transpiration values we obtained in *V. paradoxa* are lower than those found by Köhler et al. (2009) in Indonesia in more humid tropics (2092 mm of annual rainfall) in *Gliricidia sepium* trees (14 L day⁻¹) and *Theobroma cacao* (10 L day⁻¹) with a similar diameter (15 and 10.1 cm, respectively) with probes inserted at three depths (0–72 mm). The maximum SFD values obtained in our study in *V. paradoxa* (DBH = 14.7 cm) are of the same order of magnitude as those obtained in *Acacia tortilis* var. *raddiana* trees (28 L dm² day⁻¹) with smaller diameters (17 cm) in a typical Sahelian climate (280 mm of annual rainfall; Do et al. 2008). Hence, the variation in transpiration between species does not appear to be directly related with the average annual rainfall of the environment in which these species grow but more likely with each species' intrinsic functional adaptive traits to their environment.

The lower transpiration expected during the dry than during the rainy season in the two species was confirmed. The difference was small, which could be linked to the availability of water in the soil all year round and to only short-term (a month at most) partial defoliation during the dry season. Higher rates of transpiration are possible depending on the species. In *Acacia tortilis* var. *raddiana* in a Sahelian climate, Do et al. (2008) observed 70 % of rainy season transpiration during the dry season when it still has leaves, because this species has access to groundwater. Even higher transpiration rates were measured in five species of eucalyptus (*E. miniata*, *E. tetradonta*, *E. latifolia*, *E. capricornia*, and *E. terminalis*) at three sites with, respectively, 1700, 900, and 500 mm of annual rainfall in northern Australia, where 90 % of rainy season transpiration was measured in the dry season (Eamus et al. 2000). The much smaller (15 %) difference in transpiration we observed in *V. paradoxa* between the dry and the rainy seasons in our study indicates that an increase in tree density in agroforestry parklands could be expected to increase the income provided by its nuts, the crop production (Bayala et al. 2015), all the more if its hydraulic redistribution capacity mentioned by Bayala et al. (2008) is confirmed. However, competition between

crops and trees for light also needs to be taken into consideration.

Surprisingly, in some *I. doka* trees, we observed a small increase in transpiration during the dry season compared to the rainy season. This could be explained by evaporative demand in the dry season (average 2.40 versus 0.843 kPa in the rainy season) combined with their better access to the light resource after other trees lost their leaves.

Our study also demonstrated a radial decrease in SFD from the outer part of the sapwood toward the deep sapwood in both the studied species. This result is in agreement with the results of the majority of studies on the non-uniformity of SFD over the radial section of the sapwood, at least in large trees. In *Mangifera indica*, a tropical species, Lu et al. (2000) found that SFD could reach a maximum of 3 L dm² h⁻¹ at the periphery of the sapwood (1.5–3.5 cm), falling below 1 L dm² h⁻¹ (12–14 cm depth). In *Hevea brasiliensis*, Isarangkool Na Ayutthaya et al. (2010) found that sap flow reached maximum, i.e., 2.36 L dm² h⁻¹ (SD = ±0.45) between 0.5 and 2.5 cm below the bark and was zero in the deepest part of the sapwood. These values are in the same range as those we found for *I. doka* (2.56 L dm² h⁻¹ ± 0.88 between 11 am to 3 pm over the three-year study period) and for *V. paradoxa* (1.68 L dm² h⁻¹ ± 0.68 between 11 am to 3 pm the three-year study period). In four tropical species (*Anacardium excelsum*, *Ficus insipida*, *Cordia alliodora*, and *Schefflera morototoni*) in Panama, James et al. (2002) found that SFD was highest in the first four centimeters under the bark. The same decrease was observed in *Eucalyptus urophylla*, although it began only at a depth of 3–4 cm in the sapwood (Zhou et al. 2002). Disregarding interspecies variations in absolute flow values, several hypotheses have been put forward to explain this decrease. According to Granier (1987), it is caused by differences in the exposure of leaves to incident radiation. SFD at a given point depends on the water conductivity of the sapwood at that point, which in turn depends on the transpiring (photosynthetically active) leaf area linked to that part of the sapwood (Spicer and Gartner 2001). Another possible explanation is that the internal part of sapwood supplies the oldest branches at the bottom of the crown with water. These leaves would thus be more shaded than those on higher younger branches (Dye et al. 1991; Jiménez et al. 2000). However, according to Gartner and Meinzer (2005),

in deciduous species, there is not necessarily a direct connection between the old branches and the internal older portion of the sapwood. The lower water conductivity of the internal sapwood could be due to the presence of vessels that are less functional simply because they are older, but not necessarily related to leaf architecture (Ford et al. 2004). SFD at a given point of the sapwood also depends on the water available in the soil to which the connected root has access (Nadezhkina et al. 2007; Bart et al. 2015). Lastly, in addition to the lower value of SFD toward the center of the sapwood, the probes cover a smaller area for an equivalent segment of the radius of the sapwood than they do at the periphery (25 mm in our study), which contributes to the lower share of the internal sapwood in the total flow of the tree.

Conclusion

Transpiration per tree was found to be higher in *I. doka* than in *V. paradoxa* in our study conditions. If the same result is obtained in other situations, this would confirm that the woody cover of the Sudanian agroforestry system is less efficient in recycling local rainfall toward the atmosphere than the forest cover, not only through lower tree density but also through species composition. More investigations are needed on such processes in shea parklands, in fallows as well as in food crop fields, to fully explain their functionality and propose “environment smart” management options to improve the performance of the overall system.

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