The determinants of tropical forest deciduousness: disentangling the effects of rainfall and geology in central Africa

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Summary

1. Understanding the environmental determinants of forests deciduousness i.e. proportion of deciduous trees in a forest stand, is of great importance when predicting the impact of ongoing global climate change on forests. In this study, we examine (i) how forest deciduousness varies in relation to rainfall and geology, and (ii) whether the influence of geology on deciduousness could be related to differences in soil fertility and water content between geological substrates.

2. The study was conducted in mixed moist semi-deciduous forests in the northern part of the Congo basin. We modelled the response of forest deciduousness to the severity of the dry season across four contrasting geological substrates (sandstone, alluvium, metamorphic and basic rocks). For this, we combined information on forest composition at genus level based on commercial forest inventories (62 624 0.5 ha plots scattered over 6 million of ha), leaf habit, and rainfall and geological maps. We further examined whether substrates differ in soil fertility and water-holding capacity using soil data from 37 pits in an area that was, at the time, relatively unexplored.

3. Forest deciduousness increased with the severity of the dry season, and this increase strongly varied with the geological substrate. Geology was found to be three times more important than the rainfall regime in explaining the total variation in deciduousness. The four substrates differed in soil properties, with higher fertility and water-holding capacity on metamorphic and basic rocks than on sandstone and alluvium. The increase in forest deciduousness was stronger on the substrates that formed resource-rich clay soils (metamorphic and basic rocks) than on substrates that formed resource-poor sandy soils (sandstone and alluvium).

4. *Synthesis.* We found evidence that tropical forest deciduousness is the result of both the competitive advantage of deciduous species in climates with high rainfall seasonality, and the persistence of evergreen species on resource-poor soils. Our findings offer a clear illustration of well-known theoretical leaf carbon economy models, explaining the patterns in the dominance of evergreen versus deciduous species. And, this large-scale assessment of the interaction between climate and geology in determining forest deciduousness may help to improve future predictions of vegetation distribution under climate change scenarios. In central Africa, forest is likely to respond differently to variation in rainfall and/or evapotranspiration depending on the geological substrate.

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Introduction

The deciduous leaf habit, i.e. seasonal leaf loss due to unfavourable growth conditions, is a key functional attribute of some tree species. It indicates that tree growth is seasonally suppressed, which has effects on carbon, water and nutrient cycling. Thus, understanding which environmental factors determine the degree of forests' deciduousness, i.e. proportion of deciduous trees in a forest stand, is of great importance when predicting the impact of ongoing global climate change on the functioning of forests.

In tropical forests, the deciduous leaf habit is a successful strategy to cope with seasonal drought. Trees can avoid drought stress by shedding their leaves in the dry season (Borchert, Rivera & Hagnauer 2002). Thus, rainfall may primarily determine tropical forests' deciduousness, due to changes in soil water availability and plant water status (Reich & Borchert 1984; Borchert 1994). It has been shown that forest deciduousness increases as annual rainfall decreases, or as the length and severity of the dry season increases (Reich 1995; Borchert 1998; Condit *et al.* 2000; Bohlman 2010; Gond *et al.* 2013). It has also been highlighted that geology can significantly alter this relationship (Condit *et al.* 2000; Bohlman 2010), probably through differences in soil resource availability between geological substrates. For instance, when relating annual rainfall to the average deciduousness found on seven volcanic and ten sedimentary geological substrates in central Panama, Bohlman (2010) found a drastic difference in forest deciduousness on a limestone substrate (the Tau geological formation) compared with other substrates exposed to the same rainfall level. However, there are only a limited number of studies looking at how forest deciduousness varies with rainfall and geology or soil characteristics, and most of these are based on remotely sensed data (Bohlman 2010; Gond *et al.* 2013), or on small numbers of forest inventory plots (Condit *et al.* 2000).

In addition, whether soil water or nutrient availability modulates the response of tropical forest deciduousness to rainfall seasonality across geological substrates remains to be addressed. First, soil water reserves may buffer the effect of climatic drought, enabling the persistence of drought-intolerant evergreen species. Indeed, spatial variation in soil water content has been found to drive spatial variation in leaf habit, with evergreen species associated with high soil water content (low-elevation moist sites, Méndez-Alonzo *et al.* 2013; deep soils having high available water capacity, Murata *et al.* 2009), and deciduous species associated with low soil water content (hills or shallow soils). Second, soil nutrient availability may also drive forest deciduousness (Mackey 1993). For instance, under the same rainfall regime, evergreen vegetation is present on acid and unfertile soils, while deciduous vegetation dominates on less acid and more fertile soils in the subtropical dry forests of north-western Mexico (Goldberg 1982) and Thailand (Ishida *et al.* 2006).

Plant species world-wide are distributed along a general continuum of plant strategies, from the conservative strategy of resource use to the acquisitive strategy (Wright *et al.* 2004; Reich 2014). The resource-conservative strategy is associated with plant traits that allow persistence in stressful environments, these include slow growth, low nutrient loss rates, and long life span and high density of the tissues. The strategy of rapid acquisition of resources, which confers an advantage in resource-rich environments, is associated with the opposite suite of traits. A long leaf life span is a key trait attribute of conservative species, and is usually associated with the evergreen leaf habit (Chabot & Hicks 1982). Therefore, nutrient-poor soils should favour species with a conservative strategy, i.e. with a long leaf life span and thus an evergreen leaf habit, while nutrient-rich soils should favour acquisitive fast growing species with short leaf life span and a deciduous leaf habit to avoid the unfavourable growth period (Aerts 1995; Givnish 2002). Thus, in climates with seasonal drought, we should expect a trade-off between a deciduous habit enabling plants to cope with drought and an evergreen habit enabling them to cope with nutrient shortages.

In this study, we aimed: (i) to examine how forest deciduousness varies in relation to climate and geology across large spatial scale in central African moist forests, and (ii) to determine in which extent an effect of geology on the deciduousness-climate relationship could be explained by differences in soil nutrient content and water availability between geological substrates. For this purpose, we combined information on forest composition at genus level based on a huge data set of commercial forest inventories compiled by logging companies (62 624 0.5 ha plots scattered over 6 million ha of land); leaf habit from a trait database; rainfall and geological maps; and published and unpublished soil data. Unlike Condit *et al.* (2000) and Bohlman (2010), who focused on annual rainfall, we assumed that the relevant feature of the highly seasonal rainfall regime in central Africa that determines forest deciduousness is the climatological water deficit accumulated over the long dry season (Maximum Climatological Water Deficit (MCWD) index, Aragão *et al.* 2007; Malhi *et al.* 2009). Indeed, it has been demonstrated that MCWD reflects the distribution of tropical forests (dry, moist and wet forests) better than annual rainfall (Zelazowski *et al.* 2011). However, to allow direct comparisons with the other studies, we also related forest deciduousness to annual rainfall. Finally, we specifically expected to find evidence of a strong influence of geology on forest deciduousness, as geology is the primary factor driving tree species distribution in the study area (Fayolle *et al.* 2012). Under the same rainfall regime, forest

deciduousness should be lower on geological substrates that led to nutrient-poor soils (evergreen conservative species should be favoured) than on geological substrates that led to nutrient-rich soils.

Materials and methods

VEGETATION DATA

The study was conducted in the northern part of the Congo basin (0°3′–4°4′ N, 13°3′–18°7′ E), spanning the borders of Cameroon, Central African Republic, and Republic of Congo (Fig. 1). The vegetation corresponds to the mixed moist semi-deciduous forests of the Guineo-Congolian Region including patches of evergreen forests (White 1983), or to the central African moist forests (Fayolle *et al.* 2014b). Both geological and historical factors have influenced forest composition (Fayolle *et al.* 2012, 2014b). In semi-deciduous forests (composed of a mix of deciduous and evergreen species), most canopy species are deciduous and light-demanding (White 1983), and their local abundance can be explained by short- and long-term human disturbances (shifting cultivation, Morin-Rivat

et al. 2014). They mostly belong to Malvaceae (Sterculiaceae), Meliaceae, Sapotaceae, Ulmaceae (Cannabaceae) and Fabaceae families.

Commercial forest inventories were conducted in 21 logging concessions between 2000 and 2007. Sampling was standardized and systematic in all concessions, and consisted of continuous 25 m wide transects, separated on each side by 2–3 km, and subdivided into rectangular 0.5-ha plots of 25 m by 200 m or 20 m by 250 m (Réjou-Méchain *et al.* 2011; Fayolle *et al.* 2012, 2014a). All trees with diameter at breast height (dbh ≥ 30 cm) were measured for their dbh, and identified with a vernacular name in 62 624 plots of 0.5 ha (98.96% of the plots were of 0.5 ha, others range between 0.05 and 1 ha). Vernacular names were converted to species-level scientific names when possible. Taxonomy was revised and homogenized according to the African plant database (available online http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php). The analyses were conducted at the genus level because vernacular names used in the field during forest inventory are more reliable at genus level than at the species level (Réjou-Méchain *et al.* 2011). A total of 247 genera were recorded in the study area.

We considered two traits: (i) leaf habit (evergreen or deciduous) considering that a deciduous leaf habit meaning that the species was
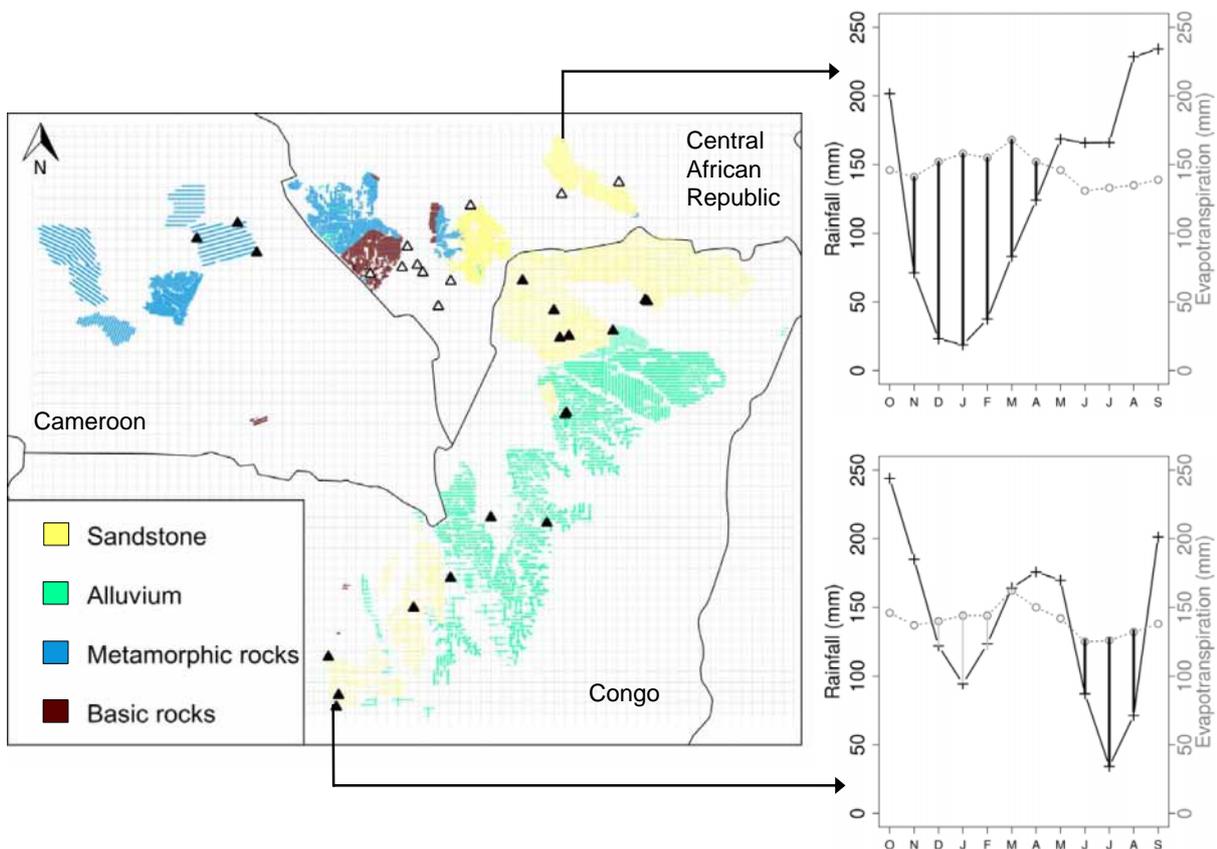
Fig. 1. Location of the 62 624 0.5 ha inventory plots coloured according to the geological substrate. The locations of the 19 soil pits dug for the purpose of this study (dark triangle) and of the 18 pits gathered from published studies (triangle) are also indicated. The 8 × 8 km grid (light grey) constructed to work out the fraction of deciduous trees and country borders (dark grey) are shown in the background. The right panel shows two contrasting 8 × 8 km cells in terms of rainfall regime (black crosses) and evapotranspiration (grey circles). The main seasonal cycle of rainfall is a pronounced dry season during boreal winter. In the south of the area, this pattern is associated with an additional short dry season during boreal summer. During dry seasons, evapotranspiration is higher than rainfall, the difference between evapotranspiration and rainfall being the water deficit (WD, in mm). For each dry season, a cumulative WD over the dry months can be computed as the sum of WD over those dry months (area hatched). Maximum climatological water deficit (MCWD) is defined as the cumulated WD of the driest dry season, i.e. the dry season with the greatest cumulated WD (area hatched in black).

totally leafless for some period of the year; (ii) regeneration guilds *sensu* Hawthorne (1995): pioneers (P) require gaps for establishment, non-pioneer light-demanding (NPLD) species can establish in shade but need a gap to grow to their full height, and shade bearer (SB) species can be found in shade both as young and older plants. Among pioneers, we distinguished short-lived and long-lived pioneer species (Meunier, Moumbogou & Doucet 2015). Traits information (leaf habit and regeneration guild) at genus level was obtained from a trait data base at species level (see data accessibility section). The most frequent leaf habit or regeneration guild observed within a genus was attributed to this genus. The resulting list was then improved by field expertise (J.-L. Doucet). When there was no information available, or no tendency of trait conservatism at the genus level, the genus was ignored in the trait calculation. Among the 247 genera, 62 were recorded as deciduous and 150 as evergreen, 52 as short-lived P, 13 as long-lived P, 47 as NPLD and 97 as SB (see Appendix S1 and S2 in Supporting Information).

CLIMATE DATA

Monthly rainfall was modified from WorldClim database (Hijmans *et al.* 2005) to correct for an anomalous rainfall spatial pattern in the centre of the study area due to an outlier pattern (reverse seasonality) in a FAOCLIM 2.0 Ngoundji climate station (Gommes, Grieser & Bernardi 2004). This station is located at the border between Cameroon and Central African Republic (3°54′3.71″ N 15°6′54.65″ E). We removed the area seemingly influenced by the anomaly, and reapplied WorldClim interpolation methodology, i.e. thin-plate spline using latitude, longitude and elevation as independent variables, to the remaining data and to the 10 FAOCLIM 2.0 rainfall station 1960–1990 data (as used to compute WorldClim data, Gommes, Grieser & Bernardi 2004) in the removed area (see Appendix S3 for an illustration).

Monthly potential evapotranspiration was taken from CGIAR-CSI Global-Aridity and Global-PET Database (Zomer *et al.* 2007, 2008), which was estimated from WorldClim temperature data according to Heargraves method. As Ngoundji station did not provide any temperature data, we did not have to remove the area influenced by this station as for rainfall. Hence, the PET data base was consistent with the WorldClim rainfall data, despite the necessity to manipulate the later.

The annual rainfall varied between 1492 mm and 1737 mm over the study area. The main seasonal cycle of rainfall is a pronounced dry season lasting from 3 to 6 months during boreal winter. In the southern part of the study area, this pattern is associated with an additional short dry season lasting from 1 to 3 months during boreal summer (Fig. 1). During dry seasons, evapotranspiration is higher than rainfall, the difference between evapotranspiration and rainfall being the water deficit (WD, in mm). For each dry season, a cumulative WD over the dry months can be computed as the sum of WD over those dry months. Maximum climatological water deficit (MCWD) is defined as the cumulated WD of the driest dry season, i.e. the dry season with the greatest cumulated WD (Fig. 1). This measure of climatological dryness has been shown to be a good predictor of the distribution of humid tropical forest and other biomes within the tropics (Malhi *et al.* 2009; Zelazowski *et al.* 2011).

GEOLOGY AND SOIL PROPERTIES

We analysed the relationship between forest deciduousness and MCWD for four contrasting geological substrates (Fig. 1): sandstone (32% of the plots), alluvium (39%), metamorphic rocks (23%) and basic rocks (6%). We selected these four substrates from the eight

previously identified in the study area (Fayolle *et al.* 2012) based on their dominance and the presence of soil data.

To understand the relationship between forest deciduousness and MCWD for the geological substrates, we estimated soil nutrients and water availability for each of the substrates. We first used the Harmonized World Soil Database (HWSD, FAO, IIASA, ISRIC, ISS-CAS & JRC 2008) to determine the most common HWSD soil map unit that occurred on each substrate (Appendix S4). An HWSD soil map unit is composed of several soil types in estimated proportions (ISRIC-WISE global dataset of soil properties, Batjes 2006). We chose the most common soil type to estimate soil properties (Appendix S4). The ISRIC-WISE global data set of soil properties (Batjes 2006) provides for each soil type estimates of water-holding capacity, clay content and common indicators of soil chemical fertility, such as total organic carbon content (C), cation exchange capacity (CEC), pH in water and the ratio between C and nitrogen content.

The indicators of soil fertility and water-holding capacity for the geological substrates could only be roughly estimated from the global soil map and the ISRIC-WISE soil properties. We thus compared those estimations with physical and chemical properties measurements of soil samples taken from a total of 37 pits. Namely, we assembled soil data from 19 pits dug in the study area in 2010 and 2011 (V. Freycon & J.F. Gillet, unpubl. data), and soil data from 18 pits described in grey literature (Fig. 1, Appendix S5). Of the 37 pits, 20 were over sandstone, five over alluvium, seven over metamorphic rock and five over basic rock. In the first 19 pits, with a maximum depth of between 90 and 140 cm, layers were delineated and a sample was collected for each layer. The percentage of coarse fragments (> 2 mm, cf, %) of each sample was visually estimated at this time. Samples were then analysed at the Water, Soil and Plant Analysis laboratory of CIRAD (centre de Coopération Internationale en Recherche Agronomique pour le Développement), Montpellier (France). Soil texture (clay, sand and silt fractions) was determined using the pipette method, soil bulk density (bd, g cm^{-3}) was determined using the cylinder method, and the amounts of water held in the soil at field capacity (θ_{FC}, pF2, matric potential of -0.01 MPa) and at the permanent wilting point (θ_{PWP}, pF 4.2, matric potential of -1.5 MPa) were quantified. Soil pH was measured both in water and KCl 1 mol L^{-1}; organic carbon (C) and nitrogen (N) fractions were measured by the dry combustion method; cation exchange capacity (CEC) was determined using the ammonium acetate (pH 7) method (exchangeable basic cations potassium (K), Sodium (Na), Calcium (Ca), Magnesium (Mg), and exchangeable acid cations Hydrogen (H), and Aluminium (Al) were measured). Available phosphorus (P) was measured using the Bray II method and total phosphorus was determined colorimetrically by a molybdenum blue method. These first 19 pits did not cover basic rock substrate, so we collected from the literature additional measures of soil characteristics, i.e. clay, sand and C content and cf (18 pits, Appendix S5).

To estimate indicators of soil chemical fertility for each substrate, we used the soil properties measured in the topsoil layers, which varied between 0–5 and 0–20 cm. We selected the same indicators as those estimated from the ISRIC-WISE data base (clay content, C, CEC, pH in water, and C/N ratio), as well as available P and exchangeable Ca concentration, which have been found to determine tree species distribution in lowland tropical forests (Sollins 1998). Clay and carbon content were measured for all 37 pits covering all geological substrates. In contrast, C/N ratio, CEC, available P and exchangeable Ca concentration were only measured for the first 19 pits, these indicators were thus not measured for basic rock substrate. We tested if our soil data set, which was derived from heterogeneous

sources, showed the expected relationships between soil clay content and (i) carbon content (Ohta *et al.* 1993), (ii) CEC (Martel, De Kimpe & Laverdière 1978; Parfitt, Giltrap & Whitton 1995), and (iii) water-holding capacity (Pidgeon 1972; van den Berg *et al.* 1997), by using Pearson correlations when the number of observations *n* was > 30 and Spearman rank correlations when $n \leq 30$.

We calculated the soil Plant-Available Water capacity (PAW, in millimetres of water) for each layer of the 37 pits following Cazemier, Lagacherie & Martin-Clouaire (2001):

$$PAW = dh * bd * [(100 - cf)/100] * (\theta_{FC} - \theta_{PWP}) \qquad \text{eqn 1}$$

where dh is the width of the soil layer, bd is the bulk density, cf is the percentage of coarse fragments, θ_{FC} is the amount of water held in the soil at field capacity, and θ_{PWP} is the amount of water held in the soil at the permanent wilting point. For the 18 pits described in the grey literature, missing values (bd, θ_{FC}, and θ_{PWP}) were predicted based on the observed relationship with clay and sand content for θ_{FC} and θ_{PWP} (Batjes 1996; van den Berg *et al.* 1997), and with total organic carbon content for bd (Appendix S6). PAW was calculated for each soil layer, and we summed the layers' values to obtain a PAW for each pit. Because rooting depth was unknown, we could not define the maximum PAW. We thus standardized PAW and expressed it for a depth of 1 m of soil to account for differences in $PAW_{1\ m}$ across geological substrates.

DATA ANALYSIS AND MODELLING

To examine how forest deciduousness varies in relation to rainfall seasonality and geology over the large scale, we smoothed local heterogeneity by calculating forest deciduousness on an 8 × 8 km (6400 ha) grid. This also reduced the spatial autocorrelation between observations. To create homogeneous cells within each geological substrate, we built a grid for each geological type and excluded cells with < 10 ha total inventoried area. A total of 320 cells totalling 2709 plots were excluded, and these plots are not included in the previously mentioned 62 624 plots. This resulted in a total of 890 cells with a total sampled area ranging from 10 to 99.5 ha in each cell: 321 cells were located on sandstone substrate, 349 on alluvium, 179 on metamorphic rocks and 41 on basic rocks. The index for the severity of the dry season MCWD and annual rainfall initially available at 1 km spatial resolution were averaged for each cell. We also estimated for each cell the most common HWSD soil map unit by the proportion of plot occurrences. We then estimated the most common soil type and corresponding ISRIC-WISE indicators of resource availability. We found a total of 17 soil map units in our study area. Because different soil map units may have similar most common soil type, it resulted in seven dominant soil types in the study area (Appendix S4).

For each cell, forest deciduousness (%) was calculated as the fraction of trees' basal area (dbh $\geq$ 30 cm) that belonged to a genus recorded as deciduous. As plots can have a different sampled area (from 0.05 to 1 ha), we expressed trees' basal area for one ha plot before calculations. Forest deciduousness was computed for only trees belonging to long-lived P, NPLD, and SB genera. Indeed, stands that are recovering from recent disturbance tend to be more deciduous than late-successional stands (Réjou-Méchain *et al.* 2014, in this study 38.7% of the genera recorded as deciduous were short-lived pioneers, Appendix S2). Nevertheless, it should be noted that calculating the fraction across all genera produced similar results (Appendix S7).

We used a weighted multiple regression to examine the effect of (i) MCWD (quantitative variable), (ii) geological substrate (qualitative variable), and (iii) the interaction between (i) and (ii) on forest deciduousness (%). The sampled area within each cell was used to weight the observations (weights ranged from 10/99.5 = 0.1 for the smallest cell to 99.5/99.5 = 1 for the largest cell). We further checked whether there was any residual effect of the successional stage (*sensu* Réjou-Méchain *et al.* 2014) on forest deciduousness (Appendix S8). To compare our results with those of Condit *et al.* (2000) and Bohlman (2010), we also explored the relationship between forest deciduousness and annual rainfall instead of MCWD. In order to investigate the influence of soil physical and chemical properties on forest deciduousness, we removed the effect of climate by considering the residuals of the overall model between forest deciduousness and MCWD. We assessed how soil water and nutrient availability co-varied in the study area by using Spearman rank correlations (*n* = 7). We then performed weighted simple linear regressions (the weights still being the sampled area) of these residuals against each indicator of soil nutrient and water availability separately. All analyses were conducted using R software (R Core Team 2013).

Results

DETERMINANTS OF FOREST DECIDUOUSNESS

Forest deciduousness was strongly variable over the study area, ranging from 6.0% to 88.5%. The multiple regression model fitted the data well (Appendix S8), and explained 65.73% (R^2) of the total variation in deciduousness. The relative contribution of geology to the variation in forest deciduousness was 46.3%, three times stronger than the one of the severity of the dry season (MCWD, 14.2%). The interaction between geology and MCWD was also significant and explained 5.2% of the variation. As expected, forest deciduousness increased with MCWD, and geology significantly altered the relationship (Fig. 2). The overall equation for predicting deciduousness from MCWD was $0.22 + MCWD * 6.4 \times 10^{-4}$ (Table 1). Regression slope estimates were significantly higher on metamorphic and basic rocks (slope between 9.2×10^{-4} and 21.1×10^{-4}) than on alluvium and sandstone substrates (slope between 4.3×10^{-4} and 8.9×10^{-4}, Table 1a), suggesting that forest deciduousness increased with MCWD significantly faster on metamorphic and basic rocks than on alluvium and sandstone. Furthermore, the intercept was significantly higher on alluvium than on sandstone substrate (Table 1b), suggesting that although deciduousness increased with MCWD equally slowly on these two substrates, deciduousness was generally higher on alluvium than on sandstone.

When forest deciduousness was related to annual rainfall instead of MCWD, the relationship was less clear overall and not conserved for some geological substrates (Appendix S9). In some areas (especially on alluvium substrates), annual rainfall was not correlated with MCWD, and a strong variability in the severity of the dry season could be found for similar amounts of annual rainfall.
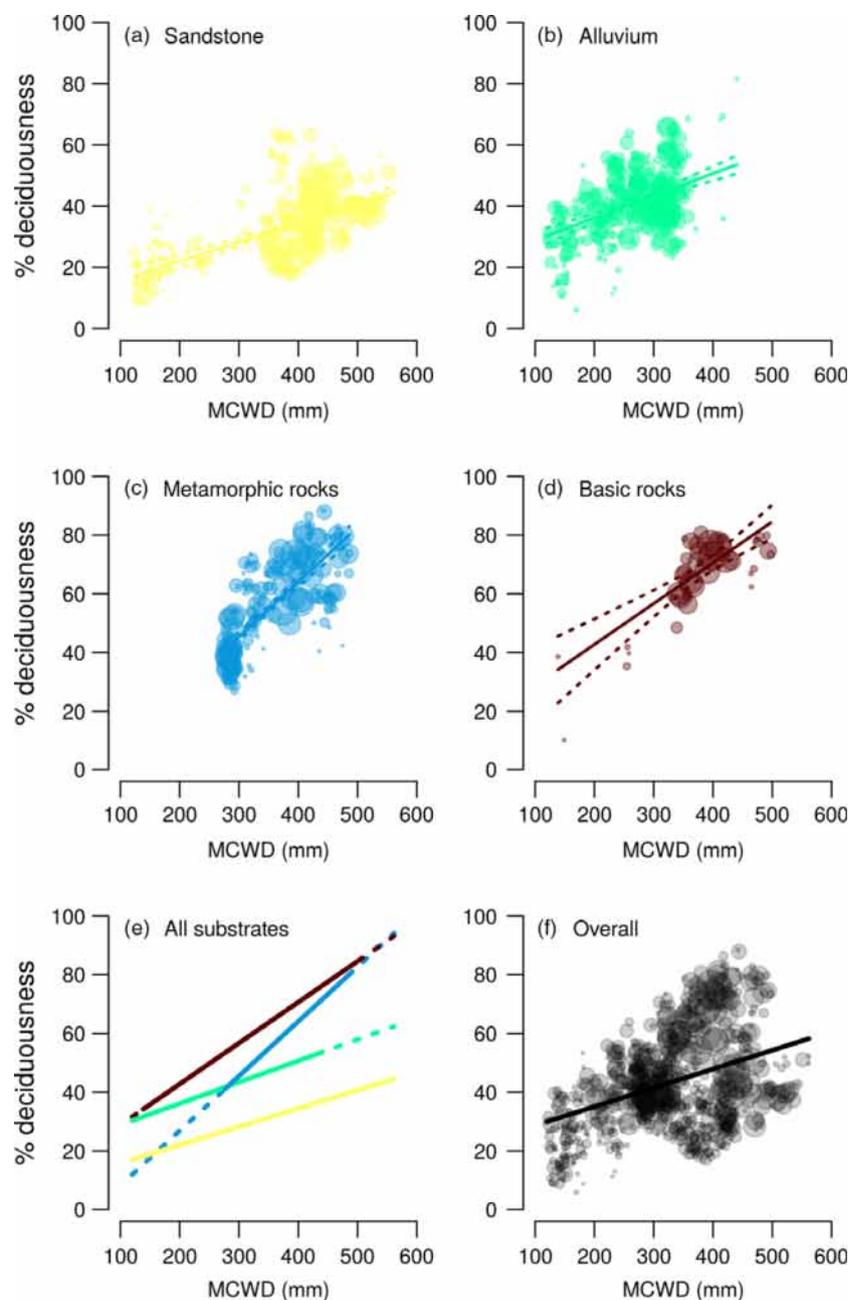
Fig. 2. Relationships between forest deciduousness (%) and Maximum Climatological Water Deficit (MCWD) for the four geological substrates – (a) sandstone, (b) alluvium, (c) metamorphic rocks and (d) basic rocks) – with model fitted values (solid lines) and 95% confidence intervals (dotted lines). Symbol size corresponds to sampled area that was used as weights in the model. For easier comparison of the relationships between substrates, model fitted values of all substrates are shown in (e). The overall relationship between forest deciduousness and MCWD whatever the geological substrate is shown in (f).

SOIL NUTRIENTS AND WATER-HOLDING CAPACITY ACROSS GEOLOGICAL SUBSTRATES

Using the world soil map HWSD, we found that dominant soil types differed between the four geological substrates (Appendix S4). Arenosols were the most common soils on sandstone, whereas Xantic Ferralsols dominated on alluvium, and Orthic Ferralsols on metamorphic and basic rocks (Table 2a). According to the ISRIC-WISE data base, soil properties differed between soil types with increasing water-holding capacity and chemical fertility (as suggested by clay content, organic carbon content and CEC) between Arenosols, Xantic Ferralsols and Orthic Ferralsols (Table 2b).

Remarkably, the gradient in fertility indicators (clay content, CEC, organic carbon content) and water-holding capacity

($PAW_{1\ m}$) estimated from the ISRIC-WISE global data base found across the geological substrates was confirmed by the measurements from the 37 pits (Table 2, Appendix S5). Soils that developed on sandstone were characterized by low chemical fertility and water-holding capacity compared to soils that developed on metamorphic and basic rocks, and to a lesser extent on alluvium. First, the four substrates differed in topsoil texture: clay content was lower on sandstone (10%), alluvium (24%) and metamorphic rocks (30%) than on basic rocks (69%, Table 2c), while sand content exhibited the opposite pattern (Appendix S5). Second, as expected, clay content turned out to be a good proxy for soil carbon content and CEC, as well as for water-holding capacity. Topsoil clay content was correlated with C which was relatively low on sandstone, medium on alluvium and basic rocks, and high on

Table 1. (a) Slope and (b) intercept estimates of the linear relationship between forest deciduousness and Maximum Climatological Water Deficit (MCWD) for the four geological substrates and overall, with their standard errors (se), and lower (CI_{low}) and upper bounds (CI_{up}) of their 95% confidence interval

	Geological substrates				
Model parameters	Sandstone	Alluvium	Metamorphic rocks	Basic rocks	Overall
(a) Slope					
Estimate	6.2×10^{-4}	7.3×10^{-4}	18.6×10^{-4}	13.9×10^{-4}	6.4×10^{-4}
Se	1×10^{-4}	0.8×10^{-4}	1.3×10^{-4}	2.4×10^{-4}	0.5×10^{-4}
CI_{low}	4.3×10^{-4}	5.7×10^{-4}	16.1×10^{-4}	9.2×10^{-4}	5.4×10^{-4}
CI_{up}	8.2×10^{-4}	8.9×10^{-4}	21.1×10^{-4}	18.7×10^{-4}	7.4×10^{-4}
(b) Intercept					
Estimate	0.0956	0.2161	−0.1035	0.1488	0.2229
Se	0.0310	0.0225	0.0411	0.0921	0.0181
CI_{low}	0.0347	0.1720	−0.1841	−0.0319	0.1872
CI_{up}	0.1566	0.2603	−0.0228	0.3296	0.2585

Table 2. Soil indicators estimated for the four geological substrates: (a) dominant soil type (see appendix S4); (b) ISRIC-WISE derived soil properties; and (c) median values of the soil properties measured for topsoil samples collected from 37 pits covering the four substrates (20, 5, 7 and 5 pits located on sandstone, alluvium, metamorphic rocks and basic rocks respectively). In (c) the 5th and 95th percentiles are also shown in parentheses

	Geological substrates			
Soil indicators	Sandstone	Alluvium	Metamorphic rocks	Basic rocks
(a) Dominant soil type				
Soil type	Arenosols	Xantic Ferralsols	Orthic Ferralsols	Orthic Ferralsols
(b) ISRIC-WISE soil properties				
Clay (%)	6	34	39	39
Sand (%)	89	54	43	43
Organic C (%)	3.3	13.2	15.2	15.2
CEC ($cmol_c$ kg^{-1})	2.5	6.3	9.7	9.7
pH in water	5.6	4.5	4.9	4.9
C/N	13	13	13	13
$PAW_{1\ m}$ (mm)	88	204	300	300
Drainage	Extremely drained	Well drained	Well drained	Well drained
(c) Measured soil properties				
Clay (%)	10 (5; 21)	24 (17; 34)	30 (21; 48)	69 (31; 77)
Sand (%)	88 (77; 93)	73 (63; 82)	60 (39; 72)	17 (10; 59)
Organic C (%)	1.7 (0.7; 2.9)	2.3 (1.1; 3.5)	2.8 (2.0; 5.3)	2.2 (1.9; 4.3)
CEC ($cmol_c$ kg^{-1})	3.7 (2.3; 6.7)	5.0 (3.9; 8.6)	8.3 (7.5; 10.5)	–
pH in water	3.9 (3.6; 4.7)	4.2 (3.6; 4.8)	4.7 (4.2; 4.9)	–
C/N	16 (14; 20)	16 (13; 22)	12 (11; 12)	–
Exchangeable Ca ($cmol_c$ kg^{-1})	0.05 (0.04; 0.24)	0.08 (0.04; 0.79)	1.25 (0.89; 3.04)	–
Available P (mg kg^{-1})	5.3 (3.6; 10.8)	7.4 (4.6; 24.3)	4.4 (4.4; 5.6)	–
$PAW_{1\ m}$ (mm)	50 (42; 83)	71 (50; 99)	87 (32; 112)	135 (97; 139)

metamorphic rocks (Table 2c, $r = 0.44$, P-value = 0.006, $n = 37$). Clay content was also strongly positively correlated to CEC ($r_S = 0.77$, P-value = 0.014, $n = 19$), and $PAW_{1\ m}$ ($r = 0.85$, P-value = 4.8×10^{-11}, $n = 37$), which gradually increased from sandy soils on sandstone (50 mm) and on alluvium (71) to clay soils on metamorphic (87) and basic rocks (135). These figures suggest a gradient in chemical fertility and water-holding capacity from soils on sandstone, alluvium and metamorphic rocks, to those on basic rocks.

The gradient in chemical fertility could be refined for the three substrates for which C/N ratio, Ca, and available P content were available. C/N ratio was higher and similar on sandstone and alluvium (16, Table 2c) than on metamorphic rocks (12), suggesting that soils on sandstone and alluvium have similar levels of reduced soil biological activity leading to slow decomposition rates. Exchangeable Ca concentration was relatively higher on metamorphic rocks (1.25 $cmol_c$ kg^{-1}) than on sandstone and alluvium (0.05 and 0.08 respectively), whereas available P content was relatively higher on alluvium (7.4 mg kg^{-1}) than on sandstone (5.3) and metamorphic rocks (4.4).

RELATIONSHIP BETWEEN FOREST DECIDUOUSNESS AND SOIL PROPERTIES

Forest deciduousness (after removing the effect of climate) significantly increased with clay content, organic carbon content and CEC (Fig. 3). It significantly decreased with

sand content, C/N ratio and pH. These relationships (except for pH) suggest an increase in forest deciduousness with soil chemical fertility, in agreement with the analysis of the geological substrates. The strength of the relationship between forest deciduousness and soil properties was found to be higher for clay content (R^2 = 0.36), than for pH (0.15) and CEC (0.07). The relationship between forest deciduousness and soil pH appeared ambiguous. Deciduousness was negatively correlated with pH (Fig. 3), whereas it increased from sandstone (pH = 3.9), alluvium (pH = 4.2), to metamorphic rocks (pH = 4.7, Table 2c), suggesting a positive relationship between deciduousness and pH at geological level.

Forest deciduousness (after removing the effect of climate) significantly increased with soil water availability ($PAW_{1\,m}$, Fig. 3), and this seems counterintuitive, but could be easily explained by the co-variation between soil nutrient and water availability observed in the area. Indeed, we found that $PAW_{1\,m}$ was positively correlated with clay content (r_S = 0.84, *P*-value = 0.02, *n* = 7), soil organic carbon content (r_S = 0.99, *P*-value = 1.46 × 10^{-5}, *n* = 7) and CEC (r_S = 0.93, *P*-value = 0.01, *n* = 6).

Discussion

In this study, we showed that forest deciduousness increases with increasing severity of the dry season, and that geology clearly alters this relationship through differences in soil resource availability between geological substrates. To our knowledge, this is the first time that the effect of soil properties on the deciduousness–climate relationship has been evidenced at a large scale. This was possible by collating forest inventory data, trait information, environmental data (rainfall, geological and soil maps), and physical and chemical properties of soils at specific sites.

THE ADVANTAGE OF SHORT-LIVED LEAVES WHEN SEASONALITY INCREASES

As expected, forest deciduousness increased with the severity of the long dry season (MCWD) for the four geological substrates studied. This result suggests the benefits of the deciduous leaf habit at sites with high rainfall seasonality because it acts as a drought avoidance mechanism (Chabot & Hicks 1982; Givnish 2002). Shedding leaves during the season
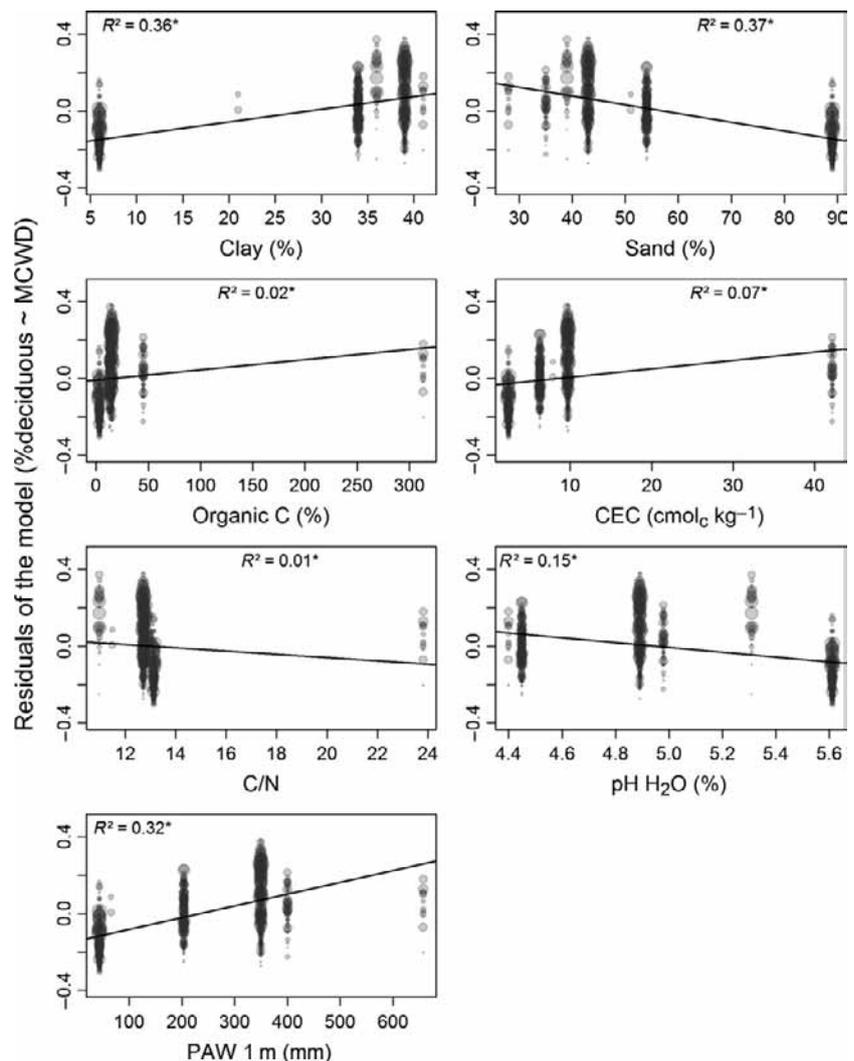

Fig. 3. Residuals of the overall regression between forest deciduousness and MCWD against estimated soil properties. These residuals can be considered as deciduousness after removing the effect of climate. Soil properties were the soil properties estimated for the most common soil type of a soil map unit. The coefficient of determination R^2 is indicated, a star meaning that the slope was significantly different from 0 (*P*-value < 0.05).

unfavourable for growth enables plants to avoid the costs associated with mechanisms of stress-tolerance. At the same time, it may maximize resource capture and growth during a limited growing season (Markesteijn & Poorter 2009; experimental study on seedlings; Givnish 2002; modeling study) thanks to the high rate of photosynthesis exhibited by young leaves. On an annual basis, deciduous species with short-lived leaves may have an advantage over evergreen species with long-lived leaves because of their higher growth rate. Indeed, slow growth is associated with the strategy of resource conservation and stress-tolerance, as well as having dense and long-lived tissues (Chapin, Autumn & Pugnaire 1993; Wright et al. 2004; Reich 2014). For instance, it has been found in a semi-deciduous forest adjacent to the study area that trees which that tolerate shade and drought better are those with the lowest potential growth rate (Ouédraogo et al. 2013, M'Baïki, central African Republic).

It should be noted that when forest deciduousness was related to annual rainfall instead of MCWD, for easier comparison with the studies of Condit et al. (2000) and Bohlman (2010), the relationship was less clear. Consequently, we recommend using MCWD instead of annual rainfall in studies modelling forest response to climate change, to avoid potential misinterpretation if the severity of the dry season varies independently from annual rainfall. Specifically, potential evapotranspiration will be very sensitive to temperature increase and its effect might be more important than rainfall variations, even in regions where annual rainfall is predicted to increase.

THE ADVANTAGE OF LONG-LIVED LEAVES ON RESOURCE-POOR SOILS

This study confirmed that the geological substrate significantly altered the deciduousness–climate relationship (Condit et al. 2000; Bohlman 2010). Forest deciduousness increased with the severity of the dry season significantly slower on sandstone and alluvium substrates than on metamorphic and basic rocks. Thus for a comparable climate (same severity of dry season), deciduousness was lower on sandstone and alluvium than on metamorphic and basic rocks, confirming the observed filtering effect toward evergreen species on sandstone (Fayolle et al. 2012; an environmental filter being an abiotic barrier to the establishment and/or survival of particular species from the regional species pool). The alteration of the relationship between forest deciduousness and climate could be explained by differences in soil fertility associated with the different geological substrates. Indeed, we showed that soils that developed on sandstone and alluvium were characterized by a low and a medium chemical fertility respectively, whereas soils on metamorphic and basic rocks were characterized by a relatively high chemical fertility (high CEC). The hypothesis that nutrient-poor soils can favour an evergreen leaf habit (Aerts 1995) is consistent with the slower increase in deciduousness with rainfall seasonality observed on sandstone and alluvium. On resource-poor soils, many deciduous species with short-lived leaves may not be able to

maximize their growth during the favourable growing period to out-compete evergreen species with long-lived leaves. The later may, indeed, benefit from a longer growing period than deciduous species. For instance, differential growth and survival among species on soil types differing in texture have been found to drive tree species distribution patterns in a Bornean rain forest (Russo et al. 2005). The differences between the regression intercepts on sandstone and alluvium also support the nutrient limitation hypothesis (i.e. the nutrient theory of evergreenness sensu Chabot & Hicks 1982). Although the response to rainfall seasonality was similar between sandstone and alluvium, forest deciduousness was significantly higher on alluvium, characterized by soils with medium fertility, than on sandstone, characterized by soils with low fertility, suggesting that conservative species with an evergreen leaf habit were favoured on sandstone substrates.

The direct correlation we identified between forest deciduousness and soil chemical fertility reinforces the hypothesis that geology alters the deciduousness–climate relationship through differences in soil nutrient availability between the geological substrates. Forest deciduousness (after removing the effect of climate) significantly increased with clay content, organic carbon content, and CEC; and decreased with pH. This suggests that soil properties favour particular strategies for resource use and thus particular attributes for leaf functional traits, which has consequences on forest deciduousness. Indeed, a relationship between leaf functional traits and soil fertility was demonstrated at global scale. Ordoñez et al. (2009) found a consistent increase in specific leaf area (SLA) with soil fertility (decreasing C/N ratio). Maire et al. (2015) also recently evidenced at global scale that SLA increases with soil organic C, and decreases with soil pH. SLA is a key leaf functional trait for characterizing plant species along the continuum of strategies for resources use (Wright et al. 2004), with conservative species having lower SLA than acquisitive species. The increase in SLA with soil chemical fertility suggests that nutrient-rich soils favour acquisitive species, and conversely that nutrient-poor soil favour conservative species, which has consequences on SLA. In this study, we showed that this process also has consequences on another leaf functional trait: the leaf habit (at least in central African semi-deciduous forests).

Finally, we found that soil chemical fertility and water-holding capacity ($PAW_{1 m}$) varied in the same way in the study area. Assuming that plant-available soil water content (which depends on rooting depth) followed the same pattern, the filtering effect we observed on sandstone could result from nutrient- as well as from water limitation. Indeed, the high wood density observed in species growing on sandstone (Gourlet-Fleury et al. 2011), which is typical of the conservative strategy (Chave et al. 2009), affords greater resistance to cavitation (Markesteijn et al. 2011). Similarly, in Amazonian forests, species with high wood density were found in environments with limited soil water and nutrient availability (Fortunel et al. 2014). Indeed, there is increasing evidence that the trade-off between 'acquisition' and 'conservation' of resources occurs for nutrients as well as for water and light

(Reich 2014), and the conservative strategy may be favoured in habitats with low nutrient, water or light availability. However, the hypothesis that the filtering effect we observed on sandstone results from water limitation seems unlikely. Indeed, Freycon *et al.* (2015) recently suggested a maximum rooting depth of 10 m for semi-deciduous tropical forests in Central Africa. With this value and assuming a constant soil water-holding capacity ($PAW_{1\,m}$) irrespective of depth, trees on soils with the lowest water-holding capacity (on sandstone) may have around 500 mm of soil water reserve to cope with a climatological water deficit ranging from 124 to 562 mm, suggesting that these trees experienced little water stress. Furthermore, the presence of a root mat on sandstone (Freycon *et al.* 2015) also argues in favour of the nutrient limitation hypothesis, as root mats support the direct recycling of nutrients on poor soils (Vitousek & Sanford 1986).

Conclusion

We found evidence that tropical forest deciduousness is the result of both the competitive advantage of deciduous species in climates with high rainfall seasonality, and the persistence of evergreen species on resource-poor soils. Our findings could be used to improve future predictions of vegetation distribution under climate change scenarios. For instance, in central Africa, forest is likely to respond differently to variations in rainfall and/or evapotranspiration depending on the geological substrate. Moreover, the relative contribution of geology to the variation in forest deciduousness was three times stronger than the one of climate (46.3% and 14.2% of the total variation, respectively), highlighting the importance of geology and soil for predicting vegetation functional characteristics. It was similarly found at global scale that soil properties were better explanatory variables than climate for variation in leaf photosynthetic traits (Ordoñez *et al.* 2009; Maire *et al.* 2015).

Our findings also offer a clear illustration of well-known theoretical leaf carbon economy models explaining the patterns in the dominance of evergreen versus deciduous species. To find evidence of these patterns at a large scale, we had to adjust the resolution of our variables by making several approximations. In particular, the degree of forest deciduousness was approximated as the fraction of canopy trees belonging to a genus recorded as deciduous; rainfall and evapotranspiration records were interpolations from widespread meteorological stations, and soil properties were roughly evaluated. However, despite these very large approximations, we found significant patterns, indicating that they are strong and have great importance. A significant part of the deviation that we observed in the data relative to the trend might be explained if a more detailed map of soil properties or a better knowledge of the local climate was available, highlighting the need for higher spatial resolution ground data for central Africa.

Acknowledgements

Data accessibility

Data deposited in the Dryad repository: http://dx.doi.org/10.5061/dryad.264j9 (Ouédraogo *et al.* 2016). To respect the industrial secret imposed by the logging companies on the vegetation data set at plot level, only anonymous genera names are available from the Dryad repository. The complete vegetation data set is archived in the CIRAD institute (http://www.cirad.fr/en), and due to the highly sensitive nature of the data it should be used solely for research purposes, with the understanding that researchers use the data with discretion. Researchers interested in using this data set are thus invited to contact Fabrice Bénédet (fabrice.benedet@cirad.fr) with a short description of the research project. This is in order to establish, after acceptance of the project by CIRAD, a formal convention for use of the data.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of the 247 genera found in the study area with corresponding number of species, number of 8 × 8 km cells where the genus occurred, regeneration guild and leaf habit.

Appendix S2. Contingency table of leaf habit and regeneration guild of the genera.

Appendix S3. Correction procedure of the WorldClim rainfall data.

Appendix S4. Identification of dominant soil type of geological substrates using the Harmonized World Soil Data base.

Appendix S5. Topsoil data, including sample coordinates, sampling depth, soil texture and chemical properties.

Appendix S6. Estimates of the missing soil parameters bd, θ_{FC}, θ_{PWP}.

Appendix S7. Relationships between forest deciduousness computed over all genera and MCWD.

Appendix S8. Statistics and validation of the weighted multiple regression model.

Appendix S9. Comparison of the response of forest deciduousness to annual rainfall and rainfall seasonality (MCWD).