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La réponse des forêts tropicales humides aux variations climatiques

Évolution de la structure et de la dynamique des
peuplements forestiers guyanais

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Résumé

L'importance des forêts tropicales dans le cycle du carbone à l'échelle planétaire est majeure, tant en terme de stock qu'en terme de flux de CO_2 . Plusieurs études mettent en évidence des changements au sein des forêts tropicales au cours des 20 dernières années, notamment des changements de la dynamique forestière et une augmentation de la biomasse aérienne. Les déterminants de ces variations sont aujourd'hui discutés et nous proposons ici d'apporter une contribution à ce débat. Les données utilisées dans ce travail proviennent du dispositif de suivi forestier à long terme de Paracou, Guyane Française, mis en place en 1984 et qui recouvre plus de 120 ha de forêt tropicale humide. Les données météorologiques proviennent de la tour à flux du dispositif, Gyaflux. Les mesures de diamètre proviennent de la base Guyafor pour les données annuelles et bisannuelles, et des mesures de 260 arbres à proximité de la tour à flux pour les mesures diamétriques intra-annuelles. Cette thèse se divise en deux grandes parties. La première concerne l'analyse de la biomasse du dispositif de suivi forestier de Paracou en Guyane et l'implication des changements de structure de cette forêt sur le bilan de carbone. Cette partie est constituée de deux points. (i) Quelles échelles temporelles et spatiales sont pertinentes pour analyser les composantes de structure (biomasse, aire basale et nombre de tiges) et de dynamique (croissance, recrutement et mortalité) des forêts tropicales afin de minimiser les effets d'échantillonnage ? Nous avons établi une méthodologie permettant de relier les intervalles de temps et la surface de mesure aux coefficients de variation de chacune des variables de structure et de dynamique de la forêt. (ii) Quels processus démographiques sont prépondérants dans l'explication des variations de biomasse et comment se redistribue la biomasse accumulée dans le système ? L'augmentation de la biomasse observée sur le dispositif de Paracou serait liée à la rareté des événements de mortalité des gros arbres qui portent une part très importante de la biomasse. La deuxième partie de la thèse concerne l'analyse de l'effet du climat à moyen terme, inter et intra-annuel, et les effets directs du climat dans les changements de dynamique de la forêt. Cette partie se divise en 3 points. (i) Comment quantifier le stress hydrique en forêt tropicale humide ? Nous avons réalisé un modèle journalier de réserve en eau du sol pour les arbres en forêt tropicale. (ii) Quelles variables sont explicatives de la croissance des arbres en forêt guyanaise ? Nous avons montré que l'eau dans le sol est le facteur le plus explicatif du déterminisme climatique parmi un panel de variables climatiques. (iii) Quels traits fonctionnels sont prédicteurs de la réponse des arbres aux variations climatiques ? Nous avons déterminé que des traits spécifiques, la densité du bois et la hauteur maximale, ainsi que le diamètre de l'arbre au moment de la mesure, modulent la croissance des arbres en réponse au climat.

Abstract

At a global scale tropical forest play a major role in term of carbon stock as well as in term of CO₂ fluxes. Several studies have highlighted changes in tropical forest functioning during the last 20 years including a faster turnover and an increase of above ground biomass. The drivers of these changes are discussed and throughout this thesis we propose to contribute to this debate. We use the data from the Paracou experimental site in French Guiana established in 1984 on 120 hectares of moist tropical forest. Meteorological data come from the flux tower of the site, Gyaflux. We use annual and bisannual diameter measurements from the Gyafor database, and intra-annual diameter increments from the measurements of 260 trees near the flux tower. This thesis has two main parts. In the first part we present the biomass analysis of the Paracou permanent plots and the impact of structural changes in this forest on the carbon budget. The first part is constituted by two points. (i) Which temporal and spatial scale used to analyze the structure (biomass, basal area and stem density) and dynamics (tree growth, recruitment and mortality) components of tropical forest in order to minimized sample bias? We establish a simple method to rely measurement interval between census and surface of measurement to the coefficient of variation of forests structure and dynamic components (ii) Which demographic process are involved in the explanation of biomass variation and how the biomass is distributed in the system? The observed increase of biomass at Paracou could be link to the rarity of big trees mortality events. These big trees represent the larger part of the biomass. In the second part, we present the analysis of intra and inter-annual climate variation effects on forest dynamic changes. This part is divided in two points. (i) How to model drought stress in moist tropical forest? We built a daily water balance model for tropical trees. (ii) Which climate variables explain the tree growth in guianian forests? We shown that soil water availability is the determinant factor of tree growth among a panel of climate variables. (iii) Which functional traits are involved in the tropical tree growth responses to climate? In this analysis, we determined that wood specific gravity, maximum tree height and tree diameter modulate the tree growth response to climate variations.

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Introduction

L'objectif de cette thèse est de comprendre la réponse des forêts tropicales humides (FTH) aux variations climatiques en utilisant une approche de modélisation et les données provenant du dispositif expérimental forestier de Paracou en Guyane française. Les données comprennent des mesures climatiques et des mesures de dynamique forestière, i.e. recrutement, mortalité et croissance des arbres. La première partie de la thèse concerne les stocks et les flux de carbone. La seconde partie concerne spécifiquement le flux entrant de carbone à travers la croissance des arbres et présente l'analyse de l'effet du climat sur cette composante de la dynamique forestière. La partie introductive suivante fait une présentation (i) du contexte générale de la thèse, le changement climatique ; (ii) de l'importance des forêts tropicales face aux changements climatiques ; et (iii) de l'effet du climat sur la croissance des arbres en forêt tropicale.

1 Changement climatique, atmosphère et climat

Depuis la création du Groupe intergouvernemental d'experts sur l'évolution du climat en 1988 (GIEC, International Panel on Climate Change en anglais, IPCC) et la conférence de RIO en 1992, le 'Sommet de la Terre', la communauté internationale se préoccupe du changement climatique et prend des mesures pour limiter son impact sur la communauté humaine. Ainsi lors du sommet de Rio, la Convention-cadre des Nations Unies sur les changements climatiques (CCNUCC) a été mise en place. L'article 2 de

cette convention, aussi appelé objectif ultime de la convention, a pour but de stabiliser les concentrations de GES (gaz à effet de serre) afin de minimiser l'interférence anthropique sur le système climatique. En 1997, le protocole de Kyoto, signé par 141 pays, définit les devoirs et les objectifs des pays signataires pour lutter contre l'augmentation des GES. Il définit des mesures contraignantes pour réduire les émissions des GES de 5% par rapport à 1990, objectif à réaliser sur la période 2008-2012. L'accord de Copenhague s'ajoute aux objectifs du protocole de Kyoto. Il est signé lors de la conférence du même nom en 2009 par 112 pays et il renvoie à un autre objectif chiffré, celui de réduire les émissions de GES pour que la température n'augmente pas de plus de 2 °C par rapport à l'ère pré-industrielle.

Le changement climatique est aujourd'hui reconnu par la communauté internationale et par la communauté scientifique comme étant en partie dû aux émissions de GES anthropique (Solomon *et al.*, 2007). Le changement climatique est attribué à l'augmentation de la concentration GES et notamment du CO₂. La concentration atmosphérique en CO₂ a augmenté de 14 % entre 1975 et 2005, passant de 330 à 377 ppm (Clark, 2007a) suite à l'augmentation des émissions anthropiques de CO₂ d'environ 80 % entre 1970 et 2004 (Solomon *et al.*, 2007). Ces concentrations sont très supérieures aux 300 ppm, maxima relevés pour les 420 000 ans avant l'ère industrielle (Petit *et al.*, 1999). L'augmentation de CO₂ atmosphérique a accéléré pour la période 2000-2005 se rapprochant des scénarios les moins optimistes du premier rapport de l'IPCC (Raupach *et al.*, 2007). Malgré leurs efforts, la plupart des états ne sont pas arrivés à leurs objectifs de réduction de leurs émissions de GES en 2008 (UNFCCC, 2010). L'augmentation de la concentration GES devrait perdurer si aucun changement contraignant n'est opéré concernant l'utilisation des terres et la combustion de carbone fossile. Récemment, Solomon *et al.* (2009) ont montré que le changement climatique dû à la concentration en CO₂ est irréversible pour au moins mille ans même si les émissions s'arrêtaient aujourd'hui.

2 Climat des régions de forêts tropicales et de Guyane française

2.1 Généralités au niveau mondial

La FAO (Food and Agriculture Organization) définit les forêts tropicales comme des forêts dont la température moyenne mensuelle est toujours supérieure à 18 ° C. Elles sont classées en 3 catégories, avec 0 à 3 mois secs : rainforests, ou 3 à 5 mois secs : moist deciduous forests, ou 5 à 8 mois secs : dry forests. Les mois secs sont définis comme les mois où la somme des précipitations est égale ou inférieure à deux fois la température moyenne en degré Celsius (FAO, 2000). Les forêts tropicales se retrouvent sous différents régimes de précipitations dont les patterns varient grandement, ce qui entraîne différentes alternances et intensités de saisons sèches (Malhi & Wright, 2004; Walsh & Newbery, 1999). Même en forêts très humides (rainforests), connues pour n'avoir aucune saisonnalité, une sécheresse se produit typiquement tous les trois à six ans, déclenchée par des événements El Niño (El Niño Southern Oscillation, ENSO) (Allan *et al.*, 1996). En Amazonie, la plupart des forêts tropicales sont soumises à une alternance régulière de saisons humides et sèches (Malhi & Wright, 2004; Marengo, 1992; Sombroek, 2001).

2.2 Le climat de la Guyane française

Climat passé

Lors des 20 000 dernières années (pleistocène et holocène), le climat du plateau des Guyanes aurait subi des variations de températures et de précipitations. Lors du dernier maximum glaciaire (-20 000 ans), figure 1 et figure 2, les températures moyennes étaient plus basses de 2 à 6 °C selon les scénarios (Anhuf *et al.*, 2006; Broccoli, 2000; Cowling *et al.*, 2001). De plus, quelques indices suggèrent qu'au début et au milieu de l'holocène (-8000 à -4000) les conditions climatiques étaient plus sèches qu'aujourd'hui (Baker *et al.*, 2001; Mayle & Power, 2008) avec une réduction des précipitations comprise entre 20 et 30% (Cowling *et al.*, 2001; Stute *et al.*, 1995).

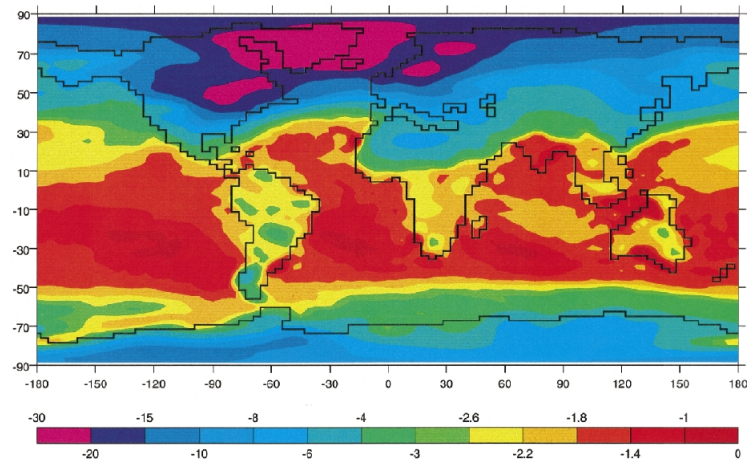


FIGURE 1 – Carte de la différence des moyennes annuelles de la température de l'air entre le dernier maximum glaciaire (-21 000 ans) et aujourd'hui en °C, carte tirée de Broccoli (2000)

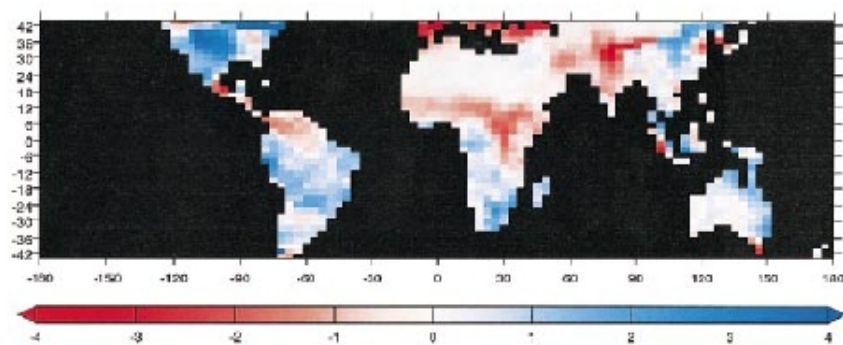


FIGURE 2 – Carte des différences des moyennes annuelles d'humidité du sol entre le dernier maximum glaciaire (-21 000 ans) et aujourd'hui en cm, carte tirée de Broccoli (2000)

Cependant, les analyses de pollen et les modèles de dynamique de végétation suggèrent que la majeure partie de l'Amazonie est restée boisée lors du dernier maximum glaciaire (Malhi & Wright, 2004). En Guyane, plusieurs auteurs ont montré que des perturbations ont entraîné des changements de composition spécifique de la forêt à la fin de l'Holocène (-3000) (Charles-Dominique *et al.*, 1998; Ledru, 2001) mais les causes de ces perturbations sont toujours débattues. D'autres travaux suggèrent que cette région a subi

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des perturbations majeures de composition spécifique pendant la fin du pleistocène (entre -20000 et -10000 ans); des forêts refuges ont également été identifiées (de Granville, 1982; Dutech *et al.*, 2003).

Climat actuel

Les forêts de Guyane française bénéficient d'un climat tropical. Elles font partie de la catégorie forêt tropicale humide (FTH) de la FAO (en anglais : moist deciduous forest). Comme dans tous les milieux tropicaux le climat est plus influencé par le régime des pluies que par les variations de températures. Les précipitations moyennes sont comprises entre 2000 et 4000 mm par an et montrent une grande variabilité spatiale et temporelle, figure 3 et figure 4. Il existe un fort gradient de précipitations d'ouest en est avec des précipitations annuelles parfois supérieures à 4000 mm à l'est et des précipitations annuelles proche de 1500 mm pour certaines stations à l'ouest du département. La variabilité saisonnière des précipitations est importante en Guyane, figure 4. Ces variations temporelles sont dues au déplacement de la Zone Intertropicale de Convergence (ZIC), définie comme la zone de contact des vents de l'anticyclone des Açores et des vents de l'anticyclone de Sainte-Hélène. La rencontre de ces deux masses d'air crée une ceinture dépressionnaire responsable de la formation des cumulonimbus qui entraînent des précipitations tropicales. La ZIC se déplace au cours de l'année passant de part et d'autre de l'équateur. Lorsque la ZIC est au-dessus de la Guyane, elle provoque des épisodes pluvieux. Les saisons se décomposent en une longue saison humide de avril à mi-juillet suivi d'une saison sèche avec des mois où les précipitations sont inférieures à 50 mm de mi-juillet à mi-novembre (Bonal *et al.*, 2008). Entre mi-novembre et avril les pluies reprennent et parfois une petite saison sèche est observée vers le mois de mars, période appelée petit été de mars. D'autres facteurs tels que les évènements El Niño et/ou l'augmentation des températures de surface (Sea Surface Temperatures, SST) du nord de l'océan Atlantique sont associés à l'intensité de la saison sèche en Amazonie, (Marengo & Camargo, 2008; Nepstad *et al.*, 1999). La température présente très peu de variations au cours de l'année avec une moyenne annuelle de

26.1 °C. Seule l'amplitude journalière varie au cours de l'année, elle est plus importante en saison sèche, figure 4.

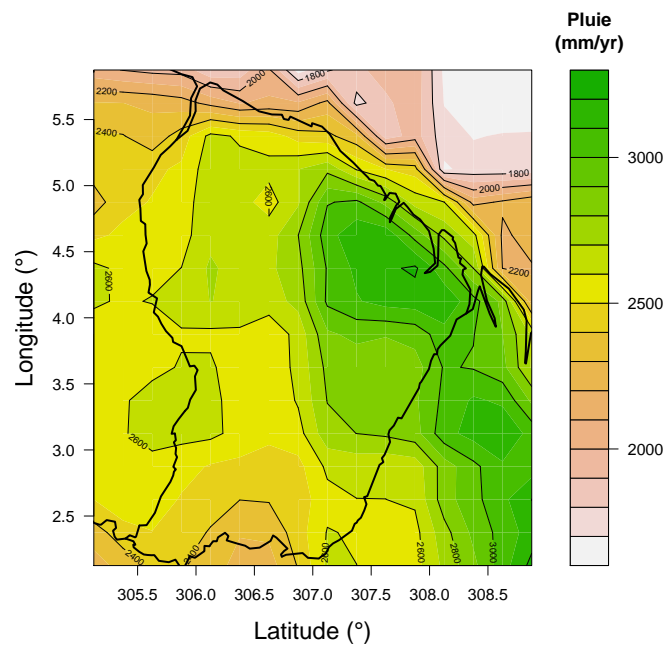


FIGURE 3 – Carte des isohyètes de précipitations annuelles de la Guyane, à partir des données satellites TRMM mensuelles de 1998-2011 (Tropical Rainfall Measurements Mission)

3 Changements du climat des forêts tropicales

Les changements de concentration de gaz atmosphériques à effet de serre ont entraîné des modifications du climat dans la plupart des régions tropicales.

3.1 Augmentation de la température

Les forêts tropicales ont subi une hausse moyenne de la température de $0.26 \pm 0.05^{\circ}\text{C}$ par décennie depuis 1970 (Malhi & Wright, 2004). Cette augmentation est synchrone avec l'augmentation globale des températures attribuée à l'effet de serre d'origine anthropique. Pour la Guyane, les températures

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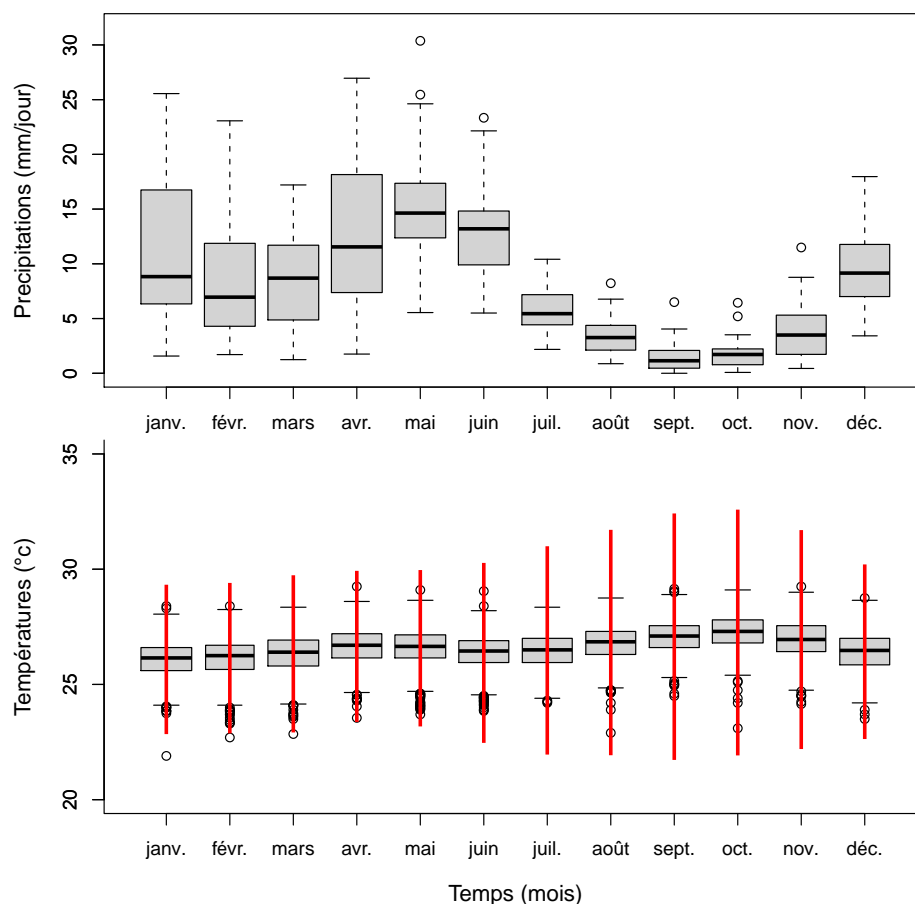


FIGURE 4 – Graphique ombrothermique de la station de Pointe-Combi (15 km de Paracou) de 1981 à aujourd’hui (l’amplitude des températures est représentée par une barre verticale).

montrent une tendance similaire, une augmentation de 0.25°C par décennie, figure 5 et figure 6.

Une augmentation des températures minimales est observée pour toutes les stations météorologiques de Guyane. La plupart de ces stations montrent aussi une augmentation des températures maximales. Cela entraîne une augmentation de la moyenne des températures. Sans action internationale pour limiter les émissions de gaz à effet de serre, la température moyenne de la planète pourrait augmenter de $1,8$ à 4°C supplémentaires d’ici 2100 et jusqu’à $6,4^{\circ}\text{C}$ dans le scénario le plus pessimiste selon le quatrième rapport de

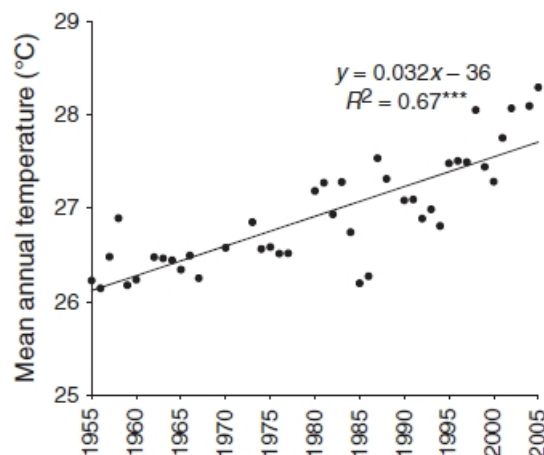


FIGURE 5 – Moyenne annuelle des températures de la station de Régina, Guyane, carte tirée de Fonty *et al.* (2009)

l’IPCC (Solomon *et al.*, 2007). Concernant les forêts tropicales, les prévisions des modèles climatiques suggèrent une augmentation comprise entre 3 et 8 °C d’ici 2100 (Malhi *et al.*, 2009; Petit & Prudent, 2008; Seneviratne *et al.*, 2006; Solomon *et al.*, 2009) .

3.2 Changement de régime des pluies

Le régime des précipitations de certaines régions tropicales a subi des modifications pendant cette même période. En moyenne, pour les régions de forêts tropicales, une diminution de 1.0 ± 0.8 % des précipitations par décennie a été observée pour la période 1960-1998. La diminution est plus importante pour les régions de l’Afrique tropicale avec une diminution de 3 à 4 % des précipitations par décennie. Les précipitations diminuent marginalement pour les pays tropicaux d’Asie et aucune tendance significative à la réduction n’a été observée en Amazonie (Malhi & Wright, 2004). Bien que les moyennes annuelles des précipitations n’aient pas varié, une augmentation significative de la fréquence des événements de sécheresse a été observée pour le sud de l’Amazonie sur la période 1970-1999 (Li *et al.*, 2008). La plupart des modèles de prévisions issus des scénarios de l’IPCC prévoient une diminution des précipitations en Amazonie. Le modèle HadCM3 du Had-

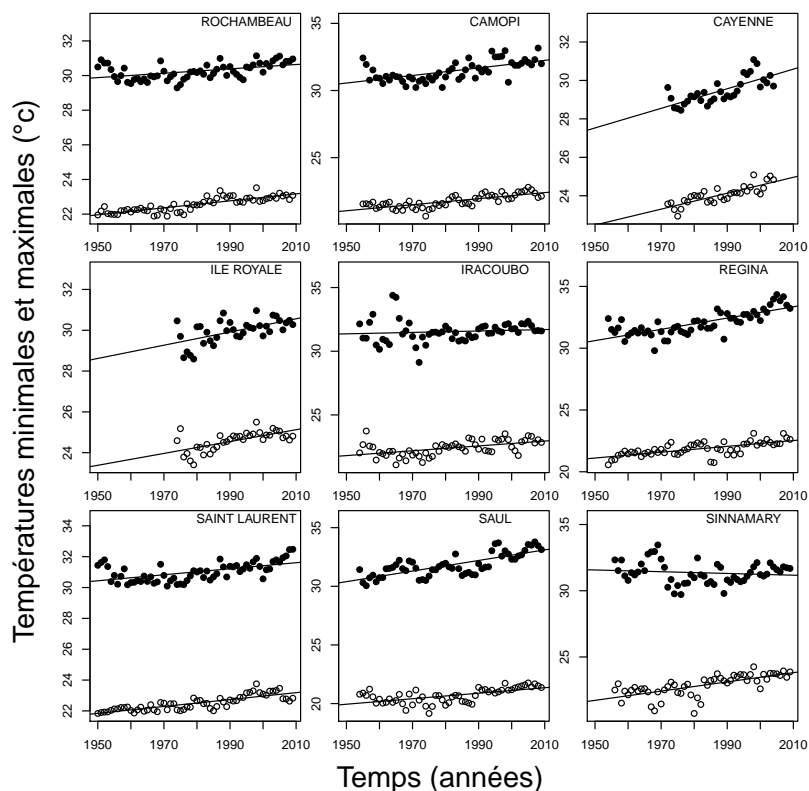


FIGURE 6 – Températures minimales et maximales annuelles avec leurs courbes de tendance (régression linéaire) pour 9 stations Météo-France de Guyane

ley center prévoit un climat plus sec sur l'ensemble de l'Amazonie pour le XXI^{ème} siècle (Burke *et al.*, 2006; Johns *et al.*, 2003). Concernant le bassin des Guyanes, un consensus des 23 modèles de L'IPCC prévoit que l'augmentation de l'intensité de la saison sèche est probable à plus de 80 % (Malhi *et al.*, 2009). Récemment, par une approche de modélisation, un lien entre augmentation des températures et changement de la distribution des précipitations mensuelles a été établi. Ce modèle prévoit que l'intensité de la saison sèche augmentera d'autant plus que la température globale augmente (Solomon *et al.*, 2009).

3.3 Variation de l'irradiance solaire

Il n'est pas établi qu'un changement de l'ensoleillement en général et du rapport des composantes rayonnements direct et diffus ait eu lieu au cours des dernières décennies pour les régions tropicales (Lewis *et al.*, 2004). Mais si la sécheresse augmente en intensité et en durée, il est probable que cela entraîne une diminution du couvert nuageux et par conséquent une augmentation de l'ensoleillement (Nemani *et al.*, 2003). Très récemment, pour les forêts d'Amazonie, Arias *et al.* (2011) ont rapporté une diminution du couvert nuageux et une augmentation de l'irradiance pour la période 1984–2007. Leur étude se base sur des données satellitaires de couvert nuageux et des mesures de surface du flux radiatif.

4 Importance des forêts tropicales

4.1 Stock de carbone

La forêt tropicale est associée à la concentration de GES atmosphériques par deux processus principaux, la séquestration du CO₂ par la photosynthèse et l'émission de CO₂ dans l'atmosphère par la déforestation. Les forêts tropicales séquestrent et stockent plus de carbone que tous les autres écosystèmes terrestres. A l'échelle planétaire, elles stockent environ 40 % du carbone de la végétation terrestre (Houghton, 2005; Malhi *et al.*, 2006). Le stock de carbone total des forêts tropicales est estimé à 247 Pg C (193 Pg C aérien et 54 Pg C souterrain). Cette biomasse est répartie sur l'Amérique latine, l'Afrique sub-saharienne et L'Asie du sud-est, respectivement 49%, 25%, and 26% du stock total (Saatchi *et al.*, 2011). Les forêts tropicales sont responsables de plus du tiers de la productivité primaire globale terrestre (Melillo *et al.*, 1993) et fournissent de nombreux services à la communauté humaine, notamment via la production de bois tropicaux et de produits dérivés. De plus, les forêts tropicales sont le milieu de vie et la ressource de base d'un part majeure de la diversité animale terrestre. Des changements de composition, de structure, de dynamique et/ou du cycle du carbone de ces forêts peuvent potentiellement avoir des conséquences très importantes pour la communauté humaine,

4. IMPORTANCE DES FORÊTS TROPICALES

TABLE 1 – Bilan de carbone forestier sur la période 1990-2007, adapté de Pan *et al.* (2011).

Carbon sink and source in biomes ^{a b}	1990-1999	2000-2007	1990-2007
Boreal forest	0.50 ± 0.08	0.50 ± 0.08	0.50 ± 0.08
Temperate forest	0.67 ± 0.08	0.78 ± 0.09	0.72 ± 0.08
Tropical intact forest ^c	1.33 ± 0.35	1.02 ± 0.47	1.19 ± 0.41
Total sink in global established forests ^d	2.50 ± 0.36	2.30 ± 0.49	2.41 ± 0.42
Tropical regrowth forest ^e	1.57 ± 0.50	1.72 ± 0.54	1.64 ± 0.52
Tropical gross deforestation emission ^f	-3.03 ± 0.49	-2.82 ± 0.45	-2.94 ± 0.47
Tropical land-use change emission ^g	-1.46 ± 0.70	-1.10 ± 0.70	-1.30 ± 0.70
Global gross forest sink ^h	4.07 ± 0.62	4.02 ± 0.73	4.05 ± 0.67
Global net forest sink ⁱ	1.04 ± 0.79	1.20 ± 0.85	1.11 ± 0.82

a. $F_{Established\ Forests} = F_{Boreal\ Forests} + F_{Temperate\ Forests} + F_{Tropical\ Intact\ Forests}$ (Eq.1), $F_{Tropical\ Land-use\ Change} = F_{Tropical\ Gross\ Deforestation} + F_{Tropical\ Regrowth\ Forests}$ (Eq.2); $F_{Gross\ Forest} = F_{Established\ Forests} + F_{Tropical\ Regrowth\ Forests}$ (Eq.3); $F_{Net\ Forest} = F_{Established\ Forests} + F_{Tropical\ Land-use\ Change}$ (Eq.4)

b. Sinks are positive values and sources are negative values

c. Tropical Intact Forests : Tropical forests that have not been substantially affected by direct human activities, but the flux accounts for the dynamics of natural disturbance-recovery processes

d. Global Established Forests : The forest remaining forest over the study periods plus afforested land in boreal and temperate biomes, plus intact forest in the tropics (Eq. 1)

e. Tropical Regrowth Forests : Tropical forests that are recovering from past deforestation and logging

f. Tropical Gross Deforestation : The total C emissions from tropical deforestation and logging, not counting uptake of C in tropical regrowth forests

g. Tropical Land-use Change : Emissions from tropical land-use change, which is a net balance of tropical gross deforestation emissions and C uptake in regrowth forests (Eq. 2). May be referenced as a tropical net deforestation emission in the literature

h. Global Gross Forest sink : The sum of total sinks in global established forests and tropical regrowth forests (Eq. 3)

i. Global Net Forest sink : the net budget of global forest fluxes (Eq. 4). It can be calculated in two ways : (i) total sink in global established forests minus tropical land-use change emission; and (ii) total global gross forest sink minus tropical gross deforestation emission

la biodiversité et le climat de la terre.

La déforestation des forêts tropicales a libéré dans l'atmosphère 1 à 2 milliards de tonnes de carbones par an depuis les années 1990, soit environ 15 à 25 % des émissions annuelles de GES (Fearnside & Laurance, 2004; Houghton, 2005; Malhi & Grace, 2000). La déforestation et la dégradation

des forêts sont les plus importantes sources d'émission de gaz à effet de serre dans la plupart des pays tropicaux (FAO, 2005; Gibbs *et al.*, 2007). La vitesse de déforestation diminue depuis les années 90 mais reste très élevée et 13 millions d'hectares de forêts sont convertis à un autre usage ou perdus lors de perturbations naturelles chaque année (FAO, 2010). La destruction de ces hectares de forêts a deux conséquences : une libération du carbone stocké sous forme de biomasse et la diminution du stockage potentiel.

4.2 Dynamique des flux de carbone forestiers

L'étude de la dynamique forestière dans ce contexte de changement climatique est très importante, notamment pour établir si les forêts tropicales sont des sources ou des puits de carbone et quel sera leur rôle pour les siècles à venir : augmentation ou atténuation de la concentration du CO₂ atmosphérique. Pan *et al.* (2011) ont récemment établi que les forêts tropicales ont été des puits de carbone sur la période 1990-1999 et 2000-2007 avec respectivement un flux entrant de 1.3 ± 0.3 et 1.0 ± 0.5 Pg C, tableau 1. Plusieurs hypothèses font actuellement débat concernant les effets du changement climatique sur le stock de carbone que constituent les forêts tropicales. Ces hypothèses essaient d'expliquer les causes des changements déjà observés de la dynamique des forêts tropicales. L'analyse des données issues de forêts néotropicales suivies sur le long terme ont suggéré des changements importants dans les processus de dynamique forestière (Lewis *et al.*, 2006). Ces changements se traduisent par une augmentation générale du turn-over des arbres en forêt tropicale humide (Phillips *et al.*, 1998). Cette augmentation globale se déclinant elle-même en des taux de recrutement et de mortalité s'élevant régulièrement (Phillips *et al.*, 2004). La biomasse aérienne des forêts tropicales montre une augmentation en Amazonie et en Afrique (Baker *et al.*, 2004; Lewis *et al.*, 2009). Cette augmentation de biomasse a une très grande importance puisque qu'elle constituerait le principal puits de carbone en région tropicale (Lewis, 2006). Ces changements et les mécanismes qui permettent de les expliquer sont largement débattus et il en ressort deux principales hypothèses, celle de la fertilisation des forêts tropicales par l'augmentation

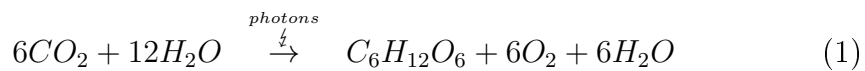
du CO₂ atmosphérique (Phillips *et al.*, 1998) et celle de la régénération de la biomasse après perturbation naturelle (Chave *et al.*, 2008; Korner, 2003; Wright *et al.*, 2005). Dans cette dernière, les auteurs considèrent que le flux entrant de biomasse (croissance et recrutement) et le flux sortant (mortalité) n'ont pas la même dynamique. Le flux entrant de biomasse serait lent et régulier alors que le flux sortant serait comparable à une perturbation, un événement ponctuel entraînant des changements importants de la biomasse. De ce fait, si la somme des flux est observée sur de courtes périodes, il serait plus probable d'observer une augmentation de la biomasse.

5 Effet direct du climat sur la croissance des arbres

Parmi les processus de la dynamique forestière (recrutement, croissance et la mortalité), la croissance est un des processus clés dans ce contexte de changement climatique. En effet, cette croissance constitue le principal flux entrant de carbone dans les forêts tropicales (Blanc *et al.*, 2009; Rutishauser *et al.*, 2010).

5.1 Rappels sur la photosynthèse

Les variables climatiques ont un rôle direct dans la formation de la matière organique au cours de la photosynthèse. L'eau et la lumière sont les substrats clés de la photosynthèse avec le CO₂, eqn 1. La température agit sur la cinétique de la réaction photosynthétique (c.f. 5.4). Les composés créés lors de la photosynthèse permettent aux arbres de survivre, grandir et se reproduire. C'est le processus biochimique le plus important pour les écosystèmes, il permet de synthétiser de la matière organique, la base de la chaîne alimentaire.



Les carbohydrates produits lors de la photosynthèse sont utilisés pour la respiration, la croissance des nouvelles pousses (croissance primaire), la croissance cambiale (croissance en diamètre, croissance secondaire), la croissance des racines et l'investissement reproducteur (Kozlowski, 1992). La croissance secondaire utilise une grande quantité de carbohydrates, par exemple, pour l'*Eucalyptus regnans* pour produire un gramme de cellule du tronc (quel que soit son type, phloème, xylem, . . .), il faut plus d'un gramme de glucose. Pour les arbres de milieu tempéré, on observe une transition dans l'utilisation des carbohydrates au cours de la saison de végétation. Les carbohydrates de réserve sont utilisés en début de saison de végétation, avant que la photosynthèse commence, pour la mise en place des nouvelles branches et feuilles. Ces structures sont des puits importants de carbohydrates et absorbent la plus grande partie des produits de la photosynthèse du début de la saison de végétation. Pendant cette période débute la croissance cambiale qui est associée avec une utilisation des carbohydrates de réserve de la tige. Une transition est ensuite observée dans l'utilisation des produits de la photosynthèse des nouvelles branches et feuilles vers les cellules du tronc. En milieu tropical, les carbohydrates peuvent être utilisés une grande partie de l'année voire toute l'année, ce qui expliquerait les absences de cernes annuels, bien que des cernes soient observés dans les climats tropicaux saisonniers (Kozlowski, 1992). En Guyane, Détienne & Barbier (1988) ont observé que les essences de forêts guyanaises produisent des cernes annuels mais que ceux-ci sont plus ou moins marqués et difficiles à identifier. La production des cellules du tronc peut être répartie inégalement de haut en bas de la tige. Des excentricités sont parfois observées dans la croissance autour de la tige, la croissance cambiale peut former des arcs de cercle de nouvelles cellules (Kozlowski, 1992). Les paragraphes suivants décrivent les effets observés du climat sur la croissance des arbres en forêt tropicale.

5.2 Précipitations

L'eau est un élément majeur de la photosynthèse. L'eau intervient d'une part dans la fabrication de matière organique dans la réaction chimique de

5. EFFET DIRECT DU CLIMAT SUR LA CROISSANCE DES ARBRES

photosynthèse et d'autre part dans le mécanisme de la transpiration. Bien que les forêts tropicales reçoivent plus de 1500 mm de précipitations par an, la plupart de ces régions ont une saisonnalité avec une saison sèche plus ou moins prononcée (Malhi & Wright, 2004; Marengo, 1992; Sombroek, 2001; Xiao *et al.*, 2006), figure 7 et figure 3. Les articles traitant de l'effet de l'eau sur la croissance des arbres en forêt tropicale étudient principalement la sécheresse bien que certains auteurs étudient aussi l'effet des périodes d'inondations (Parolin *et al.*, 2010).

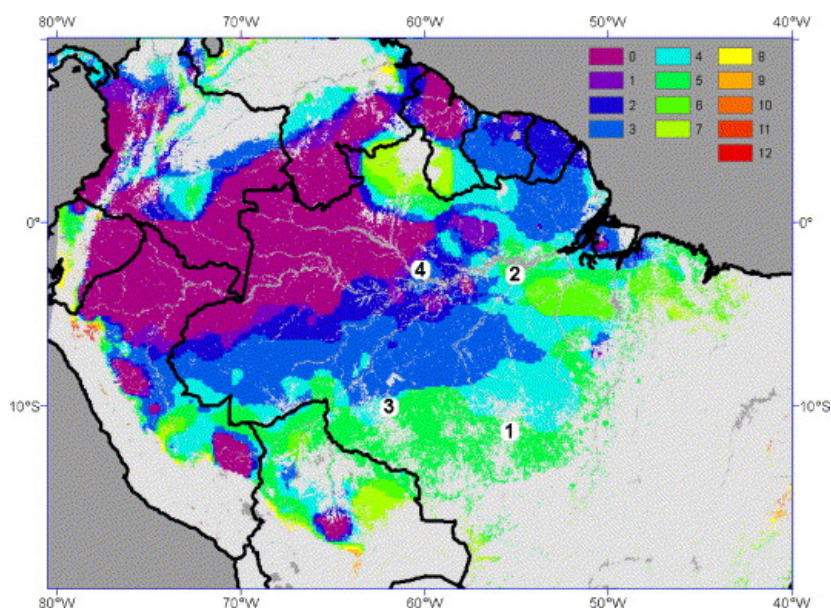


FIGURE 7 – Répartition spatiale de la saison sèche pour la zone tropicale de l'Amérique du Sud. La durée de la saison sèche est définie par le nombre de mois avec des précipitations inférieures à 100 mm. Carte tirée de Xiao *et al.* (2006)

La sécheresse est un évènement majeur en forêt tropicale pour la dynamique des arbres. Son intensification dans le siècle à venir est considérée comme une des composantes du changement climatique qui va le plus influencer les forêts tropicales (Chambers & Silver, 2004; Clark, 2004; Lloyd & Farquhar, 2008; Malhi *et al.*, 2008; Nepstad *et al.*, 2004; Wright, 2005). Le manque d'eau entraîne une réduction de la croissance en diamètre et une hausse des taux de mortalité des arbres (Brando *et al.*, 2008; Nepstad *et al.*,

2007). Les taux de mortalité augmentent lors des sécheresses comme lors de la sécheresse de 2005 en Amazonie (Phillips *et al.*, 2009). D'un point de vue uniquement climatique, Cook & Vizy (2008) ont montré par des simulations de climats qu'avec une augmentation de la concentration de CO₂ à 775ppm, la surface des forêts d'Amazonie serait réduite de 70%. Cette réduction serait due à des climats trop secs qui ne seraient plus propices à la forêt tropicale mais plutôt à l'installation de savanes, de végétations arbustives et de forêts ouvertes. Les causes de la sécheresse sont multiples : soit annuelles pour les forêts soumises à une saisonnalité, soit pluri-annuelles dans le cas d'évènement El ninõ ou de réchauffement des températures de surface de l'Atlantique. Les effets de la sécheresse sur la physiologie des arbres en milieu tropical ont très bien été décrits dans l'article de Nepstad *et al.* (2002). Quand la pluie est inférieure à l'évapotranspiration, l'eau du sol diminue graduellement entraînant une augmentation de la tension de la sève du xylème. Cela peut éventuellement déclencher la fermeture des stomates et entraîner d'autres réponses physiologiques telles que la baisse des potentiels hydriques foliaires, la réduction de la capacité polysynthétique et l'augmentation de la chute des feuilles. Les auteurs qui analysent l'effet de la sécheresse ont déjà observé des effets sur la croissance en diamètre (croissance secondaire). Ces articles peuvent être classés en plusieurs types. Soit les auteurs s'intéressent à peu d'espèces et utilisent la dendrochronologie. Soit les auteurs utilisent les données de différents dispositifs permanents forestiers le plus souvent sans s'intéresser à l'espèce, mais plutôt à l'ensemble du peuplement (moyenne de croissance annuelle du peuplement, augmentation annuelle de biomasse). Les indices utilisés pour analyser l'effet de la quantité d'eau sur la croissance sont souvent issus de mesures directes de précipitation, par exemple : précipitation journalière, mensuelle ou annuelle, mois où les précipitations sont inférieures à 100 mm, nombre de jours de pluie en saison sèche, etc. . . . Peu d'auteurs utilisent des indices permettant d'estimer une quantité d'eau disponible pour la plante comme il en existe en forêt tempérée (Granier *et al.*, 1999; Nepstad *et al.*, 2004). Seules quelques études ont développé des indices simples pour approcher l'eau disponible pour la plante en milieu tropical à différentes résolutions temporelles, indices annuels (Enquist & Leffler, 2001),

mensuels (Tian *et al.*, 1998) et journaliers (Phillips *et al.*, 2009). Un autre problème apparent est la quasi absence d'étude sur l'effet du climat à l'échelle intra-annuelle bien que la plupart des forêts tropicales aient une saisonnalité. La littérature sur la croissance des arbres donne des résultats contradictoires, cependant quelques résultats majeurs sont à noter.

En Amazonie, deux dispositifs expérimentaux d'exclusion des pluies ont été mis en place pour décrire les effets de l'intensification de la saison sèche sur la dynamique forestière. Dans ces dispositifs au Brésil, après deux ans d'exclusion partielle des pluies (50%), les auteurs ont montré une nette réduction de la croissance des arbres de plus de 14 cm de diamètre et une diminution d'un quart de la productivité primaire (Nepstad *et al.*, 2002). En 2005 a eu lieu la saison sèche la plus intense depuis 100 ans en Amazonie. Phillips *et al.* (2009) ont montré que cette saison sèche avait entraîné une réduction de la biomasse due à une forte mortalité. Ces auteurs n'ont pas mis en évidence de lien direct avec la croissance des arbres. Dans un article sur trois sites de forêt tropicale au Panama : Sherman, BCI et Cocoli (respectivement 2892 mm, 2616 mm et 1950 mm de précipitations annuelles en moyenne), Condit *et al.* (2004) ont montré que la plupart des espèces étudiées avaient une croissance plus importante lors de l'année El ninõ de 1997, en comparaison aux périodes précédentes et suivantes, et malgré des conditions de sécheresse plus intenses. Au Costa Rica, dans le dispositif de La Selva (4142mm de précipitations par an), Clark *et al.* (2010) ont montré que la quantité de pluie lors de la saison sèche était associée positivement à la croissance des arbres, en d'autres termes que les années de sécheresse, une croissance plus faible est observée. Dans une récente revue de la littérature sur la dendrochronologie en forêt tropicale, Rozendaal & Zuidema (2011) ont établi les associations entre précipitations et croissance pour 36 espèces de forêt tropicale sèche provenant de différents sites (précipitations annuelles différentes). Ils ont identifié plusieurs types de réponses à la quantité de pluie. La croissance des espèces de forêt tropicale sèche peut être associée à la quantité totale de pluie en saison humide, à la quantité totale de pluie en saison sèche, à la quantité de pluie pendant la transition entre saisons et à la quantité de pluie de l'année précédente. Selon les auteurs, ces réponses spécifique reflètent des différences

dans les stratégies de croissances de ces espèces. Il existe beaucoup d'incertitudes concernant la réponse en terme de croissance des arbres à l'eau en forêt tropicale pour deux raisons principales : (i) les indices climatiques ne semblent pas adaptés, il faudrait avoir accès à la quantité d'eau journalière disponible pour les plantes, et (ii) les données des dispositifs permanents de forêts tropicales ne sont pas adaptées pour une analyse intra-annuelle des effets du climat, dans ces dispositifs les arbres sont mesurés en moyenne tous les 2-3 ans (Clark & Clark, 2011).

5.3 Ensoleillement

La lumière est un élément indispensable à la réalisation de la photosynthèse. Il existe peu d'expériences en forêt tropicale qui relient la quantité de lumière à la croissance des arbres. Dans une expérience de référence au Panama où des arbres étaient éclairés artificiellement lorsque des nuages réduisaient le flux de photons photosynthétique, Graham *et al.* (2003) ont montré pour une augmentation de la photosynthèse, de l'absorption de CO₂ et de la croissance primaire (croissance des branches). La couverture nuageuse peut diminuer la lumière et cela serait un facteur limitant important pour la production primaire en région tropicale mais les niveaux critiques où l'irradiance deviendrait un facteur limitant sont rarement atteints (Bonal *et al.*, 2008; Graham *et al.*, 2003; Nemani *et al.*, 2003). Une association positive entre lumière et croissance a été établie sur les données du dispositif de BCI au Panama, en utilisant le nombre de jours sans pluie comme indice d'insolation (Feeley *et al.*, 2007). Les auteurs expliquent cette augmentation de croissance à BCI par l'augmentation de la lumière disponible due à une réduction du couvert nuageux. Cette association n'a pas été retrouvée pour le dispositif de Pasoh (Feeley *et al.*, 2007). Très récemment, Arias *et al.* (2011) ont reporté une diminution du couvert nuageux et une augmentation de l'irradiance pour la période 1984–2007 pour les forêts d'Amazonie. Ces auteurs suggèrent que l'augmentation de l'irradiance sur la période d'étude pourrait être responsable de l'augmentation de biomasse observée ces dernières décennies en forêt tropicale. Il existe un autre moyen indirect pour analyser

l'effet de la lumière sur la croissance des arbres. Certaines études réalisées à partir de mesures satellitaires (capteurs MODIS, NASA, satellites Terra et Aqua, depuis 2000) essayent de caractériser la capacité photosynthétique et la surface du couvert végétal en fonction de la quantité lumineuse reçue. Les deux indices de végétation principaux issus de ces mesures sont l'indice de différence de végétation normalisé (Normalized Difference Vegetation Index, NDVI) et l'indice de végétation amélioré (Enhanced Vegetation Index, EVI). Bien qu'étant issus de mesures indirectes de capacité photosynthétique, ces indicateurs renseignent sur le potentiel de photosynthèse et la phénologie, et donc indirectement sur la croissance des arbres. Si le couvert a une forte valeur de l'indice de végétation (EVI ou NDVI), cela traduit une forte capacité photosynthétique qui devrait se traduire par une forte croissance. Huete *et al.* (2006) ont montré que la capacité photosynthétique de la canopée augmentait avec la lumière du soleil pendant la saison sèche. Ils ont utilisé le NDVI, l'indice de végétation de la différence normalisée des réflectances dans le proche-infrarouge et le rouge, qui reflète la quantité de chlorophylle de la canopée. Leur résultat est le contraire de ce qui est généralement admis, i.e. l'activité photosynthétique diminue en saison sèche à cause de la limitation en eau. Une autre étude avec indice provenant des mêmes satellites, l'EVI qui reflète l'indice de surface foliaire (surface totale des feuilles par surface de sol, Leaf Area Index, LAI) plus que la capacité photosynthétique, a montré que dans les forêts tropicales, en 2002 les maximums d'EVI ont eu lieu à la fin de la saison sèche et au début de la saison humide (Xiao *et al.*, 2006). En Guyane, les pics de photosynthèse sont aussi observés en saison sèche (Bonal *et al.*, 2008). Ces résultats suggèrent que la phénologie des feuilles n'est pas déterminée par la saisonnalité des précipitations mais qu'elle pourrait être déterminée par la disponibilité en lumière (Xiao *et al.*, 2006). En Guyane, les mêmes données que celles ayant servi pour l'article de Huete (capteurs MODIS, NDVI et EVI) suggèrent que la capacité photosynthétique de la forêt a tendance à augmenter en saison sèche (Pennec *et al.*, 2011). Reste que le lien entre la capacité photosynthétique du couvert et la croissance diamétrique de l'arbre n'est pas clairement établi. Les observations des tours à flux suggèrent une augmentation de la photosynthèse en saison sèche mais le pic

de croissance en diamètre des arbres ne semble commencer qu'en début de saison humide. Ce phénomène pourrait être lié à une allocation des photosynthétats pour les réserves de la plante ou à des processus autres que la croissance secondaire (Kozlowski, 1992).

Pour résumer, l'effet de la lumière sur la croissance pourrait être : (i) positif si la quantité de lumière augmente du fait de la réduction du couvert nuageux, ou (ii) négatif de manière indirecte, si la phénologie est dépendante de la lumière et que les feuilles tombent pendant les périodes où l'irradiance est la plus élevée.

5.4 Température

La température est impliquée de façons directe et indirecte dans la photosynthèse (Lloyd & Farquhar, 2008). Elle module les taux d'activités d'enzymes de la photosynthèse et de la chaîne de transport des électrons (Rubisco et RuBP), figure 8. De façon indirecte, la température intervient dans la fermeture des stomates. Les stomates se ferment quand la demande évaporative est trop importante. L'humidité de l'air est plus ou moins constante en forêt tropicale pendant la journée et la demande évaporative est principalement sous l'influence de la température. Ce rôle de la température dans l'ouverture des stomates influence indirectement la photosynthèse.

Les espèces tropicales pourraient être particulièrement sensibles à la température pour deux raisons : (i) ces espèces vivent à des températures moyennes annuelles proches des maxima sur terre et il y a un manque de populations biologiques adaptées à une température plus élevée ; (ii) les variations saisonnières sont très limitées, moins de 4 °C en moyenne dans l'espace compris entre les latitudes 20° de part et d'autre de l'équateur, et de ce fait, les espèces sont adaptées à des petits intervalles de températures (Wright, 2010).

Plusieurs études en forêts tropicales ont analysé l'association entre température et croissance des arbres. Les liens entre ces deux variables ne sont toujours pas clairement établis, ils dépendent de la stratégie que la plante adopte pour l'allocation des molécules formées lors de la photosynthèse (Kozlowski, 1992). Dans une récente review de la littérature traitant de l'effet de

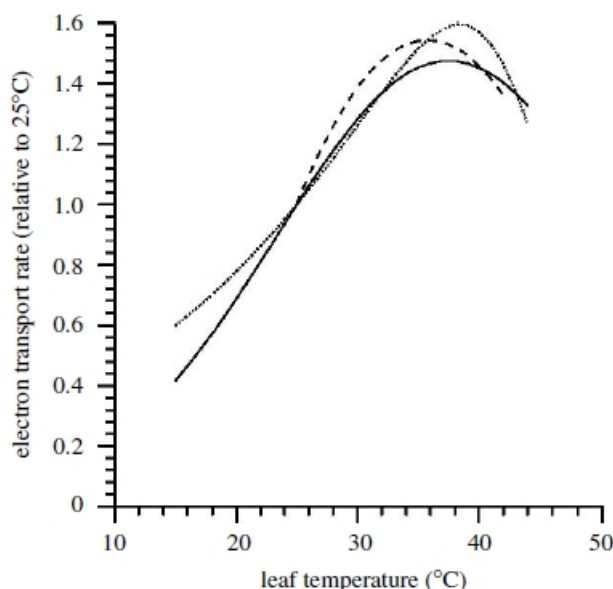


FIGURE 8 – Sensibilité du transport des électrons lors la photosynthèse à la température, pour des plants de soja (traits discontinus) et des arbres de forêt Amazonienne (ligne en pointillés et traits pleins), tiré de Lloyd & Farquhar (2008)

la température sur les forêts, Way & Oren (2010) ont montré que les espèces des forêts tropicales sont plus sensibles à la diminution de la croissance causée par l'augmentation de la température que les espèces des forêts tempérées ou boréales. De plus, Doughty & Goulden (2008) suggèrent que les espèces d'arbres de forêts tropicales pourraient être proches du seuil de température pour la photosynthèse, figure 8. Un dépassement de ce seuil entraînerait une réduction de l'assimilation de CO_2 par la plante et de la croissance des arbres.

Plusieurs études ont observé un lien entre la croissance en diamètre et la température minimale annuelle. Avec les données du dispositif de La Selva (Costa Rica, précipitations 4142 mm/an), Clark *et al.* (2003) ont montré que la température avait un effet sur la productivité primaire, avec une réduction de l'incrément annuel en diamètre inversement corrélé avec les températures minimums (moyennes annuelles). Plus récemment, toujours à La Selva, Clark *et al.* (2010), ont montré que l'accroissement annuel en diamètre du peuplement était associé aux températures moyennes nocturnes annuelles.

Les températures nocturnes sont très proches des températures minimales. Feeley *et al.* (2007) ont trouvé le même effet sur les données du dispositif de Barro Colorado Island (BCI, Panama, précipitations : 2551 mm/an) et de Pasoh (Malaysie, précipitations : 1788 mm/an). Pour ces deux sites, la croissance des arbres était négativement corrélée avec les températures minimales (moyennes annuelles).

D'autres auteurs ont observé une corrélation avec la température maximale. Dans une forêt tropicale d'Amazonie centrale à 80 km au nord de Manaus (Brésil, précipitations : 2600 mm/an, saison sèche modérée de juin à aout), Laurance *et al.* (2009a) ont montré que les taux de croissance des arbres était fortement corrélés positivement avec les moyennes des températures journalières maximales sur des périodes pluriannuelles.

L'absence de lien entre température et croissance à aussi été observé. Brien *et al.* (2011), concernant une forêt tropicale sèche (sud du Mexique, précipitations 930 mm/an), ont montré que les variations inter-annuelles d'activité photosynthétique de l'espèce *Mimosa acantholoba* n'étaient pas associées avec les températures moyennes. Enquist & Leffler (2001) en forêt tropicale sèche (Costa Rica, précipitations 1535 mm/an), n'ont pas pu mettre en évidence de corrélations entre les températures mensuelles et l'accroissement observé pour deux espèces sur la période 1976-1995.

Par une approche basée sur des données satellitaires de températures et de mesures de NDVI, Braswell *et al.* (1997) ont montré que les écosystèmes tropicaux étaient moins productifs les années chaudes (réduction de NDVI).

Ces résultats sont très contrastés, et de façon similaire aux conclusions des études sur l'effet des précipitations, les auteurs ont tendance à interpréter avec un lien causal les effets des variations de température sur la croissance. La température peut faire varier la cinétique de la photosynthèse, certes, mais il semble difficile d'interpréter un lien entre une température moyenne annuelle et une variation de croissance, d'autant plus qu'il existe une saisonnalité pour ces variables. Les variables climatiques sont très corrélées entre elles et l'une des hypothèses de cette thèse est que la température minimale sort bien dans certaines analyses parce qu'elle est corrélée à une variable plus importante : la disponibilité en eau du sol. D'autre part, elle serait un

meilleur indicateur de l'eau disponible que la quantité de précipitations. Ceci apparaît encore plus clairement pour les zones avec des précipitations annuelles supérieures à 4000 mm et une faible saisonnalité comme le dispositif de la Selva au Costa Rica , où les températures minimales annuelles sont plus élevées lors des années qui ont une saison sèche avec des mois où les précipitations sont inférieures à 50 mm (Clark *et al.*, 2010). Au vue des changements déjà observés et des changement attendus pour cette variable, comprendre le rôle direct ou indirect de la température sur la croissance apparaît comme une urgence (Cox *et al.*, 2000).

5.5 Dioxide de carbone, CO₂

L'effet de l'augmentation du CO₂ atmosphérique sur la croissance fait aujourd'hui l'objet d'un débat en milieu tropical. Certains attribuent l'augmentation de la biomasse à l'augmentation de la concentration en CO₂ alors que d'autres auteurs attribuent cette croissance au phénomène de régénération après perturbation. Les résultats venant des dispositifs forestiers de suivi permanent sont contradictoires. Du point de vue théorique l'augmentation de CO₂ devrait être bénéfique pour la plante, le CO₂ étant un substrat clé de la photosynthèse. Certains auteurs ont montré un lien entre l'augmentation du CO₂ atmosphérique et l'augmentation de la croissance en forêt tropicale mais ce résultat n'est pas toujours retrouvé. Clark *et al.* (2010) ont montré que l'augmentation annuelle de la surface terrière du dispositif de La Selva était liée au climat mais pas à l'augmentation de la concentration en CO₂. D'un autre coté, certaines espèces de forêts tropicales sèches au sud du Mexique montrent une forte réaction à l'augmentation du CO₂ depuis 40 ans. Cette association a été mise en évidence par des données dendrochronologiques (Brienen *et al.*, 2011). Les données provenant de 50 dispositifs forestiers permanents en Amérique du Sud sur la période 1971-2002 montrent une augmentation du stock de biomasse et cette augmentation a été attribuée au CO₂ par Lewis *et al.* (2004). Le débat pour conclure si l'augmentation vue sur la biomasse en Amazonie est due à l'augmentation du CO₂ ou à un mécanisme de régénération est toujours en cours (Muller-Landau, 2009).

5.6 Vent

L'effet du vent est très peu étudié en Amazonie. La plupart des études associant vent et dynamique des forêts tropicales sont menées dans les régions tropicales où sont observés des cyclones et ouragans, i.e. dans les Caraïbes, en Amérique du Sud, en Amérique du Nord et en Australie, e.g. Gleason *et al.* (2008); Uriarte *et al.* (2004). Dans l'océan Atlantique, ces phénomènes météorologiques montrent une augmentation de fréquence depuis le début des années 90, due principalement à l'augmentation des températures de surface de l'Atlantique (Saunders & Lea, 2008). Leur effet sur les systèmes forestiers est considéré comme une perturbation avec des conséquences directes sur la mortalité, le recrutement, l'accès à la lumière et la structure. Consulter Gleason *et al.* (2008) pour une review des effets observés du vent sur les arbres. Un effet direct n'est pas attendu pour la croissance, cependant les vents violents peuvent provoquer un ralentissement de la croissance en réaction au traumatisme. C'est ce qu'ont observé Gleason *et al.* (2008) après le passage du cyclone Larry (Mars 2006) sur une forêt tropicale d'Australie : les arbres de 63 espèces ont diminué leur croissance en diamètre de 80% sur la période suivant le passage du cyclone. En Guadeloupe, Imbert & Portecop (2008) ont observé pour une forêt sèche des Caraïbes que neuf ans après le passage de l'ouragan Hugo (1989), la croissance en diamètre n'était pas revenue aux valeurs précédant l'ouragan.

5.7 Évènements El Niño

Le phénomène El Niño se caractérise par des températures de l'eau plus élevées que la normale dans la partie est de l'océan Pacifique sud (Beucher, 2010). De plus il est associé avec le cycle de variation de la pression atmosphérique globale entre l'est et l'ouest du Pacifique. Il entraîne des changements de climat dans la plupart des régions du globe. Ces évènements El Niño, interviennent à une échelle supra annuelle (exemples d'année El Niño : 1982-83, 1997-98, 2002-03) et entraînent des conditions climatiques plus sèches et plus chaudes pour le bassin amazonien. Ce phénomène est bien documenté pour l'Amazonie (Laurance *et al.*, 2009a; Marengo, 2004; Marengo *et al.*,

2001; Tian *et al.*, 1998). Plusieurs auteurs ont analysé l'effet de El Niño sur la dynamique des forêts tropicales en Amazonie. Les effets de El Niño observés jusqu'à présent sur la forêt tropicale amazonienne se traduisent par une augmentation de la mortalité et une augmentation de la vulnérabilité aux incendies (Aragao *et al.*, 2007; Condit *et al.*, 2004; Lewis *et al.*, 2004). Lors de l'année El Niño de 2001 qui a entraîné un épisode de sécheresse intense, Nepstad *et al.* (2004) ont montré que la production de biomasse de l'ensemble de l'Amazonie était inférieure de 0.19 Pg à ce qui pouvait être attendu sans inhibition de la croissance par la sécheresse. L'effet de l'El Niño peut avoir un effet inverse sur la croissance des arbres, par exemple sur des arbres de plaines inondées d'Amazonie dont la croissance s'arrête lors des inondations Schongart *et al.* (2004). Ces derniers ont montré que El Niño entraîne par la diminution des pluies, une diminution de la durée des inondations, un allongement de la durée de la saison de végétation et une augmentation de la croissance. Ces auteurs ont aussi montré une intensification des sécheresses induites par les événements El Niño au cours des deux derniers siècles en Amazonie. Même si les évidences de l'effet de El Niño sur la croissance des arbres sont peu nombreuses, potentiellement, son effet pourrait entraîner des changements dans la croissance des arbres. Ces derniers seraient à mettre en lien avec la sécheresse intense provoquée par la réduction du couvert nuageux (Lewis *et al.*, 2004).

5.8 Températures de surface de l'Atlantique, SST

Un autre phénomène, lié à la température de surface du nord de l'Atlantique tropical affecte le climat de l'Amazonie (SST, Sea Surface Temperature). Par exemple, la sécheresse en Amazonie de 2005 n'est pas due à un événement El Niño, mais à l'augmentation des SST de l'Atlantique (Aragao *et al.*, 2007; Marengo *et al.*, 2008; Marengo & Camargo, 2008). Les SST de l'Atlantique tropical pourraient influencer les précipitations de la saison sèche de l'Amazonie en déplaçant la ZIC et en modifiant les mouvements d'air verticaux (Good *et al.*, 2008). Ces SST influencent les croissances des arbres en provoquant la sécheresse dans le sud de l'Amazonie. L'implication

potentielle des températures de surface dans la croissance des arbres est la même que pour les événements El Niño.

6 Apport des traits fonctionnels à l'analyse de la croissance

Ces dernières années, plusieurs études ont permis de connaître la réponse des forêts tropicales à des événements climatiques (Brando *et al.*, 2008; Clark *et al.*, 2010; Lloyd & Farquhar, 2008; Wagner *et al.*, soumis). Ces études se focalisent particulièrement sur les variables climatiques pour lesquelles un changement est attendu, la température et les précipitations. Le problème principal, pour la modélisation de la dynamique des forêts tropicales, est qu'elles ont une richesse spécifique très importante et qu'il est difficile voire impossible de suivre expérimentalement la dynamique de toutes les espèces et donc de paramétrer des modèles espèce-spécifiques. Une méthode de plus en plus utilisée pour répondre aux questions écologiques à l'échelle de l'écosystème est de classer les plantes sur leurs ressemblances fonctionnelles et non sur leur taxonomie (Diaz *et al.*, 2004; Grime *et al.*, 1997; Lavorel & Garnier, 2002). Ces ressemblances fonctionnelles sont estimées en mesurant des traits fonctionnels clés de la plante. Ces traits peuvent être de plusieurs types : morphologiques, physiologiques ou phénologiques. La combinaison de plusieurs traits fonctionnels permet de caractériser le fonctionnement de la plante et de mettre en évidence les stratégies adaptatives de l'espèce (Diaz *et al.*, 2004; Grime *et al.*, 1997). Westoby (1998) et Westoby *et al.* (2002) ont établi le lien entre les traits fonctionnels et les stratégies universelles des plantes selon l'investissement dans les feuilles, la taille et la reproduction (Leaf Height Seed strategy scheme, LHS). Pour les traits fonctionnels foliaires Wright *et al.* (2004) ont établi l'existence d'un compromis entre la vitesse d'acquisition et la capacité de conservation des ressources, qui exercerait une contrainte majeure dans l'évolution de la physiologie des plantes. Ce compromis est connu sous le nom de 'leaf economic spectrum'. Un autre compromis sur les traits des tiges des arbres a été mis en évidence sur les me-

6. APPORT DES TRAITS FONCTIONNELS À L'ANALYSE DE LA CROISSANCE

sures de traits fonctionnels de 668 espèces tropicales (Baraloto *et al.*, 2010). Les auteurs ont montré qu'il existait un second compromis orthogonal au 'Leaf Economic Spectrum', figure 9, le 'Stem Economic Spectrum', les arbres avec une faible densité et une forte teneur en eau versus les arbres à forte densité et faible teneur en eau. Le but de l'analyse par les traits fonctionnels est de décrire les différentes stratégies des espèces de la communauté par une composition de traits fonctionnels. Comme ces traits fonctionnels traduisent les stratégies des espèces, ils devraient permettre de faire des modèles de communauté.

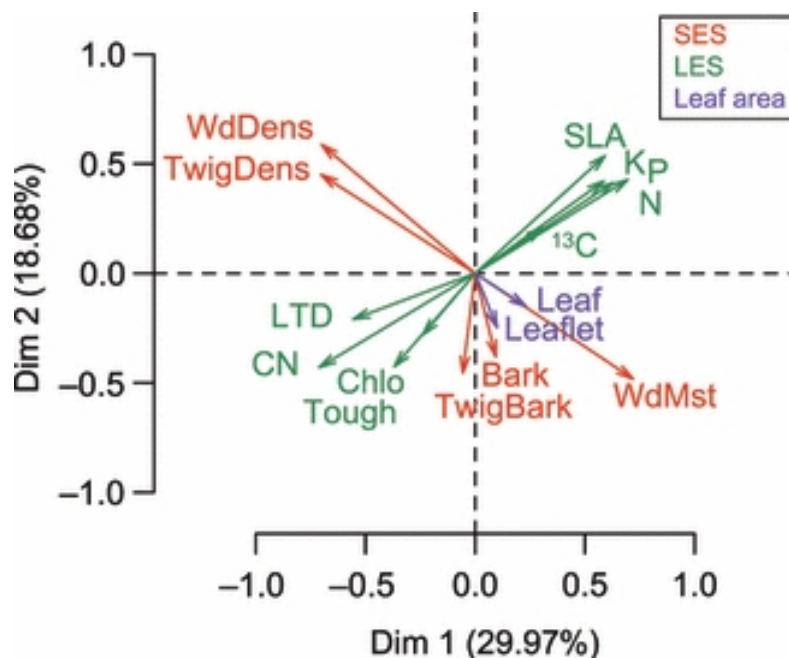


FIGURE 9 – Cercle de corrélation de 16 traits fonctionnels illustrant deux compromis dans la stratégie des arbres tropicaux, 'Stem Economic Spectrum' et 'Leaf Economic Spectrum', tiré de Baraloto *et al.* (2010)

Récemment Hérault *et al.* (2011) ont construit un modèle de croissance à l'échelle de la communauté basé sur les traits fonctionnels. Ce modèle permet d'expliquer environ 25% de la variabilité de la croissance des arbres sur une période de 14 ans avec seulement 4 traits inclus dans le modèle. Ceci permet de réduire le nombre de paramètres du modèle de communauté à un par trait alors qu'un modèle spécifique aurait demandé un jeu de paramètres par

espèce. Cette méthode par les traits simplifie considérablement la complexité de la modélisation de la communauté. Les traits qui permettent d'expliquer la croissance des arbres sont le diamètre maximal de l'espèce, la densité du bois, la hauteur maximum de l'espèce et le $\delta^{13}C$ des feuilles. Dans cette étude, les traits foliaires sont peu reliés à la croissance des arbres. Dans les paragraphes suivants sont décrits les rôles supposés de chacun des traits fonctionnels dans la réponse de la croissance des arbres au climat. Pour une définition plus complète des traits, se reporter à l'article de Cornelissen *et al.* (2003). Nous nous focalisons sur les interactions traits/climats pour les plantes adultes parce que le rôle des traits fonctionnels varie considérablement au cours de l'ontogénie (Wright *et al.*, 2010).

6.1 Traits d'histoire de vie

Les traits d'histoire de vie regroupent les traits liés à la stature (diamètre de l'arbre, diamètre maximum et hauteur maximum de l'espèce) et à la stratégie de régénération (masse des graines, type de germination). La hauteur maximum est un indicateur de la position de la plante adulte dans le profil vertical de la végétation et de son accès à la lumière (Hérault *et al.*, 2010). Poorter *et al.* (2008) font l'hypothèse que les arbres qui ont leur couronne dans la canopée sont exposés à des conditions plus sèches et qu'ils pourraient avoir plus de difficultés à maintenir leur demande évaporative lors des périodes sèches. Cette même hypothèse semble pouvoir s'appliquer au diamètre observé de l'arbre et au diamètre maximum de l'espèce. Le diamètre observé est un bon l'indicateur de la place de la couronne dans la canopée. En Guyane, Granier *et al.* (1996) ont observé, par des mesures de flux de sève, que les gros arbres ont une plus grande demande en eau. Dans cet étude, le flux de sève total journalier des arbres dominants peut atteindre 250 à 300 kg.jour⁻¹. Le débit de sève dépend de l'aire de l'aubier et cette aire est directement reliée au diamètre du tronc, certains auteurs corrigent même par le diamètre pour normaliser les flux de sève provenant de plusieurs arbres (Fisher *et al.*, 2007). Nepstad *et al.* (2007) ont montré dans une expérience d'exclusion des pluies (exclusion de 60% des pluies en saison humide) que

les gros arbres étaient les plus affectés, notamment pour la mortalité. Plus précisément, après 3.2 ans d'exclusion des pluies, la mortalité des arbres de la parcelle traitée était augmentée de 38 % par rapport aux parcelles témoins. Les taux de mortalité sont 4 à 5 fois plus importants pour les arbres aux diamètres supérieurs à 30 cm et deux fois plus importants pour les arbres entre 10 et 30 cm. On peut supposer que cette hausse de la mortalité est précédée par un ralentissement de la croissance. Sur le même site, ces deux processus, mortalité et croissance, ont vu leurs dynamiques changer lors de l'exclusion des pluies (Brando *et al.*, 2008). Selon les auteurs qui ont analysé l'augmentation de la mortalité en Amazonie en 2005, celle-ci devait s'accompagner d'une diminution de la croissance mais leur méthode n'a pas permis de l'établir à cause des intervalles de temps de plusieurs années entre les mesures (Phillips *et al.*, 2009). Notre hypothèse est que les arbres avec de gros diamètres, ainsi que les espèces avec les diamètres maximums et les hauteurs maximums les plus importants, devraient être plus sensibles aux conditions de sécheresse et que cela devrait affecter négativement leur croissance. Bien que la masse des graines ne soit pas directement reliée aux performances de la plante adulte, elle est un important indicateur de la stratégie d'histoire de vie des espèces. Par exemple, les espèces à croissance rapide ont tendance à avoir de petites graines (Moles *et al.*, 2004; Poorter & Bongers, 2006). Pour ces espèces à petites graines, on s'attend à une plus grande sensibilité de la croissance aux variations climatiques, due aux importants besoins en ressources demandées pour maintenir une croissance rapide.

6.2 Traits du 'Stem Economic Spectrum'

Les arbres à bois dense pourraient être moins sensibles à la sécheresse que les arbres à bois léger en raison d'une résistance plus élevée à l'embolisme, les espèces à densité de bois élevée ont des petits vaisseaux qui permettent une meilleure résistance à la cavitation (Chave *et al.*, 2009; Markesteijn *et al.*, 2011). Cette hypothèse a été validée empiriquement par Poorter *et al.* (2010). L'épaisseur de l'écorce n'a pas, a priori, de lien avec le climat, c'est plutôt un trait de défense de l'arbre et de résistance au feu (Paine *et al.*, 2010).

Indirectement ce trait peut être lié aux variations de diamètre, si les troncs gonflent au début de la saison des pluies et se rétractent au début de la saison sèche (Baker *et al.*, 2003; Stahl *et al.*, 2010). Les espèces à écorce épaisse devraient montrer un gonflement plus important que les autres en début de saison des pluies et cela devrait se traduire par un accroissement en diamètre supérieur à celui des espèces avec des épaisseurs d'écorce petites.

6.3 Traits du 'Leaf Economic Spectrum'

Bien qu'il existe une littérature abondante sur les liens entre valeurs de traits foliaires et réponse de la croissance au climat chez les plantules (Kitajima, 1994; Poorter & Bongers, 2006), peu d'études ont analysé cette association pour les plantes adultes. Le rapport surface de la feuille/masse de la feuille (Specific leaf area, SLA) indique l'efficacité de la feuille à capter la lumière par unité de biomasse investie (Poorter *et al.*, 2009). Le SLA n'est pas relié à la croissance chez les arbres adultes où celle-ci semble plus déterminée par le nombre méristèmes actifs que par les variations de SLA (Poorter *et al.*, 2008; Sterck & Bongers, 2001). Cependant en réponse au climat, les espèces avec un grand SLA, qui ne permet pas un contrôle important de la perte d'eau par la feuille en comparaison aux feuilles plus coriaces, pourraient être plus affectées en conditions sèches, à cause de l'importante ressource en lumière et de la diminution de disponibilité en eau du sol. Les espèces avec un grand SLA ont tendance à avoir des feuilles à durée de vie plus courte avec une haute concentration en N et P, figure 9. Ces traits sont le plus fréquemment trouvés du côté des espèces à croissance rapide du 'Leaf Economic Spectrum' et ces espèces sont connues pour être plus sensibles aux variations de disponibilités en ressources parce qu'elles ont plus de besoins par unité de temps que les espèces à croissance lente (Fyllas *et al.*, 2009; Poorter & Bongers, 2006; Wright *et al.*, 2004). La concentration de K foliaire est corrélée avec la concentration de N et de P foliaire (Baraloto *et al.*, 2010; Wright *et al.*, 2004). Le K foliaire intervient dans le contrôle des stomates, plus précisément les mouvements stomatiques résultent du transport de K⁺ à travers les membranes des cellules de garde des stomates (Roelfsema &

Hedrich, 2005). On peut imaginer que les espèces avec une grande valeur de K foliaire sont plus sensibles à la sécheresse. De plus, ce trait est corrélé positivement avec N et P . De l'autre côté du 'Leaf Economic Spectrum', les traits associés avec un faible SLA (limbe épais, petites cellules à parois épaisses) sont considérés comme des adaptations permettant de maintenir les fonctions de la feuille sous des contraintes de sécheresse importante, même chez les espèces sempervirentes (Donovan *et al.*, 2011; Wright *et al.*, 2004). Les espèces avec des valeurs élevées de ces traits (limbe épais, petites cellules à parois épaisses) devraient être capables de maintenir leur croissance en début de saison sèche, pour une période plus longue que les espèces avec de faibles valeurs pour ces traits. Le $\delta^{13}C$ est une mesure de l'efficacité d'utilisation de l'eau par la plante (Farquhar *et al.*, 1989). Ce trait est intégrateur de la réponse des stomates à la sécheresse de l'air (McMahon *et al.*, 2011; Prentice *et al.*, 2011). Il existe une corrélation entre les feuilles avec un faible SLA et une faible efficacité d'utilisation de l'eau (Fyllas *et al.*, 2009; Lamont *et al.*, 2002), mais on ne la retrouve pas chez les arbres de Guyane (Baraloto *et al.*, 2010). Les conditions sèches pourrait affecter en priorité les espèces qui ont une faible efficacité d'utilisation de l'eau, i.e. les espèces les moins économes (Bonal *et al.*, 2000).

7 Matériel et méthodes

7.1 Données de terrain

Site d'étude

Les travaux de cette thèse ont été réalisés sur les données du dispositif de recherche sylvicole de Paracou (5°18'N, 52°23'W), à 15 km de l'océan Atlantique en Guyane Française. Ce dispositif a été mis en place en 1984 par le Cirad pour étudier l'effet de différents traitements sylvicoles. Il comprend 15 parcelles forestières de 6.25 ha, dont 6 témoins (3 depuis 1984 et 3 depuis 1991) et 9 parcelles exploitées avec différents traitements sylvicoles (Gourlet-Fleury *et al.*, 2004), figure 10. Sur les parcelles témoins plus de 90 % des arbres sont identifiés à l'espèce. Dans cette thèse seules les données

des parcelles témoins ont été utilisées.

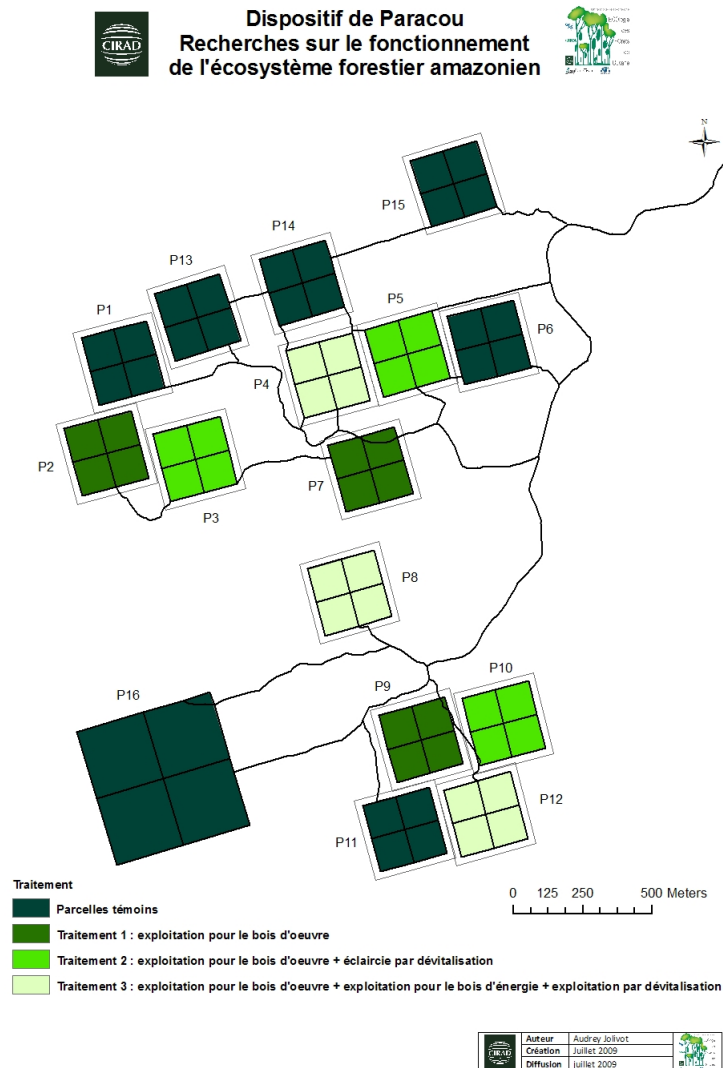


FIGURE 10 – Carte du dispositif de suivi forestier permanent de Paracou

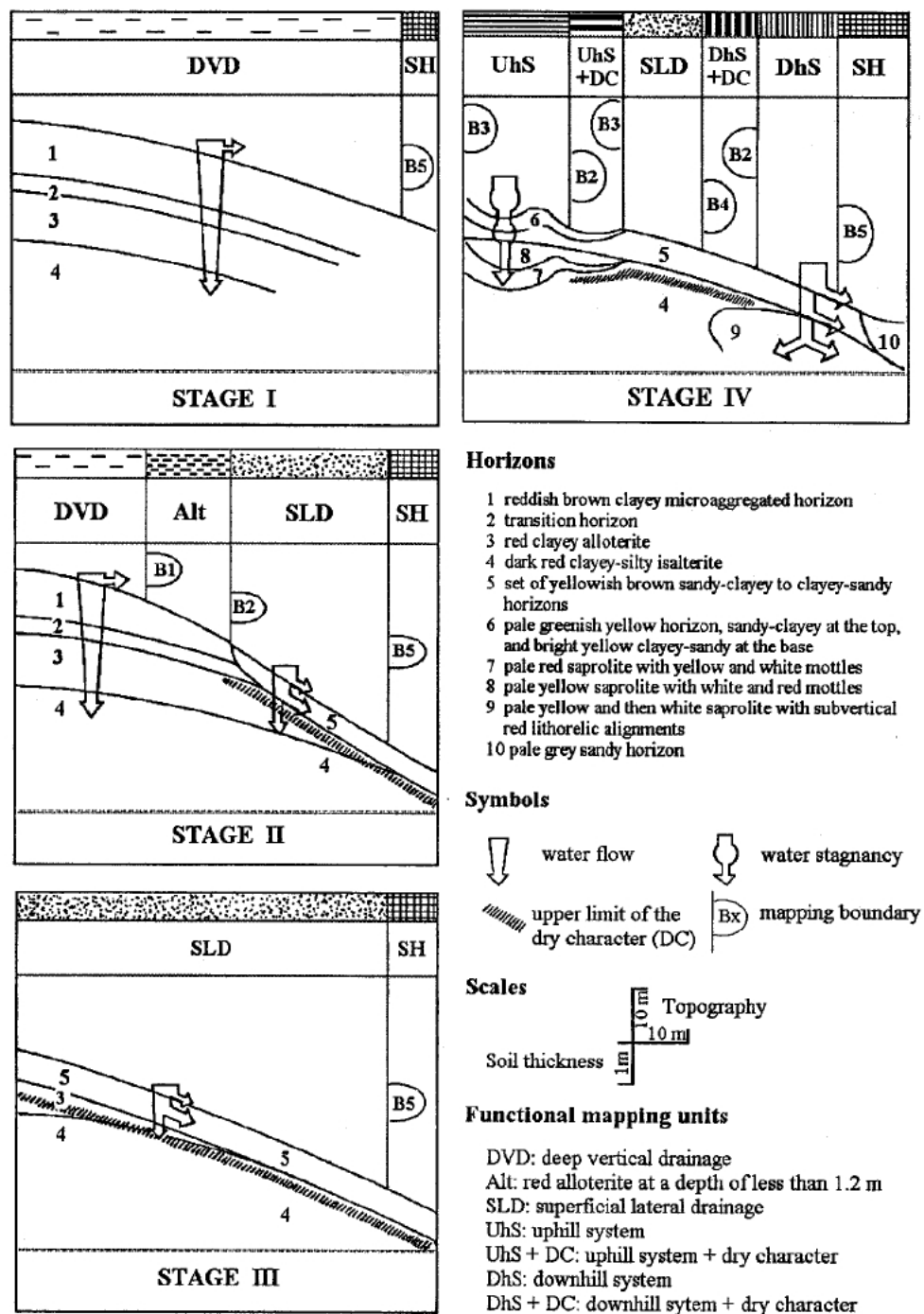
La forêt de Paracou est classifiée comme étant une forêt tropicale humide de basse altitude sur terra firme (terre ferme), un type forestier typique du bouclier des Guyanes (ter Steege *et al.*, 2006). Plus de 550 espèces ligneuses atteignant 2 cm de DBH (Diameter at Breast Height, 130 cm) ont été décrites à Paracou, avec une moyenne du nombre d'espèces de DBH supérieur à 10 cm comprise entre 160 et 180 par hectare. Les familles dominantes comprennent

les Leguminosaeae, Chrysobalanaceae, Lecythidaceae, Sapotaceae et les Burseraceae. La topographie du site est formée de petites collines d'environ 40 m au dessus du niveau de la mer entrecoupées par des bas-fonds.

Les sols de Paracou sont définis par sept unités fonctionnelles qui correspondent à différents stades d'évolutions d'un sol ferralitique, figure 11 (Sabatier *et al.*, 1997). Ces différents stades sont reliés à différents fonctionnements hydrodynamiques et aux propriétés chimiques du sol. Les sols les plus communs à Paracou sont des sols ferralitiques peu profonds limités en profondeur par une couche d'allotérite rouge limoneuses (dégradation de la roche mère). Hormis les bas-fonds, les sols montrent un drainage très important avec une conductivité hydraulique des horizons de surface pouvant approcher 500 mm par jour (Guehl, 1984). Le site de Paracou reçoit annuellement environ 3000 mm de précipitations en moyenne (Bonal *et al.*, 2008; Gourlet-Fleury *et al.*, 2004). Ces précipitations sont inégalement réparties au cours de l'année avec une grande saison sèche de mi-août à mi-novembre et une saison des pluies de décembre à juillet, figure 4. En saison sèche, certains mois ont des précipitations inférieures à 50 mm. Une petite saison sèche a lieu en mars mais elle est d'intensité variable et parfois même absente. Les températures moyennes varient très peu, seule l'amplitude varie au cours de l'année, montrant une augmentation en saison sèche.

Mesures de diamètres

Pour les mesures de diamètres, nous disposons de trois types de données : (i) des données d'inventaire mesurées avec des mètres à ruban ; (ii) des données provenant de dendromètres installés sur les arbres et relevés tous les 2 mois environ ; et (iii) des données provenant de dendromètres automatiques (mesure automatique toutes les 30 minutes). Dans chaque parcelle de Paracou, tous les arbres de diamètres supérieurs à 10 cm de diamètre sont spatialement référencés, étiquetés, identifiés au plus bas niveau taxonomique et leur circonférence mesurée annuellement ou bi-annuellement. Ces données sont stockées dans une base Firebird (GUYAFOR v. 2.1). Pour les 6 parcelles témoins, cela représente environ 28200 arbres et plus de 316000 mesures d'ac-

FIGURE 11 – Stade d'évolution du sol à Paracou, tiré de Sabatier *et al.* (1997)

croissements. La précision de mesure de ces accroissements est de 0.5 cm en circonférence. Les changements de circonférence à une échelle saisonnière, environ 40 jours, sont suivies depuis 2007 sur 235 arbres de 67 espèces avec des dendromètres à ruban en acier (Stahl *et al.*, 2010). Des dendromètres automatiques équipent 10 arbres dominants depuis 2007. Ces dendromètres mesurent les variations de circonférence toutes les 30 minutes. Les données sont enregistrées par une centrale d'acquisition de données (CRX10 datalogger, Campbell Scientific Inc.).

Données climatiques

Une convention entre le Cirad et Météo France a permis d'obtenir les données météorologiques journalières : précipitations, températures minimales et maximales, vent, rayonnement et évapotranspiration sur l'ensemble des 35 stations de Guyane française pour la période 1950-2009, lorsque celles-ci étaient disponibles.

Sur le dispositif de Paracou, une tour à flux de 55 m, Guyaflux, a été construite par l'INRA en 2003 dans un chablis naturel de 100 m² (Bonal *et al.*, 2008). Le haut de la tour, où sont installés les capteurs météorologiques, se trouve 20 m au dessus de la canopée. Ces capteurs mesurent plusieurs variables climatiques (précipitations, rayonnement, température, vent, pression atmosphérique, humidité de l'air, déficit de vapeur saturante), ainsi que des mesures d'eddy covariance, notamment les flux de CO₂ et d'H₂O. Les mesures sont sommées ou moyennées toutes les demi-heures, tous les détails des capteurs et des mesures sont disponibles dans l'article de Bonal *et al.* (2008).

La teneur en eau du sol provient de mesures réalisées toutes les trois semaines avec une sonde 'Time Domain Reflectometry' (TDR, TRIME FM3 ; Imko, Ettlingen, Germany) dans 10 tubes de 0.2 à 2.6 m avec une mesure tous les 0.2 m de profondeur, sur un transect qui traverse un gradient de sols typiques de Paracou.

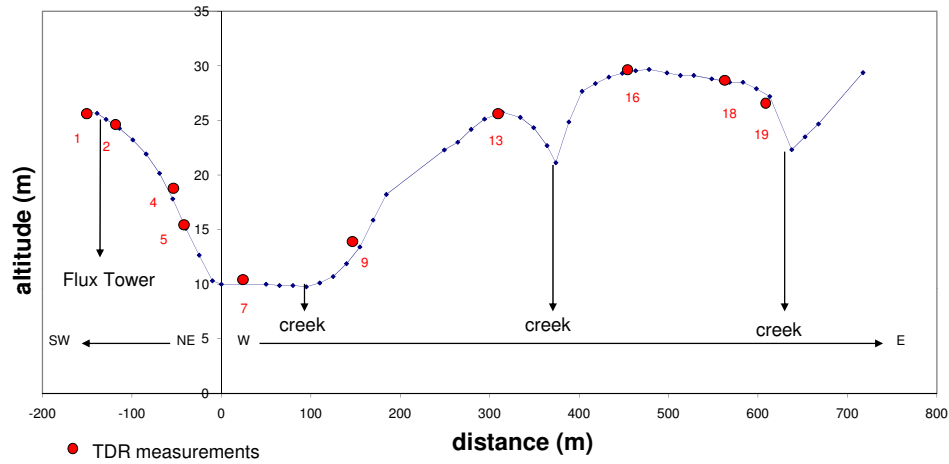


FIGURE 12 – Profil topographique du transect des mesures de l’humidité du sol, les points représentent l’emplacement des tubes TDR

Traits fonctionnels

Les mesures des traits fonctionnels des espèces de Guyane sont rassemblés dans une base de données, la base Mariwenn (Ollivier *et al.*, 2007). Cette base est accessible en ligne sur le site de l’UMR Ecofog (www.ecofog.gf/Mariwenn). Pour cette thèse d’autres données de traits fonctionnels provenant de la base Bridge ont été utilisés (<https://bridgedata.ecofog.gf/>) (Baraloto *et al.*, 2010). Ces traits fonctionnels ainsi que leur rôle écophysiologicals sont présentés dans le tableau 2.

7.2 Logiciel

L’ensemble des calculs, des analyses statistiques, des programmes développés et des graphiques présentés dans ce mémoire ont été réalisés grâce au logiciel R, version 2.10.1 (R Development Core Team, 2009). Le modèle de la disponibilité en eau et son inférence sont codés en langage C++, cf. chapitre 2.

	rôles	unités	valeurs
<i>histoire de vie</i>	DBH _{max}	mm	190 – 980
	hauteur _{max}	m	18 – 50
	masse des graines	g	<0.01 – >20
<i>stem economic spectrum</i>	densité du bois	g.cm ⁻³	0.38 – 0.84
	épaisseur de l'écorce	mm	(-4.7) – 13
<i>leaf economic spectrum</i>	SLA	cm ² .g ⁻¹	5.41 – 16
	K	g.g ⁻¹	2 × 10 ⁻³ – 2 × 10 ⁻²
	N	g.g ⁻¹	1 × 10 ⁻² – 4 × 10 ⁻²
	P	g.g ⁻¹	3 × 10 ⁻⁴ – 2 × 10 ⁻³
	C/N	g.g ⁻¹	13 – 34
	densité du tissu foliaire	g.cm ⁻³	2.5 × 10 ⁻⁵ – 5.6 × 10 ⁻⁵
	chlorophylle	μg.mm ⁻²	48 – 100
	épaisseur du limbe	N	0.85–3.4
	δ ¹³ C	‰	(-1.7) – 2.5

TABLE 2 – Traits fonctionnels utilisés dans la thèse, adapté de Baraloto *et al.* (2010)

7.3 Statistique bayésienne

Des méthodes bayésiennes numériques ont été utilisées pour inférer certains modèles. La statistique bayésienne permet de répondre à des questions auxquelles il serait plus difficile de répondre avec les méthodes de statistique fréquentiste, le problème principal provenant de la quantité de données. L'agriculture et l'écologie font partie des domaines pour lesquels l'approche bayésienne est de plus en plus utilisée (Buckland *et al.*, 2007). En effet ces domaines impliquent des systèmes dynamiques où la fréquence des observations est faible et où les séries temporelles sont courtes, typiquement une observation une fois par an sur quelques dizaines d'années. Pour cette raison, l'application de méthodes fréquentistes, basé sur un grand nombre d'observation est difficile dans ces domaines. L'autre avantage de ces méthodes est la possibilité intégrer un avis d'expert *a priori*. Les méthodes bayésiennes constituent un outil puissant pour l'estimation de la variabilité dans les processus écologiques (Clark, 2005, 2007b). Ces statistiques s'appuient sur la généralisation de la formule de Bayes, eqn 2. Soit un vecteur d'observations *Data* que l'on doit expliquer à partir d'un modèle faisant intervenir un paramètre θ , Bayes a démontré que l'on pouvait estimer la distribution *a posteriori* du paramètre θ en utilisant les probabilités conditionnelles :

$$p(\theta|Data) = \frac{p(Data|\theta)p(\theta)}{\int_{\theta} p(Data|\theta)p(\theta)d\theta} \quad (2)$$

Où $p(\theta)$ est la distribution a priori de θ intégrant la connaissance *a priori* sur θ , $p(Data|\theta)$ est la vraisemblance du modèle, $\int_{\theta} p(Data|\theta)p(\theta)d\theta$ est la constante de normalisation et $p(\theta|Data)$ est la distribution *a posteriori* de θ . La constante de normalisation peut ne pas avoir de solution analytique. Cette constante est indépendante de θ puisqu'elle est intégrée sur θ . Le postérieur conditionnel de θ est alors estimé à partir de la relation suivante :

$$p(\theta|Data) \propto p(Data|\theta)p(\theta) \quad (3)$$

Dans quelques cas où la vraisemblance et la distribution a priori sont

conjuguées, la distribution *a posteriori* de θ est connue (Bernardo & Smith, 1994). Les paramètres de la distribution *a posteriori* seront fonctions des paramètres de la distribution *a priori*, de la vraisemblance et des données. Lorsque les lois de la vraisemblance et la distribution *a priori* ne sont pas conjuguées, des algorithmes permettent d'échantillonner des valeurs de θ dans la distribution *a posteriori*, par exemple l'algorithme de Metropolis-Hastings. Ces algorithmes construisent une chaîne de Markov par simulation de Monte-Carlo (MCMC) dont la distribution converge vers la distribution *a posteriori* de θ (Clark, 2007b; Gelman *et al.*, 2004).

8 Objectifs de la thèse

Le cadre conceptuel de la thèse est l'étude de la réponse des forêts tropicales aux changements climatiques ; en terme de stock de carbone avec des données de dispositif permanent, et plus particulièrement, sur un des paramètres de l'évolution du stock de carbone, la croissance des arbres. Pour l'augmentation de biomasse observée à Paracou et pour la plupart des forêts tropicale, notre première hypothèse est que ces forêts ne sont pas en train de changer de fonctionnement, mais que cette apparente augmentation de biomasse proviendrait directement du fonctionnement des cycles sylvigénétiques. Ces derniers seraient rythmés par une lente accumulation de biomasse jusqu'à chaque perte importante de biomasse due aux événements de mortalité des gros arbres. Quantifier la variabilité des paramètres de structure et de dynamique de la biomasse en fonction de la surface échantillonnée et du temps entre les intervalles de mesures constitue un pré-requis indispensable à l'étude de la biomasse et des flux de carbone. Notre deuxième hypothèse est que le rôle du climat et en particulier le rôle de la disponibilité en eau sur la croissance en diamètre des arbres est sous estimé dans les écosystèmes forestier tropicaux. D'une part, cela est dû aux relevés pluri-annuelle des dispositifs forestiers permanents qui ne permettent pas de prendre en compte précisément les variations inter-annuelles du climat. D'autre part, en milieu tropical, on ne dispose pas d'outils suffisamment précis pour l'étude de la disponibilité en eau sur la croissance des arbres à des échelles journalières

ou saisonnières. La troisième hypothèse de travail de cette thèse est que les traits fonctionnels peuvent traduire la réaction des espèces à des conditions climatiques particulières, notamment en terme de croissance. La compréhension de la réaction des arbres au travers des traits fonctionnels amène une nouvelle approche pour les modèles de communautés des écosystèmes forestiers. Cette nouvelle approche devrait permettre de faire des prédictions pour un arbre dont le modèle de croissance est inconnu à partir du moment où les valeurs de ses traits fonctionnels sont connues.

Cette thèse utilise la modélisation et l'analyse statistique pour investiguer ces hypothèses écologiques en utilisant des données provenant de différents champs disciplinaires de l'écologie.

Cette thèse se divise en deux grandes parties, la première concerne l'analyse de la biomasse du dispositif de suivi forestier de Paracou en Guyane et l'implication des changements de structure de cette forêt sur le bilan de carbone. Cette partie est constituée de deux points : (i) Quelles échelles temporelles et spatiales sont pertinentes pour analyser les composantes de structure (biomasse, aire basale et nombre de tiges) et de dynamique (croissance, recrutement et mortalité) des forêts tropicales afin de minimiser les effets d'échantillonnage ? (ii) Quels processus démographiques sont prépondérants dans les variations de biomasse observées et comment se redistribue la biomasse accumulée dans le système forêt. Cette analyse va permettre d'apporter une contribution sur l'explication du changement de la dynamique de la biomasse observé en forêts tropicales ces dernières décennies.

La deuxième partie de la thèse concerne l'analyse de l'effet du climat à court terme, inter et intra annuel, et les implications du climat dans les changements de dynamique de la forêt. Cette partie se divise en 3 points : (i) Quels indices climatiques utiliser pour tester l'effet du climat sur la croissance ? Nous proposons dans ce point une méthode pour déterminer l'eau disponible dans le sol pour les arbres de forêts tropicale ; (ii) Quelles variables climatiques sont explicatives de la croissance en forêt guyanaise ? (iii) Quels traits fonctionnels sont prédictors de la réponse des arbres aux variations climatiques ?

Chapitre 1

Bilan de carbone

1 Effet de la surface d'échantillonnage et de l'intervalle de temps entre les mesures sur les variations des descripteurs de structure et de dynamique de la forêt

L'étude des descripteurs de structure (densité du peuplement, surface terrière et biomasse aérienne) et de dynamique (croissance des arbres, taux de mortalité et de recrutement et flux de biomasse) de la forêt tropicale représente un enjeu majeur pour la prédiction de la réponse de cette forêt à l'augmentation de CO₂ d'origine anthropique. Dans la plupart des études menées en milieu tropical, les mesures sont effectuées sur des surfaces de l'ordre de l'hectare (Clark, 2007a; Phillips *et al.*, 2009), les descripteurs sont ensuite extrapolés à une échelle supérieure. Récemment, Fisher *et al.* (2008) ont montré par des simulations de peuplements forestiers, que l'effet de la taille de la parcelle et de la stratégie d'échantillonnage pouvait biaiser les descripteurs. Ce problème est particulièrement important pour les événements rares, par exemple pour la mortalité qui représente 1% du peuplement par an à Paracou. La base de données de Paracou offre une opportunité unique pour analyser les variations spatiales et temporelles des descripteurs dynamiques et statiques en forêt tropicale. Cette information est d'autant plus impor-

tante que le jeu de données de Paracou est utilisé comme site de référence dans le suivi de la dynamique de la biomasse des forêts tropicales à l'échelle mondiale (Phillips *et al.*, 2009). Dans cette partie, nous avons donc étudié le lien entre la variabilité des descripteurs de structure et de dynamique en fonction (i) de la surface échantillonnée et (ii) du temps entre les intervalles de mesures. Tous les descripteurs de structure de la forêt ont des coefficients de variation de moins de 10 % pour des parcelles de taille supérieure à 2 hectares. Parmi les descripteurs de la dynamique forestière, le flux sortant de biomasse aérienne (mortalité) est le plus variable. Cinq parcelles de 6.25 ha sont nécessaires pour estimer sa moyenne, sur une période de 16 ans, avec un coefficient de variation de 20 %. Ceci contraste avec un flux entrant de biomasse aérienne, via la croissance des arbres présents et le recrutement de nouveaux individus, relativement constant. La croissance moyenne des arbres est remarquablement bien estimée avec un coefficient de variation de 15 % pour une parcelle de 2 ha recensée tous les 2 ans. Ce travail fournit une méthode simple de quantification des limitations des jeux de données utilisés pour estimer les descripteurs de structure et de dynamique forestière. Cette analyse est un pré-requis à l'analyse et l'interprétation des effets du changement climatique sur les forêts tropicales.

Ce travail est présenté dans la publication ci-après, Wagner *et al.* (2010).

Effects of Plot Size and Census Interval on Descriptors of Forest Structure and Dynamics

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ABSTRACT

This study was designed to explicitly formulate the effect of census interval and plot size on the variability of descriptors of tropical forest structure (stand density, basal area, aboveground biomass [AGB]) and dynamic (tree growth, mortality and recruitment rates, biomass fluxes). A unique dataset from a broad plot network (37.5 ha) surveyed every 2 yr over a 16-yr period was used to develop and parameterize a new statistical model predicting the coefficients of variation for each forest descriptor. More than 90 percent of the inherent variability of these coefficients was predicted using a simple model including plot size and census interval in a Bayesian modeling framework. All descriptors of forest structure varied by < 10 percent for plot sizes > 2 ha. Among the descriptors of forest dynamics, AGB loss was the most variable. The number of 6.25 ha plots required to estimate its mean, over a 16-yr period, within a 20 percent error of the mean remains above four. This contrasts with a relative constant flux of biomass entering the plot through tree growth and tree recruitment. Tree growth was remarkably well estimated with < 15 percent variability for a 2-yr census in a plot of 2 ha. This study provides an easy method to assess dataset limitations in efforts to estimate descriptors of forest structure and dynamic, which is of primary importance to decipher any clear consequences of global change in tropical forests.

Abstract in French is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: Amazonia; biomass fluxes; coefficient of variation; forest permanent plots; turnover rates; WinBUGS.

MOST OF OUR CURRENT KNOWLEDGE ON TROPICAL FOREST STRUCTURES and dynamics relies on observations of permanent plots (Mahli *et al.* 2002, Phillips *et al.* 2008). Descriptors of forest structures (stand density, basal area [BA], aboveground biomass [AGB]) and of forest dynamics (tree growth, mortality and recruitment rates, biomass fluxes) are estimated from repeated inventories on long-term forest plots (Swaine *et al.* 1987). These plots are the empirical basis for the current debate on tropical forest dynamics that has been focused on the detection of recent changes in AGB fluxes and stocks (Lewis *et al.* 2004, Clark 2007a, Phillips *et al.* 2008, Pyle *et al.* 2008). Deciphering unambiguous trends in tropical forest dynamics, especially those associated with global change, remains complicated because of the high levels of variability among and within tropical forest plots. First, because a single plot strategy is unlikely to represent the structural and dynamic variability of tropical forests (Clark 2007a), large-scale analyses are now performed through broad plots networks, such as RAINFOR or the pan-tropical CTFs network (Mahli *et al.* 2002, Losos & Leigh 2004). Second, descriptors of forest structure and of forest dynamic in a given forest plot are obviously linked to the spatial and temporal scales of investigation (Spies 1998). For example, Fisher *et al.* (2008) have recently attempted to highlight how plot size and sampling strategy may introduce bias in large-scale estimates in AGB, notably if mortality events are clumped and if large tree distribution is spotty (Brown *et al.* 1995). Even if some very recent studies (Gloor *et al.* 2009, Lewis *et al.* 2009, Lloyd *et al.* 2009) questioned the use by

Fisher *et al.* (2008) of least squares regression to fit power laws (but see Chambers *et al.* 2009), a correct estimation of the uncertainty due to plot size and census interval remains of primary importance to make accurate inferences based on representative descriptors of forest structure and dynamic (Sheil 1996, 1997; Phillips *et al.* 1997, 2002; Clark 2002, 2007a; Chave *et al.* 2004; Wright 2005). To our knowledge, a few studies (Hall *et al.* 1998) explicitly investigated the range of expected variability of tropical forest descriptors through space and time.

Hall *et al.* (1998) estimated the coefficient of variation (CV) of different forest descriptors (*e.g.*, stand density, tree mortality and recruitment) between two sites of tropical forest and gave an explicit formula of the minimal plot size required to detect significant differences among sites. They concluded that the differences among tree population become more difficult to detect as variance within a tree population increases and larger plot size are therefore needed to provide statistical confidence in conclusions. They also stressed that 'within a given sample size, when the variance within a time period is high, either differences among time periods need to be very large or many time periods need to be measured to statistically identify trends over time'. Keller *et al.* (2001), using the Student's *t*-statistic, estimated the amount of plots or area needed to sample, based on variability in their biomass data. Neither study (Hall *et al.* 1998, Keller *et al.* 2001) accounted simultaneously for the effects of both space- and time-scale variation on estimates of forest descriptors, or attempted to generalize results through a mathematical-explicit formulation of the CV.

We, therefore, designed this study to assess the within-a-forest variability of a large set of tropical forest descriptors at various scales of space and time. To our knowledge, this is the first attempt to

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explicitly model this variability for both forest plot size and length of forest census. In our study, we present a unique dataset from a broad plot network (37.5 ha) surveyed every 2 yr over a 16-yr period to develop and parameterize a new statistical model predicting the range of variability expected for a given forest descriptor. The inherent variability of all these descriptors was predicted using a simple model including plot size and census interval in a Bayesian modeling framework.

METHODS

DATASET.—The study was conducted at the Paracou experimental site (5°18' N, 52°55' W), a lowland tropical rain forest near Sinnamary, French Guiana (Gourlet-Fleury *et al.* 2004). The site receives nearly two-thirds of the annual 3041 mm of precipitation between mid-March and mid-June, and < 50 mm/mo in September and October (Gourlet-Fleury *et al.* 2004). The most common soils in Paracou are the shallow ferralitic soils limited in depth by a more or less transformed loamy saprolite (Gourlet-Fleury *et al.* 2004). Some very thick ferralitic soils, with free vertical drainage, are primarily encountered on the highest residual summits of the area (*ca* 40 m asl). The forest is typical of Guianan rain forests (Ter Steege *et al.* 2003). More than 550 woody species attaining 2 cm diameter at breast height (dbh; 130 cm) have been described at the site, with an estimated 160–180 species of tree ≥ 10 cm dbh/ha. The dominant families at the site include Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae.

A total of six (three in 1986 and three in 1991) square 6.25 ha parcels were established at the Paracou site for a complete annual inventory of all trees > 10 cm dbh (detailed map in Appendix S1). Annual inventories of mortality, recruitment and diameter growth were conducted until 1995 and every 2 yr thereafter. Here, we use data from 1991 to the most recent inventory in 2007, *i.e.*, 16 yr of data. Dbh was calculated from circumference measures made to a precision of 0.5 cm. For trunks without buttresses, measurements were made at positions of 1.3 m above the soil surface and points of measurement were marked using permanent paint. For trunks with buttresses, these measures were moved to a position 10 cm above the buttresses and also marked with paint. All trees were kept in data analysis for both biomass and growth estimations.

All data are stored in an MS Access data base (GUYAFOR v 2.1).

SAMPLING STRATEGY.—We aimed to develop and parameterize a statistical model predicting the range of variability expected for a given forest descriptor through a large range of plot size (descriptors of forest structure) and census intervals (descriptors of forest dynamic). To achieve that, we first derived a set of descriptors of forest structure for different plot sizes, obtained by overlaying virtual sampling grids on all six investigated forest plots. To avoid sampling bias, the grid cell was computed by dividing the plot side length (250 m) by an integer between 1 and 12. This strategy enables to use the same tree population through the entire analysis. Plot sizes ranged from 0.04 to 6.25 ha. Descriptors of forest structure were then calculated in each grid cell at each census. Secondly,

we derived a statistical population of descriptors of forest dynamics not only for different forest plot sizes, but also for different forest census intervals (2–16 yr) using the real field data (and not estimated from the successive intermediate censuses). For every combination of plot size and census interval, we computed the mean and standard deviation (SD) of the descriptors in each forest plot.

DESCRIPTORS OF FOREST STRUCTURE.—We focused on three widely used descriptors of forest structure (summary statistics in Table 1): Stand density (number of individuals/ha), BA computed as the total cross-sectional area of trees at height of measurement (m^2/ha) and AGB (Mg/ha) estimated with allometric relationships assuming circular stems at the point of measurement but not including height measurements (Chave *et al.* 2005):

$$\text{AGB} = \rho \times \exp(0.0634 - 1.562 + (2.148 \times \log(\text{dbh})) + (0.207 \times \log(\text{dbh}))^2 + (-0.0281 \times \log(\text{dbh}))^3), \quad (1)$$

where ρ is the wood specific gravity (g/cm^3) and dbh (cm). To avoid bias due to regional data base compilation (Baraloto *et al.* 2010), wood density at 12 percent humidity was measured on wood samples coming from trees logged on the same plot network (Gourlet-Fleury *et al.* 2004) and converted into wood specific gravity through multiplication by the correction factor 0.872 (Chave *et al.* 2006). When no reliable species identification was available, we applied the mean ρ of all sampled species within a genus to all species within that genus (10.5%). A similar procedure was used at the family level (17.7%). In cases of no botanical identification (19.4%), we assigned the plot-averaged ρ (mean: $0.72 \text{ g}/\text{cm}^3$) of all stems with known or estimated ρ .

DESCRIPTORS OF FOREST DYNAMIC.—We focused on five widely used descriptors of forest dynamics (see Table 1). Mortality and recruitment rates were estimated using estimators of instantaneous rates (Sheil & May 1996):

$$\lambda_m = \ln(N_o/N_s)/\Delta t \quad \text{with } N_s = N_o - N_m, \quad (2)$$

$$\lambda_r = \ln(N_f/N_s)/\Delta t \quad \text{with } N_f = N_o - N_m + N_r, \quad (3)$$

where N_o is the initial number of trees, N_m number of dead trees and N_r number of recruited trees. Annual mortality (m) and recruitment (r) rates are then defined as $m = 1 - \exp(-\lambda_m)$ and $r = 1 - \exp(-\lambda_r)$ (Sheil 1995, Sheil & May 1996). Dbh growth rate is defined as the dbh growth per stem per year averaged over the statistical population. AGB gain is calculated as the sum of the biomass of recruited trees and the dbh growth of present trees (Pyle *et al.* 2008, Blanc *et al.* 2009). Finally, AGB loss represents the biomass of all trees that died during the census interval, even if this underestimates biomass loss due to branch falls and sub-lethal canopy damages (Palace *et al.* 2007).

STATISTICAL ANALYSIS.—We used the CV (Pearson 1894) as a normalized measure of dispersion of forest descriptors:

$$\text{CV} = \sigma/\mu \times 100, \quad (4)$$

TABLE 1. Descriptive statistics of the forest structure and dynamic descriptors at the Paracou experimental site.

Variable	Mean \pm SD	Median	Minimum–Maximum
Forest structure descriptors			
Aboveground biomass (AGB)(Mg/ha) ^a	424 \pm 18	426	385–460
Basal area (m ² /ha) ^a	30.6 \pm 0.8	30.7	28.7–31.9
Stand density (individuals/ha) ^a	621 \pm 36.7	617	560–690
Forest dynamic descriptors			
Recruitment rate (%) ^b	0.85 \pm 0.12	0.8	0.73–1.01
Mortality rate (%) ^b	1.04 \pm 0.07	1.01	0.96–1.15
dbh growth (cm/yr) ^b	0.12 \pm 0.01	0.12	0.11–0.14
AGB gain (Mg/ha/yr) ^b	4.72 \pm 0.26	4.59	4.5–5.13
AGB loss (Mg/ha/yr) ^b	3.74 \pm 0.72	3.81	2.79–4.71

^aForest structure descriptors computed using the 6.25-ha plots of the nine studied censuses.

^bForest dynamic descriptors computed using the 6.25-ha plots over the 16-yr study period.

where μ and σ are, respectively, the mean and the SD of a given forest descriptors. A CV of 100 percent indicates that mean and SD are equal. The use of the CV enabled comparison of the different forest descriptors on a similar scale. The basic statistical theory is that the CV scales inversely with the square root of sample size. Theoretically, the CV should thus be related to the inverse square root of both plot size and census interval. This would be based on the assumption of independence of sampling units across time and space. This assumption is regularly violated in community ecology (Greig-Smith 1952) and particularly in tropical forest where numerous biological processes (tree growth, tree mortality, tree recruitment) may show strong spatial and temporal positive and negative autocorrelations (Brienen *et al.* 2006). Positive spatial and temporal autocorrelations make the CV slopes steeper (*i.e.*, power-law exponents superior to 0.5) whereas negative autocorrelation make them more gentle (*i.e.*, power-law exponents inferior to 0.5).

We thus build our CV models using two predictors, the plot size and the census interval, and three parameters including the two power-law exponents. We chose a Bayesian framework to estimate model parameters, for which we used the mean of the posterior densities, and to estimate parameter uncertainties, for which we used the distribution of the posterior densities (Clark 2005):

$$CV = \alpha / (S^\beta \times T^\gamma) \times \varepsilon \quad (5)$$

can be transformed into

$$\log(CV) = \log(\alpha) - (\beta \log(S) + \gamma \log(T)) + \log(\varepsilon) \quad (6)$$

to achieve linearity

$$\text{with } \varepsilon \sim \text{Log } N(1, 1/\tau), \quad (7)$$

$$\text{with } \tau \sim \text{Gamma}(0.01, 0.01), \quad (8)$$

$$\text{with } \alpha \sim N(0, 0.001), \quad (9)$$

$$\text{with } \beta \text{ and } \gamma \sim \text{Log } N(1, 0.001), \quad (10)$$

where CV is the coefficient of variation of a given forest descriptor, S is the forest plot size (m²), T is the census interval (year), α , β , γ are the parameters of the model and ε is the fitted model residuals. We chose to use a multiplicative error term as our data showed a strong heteroskedasticity. In other words, the variance of CV decreased with both plot size and census interval. In the case of forest structure descriptors, γ is set to 0. For the computation, the model was log transformed to achieve linearity (6).

In a Bayesian framework, each model parameter needs a prior distribution and the parameters of these distributions (hyper-parameters) are also needed (Clark 2007b). These priors are given in (7)–(10). The priors were chosen to be noninformative. This kind of prior enables the parameter estimations to be driven much by the data and less by the specified prior distributions. Markov chain Monte Carlo simulations were performed for all the eight models of CV. Gibbs sampling (Geman & Geman 1984) was performed in WinBUGS 1.4 (Lunn *et al.* 2000). The first 10,000 iterations for forest structure descriptor models and the first 30,000 iterations for forest dynamic descriptor models were discarded. The parameter posterior densities were obtained with 200,000 iterations after this stage.

The coefficient of determination R^2 was computed with the following formula (Gelman *et al.* 2004):

$$R^2 = 1 - (\text{Var}_{\text{model}} / \text{Var}_{\text{data}}), \quad (11)$$

where $\text{Var}_{\text{model}}$ is the mean of the posterior density of the model variance and Var_{data} is the variance of the data. Data used for computation as well as lines of WinBUGS codes are given in Appendix S2.

Finally, we give an estimate of the number of plots n needed to estimate the mean of each forest descriptor within an error d at an error rate α with

$$n = s^2 t_{\alpha, n-1}^2 / d^2, \quad (12)$$

where t is the Student's t -statistic (set to 1.96, the value from the normal distribution, to relax its dependence on the number of observations) and s^2 the unbiased sample variance estimate.

RESULTS

The model parameters of forest structure are well estimated, as shown by the low SDs, between 1.7 and 4.2 percent of the mean for α and around 1.0 percent for β (Table 2). Moreover, the high R^2 indicate that the three models are accurate (see also Appendix S3). As shown in Fig. 1, the CV estimates of stand density have a smooth slope, due to the low value of both the parameter α (91.2) and β (0.24). The value of the latter suggests a strong negative autocorrelation. In contrast, the CVs of BA and AGB exhibit steeper slopes with higher α and β fitted close to the expected 0.5 under null autocorrelation. The CVs of all of our forest structure descriptors were < 10 percent for a 2-ha plot and the number of 0.25-ha plots required to estimate the mean of each forest descriptor within a 20 percent error of the mean with 95% CI did not exceed 4 (Table 3).

The model parameters of forest dynamics are also well estimated, as shown by the low SDs. And the high R^2 (0.90–0.96) indicate that the five models all fit the data properly (see also Appendix S3). Results of the model predictions are given as isopleth diagrams (Fig. 2). Not surprisingly, the accuracy of mortality and recruitment rates increases with both plot size and census interval. These two models exhibit similar trends for small forest plots due to comparable values of parameter α , but slightly differed for large forest plots due to different β values (Table 2). The CV of dbh growth is less affected by census interval (low γ) and has small values on the whole. Regarding biomass fluxes, the CV of AGB gain and loss show contrasted responses. The CVs of AGB gain are low even for small forest plots and seem mostly dependent on the plot size. The CVs of AGB loss are high (driven by an extremely high α), superior to all the other descriptors and depend on both census interval and plot size (β and γ close to 0.5). Consequently, the number of plots required to estimate the mean of AGB loss

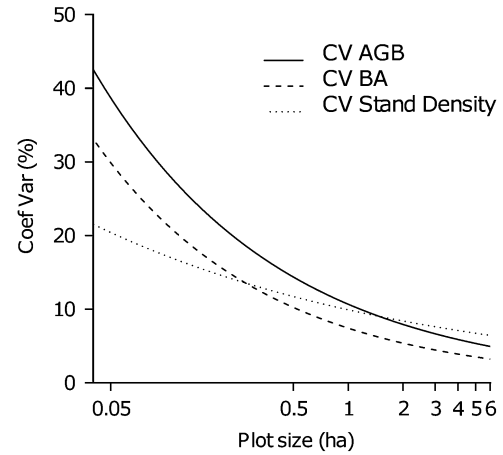


FIGURE 1. Coefficient of variations (CVs) of forest structure descriptors as a function of plot size. $\log(\text{CV}) = \log(\alpha) - (\beta \log(S)) + \log(\varepsilon)$, with S the plot size, α and β the fitted model parameters and ε the model residuals.

within a 20 percent error of the mean with 95% CI remains above four, even for 6.25-ha plots censused every 16 yr (Table 3).

DISCUSSION

The present study gives an explicit formulation of the effect of space and time variation on the accuracy of estimates of structure and dynamic descriptors in a Neotropical forest. Although spatio-temporal heterogeneity is a well-known problem in ecology, it is rarely evaluated in ecological studies (Sheil 1996, Wu *et al.* 2002, Kent *et al.* 2006). We developed a simple statistical model that links the variability of forest descriptors to plot size and census interval. As expected, we found that the CVs of the forest structure and

TABLE 2. Predicting coefficient of variation (CV) of descriptors of forest structure and dynamics. Shown are mean values \pm SD of the estimated parameters and quality of the fit of the model.

	Parameter estimates \pm SD			R^2
	α	β	γ	
Forest structure descriptors ^a				
CV aboveground biomass (AGB)	557 \pm 17	0.430 \pm 0.004		0.99
CV basal area	535 \pm 23	0.465 \pm 0.005		0.99
CV stand density	91.2 \pm 1.6	0.241 \pm 0.002		0.99
Forest dynamic descriptors ^b				
CV recruitment rate	2449 \pm 123	0.393 \pm 0.006	0.398 \pm 0.013	0.93
CV mortality rate	4883 \pm 219	0.489 \pm 0.005	0.426 \pm 0.012	0.96
CV dbh growth	266 \pm 9	0.280 \pm 0.004	0.137 \pm 0.009	0.92
CV AGB gain	1080 \pm 67	0.429 \pm 0.007	0.275 \pm 0.015	0.90
CV AGB loss	8386 \pm 446	0.451 \pm 0.006	0.438 \pm 0.013	0.94

^a $\log(\text{CV}) = \log(\alpha) - (\beta \log(S)) + \log(\varepsilon)$, with S the plot size, α and β the fitted model parameters and ε the model residuals.

^b $\log(\text{CV}) = \log(\alpha) - (\beta \log(S) + \gamma \log(T)) + \log(\varepsilon)$, with S the plot size, T the census interval, α , β and γ the fitted model parameters and ε the model residuals.

TABLE 3. Estimates of the number of plots needed to estimate the mean of each forest descriptor within a 20 percent error of the mean with 95% confidence interval.

Plot size (ha)	Estimated number of plots											
	0.25				1.56					6.25		
Forest structure descriptors												
Aboveground biomass (AGB)	4				1					1		
Basal area	2				1					1		
Stand density	2				1					1		
Census intervals (yr)												
	2	6	10	16	2	6	10	16	2	6	10	16
Forest dynamic descriptors												
Recruitment rate	84	30	20	19	39	10	6	5	28	6	2	2
Mortality rate	68	26	17	12	11	4	2	2	4	2	1	1
dbh growth	8	5	5	4	4	3	2	2	2	1	1	1
AGB gain	13	5	4	4	4	1	1	1	2	1	1	1
AGB loss	358	124	76	51	62	21	14	9	17	8	6	4

dynamic descriptors decrease with increasing plot size and census interval and we chose to use inverse power law to fit this particular curve. Even if the accuracy of the forest descriptors is expected to follow an inverse quadratic function when the forest plot size or the census interval increases, we find that several parameters set far below from the expected 0.5 (see Table 2). This suggests that negative autocorrelation is a common phenomenon in tropical forest plots and that a shared structure and dynamic between forest plots lead to less variability than expected under random tree assemblages, at least in small plot sizes and/or census intervals. As shown by Chave *et al.* (2003) and Gloor *et al.* (2009), the values of forest descriptors for small forest plot sizes may be nonnormally distributed and this may bias our results. Indeed, we need to acknowledge that our preliminary analyses using a model with an additive error term overestimated the SD (and therefore the CV) of several forest descriptors for very small forest plots (0.04 ha). We lowered this bias using a multiplicative error term in our models and, finally, this bias has disappeared (see Appendix S3).

FOREST STRUCTURE DESCRIPTORS.—Most variation of the CVs of structural descriptors is explained by a function including the plot size only. The performance of our models is remarkably good (all $R^2 \geq 99\%$), suggesting unsurprisingly that the best sampling strategy to accurately estimate AGB, BA or stand density is to have large forest plots. The CVs of all of our forest structure descriptors were smaller than 10 percent for a plot size of only 2 ha (Fig. 1) and the number of 0.25-ha plots required to estimate the mean of each forest structure descriptor did not exceed 4 (Table 3). These low values are likely due to our spatially explicit approach. Indeed, results based on Monte Carlo resampling of individual trees are likely to overestimate CVs because virtual forests are built without any constraints on tree diameter distribution. For example, using a simulation approach, the probability of obtaining a virtual forest with only large trees is not null, whereas with our more realistic spatially explicit approach, such a forest never occurred. This is the main

advantage of a spatially explicit approach: avoiding unrealistic stem distributions that bias CV estimates (Keller *et al.* 2001). In Fig. 1, all models do not reach the x -axis even in a 6-ha plot. This indicates a residual noise in our data, corresponding to the local heterogeneity among our plots that may be explained by contrasting floristic compositions as well as different type of soils and topography (Clark & Clark 2000, Gourlet-Fleury *et al.* 2004). Finally, as stand density is quite high at our site (> 630 individuals/ha) compared with other tropical forest sites (Swaine *et al.* 1987), we may expect that our CV estimates represent the lower bound and that plots with lower stand density would show higher CVs given an equivalent plot size.

FOREST DYNAMIC DESCRIPTORS.—Forest dynamic descriptors exhibited contrasting patterns: the CV of AGB loss decreased very slowly mainly because the very high value of the parameter α (Fig. 2E). But we need to acknowledge that the CV drop had an expected behavior as the CV roughly scaled with the square root of the plot size (β) and of the census interval (γ). This highlights the independence of mortality events across time and space in tropical forests (Jansen *et al.* 2008) and confirms the results of Chave *et al.* (2003), who found that at least 9-ha areas would be required to reliably estimate AGB increment but at least 40 ha to estimate AGB loss. Large variation in biomass loss is likely to be caused by the scarcity of small-scale disturbances generated by large dead trees that result in scattered and localized biomass losses (Chambers *et al.* 2004, Clark 2007a, Feeley *et al.* 2007, Rutishauser *et al.* in press). For example, Palace *et al.* (2008) showed that the effect of a single large treefall had a substantial effect on the necromass production measurement, *i.e.*, this single event more than doubled the annualized necromass production during their 4.5 yr sampling period.

At the opposite, the variation in dbh growth rates and the number of plots required to estimate mean dbh growth were always low (Table 3; Fig. 2C). This is mainly due to a very low α but it is worth to note that the power parameters β and γ set far from the

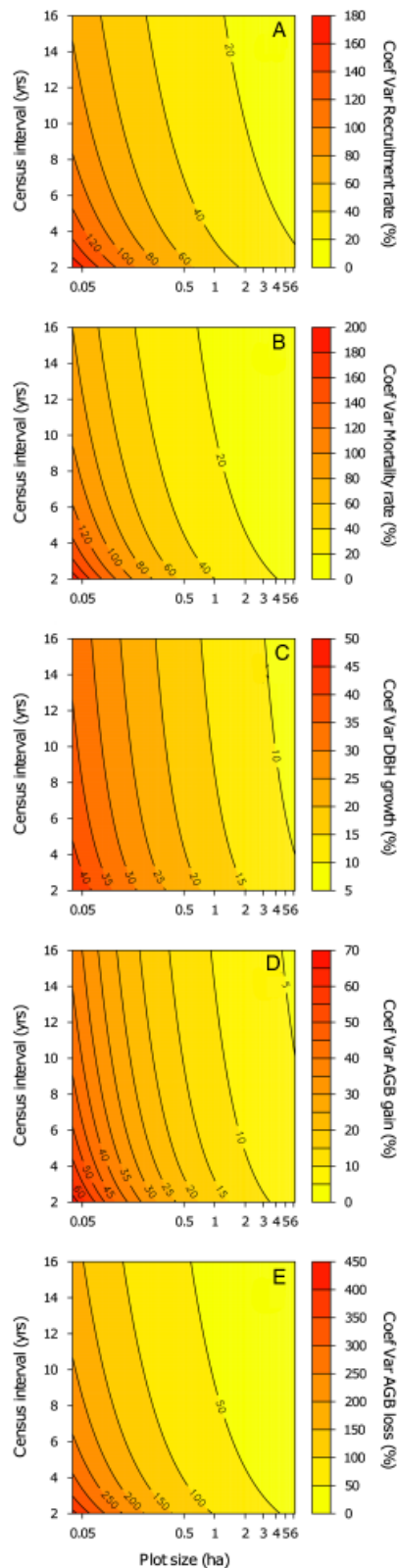


FIGURE 2. Isopleth diagrams of the coefficient of variations (CVs) of the forest dynamic descriptors ((A) Recruitment rate, (B) Mortality rate, (C) DBH growth, (D) AGB gain, (E) AGB loss) as a function of plot size and census intervals. $\log(\text{CV}) = \log(\alpha) - (\beta \log(S) + \gamma \log(T)) + \log(\epsilon)$, with S the plot size, T the census interval, α , β and γ the fitted model parameters and ϵ the model residuals.

expected 0.5 under null autocorrelation. This again suggests a shared community-level growth behavior, with forest plots always comprising low understory slow-growing species and large canopy fast growing trees, leading to less CV variability than expected under random tree assemblages. This shared community-level growth behavior might also be the influence of nutrient dynamics, localized landscape-level growth drivers and/or previous gap dynamics. In the same way, AGB gain is very well estimated, with an estimated error < 20 percent for 1 ha (Fig. 2D). This can be explained by a relative constant flux of biomass entering the plot through dbh growth and tree recruitment (Blanc *et al.* 2009), both of which are well estimated. Finally, to minimize error when estimating mortality and recruitment rates, there is a clear trade-off between plot size and census interval length. For example, for a 6-ha plot and an error < 20 percent, recruitment rate can be reliably estimated after 4 yr, but more than 20 yr are needed for a 2-ha plot (Fig. 2A).

CONCLUSIONS

Our model provides an easy way to assess variation in descriptors of forest structure and dynamics for a given set of forest plots. For the establishment of new forest plots, our results might be used as a tool to best choose census interval, plot size and the number of plots, regarding to the parameters studied and the accuracy desired. Thus, people interested in assessing descriptors of forest structure, such as AGB or stand density, might use small plots, whereas those investigating descriptors of forest dynamics, such as biomass gain or loss, would prefer large or very large plots. Although we agree that, in the context of global change, metrics derived over short-time intervals are of primary importance, our results suggest that we need to keep in mind that these short-intervals metrics are inherently very noisy, and we provide an easy way to quantify this noise.

In addition, this study provides a mean by which to estimate within-plot variability at a local scale before inferring any directional change in forest dynamics at a global scale. Our sampling design provided results on plot and census variations in a single Neotropical forest and thus our results may not be applicable to other forests with different characteristics and are unlikely to represent landscape or continental scale variability. Therefore, we strongly recommend conducting additional studies to: (1) use this method to assess variability of forest descriptors in other tropical permanent plots; and (2) extend several within-site results to among-site variability using proper error propagation statistical tools.

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SUPPORTING INFORMATION

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

- APPENDIX S1. Methods and map of study area.
- APPENDIX S2. Datasets, WinBUGS codes and Results.
- APPENDIX S3. Results: Fitting of the model.

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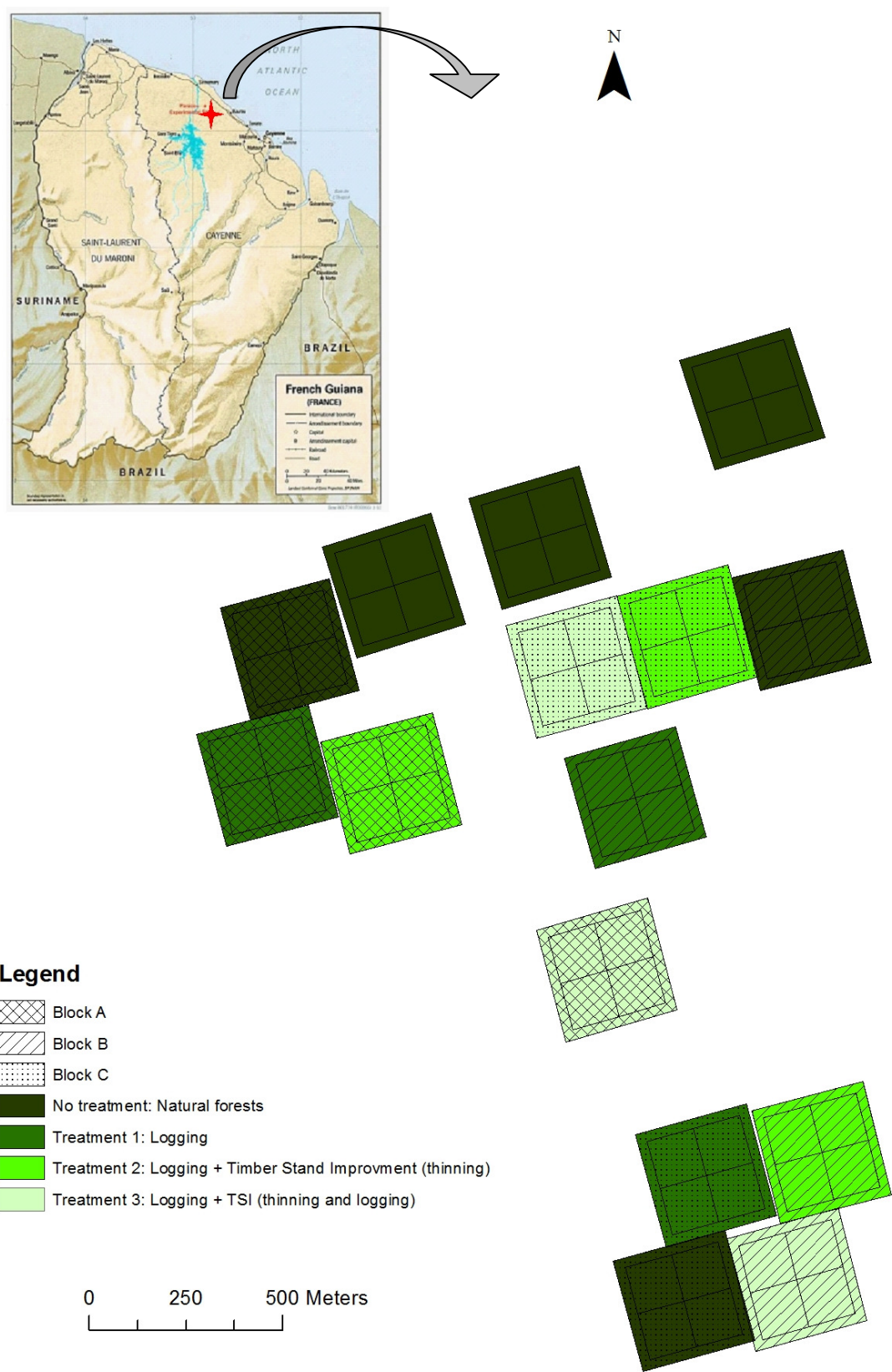
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METHODS – Map of the study site

Before the establishment of plots (1982–1984), preliminary inventories were carried out on 476 ha in the Paracou area. Three blocks of four plots (6.25 ha each) were defined with homogeneous characteristics of tree structure of the main valuable species (all commercial species and the most abundant of non commercial species). Plots were established in 1984 preferentially on hilltop with exclusion of swamp areas. From 1986 to 1988, in each block, the plots underwent three logging treatments, one plot remaining as control. Three additional control plots were also set up in the northern part of Paracou in 1991. In this study, we used the data from the control plots only.

Map: overview of the Paracou experimental plots located in the coastal part of French Guiana (5°18' N, 52°53' W).



Appendix 2: Datasets, Winbugs codes and Results

This appendix contains summary statistics (mean, standard deviation, the Monte Carlo standard error of the mean, median, 2.5 and 97.5 percentiles) for all posterior densities. Coefficient of determination (R2) and Standard deviation of the model (sd_calc) were computed in the code.

Winbugs codes and data used are given. In the datasets, CV, Area and interval are log scaled.

General model:

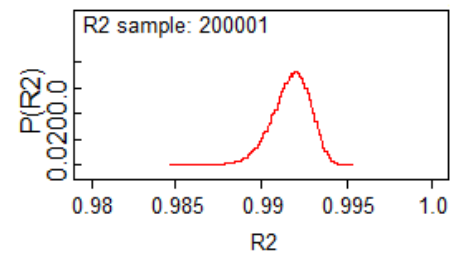
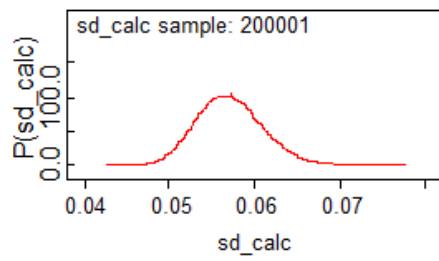
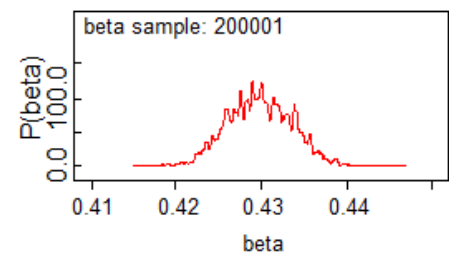
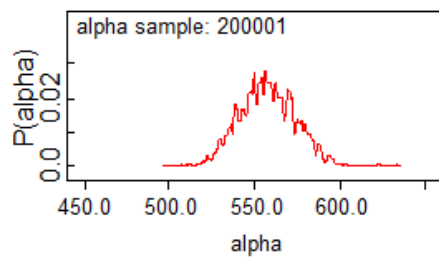
$$\log(\text{CV}) = \log(\alpha) - (\beta * \log(S) + \gamma * \log(T)) + \log(\epsilon) \quad \text{Eq.(B.1)}$$

where CV is the Coefficient of Variation of any given forest descriptor, S the forest plot size (m^2), T the census interval (year), α , β , γ the parameters of the model and ϵ the fitted-model residuals. In the case of forest structure descriptors, gamma is set to 0.

Results for forest structure descriptors

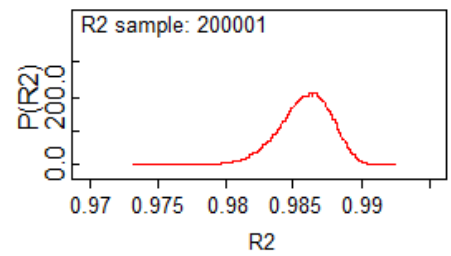
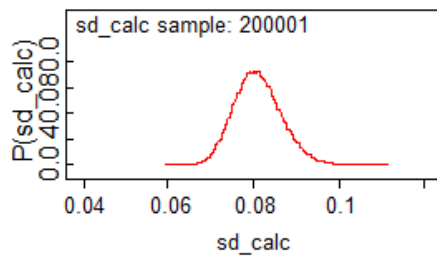
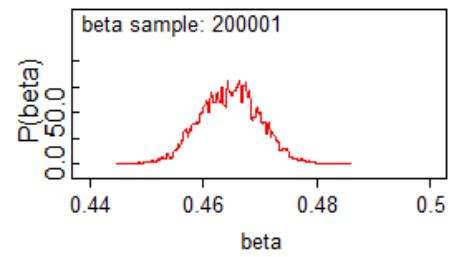
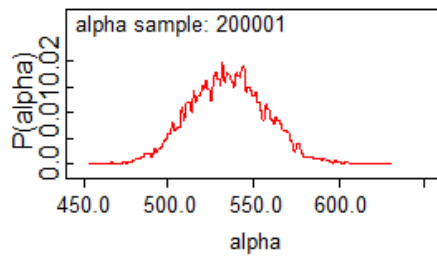
Aboveground biomass

	mean	sd	MC_error	val2.5pc	median	val97.5pc	start	sample
alpha	557.4	16.8	0.4473	526.4	556.8	589.7	10000	200001
beta	0.4298	0.003873	1.053E-4	0.4226	0.4297	0.4372	10000	200001
sd_calc	0.05711	0.003976	1.803E-5	0.04997	0.0569	0.06556	10000	200001
R2	0.9917	0.001168	5.302E-6	0.9891	0.9918	0.9937	10000	200001



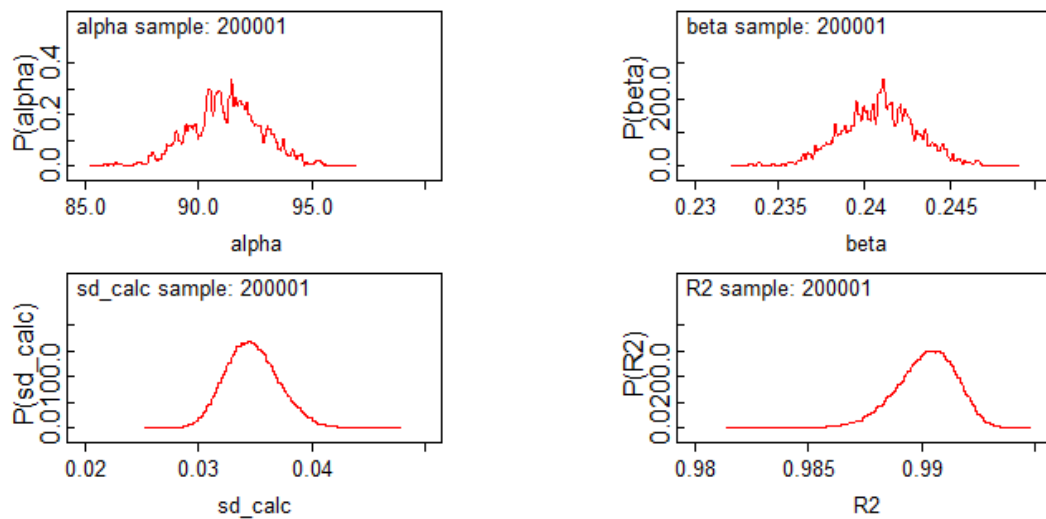
Basal Area

	mean	sd	MC_error	val2.5pc	median	val97.5pc	start	sample
alpha	534.7	22.77	0.4959	491.4	534.4	580.0	10000	200001
beta	0.4647	0.0054	1.205E-4	0.4539	0.4648	0.4752	10000	200001
sd_calc	0.081	0.005629	2.031E-5	0.07089	0.08069	0.09293	10000	200001
R2	0.9858	0.001994	7.185E-6	0.9814	0.986	0.9892	10000	200001



Stand Density

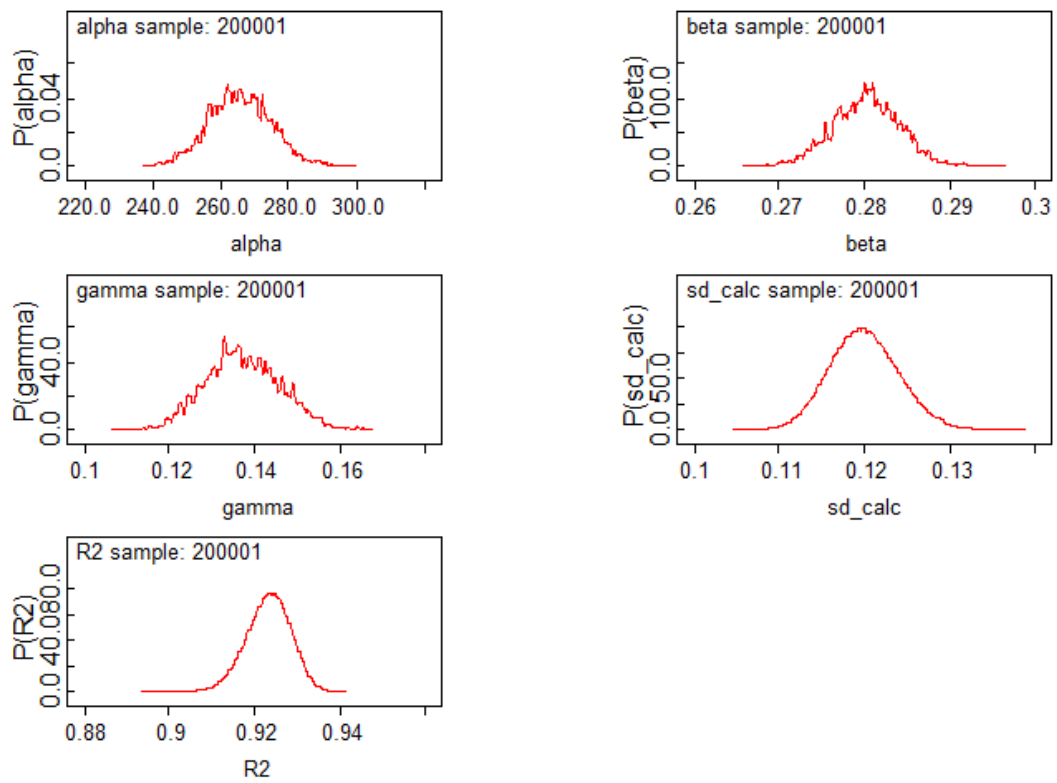
	mean	sd	MC_error	val2.5pc	median	val97.5pc	start	sample
alpha	91.23	1.618	0.07699	88.17	91.39	94.16	10000	200001
beta	0.2408	0.002273	1.085E-4	0.2367	0.241	0.2449	10000	200001
sd_calc	0.0348	0.002411	1.802E-5	0.03048	0.03467	0.03994	10000	200001
R2	0.9902	0.001378	6.293E-6	0.9871	0.9903	0.9925	10000	200001



Results for forest dynamic descriptors

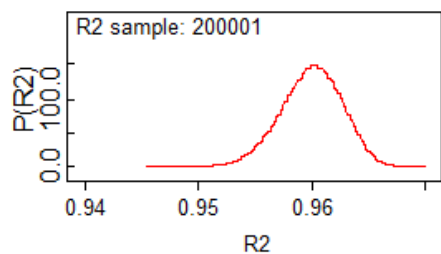
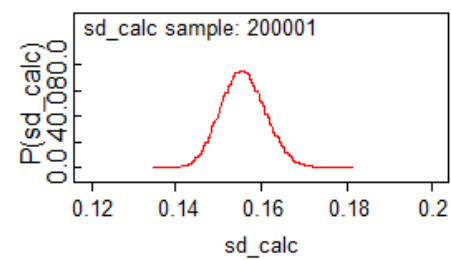
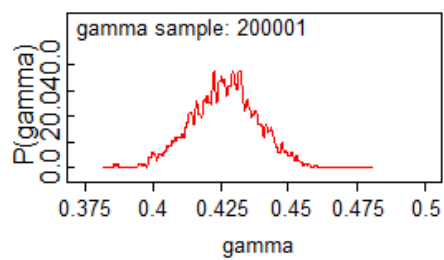
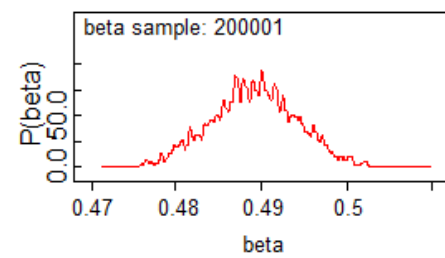
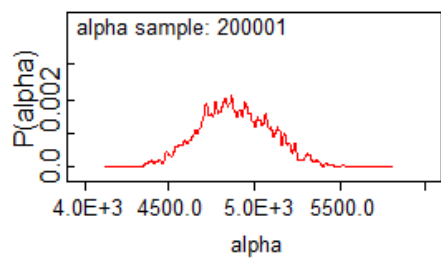
DBH growth

	mean	sd	MC_error	val2.5pc	median	val97.5pc	start	sample
alpha	265.7	9.259	0.2662	247.6	265.6	284.5	20000	200001
beta	0.2802	0.003988	1.109E-4	0.2723	0.2802	0.2879	20000	200001
gamma	0.1373	0.008817	3.625E-4	0.121	0.1367	0.1548	20000	200001
sd_calc	0.12	0.004105	1.365E-5	0.1123	0.1198	0.1284	20000	200001
R2	0.9231	0.00527	1.699E-5	0.9121	0.9234	0.9328	30000	200001



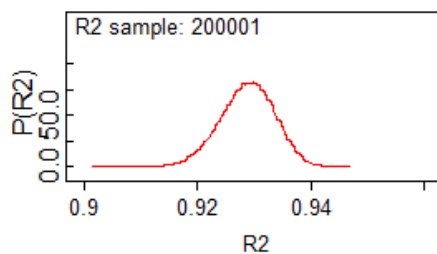
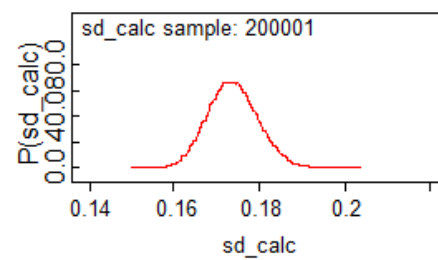
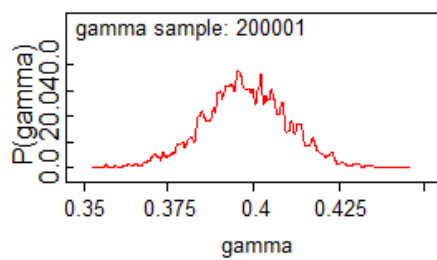
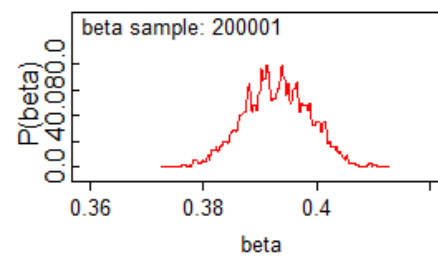
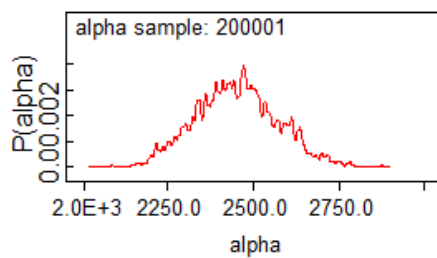
Mortality rate

	mean	sd	MC_error	val2.5pc	median	val97.5pc	start	sample
alpha	4883.0	218.8	6.099	4475.0	4871.0	5320.0	30000	200001
beta	0.4891	0.005138	1.522E-4	0.4791	0.4891	0.4992	30000	200001
gamma	0.4265	0.01239	5.192E-4	0.4015	0.4266	0.4507	30000	200001
sd_calc	0.1557	0.00534	2.045E-5	0.1457	0.1556	0.1666	30000	200001
R2	0.96	0.002752	1.053E-5	0.9542	0.9601	0.965	30000	200001



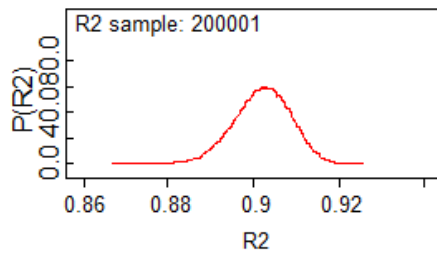
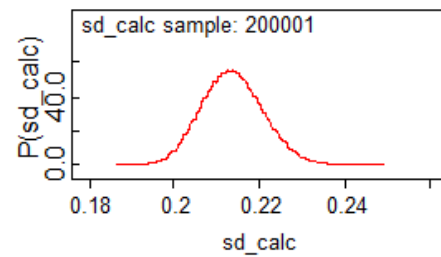
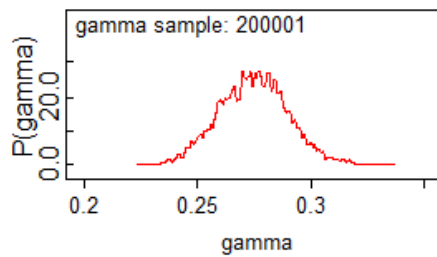
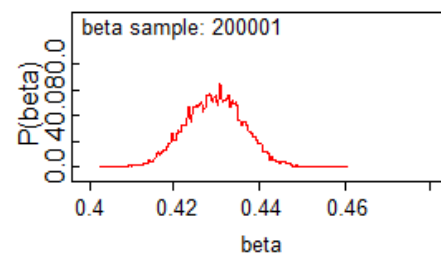
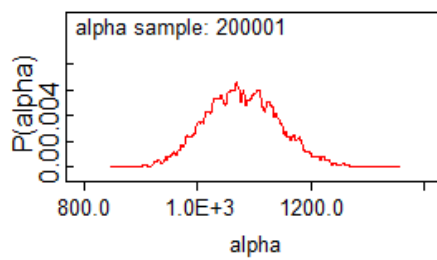
Recruitment rate

	mean	sd	MC_error	val2.5pc	median	val97.5pc	start	sample
alpha	2449.0	123.1	3.734	2215.0	2447.0	2700.0	30000	200001
beta	0.393	0.005837	1.918E-4	0.3817	0.393	0.4042	30000	200001
gamma	0.3976	0.01275	5.049E-4	0.3711	0.3974	0.4227	30000	200001
sd_calc	0.1737	0.005954	2.099E-5	0.1625	0.1736	0.1858	30000	200001
R2	0.9288	0.004891	1.723E-5	0.9186	0.929	0.9377	30000	200001



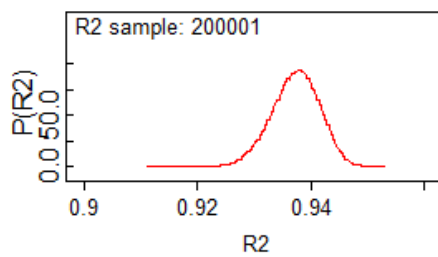
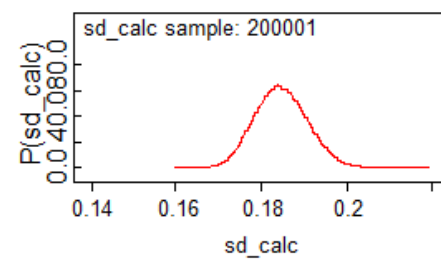
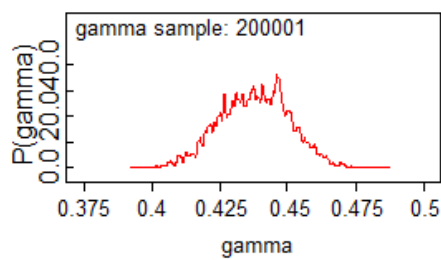
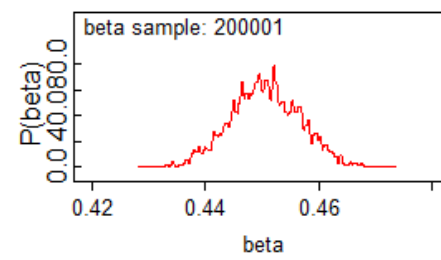
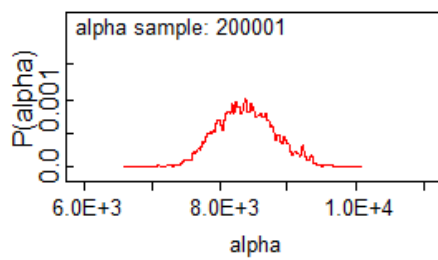
AGB gain

	mean	sd	MC_error	val2.5pc	median	val97.5pc	start	sample
alpha	1080.0	66.76	1.689	956.2	1078.0	1219.0	30000	200001
beta	0.4294	0.007081	1.81E-4	0.4158	0.4295	0.4432	30000	200001
gamma	0.275	0.01537	5.893E-4	0.2456	0.2751	0.3057	30000	200001
sd_calc	0.2137	0.007313	2.244E-5	0.1999	0.2134	0.2286	30000	200001
R2	0.9019	0.006731	2.063E-5	0.8878	0.9022	0.9142	30000	200001



AGB loss

	mean	sd	MC_error	val2.5pc	median	val97.5pc	start	sample
alpha	8386.0	446.3	13.22	7561.0	8374.0	9293.0	30000	200001
beta	0.4506	0.006214	1.993E-4	0.4383	0.4505	0.4626	30000	200001
gamma	0.4377	0.0128	5.043E-4	0.4125	0.4379	0.4621	30000	200001
sd_calc	0.1846	0.006311	1.956E-5	0.1728	0.1844	0.1975	30000	200001
R2	0.9373	0.004296	1.332E-5	0.9283	0.9375	0.9451	30000	200001



Winbugs codes

AGB, static descriptor

```

model
{
  a ~ dnorm(0,0.001)                # prior for log(alpha)
  beta ~ dlnorm(1,0.001)             # prior for beta
  tau ~ dgamma(0.001, 0.001) # prior for the precision tau
  sd_calc <- 1/pow(tau,0.5)          # sd of the model
  var_calc <- 1/tau                  # variance of the model
  R2<- 1- (var_calc / pow(sd(CV_AGB[1:108]),2)) # R²
  alpha<- exp(a)                    # coeff alpha

  for (i in 1:108)                  #for each observation
  {
    CVpred[i]<- a - beta * area[i]
    CV_AGB[i]~dnorm(CVpred[i],tau) # CV drawn from a normal distribution
  }
}

# Initial values
list(a=0,beta=0.5,tau=1)

# Data
area[] CV_AGB[]
END

```

```

#####
#####
#####
#####

```

Basal Area

```

model
{
  a ~ dnorm(0,0.001)                # prior for log(alpha)
  beta ~ dlnorm(1,0.001)             # prior for beta
  tau ~ dgamma(0.001, 0.001) # prior for the precision tau
  sd_calc <- 1/pow(tau,0.5)          # sd of the model

```

```

var_calc <- 1/tau                                # variance of the model
R2<- 1- (var_calc / pow(sd(CV_BA[1:108]),2))    # R²
alpha<- exp(a)                                  # coeff alpha

for (i in 1:108)                                #for each observation
{
  CVpred[i]<- a - beta * area[i]
  CV_BA[i]~dnorm(CVpred[i],tau)  # CV drawn from a normal distribution
}
}

# Initial values
list(a=0,beta=0.5,tau=1)

# Data
area[] CV_BA[]

END

#####
#####
#####
#####

# Stand density

model
{
  a ~ dnorm(0,0.001)                            # prior for log(alpha)
  beta ~ dlnorm(1,0.001)                        # prior for beta
  tau ~ dgamma(0.001, 0.001) # prior for the precision tau
  sd_calc <- 1/pow(tau,0.5)                      # sd of the model
  var_calc <- 1/tau                              # variance of the model
  R2<- 1- (var_calc / pow(sd(CV_N[1:108]),2))    # R²
  alpha<- exp(a)                                # coeff alpha

  for (i in 1:108)                                #for each observation

  {
    CVpred[i]<- a - beta * area[i]
    CV_N[i]~dnorm(CVpred[i],tau)  # CV drawn from a normal distribution
  }
}

```

```

# Initial values
list(a=0,beta=0.5,tau=1)

# Data
area[] CV_N[]
END

#####
#####
#####
#####

Recruitment rate

model
{
  a ~ dnorm(0,0.001) # prior for log(alpha)
  beta ~ dlnorm(1,0.001) # prior for beta
  gamma ~ dlnorm(1,0.001) # prior for gamma
  tau ~ dgamma(0.001, 0.001) # prior for the precision tau
  sd_calc <- 1/pow(tau,0.5) # sd of the model
  var_calc <- 1/tau # variance of the model
  R2<- 1- (var_calc / pow(sd(CV_recrutement[1:432]),2)) # R²
  alpha<- exp(a) # coeff alpha

  for (i in 1:432) #for each observation
  {
    CVpred[i]<- a - ( gamma * interval[i] + beta * area[i] )
    CV_recrutement[i]~ dnorm(CVpred[i],tau)
    # CV drawn from a normal distribution
  }
}

# Initial Values
list(a=0,beta=0.5,gamma=0.5,tau=1)

# Data
interval[] area[] CV_recrutement[]
END
#####
#####
#####
#####

```


Mortality rate

model

```
{
  a ~ dnorm(0,0.001)                # prior for log(alpha)
  beta ~ dlnorm(1,0.001)             # prior for beta
  gamma ~ dlnorm(1,0.001)           # prior for gamma
  tau ~ dgamma(0.001, 0.001) # prior for the precision tau
  sd_calc <- 1/pow(tau,0.5)          # sd of the model
  var_calc <- 1/tau                  # variance of the model
  R2<- 1- (var_calc / pow(sd(CV_totalMrate[1:432]),2)) # R²
  alpha<- exp(a)                    # coeff alpha

  for (i in 1:432)                  #for each observation
  {
    CVpred[i]<- a - ( gamma * interval[i] + beta * area[i] )
    CV_totalMrate[i]~ dnorm(CVpred[i],tau)
  }
}
```

Initial Values

```
list(a=0,beta=0.5,gamma=0.5,tau=1)
```

Data

```
interval[]   area[]  CV_totalMrate[]
```

END

```
#####
#####
#####
#####
```

```
# DBH growth
```

```
model
```

```
{
  a ~ dnorm(0,0.001)                # prior for log(alpha)
  beta ~ dlnorm(1,0.001)              # prior for beta
  gamma ~ dlnorm(1,0.001)            # prior for gamma
  tau ~ dgamma(0.001, 0.001) # prior for the precision tau
  sd_calc <- 1/pow(tau,0.5)           # sd of the model
  var_calc <- 1/tau                   # variance of the model
  R2<- 1- (var_calc / pow(sd(CV_dbhGrowth[1:432]),2)) # R²
  alpha<- exp(a)                     # coeff alpha

  for (i in 1:432)                   #for each observation
  {
    CVpred[i]<- a - ( gamma * interval[i] + beta * area[i] )
    CV_dbhGrowth[i]~ dnorm(CVpred[i],tau) # CV drawn from a
normal distribution
  }
}
```

```
# Initial Values
```

```
list(a=0,beta=0.5,gamma=0.5,tau=1)
```

```
# Data
```

```
interval[] area[] CV_dbhGrowth[]
```

```
END
```

```
#####
#####
#####
#####
```

```

# AGB Gain
model
{
  a ~ dnorm(0,0.001)                # prior for log(alpha)
  beta ~ dlnorm(1,0.001)             # prior for beta
  gamma ~ dlnorm(1,0.001)           # prior for gamma
  tau ~ dgamma(0.001, 0.001) # prior for the precision tau
  sd_calc <- 1/pow(tau,0.5)          # sd of the model
  var_calc <- 1/tau                  # variance of the model
  R2<- 1- (var_calc / pow(sd(CV_AGBin[1:432]),2))# R²
  alpha<- exp(a)                    # coeff alpha

  for (i in 1:432)                  #for each observation
  {
    CVpred[i]<- a - ( gamma * interval[i] + beta * area[i] )
    CV_AGBin[i]~ dnorm(CVpred[i],tau) #
  }
  CV drawn from a normal distribution
}
# Initial Values
list(a=0,beta=0.5,gamma=0.5,tau=1)

# Data
interval[]  area[]  CV_AGBin[]
END

```

```

#####
#####
#####
#####

```

```

# AGB Loss
model
{
  a ~ dnorm(0,0.001)                # prior for log(alpha)
  beta ~ dlnorm(1,0.001)             # prior for beta
  gamma ~ dlnorm(1,0.001)           # prior for gamma
  tau ~ dgamma(0.001, 0.001) # prior for the precision tau
  sd_calc <- 1/pow(tau,0.5)          # sd of the model
  var_calc <- 1/tau                  # variance of the model
  R2<- 1- (var_calc / pow(sd(CV_AGBout[1:432]),2)) # R²
  alpha<- exp(a)                    # coeff alpha

  for (i in 1:432)                  #for each observation
  {
    CVpred[i]<- a - ( gamma * interval[i] + beta * area[i] )
    CV_AGBout[i]~dnorm(CVpred[i],tau) #
  }
  CV drawn from a normal distribution
}
# Initial Values
list(a=0,beta=0.5,gamma=0.5,tau=1)

# Data
interval[] area[] CV_AGBout[]
END

```

APPENDIX 3: RESULTS – Fitting of the model**QUALITY OF FIT OF THE MODEL**

Here we present the graphics of variable predicted by the model versus variable observed. All the models were fitted with the parameters in Table 1. For each variable, the histogram of residuals is given. Normality tests were performed on these residuals with the Kolmogorov-Smirnov test. We found no statistically significant difference between the distribution of our variables and the hypothesized normal distribution function, all P -values were > 0.05 .

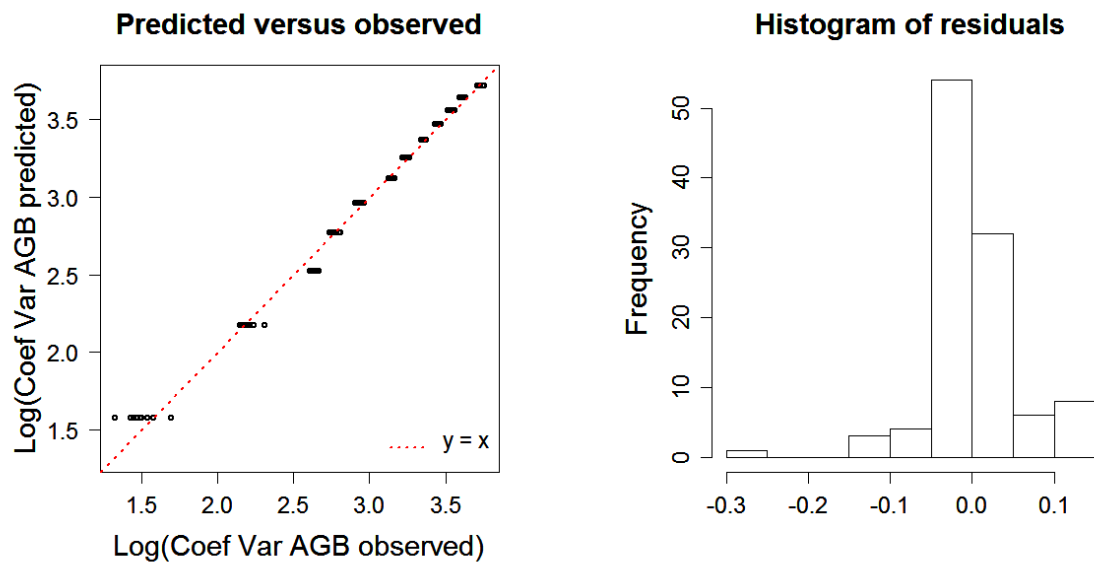


Figure 1: Fitting of the model for the AGB (static descriptor)

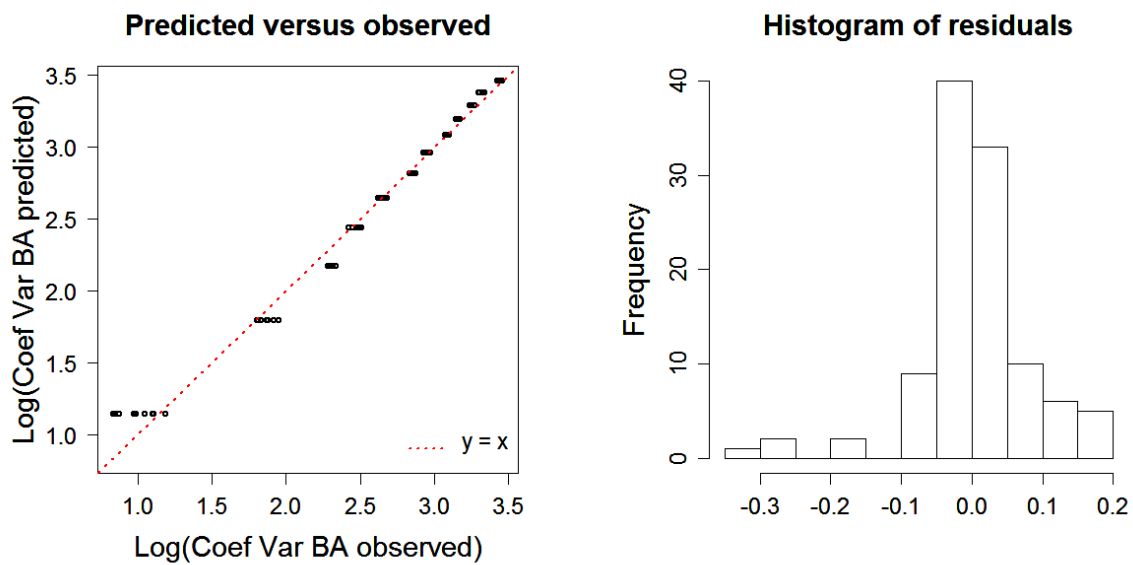


Figure 2 : Fitting of the model for the CV of BA (static descriptor)

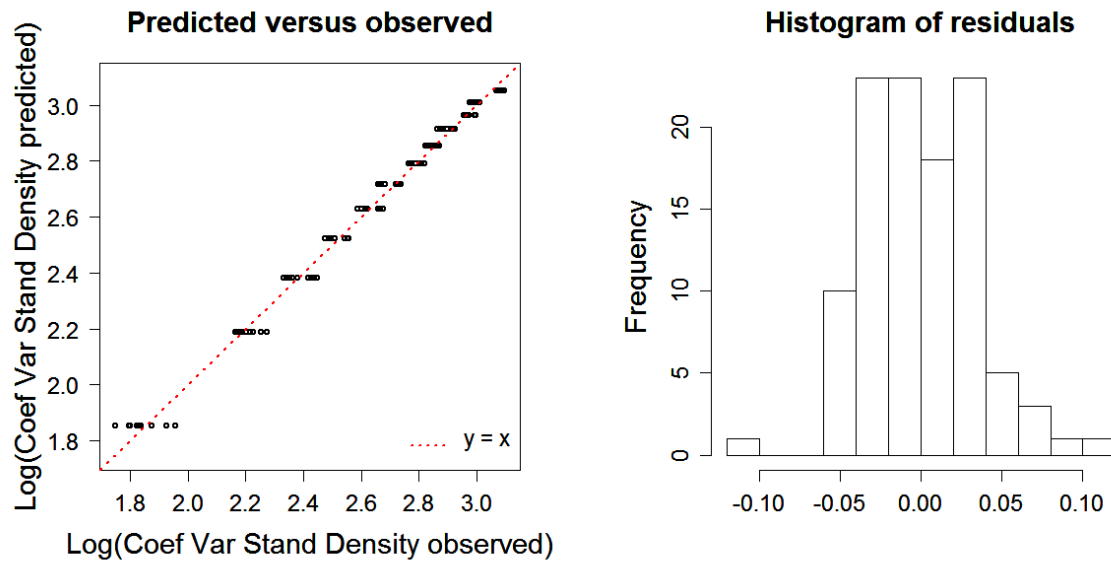


Figure 3: Fitting of the model for the CV of Tree Density (static descriptor)

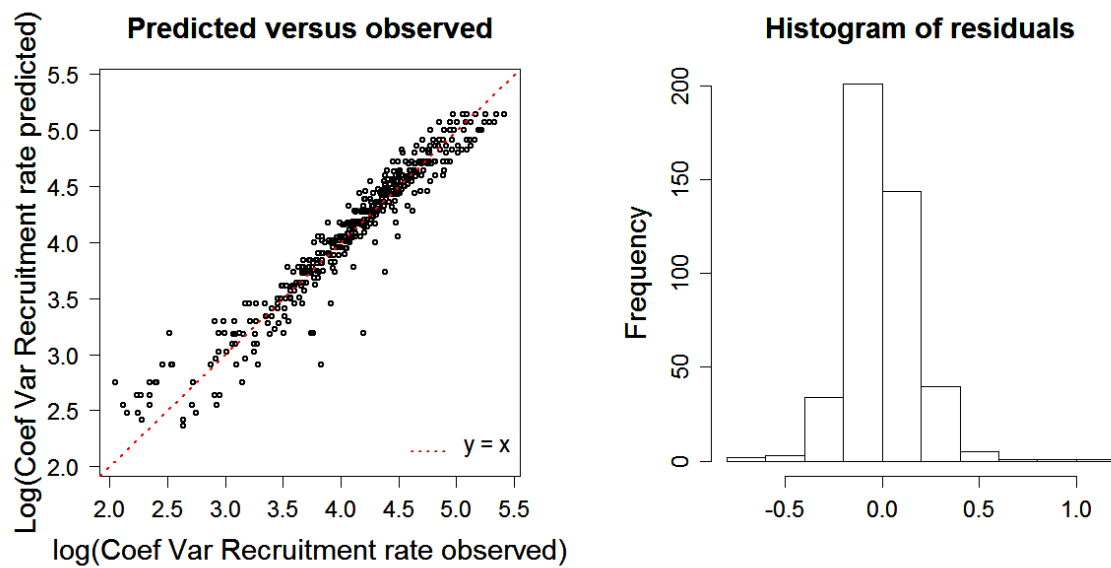


Figure 4 : Fitting of the model for the Recruitment rate (dynamic descriptor)

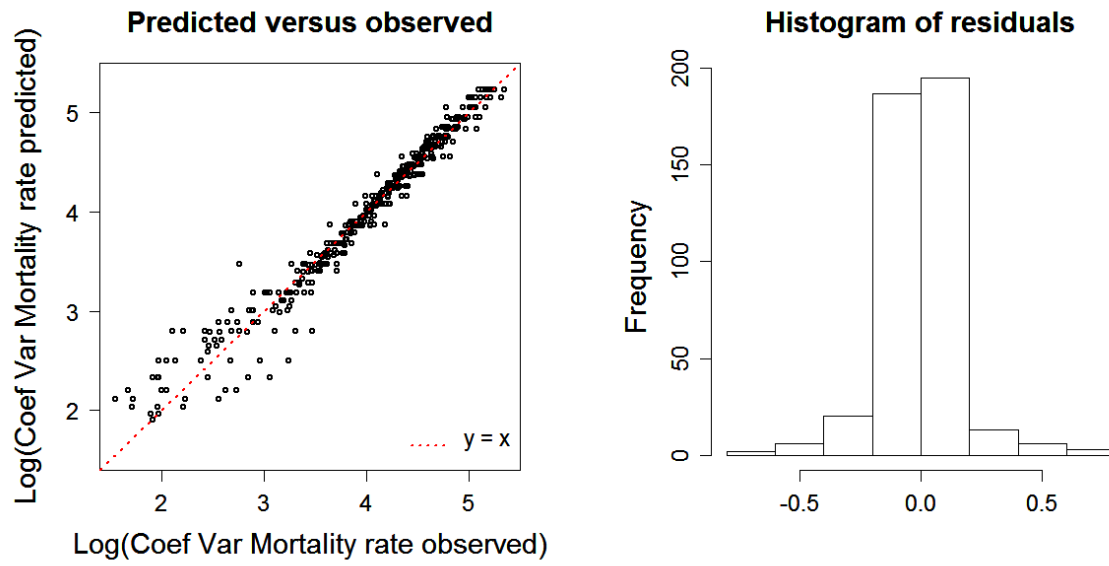


Figure 5 : Fitting of the model for the Mortality rate (dynamic descriptor)

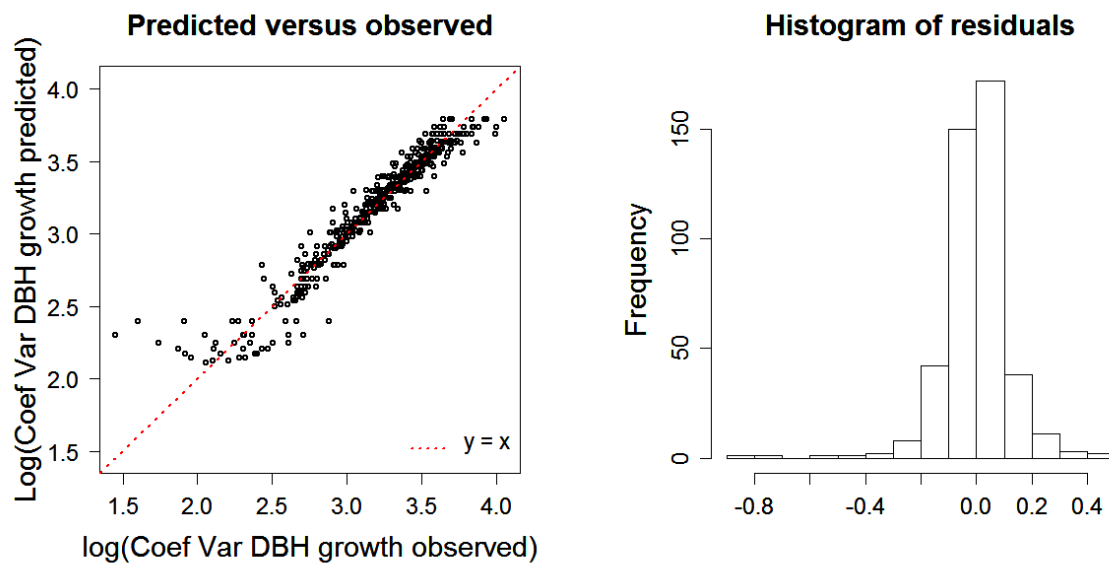


Figure 6 : Fitting of the model for the DBH growth (dynamic descriptor)

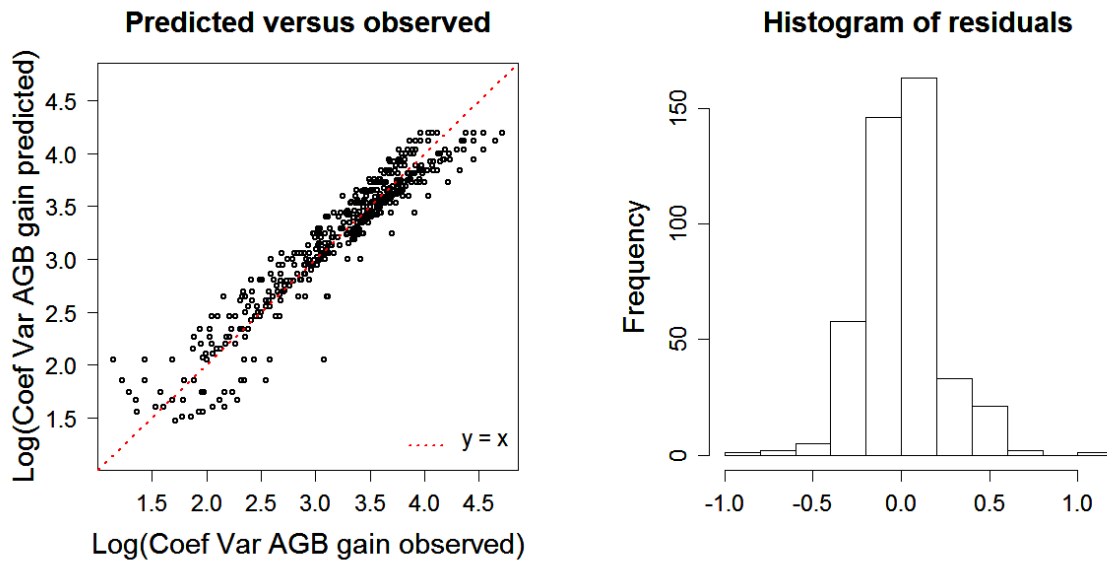


Figure 7 : Fitting of the model for the AGB gain (dynamic descriptor)

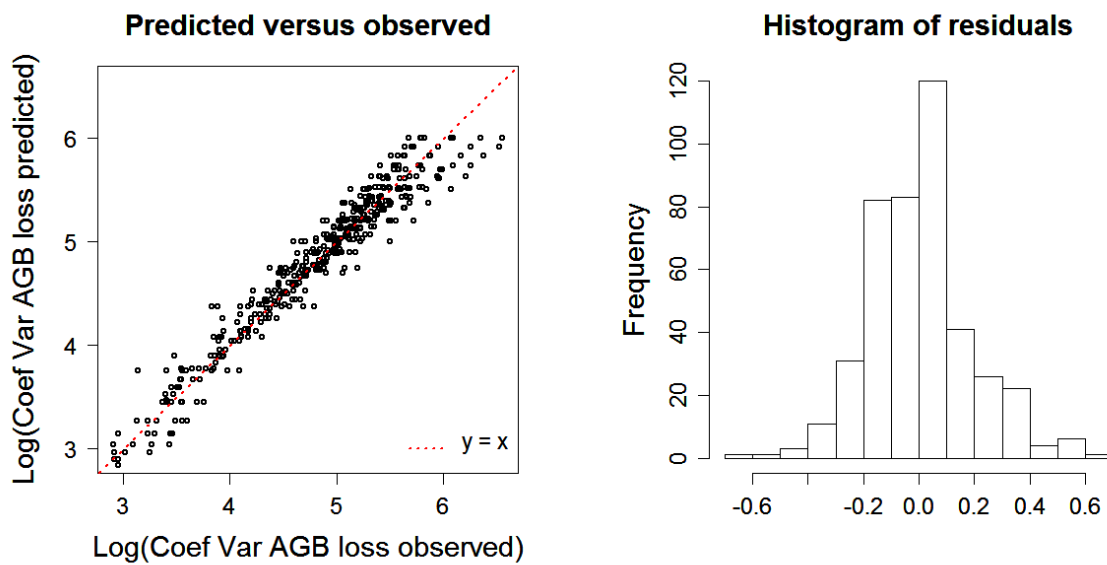


Figure 8 : Fitting of the model for the AGB loss (dynamic descriptor)

2 L'équilibre contrasté de la biomasse aérienne dans une forêt néotropicale

Le second travail de ce chapitre concerne les causes de l'augmentation de la biomasse à Paracou. Des analyses préliminaires à ce travail ont montré des bilans de biomasse positifs et équivalents à ceux de parcelles exploitées dans certaines parcelles témoins du dispositif de Paracou (L. Blanc, non publié). Nous nous sommes donc demandés si les parcelles témoins ne se trouvaient pas, elles aussi, dans une dynamique de régénération. Ces observations d'accumulation de biomasse étaient concordantes avec les observations réalisées sur les autres dispositifs permanents en forêt tropicale sur la même période. Deux grandes hypothèses font débat sur les causes de l'augmentation générale de biomasse observée en forêt tropicale, l'hypothèse de la régénération après perturbation contre l'hypothèse de la fertilisation de la forêt par l'augmentation de CO_2 . Dans ce travail, nous avons étudié comment se décomposent les bilans de biomasse entre tous les compartiments. L'étude a été réalisée avec les données de Paracou de 1991 à 2007. Les estimations de biomasse varient entre les parcelles de 395 à 443 tonnes par hectare. L'augmentation moyenne de la biomasse aérienne est de 0.9 tonnes par hectare et par an. En moyenne, les gros arbres ($\text{DBH} > 60$ cm) représentent 17.6% de la biomasse en 2007 bien qu'ils ne représentent que 1.7% des tiges. Il apparaît dans cette analyse que l'augmentation de la biomasse observée sur le dispositif de Paracou est liée à la rareté des événements de mortalité des gros arbres qui portent une part très importante de la biomasse. Ce résultat est donc en faveur de l'hypothèse de la régénération après perturbation et non de la fertilisation des forêts par le CO_2 anthropique. Ce travail est présenté dans la publication ci-après, Rutishauser *et al.* (2010).

Contrasting above-ground biomass balance in a Neotropical rain forest

Ervan Rutishauser, Fabien Wagner, Bruno Herault, Eric-André Nicolini & Lilian Blanc

Abstract

Question: What are the relative roles of tree growth, mortality and recruitment in variations of above-ground biomass in tropical forests?

Location: Paracou, French Guiana.

Methods: We quantified the contribution of growth, recruitment and mortality to total biomass of stands (trees DBH ≥ 10 cm) in six 6.25-ha permanent plots over 16 yr. Live biomass stocks and fluxes were computed for four separate size classes.

Results: All plots showed increasing biomass stocks over the study period, with an average value of $+0.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. Plots aggrading biomass were characterized by either minor biomass losses due to mortality or substantial increases in the biomass of large trees (DBH ≥ 60 cm).

Conclusions: Within the study period, the rarity of mortality events could not counter-balance the slow permanent increase in biomass, resulting in an apparent increase in biomass. Accounting for such rare events results in no net change in biomass balance.

Keywords: Biomass balance; Biomass fluxes; Forest dynamics; Permanent plots; Tropical forests.

Abbreviation: AGB: above-ground biomass; wsg: wood specific gravity; DBH: diameter at breast height (1.3 m); BA: basal area

Nomenclature: Hoff et al. (2007).

Introduction

Recent investigations of temporal fluctuations in biomass have reported changes in dynamics and structure of Amazonian and African rain forests.

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Notably, an increase in stand above-ground biomass, hereafter referred to simply as “biomass”, has been detected (Baker et al. 2004a; Lewis et al. 2004; Phillips et al. 2004). Globally, tropical forests seem to exhibit a similar trend, aggrading 1.3 Pg of carbon per year (Lewis et al. 2009).

Forests in dynamic equilibrium should theoretically remain carbon-neutral in the very long term, since accumulation of biomass in forests cannot continue indefinitely. A debate has arisen regarding the interpretation of biomass accumulation, and concentrates on two hypotheses: response to ongoing global climate change or recovery from past disturbances (Wright 2005; Clark 2007; Körner 2009; Muller-Landau 2009). The main hypothesis to explain such increases in carbon stocks is a widespread change in resource availability, among which the increasing concentration of CO₂ in the atmosphere is often cited (Lewis et al. 2004; Phillips et al. 2008). Apparent increases in biomass could also be simply explained by endogenous variations of the biomass stock (Clark 2002; Körner 2003; Wright 2006). Biomass was shown to be highly variable at both regional (Malhi et al. 2006; Lewis et al. 2009; Phillips et al. 2009) and local (Chave et al. 2003, 2008; Rolim et al. 2005; de Castilho et al. 2006; Pyle et al. 2008; Ferry et al. 2010) scales, due to the great heterogeneity of tropical forests. Variations in intensity, scale and frequency of disturbances contribute to the maintenance of such high heterogeneity. Perturbations fall into two categories: infrequent large-scale disturbances, i.e. forest fires or hurricanes, able to reset forest stand structure entirely (Nelson et al. 1994; Zimmerman et al. 1996; Vandermeer et al. 2000; Chazdon 2003; Uriarte et al. 2009) and small-scale disturbances, i.e. tree falls. In the absence of large-scale disturbances, forests can be seen as a mosaic of patches at different stages of regeneration (Bormann & Likens 1979; Oldeman 1990; Manrubia & Sole 1997; Denslow et al. 1998). These patches are likely to be characterized by different size-class structure and therefore different intrinsic biomass dynamics (Oldeman 1990; Coomes & Allen 2007; Pyle et al. 2008; Chambers et al. 2009). Patchy pattern of small-scale disturbances would result in scattered and localized biomass losses, while most of the

forest should be increasing in biomass (Körner 2003; Clark 2007; Feeley et al. 2007; Fisher et al. 2008). At the landscape level and under an equilibrium hypothesis, the dynamics of the patches would balance, and average biomass stock would remain constant (Muller-Landau 2009).

The disturbance regime is therefore of primary importance in understanding variation in biomass balance. Recent studies have explored the potential bias caused by sampling strategies that are unable to account for infrequent, large-scale disturbances. In simulating disturbances in Amazon old-growth forests, Gloor et al. (2009) found that large-scale large biomass loss were very rare, i.e. a loss of $30 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ may occur only every 1000 years. Therefore, the authors concluded that even if these occasional large mortality events had been under-sampled, they could not occur frequently enough to account for the increase in biomass observed across the Amazon basin ($+1.22 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; Baker et al. 2004a).

In the present study, we aim to contribute to the ongoing debate by investigating variations in biomass stock among six 6.25-ha plots over 16 years, to quantify the effects of three demographic processes (growth, mortality and recruitment) on biomass. Considering that tropical forests have apparently been aggrading biomass over the last decades, the present study aims to determine (1) which demographic process was involved in positive biomass net changes, and (2) how this gain was distributed among stem classes.

Methods

Study site

Our study site is a network of six 6.25-ha plots of tropical forest, located in Paracou ($5^{\circ}18'N$, $52^{\circ}23'W$) in littoral French Guiana. The site was established to study responses to different logging intensities, although in the present study we investigate only the unlogged plots. The climate of the region is equatorial, with two main seasons: a dry season from August to mid-November and a rainy season (often interrupted by a short drier period) from December to April. Annual rainfall in the vicinity of the station is 3041 mm (Gourlet-Fleury et al. 2004). The forest of Paracou is classified as lowland moist forest (*terra firme*), with low species diversity ($140\text{--}200 \text{ sp ha}^{-1}$) of trees with diameter at breast height (DBH) $> 10 \text{ cm}$ (ter Steege et al. 2000).

Dataset

In each plot, all stems with DBH $\geq 10 \text{ cm}$ were mapped, tagged and measured biannually, representing a total of 27 504 stems. Initial census of plots 1, 6 and 11 started in 1984, while plots 13, 14 and 15 were set up in 1991. For clarity and to enable comparison among the six plots, we restrict our analysis to the 1991–2007 period (mean interval: 15.8 yr). Basal area (BA in $\text{m}^2 \text{ ha}^{-1}$) refers to the projected area of the tree diameter summed overall trees DBH $\geq 10 \text{ cm}$ divided by the plot area.

Biomass estimation and wood density measurement

Biomass refers strictly to the above-ground biomass (AGB) of the stand, as we do not account for the important compartment of woody necromass (see below). For each stem, AGB was estimated using allometry developed for moist tropical forests (Chave et al. 2005) based on two predictors: wood specific gravity (wsg) and DBH:

$$\begin{aligned} \text{AGB} = & \text{wsg} \times \exp(-1,499 + 2.148 \times \ln(\text{DBH}) \\ & + 0.207 \times \ln(\text{DBH})^2 - 0.0281 \\ & \times \ln(\text{DBH})^3) \end{aligned}$$

Wood specific gravity varies widely within and among both species and sites (Wiemann & Williamson 2002; Muller-Landau 2004; Patiño et al. 2009). To avoid bias due to regional database compilation (Baraloto et al. 2010), wood density at 12% humidity were measured on wood samples (see Kollmann & Cote 1968 for methods used) from trees logged in the same plot network (Gourlet-Fleury et al. 2004). We measured wood density for 160 taxa (Digital Appendix S1) and derived wsg through multiplication by the correction factor 0.872 (Chave et al. 2006). When no wood samples or reliable species identification were available, we applied the mean wsg of all species within a genus to all species within that genus. A similar procedure was applied at the family level. In cases of no botanical identification, we assigned the plot-averaged wsg of all stems with known or estimated wsg. A total of 57.5% of all stems had wood density measured at the species level, 11.2% at the genus level, 15.9% at the family level and 15.4% at the plot level.

In order to compare the adequacy of the diameter-based allometry, we estimated above-ground biomass on a sub-sample of 1603 height-measured trees using a height-based allometry ($\text{AGB} = 0.0509 \times \text{wsg} \times \text{DBH}^2 \times H$ in Chave et al. 2005). Tree height was estimated with a laser rangefinder

(LASERACE 300[®]), from the trunk base to the tallest branch.

One species, *Swartzia polyphylla* D.C., is known to have very irregular stems that lead to large over-estimation of the volume of its trunk. We decided to correct the diameter estimate of those trees by multiplying their measured diameter by 0.56, as suggested by Nogueira et al. (2006).

Biomass fluxes

Biomass gain is given by the sum of the biomass growth of all surviving trees and the stand recruitment, defined as the summed biomass of all trees that attained the minimum size of 10-cm DBH during the census interval (Pyle et al. 2008). Biomass loss represents the biomass of all trees that die during the census interval. The biomass net change is given by biomass gain minus biomass loss. A confidence interval (CI) was constructed by sampling (with replacement) 25 subplots of 50×50 m in each plot. Biomass was then computed over this simulated 6.25-ha plot. Lower and upper CIs represent the 2.5th and 97.5th percentiles of the distribution of 1000 simulated biomass balances. We chose to bootstrap the subplots instead of the individual trees in order to conserve forest structure in the simulated data. We followed the recommendation of Chave et al. (2004), who showed that biomass distributions become normal in plots larger than 0.25 ha. The association between biomass gain, loss and net change were tested using Spearman's rank correlation.

Previous investigations of forest biomass fluctuations have generally been restricted to dynamics of carbon stocks (Lewis et al. 2004). We, however, quantified biomass fluxes (gain and loss) in four size classes: 10–20-cm DBH, 20–40-cm DBH, 40–60-cm DBH and DBH ≥ 60 cm. Biomass fluxes in each size class were defined as (i) ingrowth, the summed biomass of all trees entering from the inferior class; (ii) growth, the diameter increase of all trees staying in a class; (iii) loss, all trees that died. To allow comparison among plots, all stocks and fluxes are presented as tons of biomass per hectare per year ($\text{Mg ha}^{-1} \text{ yr}^{-1}$). Ingrowth of the 10–20-cm DBH class is smaller than stand recruitment, as few trees, such as palm trees or missed trees, might be recruited directly in the 20–30-cm DBH class. Dependence among biomass fluxes was tested using Student correlation tests and distribution of biomass stocks among size classes was compared with chi square tests.

Tree mortality

Tree death was recorded following three types: dead standing, fallen or broken. When a tree dies, we assume that its entire biomass is lost to the atmosphere. We do not account for coarse woody debris and wood decomposition, although they represent large stocks of carbon and may play an important role in the carbon budget of tropical forests (Rice et al. 2004; Pyle et al. 2008).

All statistical analyses were conducted using the R language and environment for statistical computing version 2.5.2 (R Development Core Team, R Foundation for Statistical Computing, Vienna, AT) and are available upon request from the corresponding author.

Results

Biomass stock estimation

Biomass estimates in Paracou varied among plots from 395 to 443 Mg ha^{-1} in 2007 (Table 1A). Plots had similar distributions of biomass stock among size classes ($\chi^2 = 18.3$, $\text{df} = 15$, $P = 0.25$). However, plot 6 had larger biomass stocks in the ≥ 60-cm DBH class. This was not due to one single large tree, but the consequence of the presence of many large trees (DBH ≥ 60 cm) in this plot (13.8 stems ha^{-1} compared to a mean value of 9.6 stems ha^{-1} in the other plots). On average, large trees (DBH ≥ 60 cm) comprised 17.6% of the biomass stock in 2007, even though they only accounted for 1.7% of the stems. Trees with a DBH of $20 \leq 60$ cm comprised nearly 70% of the total biomass.

Two trends were common to all plots over the study period: a decrease in biomass in the smallest size class and an increase in biomass in the two larger size classes (Table 1A). The same trend was observed for tree density: the smallest size class lost trees whereas DBH ≥ 40-cm classes increased in stem density (Table 1B).

Annual biomass fluxes

We analysed biomass change variations over the 1991–2007 period and found a significantly positive net change in three out of the six plots (Table 2), ranging from 0.34 $\text{Mg ha}^{-1} \text{ yr}^{-1}$ (95% CI: –1.40 to 1.71) to 1.59 $\text{Mg ha}^{-1} \text{ yr}^{-1}$ (95% CI: 0.90 to 2.21). In each plot, biomass net change was mainly driven by mortality fluctuations (Fig. 1). Losses showed great variability among census intervals (range: –8.9 to –1.2 $\text{Mg ha}^{-1} \text{ yr}^{-1}$), whereas

Table 1. (A) Biomass stocks (Mg ha^{-1}) by DBH class, basal area (BA in $\text{m}^2 \text{ha}^{-1}$) and mean wood specific gravity (wsg) by plot; (B) Density (stems ha^{-1}) by size class at the initial and final census by plot.

Plot census	1		6		11		13		14		15	
	1991	2007	1991	2007	1991	2007	1991	2007	1991	2007	1991	2007
<i>(A)</i>												
DBH class												
10–20	49	49	45	45	55	51	51	48	50	48	58	55
20–40	148	151	144	141	169	171	159	168	156	159	155	158
40–60	126	126	141	152	127	133	129	133	141	153	132	144
≥ 60	65	68	96	105	62	66	63	77	76	68	57	71
Total	388	395	427	443	413	421	403	426	424	429	402	427
BA ($\text{m}^2 \text{ha}^{-1}$)	28.5	28.8	30.2	31	30.5	30.5	29.9	31	30.6	30.8	30.3	31.6
Mean wsg (g cm^{-3})	0.756	0.756	0.757	0.756	0.763	0.767	0.755	0.760	0.760	0.761	0.754	0.757
<i>(B)</i>												
DBH class												
10–20	363.2	349	339.5	335.7	410.1	376.5	383.5	352.6	368.8	350.6	442.7	412.5
20–40	186.4	185.6	175.8	174.1	207.5	207	204.6	207.2	193.1	191.5	196.2	198.4
40–60	41.8	40.8	47.5	51.2	42.9	44.5	44.2	45.1	48.3	49.3	44.8	48.6
≥ 60	8.6	9.8	13.8	14.6	9.3	9.9	9	11	9.1	9.9	8.6	11
Total	600	585.1	576.6	575.5	669.8	637.9	641.3	616	619.4	601.3	692.3	670.6

Table 2. Annual recruitment, growth, mortality and net change by plot (6.25-ha). Biomass is added to the stock through recruitment and growth and lost through mortality. Confidence intervals represent the 2.5% and 97.5% values of the bootstrapped distribution of the parameter (details in text). Plots in bold had significant biomass increase during the study period.

	Annual biomass fluxes ($\text{Mg ha}^{-1} \text{yr}^{-1}$)			
	Recruitment	Growth	Mortality	Net change
Plot				
1	0.55 (0.44–0.68)	4.51 (4.14–4.90)	4.67 (3.64–5.88)	0.40 (–0.8–1.45)
6	0.48 (0.37–0.59)	4.51 (4.20–4.72)	3.96 (3.18–4.82)	1.02 (0.10–1.73)
11	0.39 (0.32–0.46)	4.27 (4.01–4.44)	4.18 (3.49–4.82)	0.48 (–0.30–1.16)
13	0.41 (0.30–0.52)	4.31 (4.05–4.56)	3.21 (2.58–3.85)	1.50 (0.81–2.17)
14	0.37 (0.30–0.44)	4.14 (3.93–4.34)	4.16 (2.82–5.95)	0.34 (–1.40–1.71)
15	0.37 (0.33–0.42)	4.15 (3.88–4.35)	2.93 (2.35–3.53)	1.59 (0.90–2.21)

gains smoothly oscillated around a mean value of $5.0 \text{ Mg ha}^{-1} \text{yr}^{-1}$ (range: 3.7 to $6.6 \text{ Mg ha}^{-1} \text{yr}^{-1}$). To determine which demographic process most affected biomass net change, we tested the correlation between biomass gains and losses and biomass net changes (Fig. 2). Biomass net changes were significantly correlated with biomass losses (Spearman's $\rho = 0.89$, $P < 0.0001$), while no correlation was found with biomass gains (Spearman's $\rho = 0.23$, $P = 0.11$). Biomass loss was independent of biomass growth (Student's test: $t = 1.54$, $\text{df} = 46$, $P = 0.13$), suggesting no common response to external drivers, e.g. drought enhancing mortality and affecting growth simultaneously.

Biomass dynamics among size classes

We analysed biomass fluxes independently for four size classes. Biomass fluxes (ingrowth, growth and loss) in classes of $\text{DBH} < 40 \text{ cm}$ were rather constant among plots, whereas biomass fluxes in

classes of $\text{DBH} \geq 40 \text{ cm}$ showed higher variation. Biomass losses differed significantly between plots (Kruskal–Wallis $\chi^2 = 10.18$, $\text{df} = 5$, $P < 0.05$). Losses in plots 13 and 15 (respectively 0.58 and $0.62 \text{ Mg ha}^{-1} \text{yr}^{-1}$) were two-times lower than values recorded in others plots (from 1.0 to 1.48). Significant biomass accumulation was the consequence of two different processes. Plots 13 and 15 had few losses and substantial growth in the largest size class. Plot 6 lost substantial biomass in the $\text{DBH} \geq 60 \text{ cm}$ size class, but this flux was more than compensated by ingrowth in the smaller size classes (Fig. 3).

Mortality process

The intensity and occurrence of strong biomass loss differed among plots (Fig. 1). Over the study period, 46.9% of the annual biomass loss was dead standing, 39.7% fallen and 13.4% broken trees. Trees of $\text{DBH} \geq 60 \text{ cm}$ contributed strongly to total biomass loss, whereas smaller trees contributed

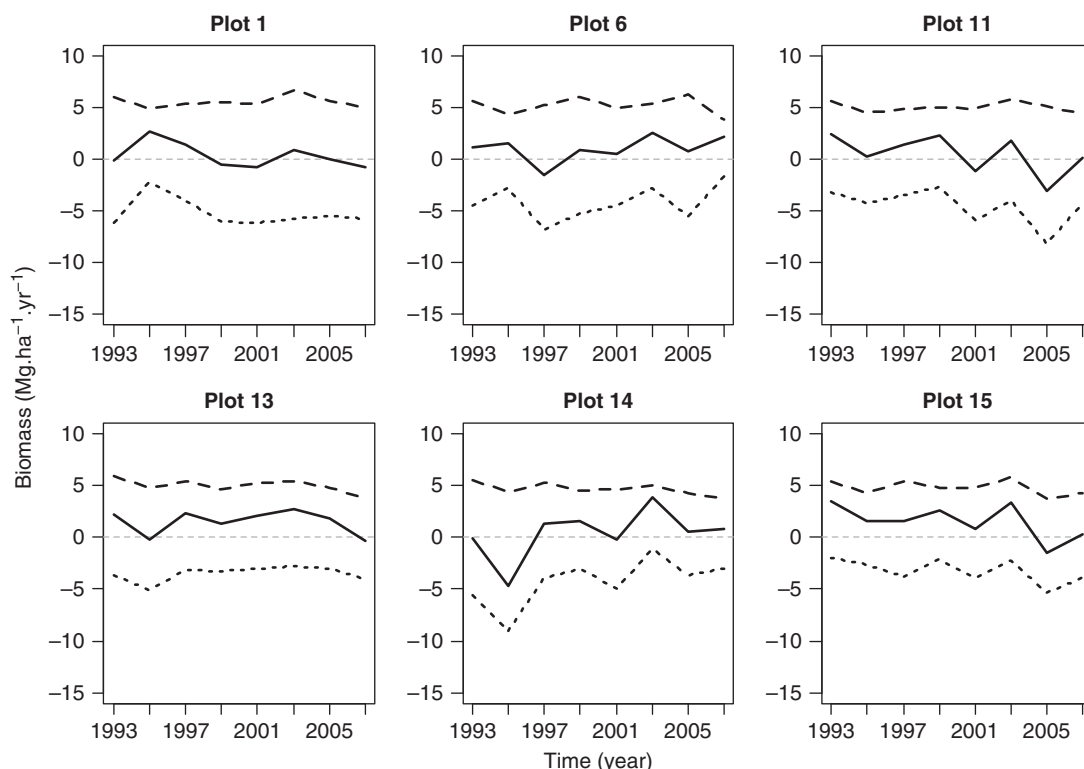


Fig. 1. Biomass gain (dashed line), loss (dotted line) and net change (straight line) over 16 years by plot.

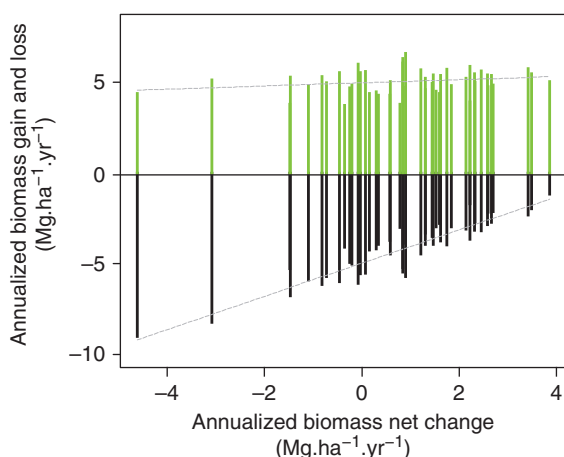


Fig. 2. Annual biomass gain (positive value – pale lines) and loss (negative value – black lines) plotted by increasing ordered values of annual biomass net change. Dotted lines represent the trend of each biomass flux along increasing biomass change. A positive significant correlation was found between annual biomass losses and biomass change (Spearman's $\rho = 0.89$, $P < 0.0001$), while no correlation was found for biomass gain (Spearman's $\rho = 0.23$, $P = 0.11$). No correlation linking biomass gains and losses was found (Spearman's $\rho = 0.21$, $P = 0.35$).

less (Fig. 4a). Large biomass losses were never due to the mortality of one single large tree. The presence or absence of a few large dead trees strongly

drove total biomass loss (Fig. 4b) and therefore biomass net change.

Discussion

Biomass stock estimation

Biomass estimates in Paracou varied among plots from 388 to 443 Mg ha^{-1} (Table 1A). These values are higher than the value ($298 \pm 51 \text{ Mg ha}^{-1}$) reported for Amazonia (Baker et al. 2004a) or the eastern part of French Guiana (Chave et al. 2008). Malhi et al. (2006) explained the higher biomass stocks in the coastal areas of Brazil and the Guyana Shield as a combination of elevated forest basal areas (BA), sustained by regular rainfall, and high average wood densities. Mean BA at our site ranged between 28.3 and 31.8 $\text{m}^2 \text{ ha}^{-1}$, corresponding to the range reported in the Amazon basin (Lewis et al. 2004). However, average wsg of the stand (0.758 g cm^{-3}) is greater at Paracou than at most other Neotropical sites (Baker et al. 2004a). 57.5% of all trees had measured wsg, 11% at the genus level, 16% at the family level and 15.5% at the plot level. Trees with plot-averaged density were equally represented among plots. In order to test for the effect of wood density estimation on our results, we ran

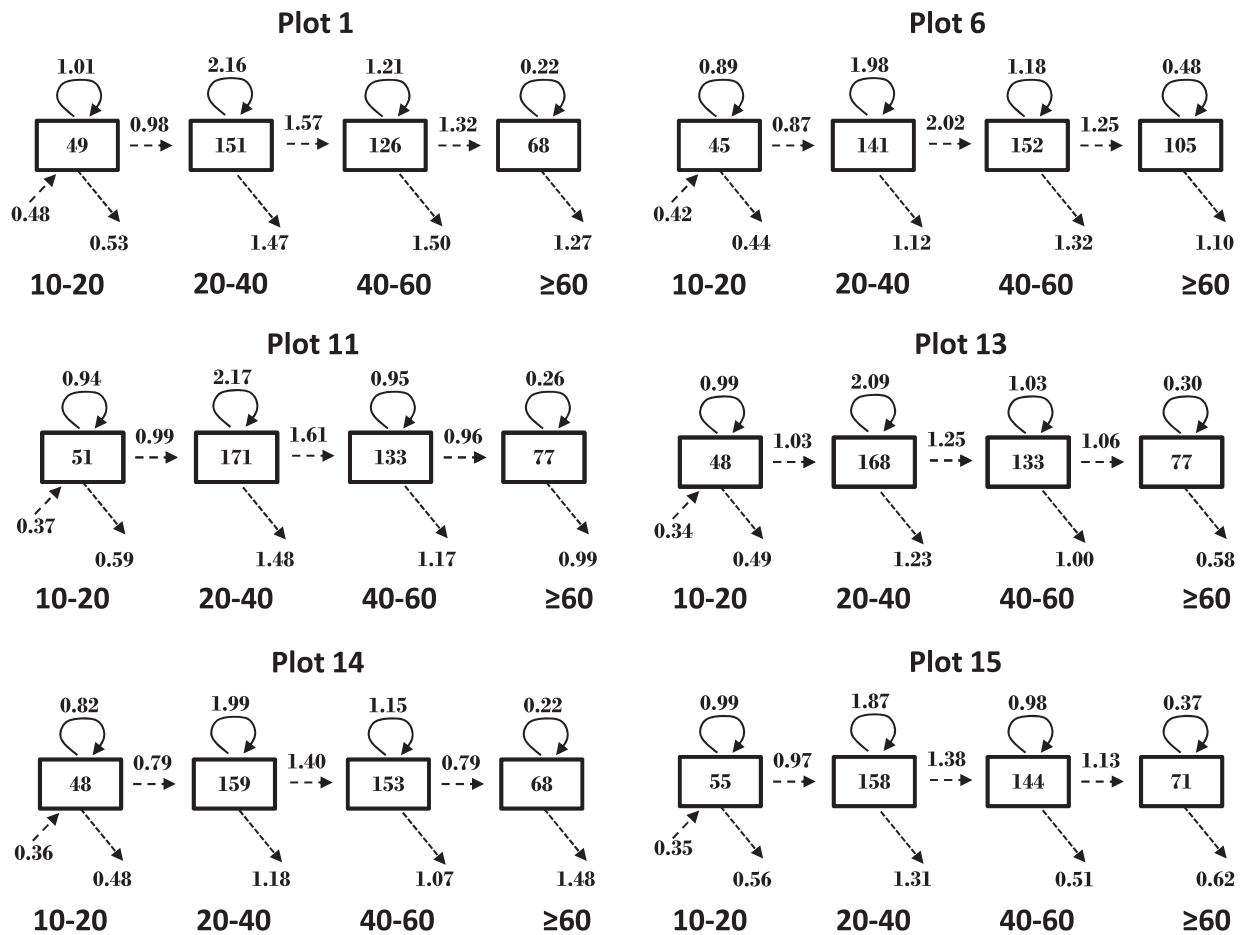


Fig. 3. Schematic diagrams of biomass stocks (Mg ha^{-1}) (boxes) and fluxes ($\text{Mg ha}^{-1} \text{yr}^{-1}$) (ingrowth: dashed arrows, growth: straight arrows, and loss: dotted arrows) by size class. Fluxes are annual values computed over the study period 1991–2007, while stocks represent initial biomass stocks (1991).

the analyses with (i) the same data set with 70% of wsg attributed at the species level (derived from cambial densities) and (ii) using wsg of the Global Wood Density Database (Zanne et al. 2009). Wider wsg attribution barely changed our biomass estimates ($<1\%$) and did not affect our results (not presented). However, plot-averaged wsg attribution may slightly overestimate total biomass stocks. Despite these known overestimations, our approach remained very conservative, as we only used local wood density rather than wood densities compiled from databases. Wood density has been shown to greatly vary among sites and species (Baker et al. 2004b; Chave et al. 2006; Patiño et al. 2009).

AGB estimates integrating height were on average only 5% lower. Height-based biomass stocks ranged from 370 to 422 Mg ha^{-1} . This difference of estimation is similar to that reported by Chave et al. (2005) and confirms the relevance of the allometry employed.

Biomass dynamics over the study period

The present study reports bi-annual censuses that are infrequent in tropical forest ecology and allow precisely quantification of the effects of forest demographic processes on biomass net changes over a 16-yr period. Tropical forests at Paracou are heterogeneous in their biomass balances. Mean annual biomass aggradation in Paracou was $0.90 \text{ Mg ha}^{-1} \text{yr}^{-1}$ over the study period. Baker et al. (2004a) found that biomass net change averaged $1.22 \text{ Mg ha}^{-1} \text{yr}^{-1}$ across Amazonia. Other studies have also reported significant biomass increases, ranging from 0.4 to $2.8 \text{ Mg ha}^{-1} \text{yr}^{-1}$ (Rice et al. 2004; Vieira et al. 2004; Chave et al. 2008; Pyle et al. 2008), which represent an increase of 0.11–0.73% of the biomass stock annually.

At our site, biomass net changes were mainly driven by large and unpredictable losses, whereas gains remained nearly constant over time. Sub-

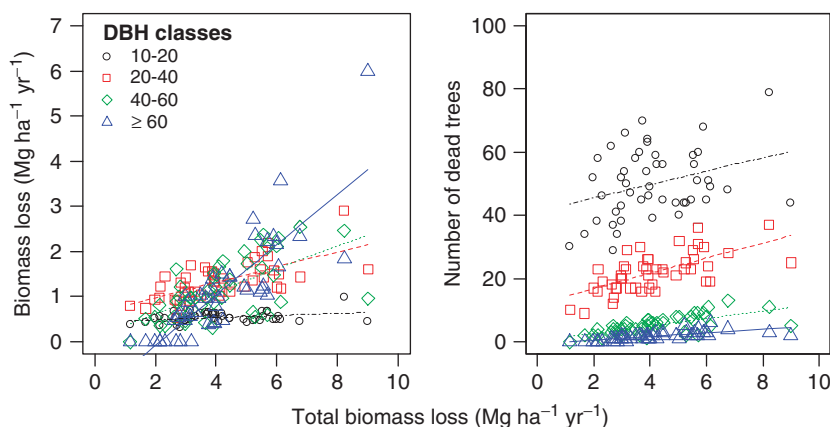


Fig. 4. (a) Relation between the biomass loss by size class and total biomass loss for all census intervals ($n = 64$); (b) Relation between the number of dead trees by size class and total biomass loss. Lines represent the correlation between both variables for each size class.

stantial losses were attributable to the death of a few large trees rather than numerous smaller ones. No evident disturbance affected any plot during the study period. On average, dead standing trees account for 47% of total biomass losses and remained nearly constant among plots and censuses. This ratio was not correlated to total biomass loss ($R^2 = 0.10$, $P = 0.47$), suggesting no large blow-down (AGB dead standing trees to AGB fallen trees) or local pathogen attacks (AGB dead standing trees to AGB fallen trees).

The role of demographic processes

In contrast to the results of Lewis et al. (2004), we found that biomass aggradation was the consequence of low mortality among large size classes, rather than biomass gains over time. Large trees represent a large portion of above-ground biomass and account for a substantial biomass loss when they die (Clark & Clark 1996; Chave et al. 2001; Nascimento & Laurance 2002; Nascimento et al. 2007). The role of these trees in biomass net change remains highly difficult to study due to their long life spans, low mortality rates and scarcity (Carey et al. 1994; Clark & Clark 1996; Nepstad et al. 2007). Hence, mortality of large trees is a punctuated and infrequent phenomenon in both space and time. We agree with the conclusion of Feeley et al. (2007), who wrote “It may be difficult to accurately capture the frequency of these rare disturbance events and adequately account for them in estimates of biomass change based on the repeated measurements of inventory plots.”

Past disturbances and forest history

Overall, some common trends arose among plots: biomass stocks as well as tree densities decreased in the 10–20-cm size class and increased in classes $\text{DBH} \geq 40$ cm. Similar trends in structure and dynamics were observed in forests regenerating from past disturbances (Chazdon 2003; Mascaro et al. 2005; Marin-Spiotta et al. 2007; Pyle et al. 2008; Blanc et al. 2009). Moreover, great variability of biomass losses among plots suggests that forest maturity in Paracou differs among plots. Both results support the hypothesis that biomass accumulation is a consequence of recovering from past disturbance.

Since plot establishment (1984), no large-scale disturbances have been recorded. At a longer time scale, exogenous past disturbances, such as extreme droughts, large blow-downs, pathogen attacks, fires or ancient human impacts, can affect biomass stocks and carbon storage of tropical forests (Rolim et al. 2005; Nepstad et al. 2007; Phillips et al. 2009). Such perturbations may have affected forests at various time and spatial scales. Regeneration may thus be spatially patchy (Turner et al. 1998; Körner 2003; Muller-Landau 2009). Some recent studies indicate the presence of pre-Colombian human communities in littoral French Guiana. Such human occupancy may have had substantial and long-lasting ecological impacts (Bush & Silman 2007; Hammond et al. 2007).

How to accurately assess rare events

Most studies of forest dynamics have been at small scales (1–5 ha) or for relatively short periods

(5–10 yr), and are therefore likely to inadequately sample the mortality of large trees. Fisher et al. (2008) showed that the estimation of biomass change was highly dependent on the spatial dispersion of disturbance events and on sampling strategy. Gloor et al. (2009) reported that a study period of 10 yr was sufficient to account for infrequent mortality events, estimating that mortality events, even though they may be under-sampled, are rare enough not to offset the increase in biomass seen across the RAINFOR network. On the basis of a study period 1.6-times longer than that advised by Gloor et al. (2009), we found that small-scale, large biomass losses were sufficient to critically affect biomass balance, resulting in no significant biomass increase. Indeed, substantial biomass losses were almost exclusively due to the death of large trees. It may be necessary to conduct studies at a scale even larger than that reported here (6×6.25 ha of forest intensively censused over 16 yr) in order to accurately capture the tail of the distribution of biomass losses (Gloor et al. 2009). Plots 1, 6 and 11 have been censused since 1985. Biomass net changes over a 22-yr period became negative in plot 1 (−0.15) and decreased in the two other plots (0.96 and 0.42). This strengthens our conclusion that short intervals may lead to apparent biomass increase, while longer periods account for infrequent events.

This can be seen as a limitation of permanent plot networks that only partly capture large-scale phenomena. Along with longer censuses, large-scale remote sensing analyses will enable better understanding of the crucial role of tropical forests in the global carbon budget.

Conclusions

In the present study, we found that forest dynamics was very heterogeneous at medium spatial (6.25 ha) and temporal (16 yr) scales. Significant positive biomass changes occurred only in plots with low mortality events recorded among large trees. Where many large trees died, on the other hand, substantial biomass losses were observed. This suggests that biomass dynamics are largely driven by endogenous processes, rather than external forcing. However, mortality of large trees remains difficult to assess accurately, even in large permanent plots. For this reason, long-term studies on large permanent plots will continue to be the cornerstone of biomass balance studies. Furthermore, we need more detailed information on the frequency and spatio-

temporal distribution of large tree mortality to understand biomass stock variations through time.

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Supporting Information

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

Appendix S1. Site-specific wood specific gravity (wsg) of tree species determined at the Paracou field station (French Guiana).

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2.1 Annexe de l'article

Valeurs de densités spécifiques du bois (wood specific gravity, wsg) déterminées pour des arbres de Paracou. Les échantillons sont stockés à l'herbier de Cayenne. La nomenclature est basée sur le format Aublet2 (www.cayenne.ird.fr/aublet2/Referentiel.html). Les niveaux d'estimations de la densité du bois font références aux niveaux de déterminations utilisés pour calculer la densité (wsg) ; wsg CIRAD : density du bois utilisée dans cette étude ; wsg GWDD : valeur moyenne calculée à partir de la base de données : 'Global Wood Density Database' (Zanne *et al.*, 2009), et N : nombre d'échantillons de bois mesurés.

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Abarema jupunba (Willd.)Britton & Killip	Mimosaceae	species	0,585	0,585	22
Abarema mataybifolia (Sandwith)Barneby & J.W.Grimes	Mimosaceae	genus	0,585	0,585	3
Abarema sp.	Mimosaceae	genus	0,585	0,585	21
Agonandra silvatica Ducke	Opiliaceae	species	0,721	0,831	5
Amaioua guianensis Aubl.	Rubiaceae	species	0,779	0,625	6
Amanoa congesta W.J.Hayden	Euphorbiaceae	genus	0,858	0,843	3
Amanoa guianensis Aubl.	Euphorbiaceae	species	0,858	0,843	4
Ambelania acida Aubl.	Apocynaceae	species	0,493	0,525	56
Amphirrhox longifolia (A.St.-Hil.)Spreng.	Violaceae	species	0,881	0,710	1
Anacardiaceae indet.	Anacardiaceae	family	0,561	0,504	28
Anacardium spruceanum Benth. ex Engl.	Anacardiaceae	species	0,424	0,479	13
Anartia meyeri (G.F.W. Meyer ex G. Don) Miers	Apocynaceae	family	0,596	0,608	7
Anartia sp.	Apocynaceae	family	0,596	0,608	8
Anaxagorea dolichocarpa Sprague & Sandwith	Annonaceae	species	0,677	0,580	4
Andira coriacea Pulle	Fabaceae	species	0,816	0,732	40
Aniba sp.	Lauraceae	family	0,477	0,473	1
Annona foetida Mart.	Annonaceae	species	0,677	0,572	1
Annonaceae indet.	Annonaceae	family	0,677	0,596	132
Antonia ovata Pohl	Loganiaceae	species	0,711	0,467	2
Apeiba glabra Aubl.	Tiliaceae	species	0,497	0,320	14
Apeiba sp.	Tiliaceae	genus	0,497	0,320	29
Apocynaceae indet.	Apocynaceae	family	0,596	0,608	21
Aspidosperma album (Vahl)Benoist ex Pichon	Apocynaceae	species	0,744	0,766	4
Aspidosperma cruentum Woodson	Apocynaceae	species	0,898	0,789	9
Aspidosperma excelsum Benth.	Apocynaceae	species	0,794	0,792	2
Aspidosperma marcgravianum Woodson	Apocynaceae	species	0,812	0,733	4
Aspidosperma oblongum A.DC.	Apocynaceae	species	0,794	0,865	1
Aspidosperma sandwithianum Markgr.	Apocynaceae	species	0,724	0,792	1
Aspidosperma sp.	Apocynaceae	genus	0,794	0,789	53
Balizia pedicellaris (DC.)Barneby & J.W.Grimes	Mimosaceae	species	0,586	0,497	21
Bocoa prouacensis Aubl.	Caesalpiniaceae	species	1,082	1,054	536
Bombacaceae indet.	Bombacaceae	family	0,617	0,492	108
Bonafousia undulata (M. Vahl) A.L. De Candolle	Apocynaceae	family	0,596	0,608	1
Brosimum guianense (Aubl.)Huber	Moraceae	species	0,898	0,843	28
Brosimum rubescens Taub.	Moraceae	species	0,945	0,825	26
Brosimum utile (Kunth)Pittier	Moraceae	species	0,921	0,506	8
Buchenavia grandis Ducke	Combretaceae	species	0,881	0,755	3
Buchenavia guianensis (Aubl.)Alwan & Stace	Combretaceae	genus	0,881	0,755	1
Buchenavia nitidissima (Rich.)Alwan & Stace	Combretaceae	genus	0,881	0,755	1
Buchenavia sp.	Combretaceae	genus	0,881	0,755	1

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Burseraceae indet.	Burseraceae	family	0,585	0,625	55
Byrsonima aerugo Sagot	Malpighiaceae	species	0,750	0,629	1
Byrsonima densa (Poir.)DC.	Malpighiaceae	species	0,750	0,620	1
Byrsonima laevigata (Poir.)DC.	Malpighiaceae	species	0,750	0,620	6
Byrsonima sp.	Malpighiaceae	genus	0,750	0,625	6
Caesalpiniaceae indet.	Caesalpiniaceae	family	0,824	0,807	1
Caraipa racemosa Cambess.	Clusiaceae	family	0,731	0,674	3
Caraipa sp.	Clusiaceae	family	0,731	0,674	4
Carapa procera DC.	Meliaceae	species	0,618	0,564	259
Caryocar glabrum (Aubl.)Pers.	Caryocaraceae	species	0,670	0,654	63
Casearia decandra Jacq.	Flacourtiaceae	species	0,597	0,664	2
Casearia javitensis Kunth	Flacourtiaceae	species	0,597	0,753	8
Casearia sp.	Flacourtiaceae	genus	0,597	0,707	8
Casearia sylvestris Sw.	Flacourtiaceae	species	0,597	0,705	3
Cassipourea guianensis Aubl.	Rhizophoraceae	species	0,723	0,820	1
Catostemma fragrans Benth.	Bombacaceae	species	0,714	0,574	164
Cecropia obtusa Trécul	Cecropiaceae	species	0,201	0,310	21
Cecropia sciadophylla Mart.	Cecropiaceae	species	0,353	0,387	4
Cecropia sp.	Cecropiaceae	genus	0,277	0,349	3
Chaetocarpus schomburgkianus (Kuntze)Pax & K.Hoffm.	Euphorbiaceae	species	0,973	0,805	146
Chaetocarpus sp.	Euphorbiaceae	genus	0,973	0,805	59
Chaunochiton kappleri (Sagot ex Engl.)Ducke	Olacaceae	species	0,613	0,522	31
Cheiloclinium cognatum (Miers)A.C.Sm.	Hippocrateaceae	plot	0,716	0,666	2
Chimarrhis turbinata DC.	Rubiaceae	species	0,787	0,720	6
Chrysobalanaceae indet.	Chrysobalanaceae	family	0,835	0,823	117
Chrysophyllum argenteum Jacq.	Sapotaceae	species	0,734	0,784	14
Chrysophyllum cuneifolium (Rudge)A.DC.	Sapotaceae	species	0,734	0,929	5
Chrysophyllum pomiferum (Eyma)T.D.Penn.	Sapotaceae	species	0,774	0,766	9
Chrysophyllum prieurii A.DC.	Sapotaceae	species	0,734	0,861	44
Chrysophyllum sanguinolentum (Pierre)Baehni	Sapotaceae	species	0,694	0,671	40
Chrysophyllum sp.	Sapotaceae	genus	0,734	0,802	54
Clusiaceae indet.	Clusiaceae	family	0,731	0,674	2
Coccoloba mollis Casar.	Polygonaceae	species	0,714	0,675	12
Combretaceae indet.	Combretaceae	family	0,881	0,755	11
Conceveiba guianensis Aubl.	Euphorbiaceae	species	0,529	0,543	68
Conceveiba sp.	Euphorbiaceae	genus	0,529	0,543	30
Cordia sagotii I.M.Johnst.	Boraginaceae	species	0,725	0,409	13
Cordia sp.	Boraginaceae	genus	0,715	0,409	8
Couepia bracteosa Benth.	Chrysobalanaceae	species	0,907	0,770	62
Couepia caryophylloides Benoist	Chrysobalanaceae	species	0,911	0,770	20
Couepia guianensis Aubl.	Chrysobalanaceae	species	0,791	0,755	14
Couepia habrantha Standl.	Chrysobalanaceae	genus	0,870	0,762	3
Couepia obovata Ducke	Chrysobalanaceae	genus	0,870	0,762	2
Couepia parillo DC.	Chrysobalanaceae	genus	0,870	0,762	1

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Couepia sp.	Chrysobalanaceae	genus	0,870	0,762	37
Couma guianensis Aubl.	Apocynaceae	species	0,488	0,467	24
Couratari calycina Sandwith	Lecythidaceae	genus	0,561	0,500	2
Couratari gloriosa Sandwith	Lecythidaceae	genus	0,561	0,500	1
Couratari guianensis Aubl.	Lecythidaceae	species	0,568	0,507	13
Couratari multiflora (Sm.)Eyma	Lecythidaceae	species	0,555	0,448	202
Couratari oblongifolia Ducke & R.Knuth	Lecythidaceae	species	0,561	0,505	3
Couratari sp.	Lecythidaceae	genus	0,561	0,500	8
Coussarea machadoana Standl.	Rubiaceae	genus	0,779	0,650	6
Coussarea racemosa A.Rich.	Rubiaceae	species	0,779	0,650	1
Coussarea sp.	Rubiaceae	genus	0,779	0,650	5
Cupania hirsuta L.A.T. Radlkofer	Sapindaceae	genus	0,877	0,628	2
Cupania rubiginosa (Poir.)Radlk.	Sapindaceae	genus	0,877	0,628	2
Cupania scrobiculata Rich.	Sapindaceae	species	0,877	0,628	14
Dacryodes nitens Cuatrec.	Burseraceae	species	0,585	0,490	8
Dendrobangia boliviana Rusby	Icacinaceae	species	0,694	0,635	40
Dendrobangia sp.	Icacinaceae	genus	0,694	0,635	1
Dialium guianense (Aubl.)Sandwith	Cesalpiniaceae	species	0,727	0,896	1
Dialium sp.	Cesalpiniaceae	genus	0,710	0,896	2
Dicorynia guianensis Amshoff	Caesalpiniaceae	species	0,704	0,591	232
Diospyros carbonaria Benoist	Ebenaceae	species	0,725	0,730	2
Diospyros sp.	Ebenaceae	genus	0,710	0,730	2
Diploptropis purpurea (Rich.)Amshoff	Fabaceae	species	0,704	0,762	3
Diploptropis sp.	Fabaceae	genus	0,704	0,762	9
Dipteryx odorata (Aubl.)Willd.	Fabaceae	species	0,794	0,923	2
Dipteryx punctata (S.F.Blake)Amshoff	Fabaceae	species	0,794	0,920	1
Dipteryx sp.	Fabaceae	genus	0,794	0,921	5
Drypetes fanshawei Sandwith	Euphorbiaceae	genus	0,901	0,737	10
Drypetes sp.	Euphorbiaceae	genus	0,901	0,737	48
Drypetes variabilis Uittien	Euphorbiaceae	species	0,901	0,737	24
Duguétia calycina Benoist	Annonaceae	species	0,907	0,370	5
Duguétia sp.	Annonaceae	genus	0,907	0,585	1
Duguétia surinamensis R.E.Fr.	Annonaceae	species	0,907	0,800	13
Duroia aquatica (Aubl.)Bremek.	Rubiaceae	species	0,708	0,785	4
Duroia eriopila L.f.	Rubiaceae	species	0,911	0,796	6
Duroia longiflora Ducke	Rubiaceae	genus	0,809	0,794	20
Duroia micrantha (Ladbrook) Zarucchi et Kirkbride	Rubiaceae	species	0,809	0,800	5
Duroia sp.	Rubiaceae	genus	0,809	0,794	1
Ecclinusa guianensis Eyma	Sapotaceae	species	0,769	0,627	3
Ecclinusa ramiflora Mart.	Sapotaceae	species	0,769	0,961	6
Ecclinusa sp.	Sapotaceae	genus	0,769	0,794	3
Elaeoluma sp.	Sapotaceae	family	0,769	0,796	1
Emmotum fagifolium Desv. ex Ham.	Icacinaceae	species	0,732	0,727	1
Enterolobium oldemanii Barneby & J.W.Grimes	Mimosaceae	species	0,828	0,699	8
Enterolobium schomburgkii (Benth.)Benth.	Mimosaceae	species	0,833	0,699	18

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Enterolobium sp.	Mimosaceae	genus	0,831	0,699	3
Eperua falcata Aubl.	Caesalpiniaceae	species	0,714	0,719	1543
Eperua grandiflora (Aubl.)Benth.	Caesalpiniaceae	species	0,781	0,704	405
Eriotheca globosa (Aubl.)A.Robyns	Bombacaceae	species	0,617	0,410	3
Eriotheca sp.	Bombacaceae	genus	0,617	0,410	3
Erythroxylum citrifolium A.St.-Hil.	Erythroxylaceae	species	0,710	0,710	1
Eschweilera collina Eyma	Lecythidaceae	species	0,830	0,778	2
Eschweilera congestiflora (Benoist)Eyma	Lecythidaceae	species	0,827	0,860	93
Eschweilera coriacea (DC.)S.A.Mori	Lecythidaceae	species	0,908	0,852	138
Eschweilera decolorans Sandwith	Lecythidaceae	genus	0,830	0,840	113
Eschweilera pedicellata (Rich.)S.A.Mori	Lecythidaceae	species	0,820	0,909	4
Eschweilera sagotiana Miers	Lecythidaceae	species	0,766	0,800	1497
Eschweilera simiorum (Benoist)Eyma	Lecythidaceae	species	0,830	0,860	1
Eschweilera sp.	Lecythidaceae	genus	0,830	0,840	146
Eugenia cupulata Amshoff	Myrtaceae	genus	0,924	0,831	1
Eugenia patrisii Vahl	Myrtaceae	species	0,924	0,831	2
Eugenia sp.	Myrtaceae	genus	0,924	0,831	6
Euphorbiaceae indet.	Euphorbiaceae	family	0,722	0,688	10
Euplassa pinnata (Lam.)I.M.Johnst.	Proteaceae	species	0,723	0,520	1
Euterpe oleracea Mart.	Arecaceae	family	0,861	0,440	1
Fabaceae indet.	Fabaceae	family	0,794	0,689	12
Familiae indet.	Familiae indet.	plot	0,716	0,673	4026
Faramea pedunculata (Bremek.) Delprete	Rubiaceae	family	0,779	0,675	1
Ficus piresiana Vázq.Avila & C.C.Berg	Moraceae	family	0,721	0,641	2
Ficus sp.	Moraceae	family	0,721	0,641	18
Flacourtiaceae indet.	Flacourtiaceae	family	0,597	0,693	4
Fusaea longifolia (Aubl.)Saff.	Annonaceae	species	0,677	0,743	2
Garcinia benthamiana (Planch. & Triana)Pipoly	Clusiaceae	genus	0,731	0,727	3
Garcinia madruno (Kunth)Hammel	Clusiaceae	species	0,731	0,727	5
Garcinia sp.	Clusiaceae	genus	0,731	0,727	147
Glycydendron amazonicum Ducke	Euphorbiaceae	species	0,635	0,681	7
Glycydendron sp.	Euphorbiaceae	genus	0,635	0,681	12
Goupia glabra Aubl.	Celastraceae	species	0,747	0,727	105
Guarea guidonia (L.)Sleumer	Meliaceae	species	0,729	0,565	5
Guarea pubescens (Rich.)A.Juss.	Meliaceae	species	0,729	0,530	1
Guarea sp.	Meliaceae	genus	0,729	0,547	27
Guatteria citriodora Ducke	Annonaceae	species	0,637	0,596	2
Guatteria guianensis (Aubl.)R.E.Fr.	Annonaceae	species	0,576	0,596	4
Gustavia hexapetala (Aubl.)Sm.	Lecythidaceae	species	0,663	0,716	282
Gustavia sp.	Lecythidaceae	genus	0,663	0,716	7
Hebepetalum humiriifolium (Planch.)Benth.	Hugoniaceae	species	0,776	0,871	75
Heisteria densifrons Engl.	Olacaceae	species	0,829	0,650	9
Heisteria sp.	Olacaceae	genus	0,829	0,650	2
Helicostylis pedunculata Benoist	Moraceae	species	0,687	0,675	7
Helicostylis sp.	Moraceae	genus	0,608	0,645	1

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Helicostylis tomentosa (Poepp. & Endl.) Rusby	Moraceae	species	0,529	0,615	7
Henriettella flavescens (Aubl.) Triana	Melastomataceae	family	0,722	0,807	24
Hevea guianensis Aubl.	Euphorbiaceae	species	0,537	0,571	91
Hieronyma oblonga (Tul.) Müll. Arg.	Euphorbiaceae	family	0,722	0,688	1
Himatanthus sp.	Apocynaceae	family	0,596	0,608	3
Hirtella bicornis Mart. & Zucc.	Chrysobalanaceae	species	0,809	0,900	31
Hirtella glandistipula Ducke	Chrysobalanaceae	genus	0,786	0,869	1
Hirtella glandulosa Spreng.	Chrysobalanaceae	species	0,762	0,925	14
Hirtella racemosa Lam.	Chrysobalanaceae	species	0,786	0,782	1
Hirtella sp.	Chrysobalanaceae	genus	0,786	0,869	18
Humiriaceae indet.	Humiriaceae	family	0,861	0,835	31
Humiriastrum sp.	Humiriaceae	family	0,837	0,835	1
Humiriastrum subcrenatum (Benth.) Cuatrec.	Humiriaceae	species	0,837	0,835	26
Hyeronima sp.	Euphorbiaceae	family	0,722	0,688	1
Icacinaeae indet.	Icacinaeae	family	0,732	0,701	2
Inga alba (Sw.) Willd.	Mimosaceae	species	0,759	0,586	3
Inga albicoria Poncy	Mimosaceae	genus	0,759	0,552	1
Inga cayennensis Sagot ex Benth.	Mimosaceae	species	0,759	0,530	5
Inga gracilifolia Ducke	Mimosaceae	genus	0,759	0,552	1
Inga loubryana Poncy	Mimosaceae	genus	0,759	0,552	4
Inga melinonis Sagot	Mimosaceae	species	0,759	0,540	4
Inga sarmentosa Glaz. ex Harms	Mimosaceae	genus	0,759	0,552	2
Inga sp.	Mimosaceae	genus	0,759	0,552	265
Inga stipularis DC.	Mimosaceae	species	0,759	0,530	7
Inga tubaeformis R. Benoist	Mimosaceae	species	0,759	0,530	2
Iryanthera hostmannii (Benth.) Warb.	Myristicaceae	genus	0,597	0,572	264
Iryanthera sagotiana (Benth.) Warb.	Myristicaceae	species	0,597	0,572	253
Iryanthera sp.	Myristicaceae	genus	0,597	0,572	2
Jacaranda copaia (Aubl.) D. Don	Bignoniaceae	species	0,400	0,351	78
Oenocarpus bataua Mart.	Arecaceae	species	0,861	0,609	409
Lacmellea aculeata (Ducke) Monach.	Apocynaceae	species	0,279	0,490	43
Lacmellea floribunda (Poeppig) Bentham et J.D. Hooker	Apocynaceae	species	0,603	0,490	2
Lacunaria crenata (Tul.) A.C. Sm.	Quiinaceae	species	1,031	0,807	3
Lacunaria jenmanii (Oliv.) Ducke	Quiinaceae	genus	1,031	0,807	2
Lacunaria sp.	Quiinaceae	genus	1,031	0,807	2
Laetia procera (Poepp.) Eichler	Flacourtiaceae	species	0,597	0,648	25
Lauraceae indet.	Lauraceae	family	0,477	0,473	205
Lecythidaceae indet.	Lecythidaceae	family	0,782	0,726	97
Lecythis chartacea O. Berg	Lecythidaceae	species	0,935	0,819	15
Lecythis holcogyne (Sandwith) S.A. Mori	Lecythidaceae	species	0,873	0,776	1
Lecythis persistens Sagot	Lecythidaceae	species	0,797	0,860	1515
Lecythis poiteau O. Berg	Lecythidaceae	species	0,885	0,802	103
Lecythis praeclara (Sandwith) S.A. Mori, ined.	Lecythidaceae	genus	0,873	0,821	1
Lecythis sp.	Lecythidaceae	genus	0,873	0,821	18
Lecythis zabucajo Aubl.	Lecythidaceae	species	0,875	0,850	23

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
<i>Leonia glycyarpa</i> Ruiz & Pav.	Violaceae	species	0,881	0,600	4
<i>Licania alba</i> (Bernoulli)Cuatrec.	Chrysobalanaceae	species	0,994	0,887	1071
<i>Licania canescens</i> Benoist	Chrysobalanaceae	species	0,947	0,880	202
<i>Licania densiflora</i> Kleinhoonte	Chrysobalanaceae	species	0,882	0,785	7
<i>Licania heteromorpha</i> Benth.	Chrysobalanaceae	species	0,862	0,816	597
<i>Licania hypoleuca</i> Benth.	Chrysobalanaceae	species	0,882	0,909	2
<i>Licania latistipula</i> Prance	Chrysobalanaceae	genus	0,882	0,852	1
<i>Licania laxiflora</i> Fritsch	Chrysobalanaceae	species	0,882	1,033	44
<i>Licania licaniiiflora</i> (Sagot)S.F.Blake	Chrysobalanaceae	species	0,709	0,670	18
<i>Licania longistyla</i> (Hook.f.)Fritsch	Chrysobalanaceae	genus	0,882	0,852	2
<i>Licania majuscula</i> Sagot	Chrysobalanaceae	species	0,875	0,883	1
<i>Licania membranacea</i> Sagot ex Laness.	Chrysobalanaceae	species	0,911	0,880	346
<i>Licania micrantha</i> Miq.	Chrysobalanaceae	species	0,894	0,836	155
<i>Licania ovalifolia</i> Kleinhoonte	Chrysobalanaceae	species	0,868	0,850	84
<i>Licania parviflora</i> Benth	Chrysobalanaceae	species	0,882	0,820	1
<i>Licania parvifructa</i> Fanshawe & Maguire	Chrysobalanaceae	species	0,882	0,887	7
<i>Licania</i> sp.	Chrysobalanaceae	genus	0,882	0,852	93
<i>Licania sprucei</i> (Hook.f.)Fritsch	Chrysobalanaceae	genus	0,882	0,852	89
<i>Loreya arborescens</i> (Aubl.)DC.	Melastomataceae	species	0,655	0,600	2
<i>Lueheopsis rugosa</i> (Pulle)Burret	Tiliaceae	species	0,497	0,547	16
<i>Lueheopsis</i> sp.	Tiliaceae	genus	0,497	0,547	12
<i>Mabea piriri</i> Aubl.	Euphorbiaceae	species	0,619	0,598	29
<i>Mabea</i> sp.	Euphorbiaceae	genus	0,619	0,598	46
<i>Macoubea guianensis</i> Aubl.	Apocynaceae	species	0,459	0,414	15
<i>Manilkara bidentata</i> (A.DC.)A.Chev.	Sapotaceae	species	0,871	0,873	49
<i>Manilkara</i> sp.	Sapotaceae	genus	0,871	0,873	1
<i>Maquira guianensis</i> Aubl.	Moraceae	species	0,654	0,766	3
<i>Maquira</i> sp.	Moraceae	genus	0,654	0,766	1
<i>Matayba</i> sp.	Sapindaceae	family	0,946	0,628	2
<i>Maximiliana maripa</i> (J.F. Correa da Serra) Drude	Arecaceae	family	0,861	0,440	21
<i>Maytenus oblongata</i> Reissek	Celastraceae	species	0,841	0,727	42
<i>Maytenus</i> sp.	Celastraceae	family	0,841	0,727	12
Melastomataceae indet.	Melastomataceae	family	0,722	0,807	76
<i>Melicoccus pedicellaris</i> (Radlk.)Acev.-Rodr.	Sapindaceae	family	0,946	0,628	1
<i>Miconia acuminata</i> (Steud.)Naudin	Melastomataceae	family	0,574	0,807	38
<i>Miconia minutiflora</i> (Bonpl.)DC.	Melastomataceae	family	0,574	0,807	1
<i>Miconia plukenetii</i> Naudin	Melastomataceae	family	0,574	0,807	1
<i>Miconia poeppigii</i> Triana	Melastomataceae	family	0,574	0,807	1
<i>Miconia</i> sp.	Melastomataceae	family	0,574	0,807	1
<i>Miconia tschudyoides</i> Cogn.	Melastomataceae	species	0,574	0,807	44
<i>Micropholis egensis</i> (A.DC.)Pierre	Sapotaceae	species	0,627	0,600	39
<i>Micropholis eugeniifolia</i> Pierre	Sapotaceae	genus	0,691	0,614	2
<i>Micropholis guyanensis</i> (A.DC.)Pierre	Sapotaceae	species	0,650	0,657	23
<i>Micropholis melinoniana</i> Pierre	Sapotaceae	species	0,691	0,530	9
<i>Micropholis obscura</i> T.D.Penn.	Sapotaceae	species	0,899	0,614	3

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Micropholis sp.	Sapotaceae	genus	0,691	0,614	5
Micropholis venulosa (Mart. & Eichler)Pierre	Sapotaceae	species	0,587	0,670	17
Minquartia guianensis Aubl.	Olacaceae	species	0,809	0,787	7
Moraceae indet.	Moraceae	family	0,721	0,641	143
Moronobea coccinea Aubl.	Clusiaceae	species	0,816	0,832	201
Mouriri collocarpa Ducke	Melastomataceae	species	0,937	0,833	2
Mouriri crassifolia Sagot	Melastomataceae	species	0,937	0,895	94
Mouriri sagotiana Triana	Melastomataceae	species	0,937	0,900	1
Mouriri sp.	Melastomataceae	genus	0,937	0,876	29
Myrciaria floribunda (H.West ex Willd.)O.Berg	Myrtaceae	species	0,924	0,785	1
Myristicaceae indet.	Myristicaceae	family	0,495	0,487	1
Myrtaceae indet.	Myrtaceae	family	0,924	0,808	138
Naucleopsis guianensis (Mildbr.)C.C.Berg	Moraceae	species	0,721	0,650	1
Neea sp.	Nyctaginaceae	plot	0,714	0,675	2
Nyctaginaceae indet.	Nyctaginaceae	plot	0,724	0,673	3
Ocotea amazonica (Meisn.)Mez	Lauraceae	species	0,557	0,443	1
Ocotea argyrophylla Ducke	Lauraceae	genus	0,557	0,476	1
Ocotea glomerata (Nees)Mez	Lauraceae	species	0,557	0,508	1
Ocotea sp.	Lauraceae	genus	0,557	0,476	3
Oenocarpus bacaba Mart.	Arecaceae	species	0,861	0,650	133
Olacaceae indet.	Olacaceae	family	0,750	0,653	4
Ormosia coutinhoi Ducke	Fabaceae	species	0,689	0,591	43
Ormosia stipularis Ducke	Fabaceae	species	0,689	0,580	1
Ouratea sp.	Ochnaceae	plot	0,722	0,675	4
Oxandra asbeckii (Pulle)R.E.Fr.	Annonaceae	species	0,841	0,770	737
Pachira dolichocalyx A.Robyns	Bombacaceae	species	0,520	0,492	12
Palicourea sp.	Rubiaceae	family	0,779	0,675	3
Parahancornia fasciculata (Lam.)Benoist	Apocynaceae	species	0,464	0,473	2
Parinari campestris Aubl.	Chrysobalanaceae	species	0,784	0,707	53
Parinari montana Aubl. emend. Ducke	Chrysobalanaceae	species	0,703	0,710	39
Parinari rodolphii Huber	Chrysobalanaceae	species	0,706	0,722	3
Parkia nitida Miq.	Mimosaceae	species	0,496	0,383	10
Parkia pendula (Willd.)Benth. ex Walp.	Mimosaceae	species	0,541	0,521	9
Parkia sp.	Mimosaceae	genus	0,552	0,429	45
Parkia ulei (Harms)Kuhlms.	Mimosaceae	species	0,422	0,379	3
Parkia velutina Benoist	Mimosaceae	species	0,750	0,435	9
Peltogyne paniculata Benth.	Caesalpiniaceae	species	0,824	0,796	2
Peltogyne sp.	Caesalpiniaceae	genus	0,824	0,796	14
Perebea guianensis Aubl.	Moraceae	species	0,721	0,560	2
Perebea mollis (Poeppig et Endlicher) Huber	Moraceae	species	0,721	0,365	1
Perebea rubra (Trécul)C.C.Berg	Moraceae	genus	0,721	0,463	2
Platonia insignis Mart.	Clusiaceae	species	0,756	0,723	43
Platonia sp.	Clusiaceae	genus	0,756	0,723	2
Platymiscium sp.	Fabaceae	family	0,794	0,689	2

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Poecilanthe hostmannii (Benth.)Amshoff	Fabaceae	species	0,968	0,620	9
Pogonophora schomburgkiana Miers ex Benth.	Euphorbiaceae	species	0,722	0,833	836
Poraqueiba guianensis Aubl.	Icacinaceae	species	0,771	0,742	100
Posoqueria latifolia (Rudge)Roem. & Schult.	Rubiaceae	species	0,711	0,570	21
Posoqueria longiflora Aubl.	Rubiaceae	species	0,711	0,455	1
Posoqueria sp.	Rubiaceae	genus	0,711	0,512	9
Pourouma bicolor Mart.	Cecropiaceae	species	0,446	0,353	4
Pourouma guianensis Aubl.	Cecropiaceae	species	0,446	0,380	1
Pourouma melinonii Benoist	Cecropiaceae	species	0,446	0,320	12
Pourouma sp.	Cecropiaceae	genus	0,446	0,351	15
Pouteria ambelaniifolia (Sandwith)T.D.Penn.	Sapotaceae	species	0,916	0,697	21
Pouteria bangii (Rusby)T.D.Penn.	Sapotaceae	species	0,863	0,854	9
Pouteria bilocularis (H.K.A.Winkl.)Baehni	Sapotaceae	species	0,811	0,708	8
Pouteria caimito (Ruiz & Pav.)Radlk.	Sapotaceae	species	0,811	0,805	2
Pouteria coriacea (Pierre)Pierre	Sapotaceae	species	0,811	0,895	1
Pouteria engleri Eyma	Sapotaceae	species	0,671	0,774	6
Pouteria eugeniifolia (Pierre)Baehni	Sapotaceae	species	0,811	1,113	25
Pouteria fimbriata Baehni	Sapotaceae	genus	0,811	0,854	4
Pouteria flavilatax T.D.Penn.	Sapotaceae	genus	0,811	0,854	1
Pouteria gonggripii Eyma	Sapotaceae	species	0,693	0,854	21
Pouteria grandis Eyma	Sapotaceae	species	0,811	0,930	1
Pouteria guianensis Aubl.	Sapotaceae	species	0,871	0,930	36
Pouteria hispida Eyma	Sapotaceae	species	0,811	0,874	3
Pouteria jariensis Pires & T.D.Penn.	Sapotaceae	species	0,813	0,854	8
Pouteria melanopoda Eyma	Sapotaceae	species	0,811	0,969	8
Pouteria reticulata (Engl.)Eyma	Sapotaceae	species	0,811	0,794	3
Pouteria sagotiana (Baill.)Eyma	Sapotaceae	genus	0,811	0,854	2
Pouteria singularis T.D.Penn.	Sapotaceae	species	0,748	0,854	7
Pouteria sp.	Sapotaceae	genus	0,811	0,854	10
Pouteria torta (Mart.)Radlk.	Sapotaceae	species	0,913	0,769	19
Pouteria torta (Martius) L.A.T. Radlkofer subsp. glabra Pennington	Sapotaceae	genus	0,811	0,854	1
Pouteria venosa (Mart.)Baehni	Sapotaceae	species	0,811	0,920	5
Pradosia cochlearia (Lecomte)T.D.Penn.	Sapotaceae	species	0,810	0,730	310
Proteaceae indet.	Proteaceae	family	0,723	0,520	2
Protium giganteum Engler var. crassifolium (Engler) Daly	Burseraceae	genus	0,585	0,615	6
Protium guianense (Aubl.)Marchand	Burseraceae	species	0,575	0,711	27
Protium opacum Swart	Burseraceae	species	0,500	0,570	63
Protium plagiocarpium Benoist	Burseraceae	genus	0,585	0,615	3
Protium robustum (Swart)D.M.Porter	Burseraceae	genus	0,585	0,615	2
Protium sagotianum Marchand	Burseraceae	species	0,585	0,557	8
Protium sp.	Burseraceae	genus	0,585	0,615	115
Protium subserratum (Engl.)Engl.	Burseraceae	species	0,585	0,550	24
Protium tenuifolium (Engl.)Engl.	Burseraceae	species	0,585	0,570	2

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
<i>Protium trifoliolatum</i> Engl.	Burseraceae	species	0,680	0,685	1
<i>Pterocarpus officinalis</i> Jacq.	Fabaceae	species	0,794	0,383	90
<i>Qualea rosea</i> Aubl.	Vochysiaceae	species	0,651	0,580	221
<i>Quiina integrifolia</i> Pulle	Quiinaceae	genus	0,976	0,851	5
<i>Quiina obovata</i> Tul.	Quiinaceae	species	0,976	0,851	14
Quiinaceae indet.	Quiinaceae	family	1,003	0,829	2
<i>Rauvolfia paraensis</i> Ducke	Apocynaceae	species	0,596	0,550	1
<i>Rauvolfia</i> sp.	Apocynaceae	genus	0,596	0,550	1
<i>Recordoxylon speciosum</i> (Benoist)Gazel ex Barneby	Caesalpiniaceae	species	0,869	0,800	226
<i>Rhodostemonodaphne grandis</i> (Mez)Rohwer	Lauraceae	species	0,363	0,390	13
<i>Rhodostemonodaphne</i> sp.	Lauraceae	genus	0,363	0,390	7
<i>Rinorea pectino-squamata</i> Hekking	Violaceae	species	0,881	0,610	2
<i>Rinorea</i> sp.	Violaceae	genus	0,881	0,610	1
<i>Rollinia exsucca</i> (A.P. De Candolle ex Dunal) A.L. De Candolle	Annonaceae	species	0,677	0,375	1
<i>Rollinia</i> sp.	Annonaceae	genus	0,677	0,375	2
Rubiaceae indet.	Rubiaceae	family	0,779	0,675	127
<i>Ruizterania albiflora</i> (Warm.)Marc.-Berti	Vochysiaceae	species	0,584	0,576	33
<i>Sacoglottis guianensis</i> Benth.	Humiriaceae	species	0,861	0,836	8
<i>Sacoglottis</i> sp.	Humiriaceae	genus	0,861	0,836	1
<i>Sagotia racemosa</i> Baill.	Euphorbiaceae	species	0,722	0,580	1
<i>Sandwithia guyanensis</i> Lanj.	Euphorbiaceae	family	0,722	0,688	201
Sapindaceae indet.	Sapindaceae	family	0,946	0,628	55
Sapotaceae indet.	Sapotaceae	family	0,769	0,796	674
<i>Schefflera decaphylla</i> (Sagot ex Seem.)Harms	Araliaceae	species	0,483	0,446	17
<i>Schefflera morototoni</i> (Aubl.)Maguire, Steyerl. & Frodin	Araliaceae	species	0,449	0,456	1
<i>Schefflera</i> sp.	Araliaceae	genus	0,466	0,451	9
<i>Schistostemon sylvaticum</i> Sabatier	Lauraceae	family	0,477	0,473	8
<i>Sextonia rubra</i> (Mez)van der Werff	Lauraceae	species	0,512	0,552	88
<i>Simaba cedron</i> Planch.	Simaroubaceae	species	0,323	0,474	223
<i>Simaba morettii</i> Feuillet	Simaroubaceae	species	0,567	0,474	7
<i>Simaba polyphylla</i> (Cavalcante)W.W.Thomas	Simaroubaceae	genus	0,445	0,474	7
<i>Simaba</i> sp.	Simaroubaceae	genus	0,445	0,474	15
<i>Simarouba amara</i> Aubl.	Simaroubaceae	species	0,367	0,383	8
<i>Siparuna cuspidata</i> (Tul.)A.DC.	Monimiaceae	species	0,811	0,655	3
<i>Siparuna decipiens</i> (Tul.)A.DC.	Monimiaceae	species	0,811	0,641	17
<i>Sloanea brevipes</i> Benth.	Elaeocarpaceae	plot	0,727	0,672	1
<i>Sloanea latifolia</i> (Rich.)K.Schum.	Elaeocarpaceae	plot	0,727	0,672	3
<i>Sloanea</i> sp.	Elaeocarpaceae	plot	0,716	0,673	186
<i>Socratea exorrhiza</i> (Mart.)H.Wendl.	Arecaceae	species	0,861	0,230	1
<i>Sterculia multiovula</i>	Sterculiaceae	genus	0,540	0,498	30
<i>Sterculia pruriens</i> (Aubl.)K.Schum.	Sterculiaceae	species	0,540	0,486	94
<i>Sterculia</i> sp.	Sterculiaceae	genus	0,540	0,498	51
<i>Sterculia speciosa</i> K.Schum.	Sterculiaceae	species	0,540	0,510	18

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Stryphnodendron moricolor Barneby & J.W.Grimes	Mimosaceae	family	0,686	0,515	1
Swartzia arborescens (Aubl.)Pittier	Caesalpiniaceae	species	0,923	0,835	4
Swartzia grandifolia Bong. ex Benth.	Caesalpiniaceae	species	0,923	1,030	5
Swartzia guianensis (Aubl.)Urb.	Caesalpiniaceae	species	0,837	0,730	6
Swartzia leblondii R.S.Cowan	Caesalpiniaceae	species	1,125	0,830	10
Swartzia panacoco (Aubl.)R.S.Cowan	Caesalpiniaceae	species	1,006	0,920	24
Swartzia polyphylla DC.	Caesalpiniaceae	species	0,724	0,691	84
Swartzia sp.	Caesalpiniaceae	genus	0,923	0,839	94
Symphonia globulifera L.f.	Clusiaceae	species	0,621	0,600	90
Symphonia sp.	Clusiaceae	genus	0,621	0,600	427
Symphonia sp2	Clusiaceae	genus	0,621	0,600	28
Tabebuia insignis (Miq.)Sandwith	Bignoniaceae	species	0,462	0,526	18
Tabebuia sp.	Bignoniaceae	genus	0,462	0,526	3
Tachigali bracteolata Dwyer	Caesalpiniaceae	family	0,609	0,807	6
Tachigali melinonii (Harms)Zarucchi & Herend.	Caesalpiniaceae	species	0,652	0,807	43
Tachigali paraënsis (Huber)Barneby	Caesalpiniaceae	species	0,565	0,807	2
Tachigali sp.	Caesalpiniaceae	family	0,609	0,807	42
Talisia furfuracea Sandwith	Sapindaceae	family	1,015	0,628	4
Talisia hexaphylla Vahl	Sapindaceae	family	1,015	0,628	25
Talisia praealta (Sagot)Radlk.	Sapindaceae	species	1,015	0,628	15
Talisia simaboides K.U.Kramer	Sapindaceae	family	1,015	0,628	14
Talisia sp.	Sapindaceae	family	1,015	0,628	14
Tapirira guianensis Aubl.	Anacardiaceae	species	0,561	0,457	6
Tapirira obtusa (Benth.)J.D.Mitch.	Anacardiaceae	species	0,561	0,293	1
Tapirira sp.	Anacardiaceae	genus	0,561	0,375	11
Tapura capitulifera Spruce ex Baill.	Dichapetalaceae	species	0,693	0,721	143
Tetragastris hostmannii (Engl.)Kuntze	Burseraceae	species	0,585	0,720	14
Tetragastris panamensis (Engl.)Kuntze	Burseraceae	species	0,585	0,717	4
Theobroma sp.	Sterculiaceae	genus	0,562	0,470	1
Theobroma subincanum Mart.	Sterculiaceae	species	0,562	0,470	122
Thyrsodium guianense Sagot ex Marchand	Anacardiaceae	species	0,698	0,650	53
Thyrsodium puberulum J.D.Mitch. & Daly	Anacardiaceae	genus	0,698	0,645	3
Thyrsodium sp.	Anacardiaceae	genus	0,698	0,645	18
Thyrsodium spruceanum Benth.	Anacardiaceae	species	0,698	0,640	2
Tiliaceae indet.	Tiliaceae	family	0,497	0,433	1
Tovomita sp.	Clusiaceae	family	0,731	0,674	642
Trattinnickia demerarae Sandwith	Burseraceae	family	0,585	0,625	1
Trattinnickia rhoifolia Willd.	Burseraceae	family	0,585	0,625	3
Trichilia micrantha Benth.	Meliaceae	species	0,840	0,613	1
Trichilia schomburgkii C.DC.	Meliaceae	species	0,840	0,687	10
Trymatococcus oligandrus (Benoist)Lanj.	Moraceae	species	0,612	0,610	38
Trymatococcus sp.	Moraceae	genus	0,612	0,610	2
Unonopsis rufescens (Baill.)R.E.Fr.	Annonaceae	species	0,641	0,605	44
Vantanea parviflora Lam.	Humiriaceae	species	0,885	0,833	11
Vantanea sp.	Humiriaceae	genus	0,885	0,833	3

Taxon	Family	Level of wsg estimation	wsg CIRAD	wsg GWDD	N
Violaceae indet.	Violaceae	family	0,881	0,640	15
Virola michelii Heckel	Myristicaceae	species	0,486	0,470	62
Virola surinamensis (Rol. ex Rottb.)Warb.	Myristicaceae	species	0,401	0,418	5
Vismia cayennensis (Jacq.)Pers.	Clusiaceae	species	0,731	0,490	1
Vismia ramuliflora Miq.	Clusiaceae	genus	0,731	0,490	2
Vismia sessilifolia (Aubl.)Choisy	Clusiaceae	genus	0,731	0,490	4
Vismia sp.	Clusiaceae	genus	0,731	0,490	9
Vitex sp.	Verbenaceae	plot	0,710	0,671	1
Vitex triflora Vahl	Verbenaceae	plot	0,727	0,672	1
Vochysia tomentosa (G.Mey.)DC.	Vochysiaceae	species	0,516	0,378	2
Vochysiaceae indet.	Vochysiaceae	family	0,584	0,511	6
Votomita guianensis Aubl.	Melastomataceae	family	0,722	0,807	18
Vouacapoua americana Aubl.	Caesalpiniaceae	species	0,825	0,794	379
Xylopia cayennensis Maas	Annonaceae	genus	0,462	0,571	5
Xylopia crinita R.E.Fr.	Annonaceae	genus	0,462	0,571	3
Xylopia frutescens Aubl.	Annonaceae	species	0,462	0,593	2
Xylopia nitida Dunal	Annonaceae	species	0,462	0,548	24
Xylopia pulcherrima Sandwith	Annonaceae	genus	0,462	0,571	1
Xylopia sp.	Annonaceae	genus	0,462	0,571	33
Zanthoxylum ekmanii (Urb.)Alain	Rutaceae	plot	0,705	0,660	1
Zygia tetragona Barneby & J.W.Grimes	Mimosaceae	species	1,059	0,515	29

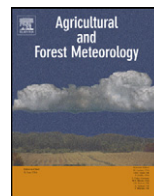
Chapitre 2

Climat et croissance des arbres tropicaux

1 Modélisation de l'eau disponible dans le sol pour les arbres des forêts tropicales

Pour analyser l'effet du climat sur la croissance, le premier travail a été de déterminer quels indices climatiques étaient les plus pertinents. Certaines variables climatiques comme la lumière ou la température ont un effet direct sur la plante. L'énergie disponible pour la plante peut être estimée par la valeur brute de ces variables climatiques, par exemple en mesurant le flux de photon photosynthétique. Les études concernant la croissance en milieu tropical utilisent les valeurs de précipitations dans leurs analyses, mais cette valeur n'est pas la quantité d'eau disponible pour la plante et ne permet pas de rendre compte de la saisonnalité de cette eau disponible. Déterminer cette quantité d'eau disponible pour la plante est beaucoup plus problématique, cela dépend de plusieurs paramètres tels que la distribution des racines et les caractéristiques du sol (capacité au champ et point de fanaison permanent). Nous avons donc développé un modèle de réserve en eau journalier pour les arbres en forêt tropicale. Ce type de modèle est déjà utilisé en forêt tempérée et a permis d'analyser la sécheresse de 2003 en Europe (Granier *et al.*, 2007). La réalisation de ce modèle est apparue d'autant plus importante que le

site de Paracou est soumis à une alternance régulière de saisons humides et de saisons sèches avec des précipitations mensuelles inférieures à 50 mm et qu'aucun outil n'était disponible en milieu tropical pour estimer l'eau disponible pour les arbres. Dans ce travail, l'eau disponible pour les arbres dans le sol a été modélisée par un modèle réalisé dans un cadre bayésien et calibré avec des données d'humidités du sol provenant de mesures TDR dans le dispositif de Paracou. Une nouvelle méthode permettant d'estimer la capacité au champ et le point de fanaison permanent est proposée. Cette méthode prend en compte l'utilisation de l'eau par la plante, ce qui n'est pas le cas des précédents modèles basés uniquement sur le fonctionnement hydrodynamique du sol. Le modèle une fois calibré permet de reconstruire l'histoire de l'eau dans le sol uniquement avec les précipitations journalières. La validation biologique du modèle a pu être réalisée avec des mesures de diamètre journalières provenant de dendromètres automatiques. Un arrêt de croissance diamétrique des arbres est observé quand la disponibilité fortement en eau diminue en saison sèche. Ce travail est présenté dans la publication ci-après, Wagner *et al.* (2011).



Modeling water availability for trees in tropical forests

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ABSTRACT

Modeling soil water availability for tropical trees is a prerequisite to predicting the future impact of climate change on tropical forests. In this paper we develop a discrete-time deterministic water balance model adapted to tropical rainforest climates, and we validate it on a large dataset that includes micro-meteorological and soil parameters along a topographic gradient in a lowland forest of French Guiana. The model computes daily water fluxes (rainfall interception, drainage, tree transpiration and soil plus understorey evapotranspiration) and soil water content using three input variables: daily precipitation, potential evapotranspiration and solar radiation. A novel statistical approach is employed that uses Time Domain Reflectometer (TDR) soil moisture data to estimate water content at permanent wilting point and at field capacity, and root distribution. Inaccuracy of the TDR probes and other sources of uncertainty are taken into account by model calibration through a Bayesian framework. Model daily output includes relative extractable water, *REW*, i.e. the daily available water standardized by potential available water. The model succeeds in capturing temporal variations in *REW* regardless of topographic context. The low Root Mean Square Error of Predictions suggests that the model captures the most important drivers of soil water dynamics, i.e. water refilling and root water extraction. Our model thus provides a useful tool to explore the response of tropical forests to climate scenarios of changing rainfall regime and intensity.

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1. Introduction

Despite annual precipitation that always exceeds 1500 mm year⁻¹, most of the Amazon's neotropical forests experience some annual dry season (less than 100 mm per month), that is variable in both duration and intensity (Malhi and Wright, 2004; Sombroek, 2001; Xiao et al., 2006; Marengo, 1992).

The consequences of annual drought on tropical forest functioning include a decrease in growth primary production and ecosystem respiration (Goulden et al., 2004; Hutrya et al., 2007; Bonal et al., 2008), and a reduction in tropical tree fluxes for both carbon (Bonal et al., 2000; Miranda et al., 2005) and water fluxes (Fisher et al., 2006). Very recently, an analysis of tree responses to the intense 2005 dry season highlighted the vulnerability of neotropical forests to moisture stress, with the potential for positive feedbacks on climate change due to increased tree mortality (Phillips et al., 2009).

Climate modeling scenarios suggest that the dry season in north-eastern Amazonian forests might lengthen during the 21st century (Cox et al., 2000, 2004; Malhi and Wright, 2004; Malhi et al., 2009). The short-term effect of soil water availability deficits on

tropical tree growth, mortality and carbon and water fluxes has recently been quantified under experimentally controlled conditions (Fisher et al., 2007; Nepstad et al., 2007). Long-term inventory plots with regular tree censuses (growth, recruitment, mortality) have been set-up widely in the past few decades throughout Amazonia (Phillips et al., 2010; Clark, 2004; Wagner et al., 2010). These plots offer an unexpected opportunity to analyze the impact of soil water availability on tropical forest dynamics on a large temporal and spatial scale (Clark, 2007). However, to the best of our knowledge, no soil water balance model explicitly accounting for tropical soil and climate characteristics, and able to compute available water for the trees on a plot scale, has ever been developed. The relation between amount of rainfall and water availability for trees is not straightforward and determined by various plant characteristics, such as the root distribution, and soil characteristics, such as the permanent wilting point and the field capacity. By contrast, other widely studied climatic variables such as light and temperature give a relatively direct indication on their effect on forest dynamics (Graham et al., 2003; Clark et al., 2010). Soil water availability to the trees, which can be characterized by Relative Extractable Water (*REW*, i.e. daily available water standardized by maximum available water), depends on soil characteristics such as structure, texture, composition and porosity, as well as on the rate of water uptake by the trees. Different soil water balance models

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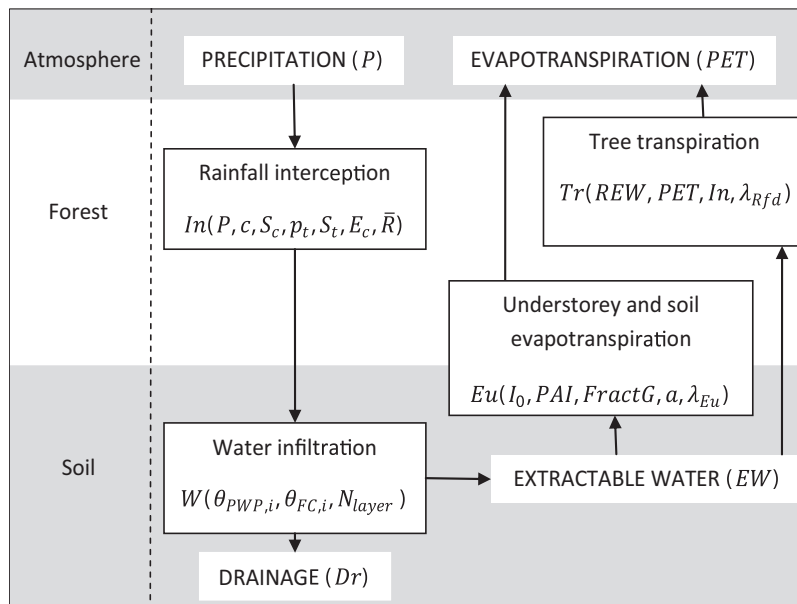


Fig. 1. Overview of the Soil Water Balance model general framework and the articulation of the different submodels. P : precipitation, c : canopy cover, S_c : canopy capacity, p_t : proportion of rain diverted to the trunks, S_t : trunk capacity, E_c : mean evaporation rate from the canopy, \bar{R} : mean rainfall rate, θ_{PWP} : soil water content at permanent wilting point, θ_{FC} : soil water content at field capacity, N_{layer} : number of layers of the model, I_0 : net radiation, PAI : plant area index, $FractG$: reflected radiation below trees, a : constant of proportionality between energy and evapotranspiration of the understorey, λ_{Eu} : understorey root density parameter, REW : relative extractable water, PET : potential evapotranspiration, λ_{Rfd} : tree root density parameter.

have been used in Amazonian tropical forests to estimate drought implications for forest flammability and tree growth (Nepstad et al., 2004), to reproduce hydrologic processes (Belk et al., 2007), to evaluate soil water controls on evapotranspiration (Fisher et al., 2007), or to evaluate the importance of deep root uptake (Markewitz et al., 2010). However, none of these models aims to estimate REW . The nearest estimate of REW is so-called plant available water (PAW) described by Nepstad et al. (2004). The spatial resolution of PAW, i.e. 8 km, is too large for use in any precise modeling of the impact of soil drought conditions on tree growth, mortality and/or recruitment. Furthermore, the modeling framework never explicitly simulates the amount of water taken up by tree roots. Modeling approaches designed to estimate REW have already been developed for temperate forests and, for instance, were used to assess soil water control on carbon and water dynamics in European forests during the 2003 drought (Granier et al., 2007). Such temperate models are not suitable for tropical forests. For instance, the polynomial rainfall interception submodel is unsuited to the stand characteristics of tropical forests. Another limit is that water extraction is not modeled and field data is needed for root density, meaning that soil pits need to be dug to quantify vertical root distribution, also meaning that the strong assumption must be made that water absorption by roots is proportional to root distribution.

In this paper we introduce a locally parameterized soil water budget model inspired by the BILJOU temperate model (Granier et al., 1999). As performed by BILJOU, this model estimates soil water availability, stand transpiration and rainfall interception in tropical forests with a daily time step and for different soil types (Fig. 1). Model inputs are daily rainfall, annual means of potential evapotranspiration (PET) and solar radiation, and averaged plant area index (PAI). The soil is filled by rainfall water passing through the canopy. The amount of rainfall intercepted by the canopy is computed in a submodel adapted to tropical forests (Gash et al., 1995). In our model, the soil consists of a succession of fine layers, each of which has a unique field capacity and permanent wilting point. We developed a new method using a Bayesian framework to estimate these two parameters using only Time Domain Reflectometer (TDR) measurements. When the water in a given

layer exceeds water content at field capacity, drainage occurs and water fills the next layer, etc. Water extraction from soil layers is due to tree transpiration in addition to soil and understorey evapotranspiration. Soil evaporation and understorey transpiration are computed based on equations developed by Granier et al. (1999), and are assumed to be proportional to the energy reaching the understorey; tree transpiration is computed using potential evapotranspiration. Both understorey and tree transpiration are extracted in accordance with estimated root distribution.

This paper has three specific objectives: (i) to present our water balance model and to describe the different submodels it contains; (ii) to present an original statistical method used to estimate permanent wilting point, field capacity, and root distribution based on Time-Domain Reflectometer (TDR) data only; and (iii) to parameterize and validate the model using TDR data collected on a soil topographic gradient in Paracou, French Guiana.

2. List of symbols and abbreviations

P	precipitation
In	rainfall interception
Th	throughfall
Tr	tree transpiration
PET	potential evapotranspiration
ρ	ratio Tr/ETP
Eu	understorey and soil evapotranspiration
Dr	drainage in depth
$\theta_{PWP,l}$	soil water content at permanent wilting point for layer l
$\theta_{FC,l}$	soil water content at field capacity of soil layer l
λ_{Rfd}	root density parameter
EW_l	extractable water of soil layer l
EW_l^{max}	maximum extractable water of soil layer l , $\theta_{FC,l} - \theta_{PWP,l}$
REW	relative extractable water of the soil
$REWC_l$	REW of soil layer l , critical when ≤ 0.4

Table 1
Interception model components adapted from Cuartas et al. (2007).

Components of interception loss	Formulation of components
For a storm insufficient to saturate the canopy	cP_G
Wetting up the canopy for a storm $>P'_G$ which saturates the canopy	$cP'_G - cS_c$
Evaporation from saturation until rainfall ceases	$\frac{\bar{E}_c}{\bar{R}}(P_G - P'_G)$
Evaporation after rainfall ceases	cS_c
Evaporation from trunks for a storm which saturates the trunk, $P_G > S_t/pt$	S_t
Evaporation from trunks for a storm insufficient to saturate the trunk	$p_t P_G$

3. The model

Our daily water balance model was constructed using discrete-time deterministic formalism. The model contains and interconnects four submodels that compute interception, water infiltration and deep drainage, tree transpiration, and soil plus understorey evapotranspiration (Fig. 1). First, part of the precipitation is intercepted by the canopy, then the remaining part reaches the soil surface and fills the soil. If the soil is at field capacity, the excess water is lost by deep drainage. Tree transpiration is assumed to absorb water from the soil depending on root distribution, and soil plus understorey evapotranspiration are assumed to absorb water from the top 1 m of soil. The daily change in soil water content is computed as:

$$\Delta EW = P - In - Tr - Eu - Dr \quad (1)$$

where ΔEW is the daily change in soil water content, P is the precipitation, In is the rainfall interception by the forest canopy, Tr is tree transpiration, Eu is evapotranspiration from soil plus understorey and Dr is drainage. We used Granier's framework for the general structure of the model (Granier et al., 1999, 2007).

3.1. Rainfall interception model

In tropical forests, rainfall interception by the forest canopy and the evaporation of intercepted rainfall constitute an important part of the ecosystem's water flux. The most commonly applied models are the original and sparse Rutter models (Rutter et al., 1971; Valente et al., 1997) and the original and sparse Gash model (Muzylo et al., 2009; Gash, 1979; Gash et al., 1995). The Gash model has been validated for tropical rainforests (Lloyd et al., 1988; Germer et al., 2006; Cuartas et al., 2007), and we estimate the daily rainfall interception using this model with a daily step, assuming one rainfall per day. To estimate In we need to determine canopy cover c , canopy capacity per unit area of cover S_c , the proportion of rain diverted to the trunks p_t , the trunk capacity S_t and the amount of rainfall needed to saturate the canopy P'_G given by:

$$P'_G = \frac{-\bar{R}S_c}{\bar{E}_c} \ln \left[1 - \frac{\bar{E}_c}{\bar{R}} \right] \quad (2)$$

where \bar{R} is the mean rainfall rate for saturated canopy conditions and \bar{E}_c is the mean evaporation rate from the canopy.

In our model we compute In under the assumption of one rainfall per day, and interception is computed as the sum of the components listed in Table 1.

3.2. Soil characteristics and drainage

The water reaching the soil (Throughfall, Th) for each day d is computed as:

$$Th_d = P_d - In_d \quad (3)$$

where P_d and In_d are precipitation and intercepted precipitation by the canopy, respectively, for day d .

The modeling of water dynamics in soil follows a layered bucket model frame. Soil is assimilated as a succession of 1 cm layers. Each layer has a field capacity and a permanent wilting point. For layer l , the difference between field capacity ($\theta_{FC,l}$) and permanent wilting point ($\theta_{PWP,l}$) is the maximum extractable water by the plant ($EW_l^{\max} = \theta_{FC,l} - \theta_{PWP,l}$). The extractable water in layer l for each day d is noted as $\widehat{EW}_{l,d}$.

When precipitation reaches the soil surface, the first layer is filled to field capacity before draining and filling the next layer to field capacity, continuing until no water remains. The model does not take account of surface runoff. If there is more water than total field capacity, the excess water is lost by deep drainage. Details of the algorithm are given in Appendix A.

A critical value is computed daily for each layer, i.e. critical relative extractable water REW_c :

$$REW_{c,l,d} = \frac{\widehat{EW}_{l,d} - \theta_{PWP,l}}{\theta_{FC,l} - \theta_{PWP,l}} \quad (4)$$

where $\theta_{PWP,l}$ and $\theta_{FC,l}$ are the permanent wilting point and the field capacity of layer l .

3.3. Understorey and soil evapotranspiration

The evapotranspiration of understorey and soil (Eu) is computed by assuming that it is proportional to the energy reaching this level (Granier et al., 1999). Available energy under the canopy is computed using the Beer Lambert equation, the extinction coefficient (k), plant area index (PAI) and net radiation (I_0), Eq. (5). Part of this energy is reflected ($FractG$) while the energy that remains is assumed to be proportional to understorey and soil evapotranspiration, applying coefficient a . We assume Eu to absorb water in the top meter of soil with an exponential function of parameter 0.5. For layer l , Eu_l is computed as:

$$Eu_l = I_0 \times \exp(-k \times PAI) \times (1 - FractG) \times a \times 0.5 \times \exp(-0.5 \times N_{layer,l}) \quad (5)$$

3.4. Tree transpiration

Tree transpiration is computed based on potential evapotranspiration (PET). Granier et al. (1999) observed, for a LAI greater than 6 and when the soil water content was unlimited (Relative Extractable Water, $REW > 0.4$), a constant ratio between tree transpiration and PET for temperate and tropical forest stands. When soil water content became limiting for plants ($REW < 0.4$), the ratio $\rho = Tr/PET$, decreased linearly (Granier et al., 1999). We made the assumption that under stress conditions ($REW < 0.4$), the ratio ρ decreases linearly to reach 0 when no water is available for the trees, Eq. (8). Tree transpiration is extracted from each layer in relation to root density. As the relationship between amount of roots and rooting depth follows an exponential function (Humbel, 1978), we used an exponential function to model fine root density (Rfd). Rfd is defined by:

$$Rfd(depth) = \lambda_{Rfd} \times \exp(-\lambda_{Rfd} \times depth) \quad (6)$$

where λ_{Rfd} is the root density parameter. The percentage of transpiration extracted between soil surface and layer l is the integral of Rfd between 0 and $depth_l$, the depth of layer l in cm. To simplify notation, we set Rfd_l as the percentage of transpiration extracted from layer l , which is defined by

$$Rfd_l = \int_{depth_{l-1}}^{depth_l} Rfd(depth) d depth$$

Tree transpiration extracted for layer l and for day d is computed as:

$$Tr_{l,d} = \rho_l \times PET \times (1 - \exp(-\lambda_{Rfd} \times N_{layer})) \times Rfd_l \quad (7)$$

where

$$\rho_l = \begin{cases} \rho & \text{if } REWC_{l,d} > 0.4 \\ (REWC_{l,d} \times \rho) / 0.4 & \text{if } REWC_{l,d} < 0.4 \end{cases} \quad (8)$$

3.5. Model output

The model outputs REW (Relative Extractable Water), a daily value between 0 and 1, is computed as follows:

$$REW_d = \sum_{l=1}^{N_{layer}} \frac{\widehat{EW}_{l,d} - \theta_{PWP,l}}{\theta_{FC,l} - \theta_{PWP,l}} \times \frac{Rfd_l}{\sum_{l=1}^{N_{layer}} Rfd_l} \quad (9)$$

REW is computed from the soil surface to the depth of the N_{layer} . When $REW=1$, the amount of extractable water by the tree is at its maximum and, when $REW=0$, no water is available for trees. A REW of less than 0.4 is considered to represent hydric stress for temperate and tropical forest trees (Granier et al., 1999; Stahl and Bonal, unpublished data). This REW is weighted by root density (Rfd) in order to limit the weight of layers that are full of extractable water but contain few or no roots.

4. Calibrating and testing the model

4.1. Site descriptions and experimental setup

The study site used for calibration is located in Paracou, French Guiana (5°18'N, 52°55'W), a lowland tropical rain forest near Sinnamary (Gourlet-Fleury et al., 2004). The forest is typical of Guianan rainforests (ter Steege et al., 2006). More than 550 woody species attaining 2 cm DBH (Diameter at Breast Height) have been described at the site, with an estimated 160–180 species of trees ≥ 10 cm DBH per hectare. The dominant families at the site include Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae. The climate is affected by the north/south movements of the Inter-Tropical Convergence Zone and the site receives nearly two-thirds of its annual 3041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month in September and October. The site is located approximately 40 m above sea level (Gourlet-Fleury et al., 2004) and is made up of a succession of small hills with slopes of less than 30% (Ferment et al., 2001; Ferry et al., 2010).

In 2003, a 55 m self-supporting metallic eddy covariance flux tower, Gyaflux, was built in the Paracou forest in a natural 100 m² gap, with minimal disturbance to the upper canopy. This location covers a range of more than 1 km of forest in the direction of the prevailing winds. The top of the tower is about 20 m higher than the overall canopy and meteorological and eddy flux sensors are mounted 3 m above the tower. Full details on tower sensors are given by Bonal et al. (2008). Potential evapotranspiration (PET in mm), was computed based on the Penman–Monteith equation (Allen et al., 1998) from meteorological data gathered by tower sensors.

Soils were mapped based on a soil classification developed in French Guiana (Boulet et al., 1993; Sabatier et al., 1997) which defines seven functional units corresponding to seven successive evolutionary stages in a ferralitic soil. The first stages involve the thinning of a miggroaggregated upper horizon, whereas the second stages describe the mineralogical changes that occur under different hydromorphic conditions. The evolutionary degree of the ferralitic cover is also related to the soil's hydrodynamic functioning and chemical properties (Sabatier et al., 1997). The seven functional soil units are referred to as DVD (deep vertical drainage), Alt (red alloterite at a depth of less than 1.2 m), SLD (superficial lateral drainage), UhS (uphill system), UhS+DC (uphill system + dry character, i.e. horizons at a depth of less than 1 m are *dry to the touch* in all seasons), DhS (downhill system) and DhS+DC (Downhill system + dry character). Humbel (1978) observed similar patterns of vertical root distribution within soils with vertical drainage (Alt, UhS, DVL), or superficial lateral drainage (SLD). Root distribution is very extensive in the upper horizon with more than 80% of the fine roots found in the top 60 cm. The presence of fine roots decreases exponentially with depth. Rooting depth has not been investigated at our study site but potentially extends to 10 m, as observed elsewhere in the Amazon basin (Markewitz et al., 2010).

Soil water content (SWC; m³ m⁻³) has been measured using a time domain reflectometry probe (TRIME FM3; Imko, Ettlingen, Germany) every 3 weeks since 2003 in depth profiles of 0.2–2.6 m every 0.2 m, in 10 tubes located along a 1 km transect that crosses the Gyaflux site. At least one tube is located in each of the four terra firme soil units Alt, UhS, SLD and DhS. Measurement error, given by the manufacturer, is 5 vol.% for a 25 vol.% water content and may reach 10 vol.% at very high contents (50 vol.%).

Within a 30 m radius of the Gyaflux tower (Alt soil type), changes in trunk circumference were monitored in 2007 and 2008 in 6 dominant trees (*Dicorynia guianensis* 34.8 cm and 41.1 cm in diameter at breast height, *Oxandra asbeckii* 16.8 cm, *Sloanea* sp. 47.5 cm, *Vouacapoua americana* 27.6 cm, *Goupia glabra* 75.5 cm) using automatic dendrometers (SLS 095; Penny + Giles, Christchurch, UK). Data were collected at 30-min intervals using a CRX10 datalogger (Campbell Scientific Inc.).

4.2. Model parameters and calibration

Model parameters were established based on the literature and field data. We performed a preliminary sensitivity analysis to quantify the impact of model parameters and their interaction on the decomposition of the REW variance. The methodology given in Wernsdorfer et al. (2008) was used. We chose to keep in the calibration those parameters that accounted for at least 10% of REW variance: the ratio $\rho = Tr/PET$, root density parameters, field capacity and permanent wilting point and the REW threshold value defining stressed conditions. Parameters that accounted for less of 10% of the variance were set at the value reported in the literature, Table 2. Canopy cover, c , 99%, was estimated by LIDAR measurements (Vincent et al., 2010). For the proportion of rain diverted to the trunks, p_t and trunk capacity S_t , values of 1.3% and 0.06 mm were used, respectively. These are the values measured by Cuartas et al. (2007) in a tropical forest 80 km from Manaus (Brazil). The mean value of k at the study site was assumed to be 0.88 (Cournac et al., 2002), i.e. a value in the upper range of photosynthetically active radiation extinction coefficients for tropical forests, from 0.7 to 0.9 (Wirth et al., 2001). A S_c of 1.9 mm was estimated with the previous fixed parameters for total 20% interception, the mean intercepted precipitation measured by Roche (1982) 30 km from Paracou in a similar forest stand. Mean PAI at Paracou is 6.92 (SD = 1.061), mean PET 3.97 mm d⁻¹ (SD = 1.15) and mean I_0 measured on the Gyaflux tower 586.8 MJ m⁻² d⁻¹ (SD = 174.91) (Bonal et al., 2008). PET , PAI and I_0 are assumed to be constant. Using the methodology of Bonal

Table 2
Fixed parameters of the model.

Parameter	Value	Unit	Origin
c	0.99	%	Vincent et al. (2010)
\bar{R}	8.64	mm	Guyaflux data
E_c	0.64	mm	Guyaflux data
p_t	0.013	%	Cuatas et al. (2007)
S_t	0.06	mm	Cuatas et al. (2007)
k	0.88	m^{-1}	Cournac et al. (2002) and Wirth et al. (2001)
threshold	0.4	–	Granier et al. (2007) and Breda et al. (2006)
S_c	1.9	mm	Roche (1982)
I_0	586.8	$MJ m^{-2} d^{-1}$	Guyaflux data
PAI	6.92	$m^2 m^{-2}$	Guyaflux data
PET	3.97	$mm d^{-1}$	Guyaflux data
a	10	%	Granier et al. (1999)

et al. (2008), we assume that a PAI of 6.92 is equivalent to a LAI above 6, the threshold value above which the ratio between tree transpiration and PET is assumed to be constant (Granier et al., 1999).

Two methods are currently used to determine θ_{PWP} and θ_{FC} at the plot scale. The first consists of plotting the water retention curve by collecting field samples and making laboratory measurements using the pressure plate, as by Granier et al. (2007) and Fisher et al. (2008). This approach is expensive and difficult to implement because the structure of the soil sample must be conserved. It is possible to retain the structure in surface samples, but a soil pit is needed to sample a depth profile. Unfortunately, in tropical soils, some horizons are extremely porous, fragile and full of roots, such that conserving the structure of these horizons is impossible. Some surface horizons show very high saturated hydraulic conductivity, with a maximum of $K_s > 500 mm d^{-1}$ (Guehl, 1984), making it difficult to saturate the sample. The other problem in this approach is to define the pressure applied to obtain θ_{PWP} and θ_{FC} . The commonly used pressure is $-1.5 MPa$, but we know that some trees can extract water under $-1.5 MPa$ (Tyree et al., 2003). In addition, this approach is not plant-centered, in other words the significance of values of θ_{PWP} and θ_{FC} are unclear in the absence of roots. The second approach is to use existing pedotransfer functions to plot the water retention curve, as has already been used in Amazonian forests (Tomasella et al., 2000; Markewitz et al., 2010). The use of pedotransfer functions and the measurement of uncertainty associated with this approach has been well described by Brimelow et al. (2010). This approach provides water retention curves at different points of pressure. It suffers from the same problem of defining the pressure applied to obtain θ_{PWP} and θ_{FC} , and of a definition of these particular points driven only by hydrology, not by plant uses. In this paper we describe a new approach used to estimate θ_{PWP} and θ_{FC} for which soil texture and physical laboratory measurements are not needed.

Parameters ρ (tree transpiration/PET), root density (λ_{Rfd}), field capacity ($\theta_{FC,l}$) and permanent wilting point ($\theta_{PWP,l}$) were estimated simultaneously. The model was calibrated at three different resolution levels, tube (M1), soil (M2) or forest level (M3), Table 3 and Appendix D, Fig. D.1. Data from 2007 to 2009 were used for model calibration, and data from 2006 were used for its validation. We

Table 3
Number of parameters used in the estimates according to model resolution level.

Parameter vector	Parameters			
Θ_m	ρ	λ_{Rfd}	θ_{PWP}	θ_{FC}
Θ_{M1} , Tube level	1	N_{tube}	$N_{tube} \times N_{layer}$	$N_{tube} \times N_{layer}$
Θ_{M2} , Soil level	1	N_{soil}	$N_{soil} \times N_{layer}$	$N_{soil} \times N_{layer}$
Θ_{M3} , Forest level	1	1	N_{layer}	N_{layer}

chose to keep 2007 and 2009 in the calibration because these years were witness to extreme events, a rare event of 180 mm of precipitation in September 2007 during the height of the dry season, and an exceptional dry period in the middle of the 2009 wet season.

We used a Bayesian framework to estimate model parameters as this is well suited to hierarchical models. Here, the value of a parameter is estimated by its posterior distribution. By definition the posterior distribution is proportional to the product of the likelihood of the model and the parameter prior distribution, Eq. (11). The user chooses the prior distribution based on his prior knowledge of the possible values of the parameter.

$$Data = \{Data_1, \dots, Data_{N_{tube}}\}$$

and

$$Data_j = \{EW_{1,1}^j, \dots, EW_{N_{obs},1}^j, EW_{1,2}^j, \dots, EW_{1,N_{day}}^j, \dots, EW_{N_{obs},N_{day}}^j\} \quad (10)$$

where $Data$ corresponds to the values of extractable water measured on number of days of field measurements N_{day} , for the number of TDR probe measurements by tubes N_{obs} and for number of tubes N_{tube} .

$$\pi_m(\Theta_m | Data) \propto \mathcal{L}(Data | \Theta_m) \pi_m^0(\Theta_m) \quad (11)$$

where $m \in \{M1, M2, M3\}$ is the model resolution level, Θ_m the parameter vector values, $\pi_m(\Theta_m | Data)$ the posterior distribution of the parameters, $\mathcal{L}(Data | \Theta_m)$ model likelihood given the parameter Θ_m and $\pi_m^0(\Theta_m)$ is the prior distribution of the parameters.

We assumed that measurement errors were distributed according to a centered normal distribution with a standard deviation of 20% around the measured value. This standard deviation was chosen to be consistent with the TDR probe error as given by its manufacturer. The error corresponds to the maximum error of the probe for soil water content near 50%, and such high soil water contents never occurred in the TDR probe data. The probe measurement error is multiplicative, increasing with soil water content. The likelihood is then given by:

$$\begin{aligned} \mathcal{L}(Data | \Theta_m) &= \prod_{p=1}^{N_{tube}} \mathcal{L}(Data_p | \Theta_m) \\ &= \prod_{p=1}^{N_{tube}} \prod_{d=1}^{N_{day}} \prod_{l=1}^{N_{layer}} \frac{\exp[-((\widehat{EW}_{l,d}^p - EW_{l,d}^p)^2) / (2(0.2 \times EW_{l,d}^p)^2)]}{\sqrt{2\pi(0.2 \times EW_{l,d}^p)}} \end{aligned} \quad (12)$$

where $\widehat{EW}_{l,d}^p$ are the extractable water values predicted by the model.

The posterior densities of the different parameters were estimated using a Monte Carlo Markov Chain algorithm (Robert and Casella, 2004). As the model contained many parameters, we built a Metropolis-Hastings algorithm within a Gibbs algorithm. Unlike the situation with a Metropolis-Hastings algorithm where the parameters are updated together, in our algorithm each parameter is updated separately and this, when many parameters need to be inferred, increases convergence speed. Details on the algorithm are given in Appendix B.

The same priors for each parameter were used at all three model resolution levels. We used uniform priors as we had no prior knowledge regarding the value of these parameters. To simplify, we give the prior distributions for the forest model, M3.

$$\pi_{\rho}^0 = \mathcal{U}_{[0,1]} \quad (13)$$

$$\pi_{\lambda_{Rfd}}^0 = \mathcal{U}_{[0,10]} \quad (14)$$

$$\pi_{\theta_{PWP}, \theta_{FC}; 1, \dots, N_{layer}}^0 = \mathcal{U}_{[0 \leq \theta_{PWP}; 1, \dots, N_{layer} < \theta_{FC}; 1, \dots, N_{layer} \leq 1]} \quad (15)$$

The algorithm was run for 120,000 iterations. The first 20,000 iterations were discarded as spin-up. Thinning of 100 iterations was

Table 4
RMSEP for model resolution levels M1, M2 and M3.

Soil	Tube	RMSEP of extractable water, median \pm (95% ci)		
		Tube level (M1)	Soil level (M2)	Forest level (M3)
Alt	1	1.696 (1.654–1.756)		
Alt	2	2.032 (1.978–2.108)		
Alt	4	1.819 (1.747–1.903)	2.631 (2.618–2.650)	
Alt	13	1.897 (1.817–1.992)		
SLD	5	1.943 (1.884–2.022)		3.582 (3.576–3.592)
SLD	9	1.770 (1.741–1.819)	3.176 (3.163–3.193)	
SLD	18	2.684 (2.663–2.716)		
DhS	19	4.420 (4.326–4.563)	4.184 (4.126–4.252)	
DhS	7	2.888 (2.815–2.998)		
UHS	16	1.570 (1.512–1.653)	1.570 (1.510–1.658)	

used to remove autocorrelation in the Monte Carlo Markov chains. We used the median of the posterior densities to estimate the parameters, and the distribution of the posterior densities to estimate parameter uncertainties 95% Bayesian credibility intervals (95% ci).

4.3. Quality of fit and validation

The three model resolution levels were compared using the Bayesian information criterion-Monte(Carlo), BICM (Raftery et al., 2007),

$$BICM = 2\hat{\mathcal{L}}_{\max} - N_{par} \times \log(N_{day} \times N_{tdr}) \quad (16)$$

where $\hat{\mathcal{L}}_{\max}$ is the maximum likelihood of the chains, N_{par} is the number of parameters, N_{day} the number of observation days, and N_{tdr} the number of TDR probe measurement. Prediction quality was

assessed by computing the root mean square errors of the predictions, RMSEP,

$$RMSEP = \sqrt{\frac{\sum_{t=1}^{N_{tube}N_{day}N_{tdr}} \sum_{d=1}^{N_{tube}} \sum_{l=1}^{N_{tdr}} (EW_{l,d}^t - \overline{EW}_{l,d}^t)^2}{N_{tube} \times N_{day} \times N_{tdr}}} \quad (17)$$

where $\overline{EW}_{l,d}^t$ is the mean of model predictions for the layer measured by the probe (from 10 cm above to 10 cm below the depth of the probe measurement).

We used EW values measured from the 1 January 2006 to 30 December 2006 for the validation (data not use in the calibration). The model was run using median values for parameter posterior densities of the parameters of the soil level model. We assigned to each 1 cm layer the median posterior density of the permanent wilting point and the field capacity of the nearest probe measurement point, from 1 to 29 cm depth. Each 1 cm layer was assigned

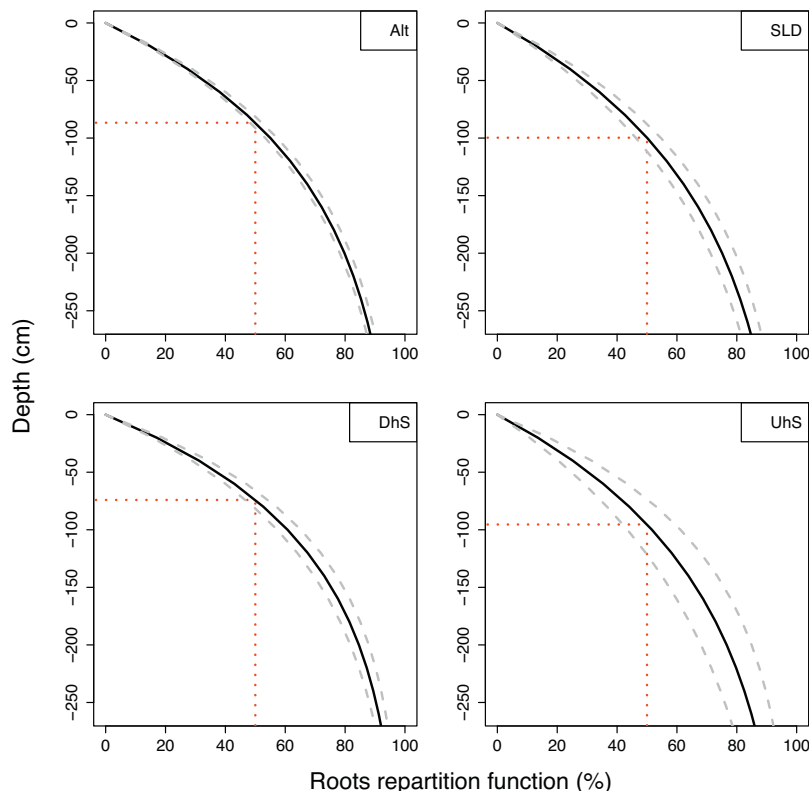


Fig. 2. Roots repartition function obtained for the soil level model M2 (Alt: alloterite at a depth of less than 1.2 m, SLD: superficial lateral drainage, DhS: downhill system, UHS: uphill system). Shown are the 95% Bayesian credibility intervals. Red dotted lines give the soil depths at 50% roots density. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

the permanent wilting point and field capacity given by the 20 cm depth TDR probe measurements, and from 30 to 49 the soil characteristics of the 40 cm depth TDR probe measurements. Predicted values of EW and REW were compared with measured values.

5. Results

5.1. Model resolution levels

The best resolution selected with the BICM was the forest level, $BICM = -4148.4$ (soil level, $BICM = -2066.7$; tube level, $BICM = -1250.0$). Extractable water RMSEP at all model resolutions ranged from 1.5 to 4.5% of water content, Table 4. With regard to the running soil level in M2, the RMSEP for Alt, SLD, DhS and UhS corresponded to 2.631, 3.176, 4.184 and 1.570 % of water content, respectively.

5.2. Parameters

5.2.1. Ratio ρ , tree transpiration/PET,

At all model resolution levels, i.e. tube (M1), soil (M2) or forest (M3), forest stand transpiration accounted for more than 98% of the PET. The median posterior density value of ρ for the forest model was 0.997 (95% ci = 0.986–0.999).

5.2.2. Root fine distribution parameter, λ_{Rfd}

Under non-stressed condition, water was extracted in all the soil layers, with a preference for the water contained in the upper layers, Fig. 2. Indeed, all the posterior values for root density parameter were between 0.005 and 0.01 ($\lambda_{Alt} = 0.0080 \pm (0.0076 - 0.0085)$, $\lambda_{SLD} = 0.0069 \pm (0.0062 - 0.0079)$, $\lambda_{DhS} = 0.0094 \pm (0.0085 - 0.0106)$, $\lambda_{UhS} = 0.0073 \pm (0.0057 - 0.0095)$, $\lambda_{Forest} = 0.0082 \pm (0.0079 - 0.0086)$). The higher the value of λ_{Rfd} the more shallow the rooting.

Values for root distribution parameters differed slightly between the soils. Alt, SLD, DhS and UhS soil had respectively 88.4%, 84.6%, 92.0% and 85.9 % of roots between 0 and 270 cm depth. Under non-stressed conditions, in the forest model, 25% of the transpiration was extracted in the horizons above 35 cm, 50% above 85 cm and 75% above 170 cm depth. Differences in root distributions in the forest model and soil model are given in Appendix E, Fig. E.1.

5.2.3. Permanent wilting point, θ_{PWP}

Median θ_{PWP} posterior density values ranged from 3.9 to 17.8% of volumetric water content in M2, Fig. 3. In Alt, SLD and UhS soil, θ_{PWP} slightly increased with depth and the θ_{PWP} profile showed smooth variations. DhS showed sharp θ_{PWP} variations from 80 to 240 cm depth, with high values for 80, 100, 120 and 240 cm in depth, i.e. 16.0, 17.3, 16.4 and 17.8% of volumetric water content, Fig. 3. Credibility intervals for all four soil types were stable above 120 cm and increased below 120 cm depth.

5.2.4. Field capacity, θ_{FC}

Median θ_{FC} posterior density values ranged from 10.4 to 24.4% of volumetric water content in M2, Fig. 3. The lowest values for estimated field capacity θ_{FC} were near 10% and the maximum value near 24% of water content. The estimated values were slightly higher below 1 m in depth. The θ_{FC} profiles correlated with the θ_{PWP} profile except for DhS between 60 and 160 cm. The credibility intervals showed small variations with depth. With the exception of soil DhS at a depth of 260 cm, all 95% credibility intervals were less than 2% of water content under or above the median value.

5.2.5. Extractable water EW

Soil extractable water profiles are given in Appendix F, Fig. F.1. The median EW value varied slightly with soil type. Median EW values ranged from 1.3% to 15.3% and correspond to extreme val-

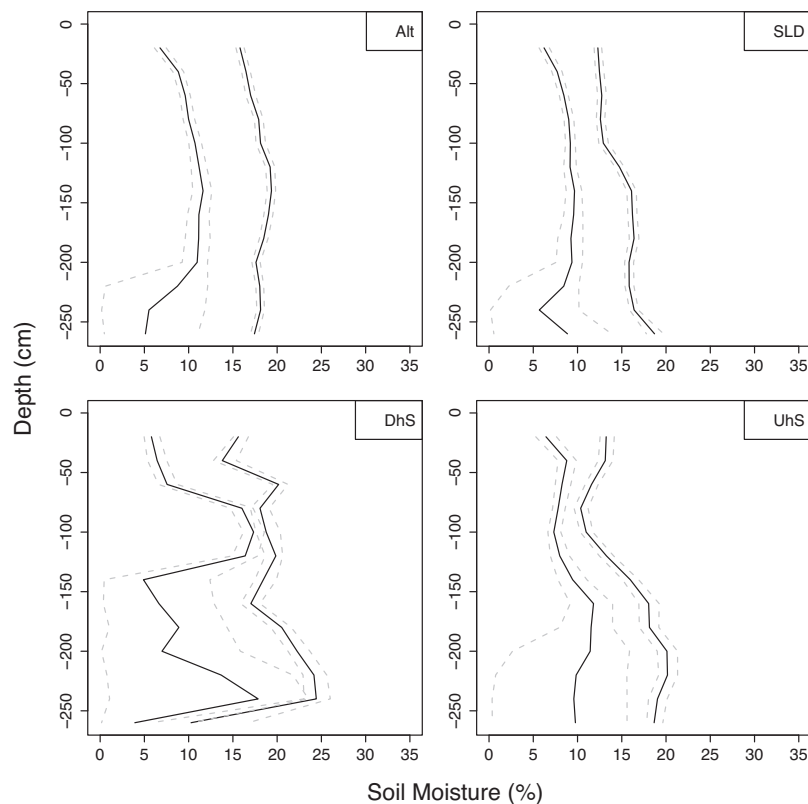


Fig. 3. Permanent wilting points and field capacities obtained for the soil level model M2 (Alt: allotrite at a depth of less than 1.2 m, SLD: superficial lateral drainage, DhS: downhill system, UhS: uphill system). Shown are the 95% Bayesian credibility intervals.

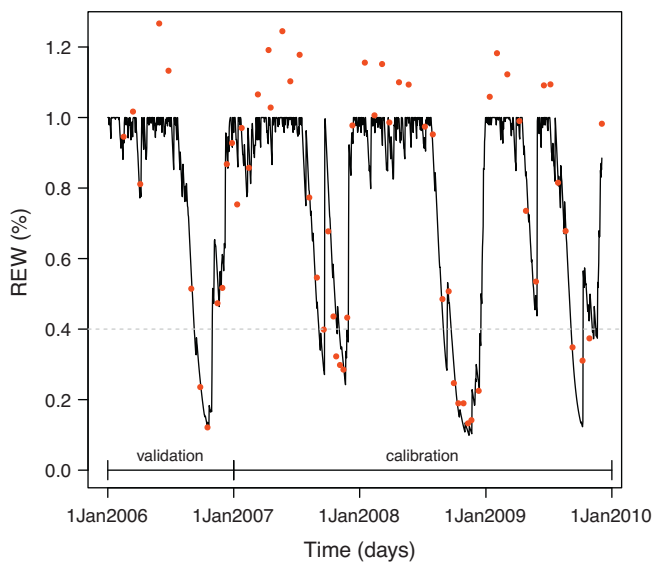


Fig. 4. Seasonal time course of predicted relative extractable water, *REW*, for 2006 (validation) and from 2007 to 2010 (calibration). The points are the observed values of *REW*.

ues for DhS soil. The *EW* profile may be described in three parts. First, a decrease in *EW* is observed in the first 100 cm. Second, from 100 to 200 cm, the *EW* profile and credibility interval remain stable or increase steadily with depth. Under 200 cm, all soils exhibited an increase in *EW* ($\geq 4\%$) coupled with a marked increase in the credibility interval.

5.3. Model validation

The model was run from 1 January 2006 to 30 December 2006 using the median posterior density values for M2 parameters. Uhs had the smaller RMSEP, 2.24% followed by Alt, SLD and DhS with a RMSEP of 5%, Appendix C, Table C.1. The model successfully reproduced the general trend seen for *REW* variations in 2006 (Fig. 4).

5.4. Variations in relative extractable water, *REW*

The model reproduced the general trend seen in soil water dynamics from 2006 to 2009, and this for all four soil types, Fig. 4. The model captured the start and end of the dry season. The two unusual events, 180 mm of rain during the dry season in September 2007, and the exceptional drought in the wet season of 2009 were also predicted by the model. In the wet season, the observed *REW* often took a value in excess of 1 whereas maximum *REW* in the model was 1. Agreement was very good between observed and predicted values of *REW*.

5.5. Relative extractable water and stem growth

REW fluctuations matched stem growth measurements in six dominant trees over the period between January 2008 and March 2009, Fig. 5. During the wet season, from January to mid-September, the trees showed different patterns of diameter growth. Four showed a decrease in diameter growth between March and June 2008. When *REW* become critical (≤ 0.4) between October and December, diameter growth ceased in all the trees.

6. Discussion

In this study we constructed a model of soil water balance for tropical forests and parameterized this model using a dataset col-

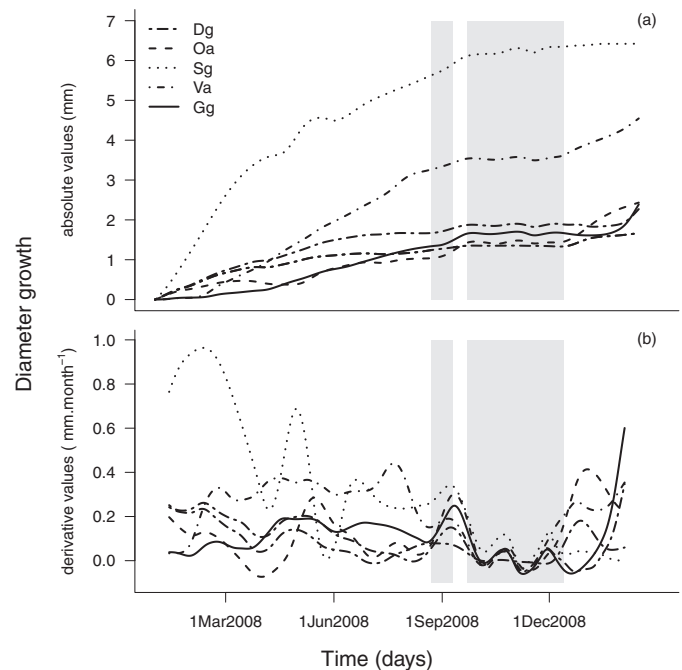


Fig. 5. Diameter growth series (a) and derivatives (b) of *Dicorynia guianensis* (Dg), *Oxandra asbeckii* (Oa), *Sloanea* sp (Sg), *Vouacapoua americana* (Va) and *Goupia glabra* (Gg). Grey font represents *REW* < 0.4

lected in Paracou, French Guiana. We then validated this model on an independent dataset from the same forest site. Extractable water is accurately predicted at the three levels of model resolution, i.e. TDR tube, soil type and forest stand, Table 4. At the soil level, RMSEP was always less than 4.2%. This is remarkable considering that precipitation is the only daily step data needed to run the model. Goodness of fit was unaffected by unusual events such as the exceptional rain event in September 2007 during the dry season (c. 180 mm) or the exceptionally dry period during the wet season in 2009, Fig. 4. However, we must acknowledge that the current model does not include porosity (deep drainage through macropores), lateral drainage, run-off, capillarity rise, or potential within-tree root redistribution of water. Our results suggest that these processes are of secondary importance in the accurate prediction of soil water content from our data. Whether they might be needed in other tropical forest sites with different topographic variability, soil properties and rainfall regimes is a worthy question that we intend to test in the near future.

Tree transpiration (*Tr*) accounts for the largest part of ecosystem evapotranspiration (*PET*). At the Paracou forest site, Granier et al. (1996), working in the dry season of 1991, determined the ratio $\rho = Tr/PET$ at 0.75 and observed that this increased up to 0.80–0.85 after a 25 mm rain event. However, other water balance models (e.g. Markewitz et al., 2010) often assume that no soil surface evaporation takes place and that ecosystem evapotranspiration is solely due to tree transpiration. In line with the latter study, we estimated *Tr/PET* at 99.7%. This high value may also suggest that we underestimated the water leaving the soil system by lateral and deep drainage. Indeed, some studies report cases where water drains below a given soil layer even though this layer has not reached field capacity (Grimaldi and Boulet, 1989–1990). This process is related to soil porosity, a parameter not taken into account in our model. Including it would greatly increase model complexity as the pores differ in nature and dimensions in the soil layers in our neotropical forest (Grimaldi and Boulet, 1989–1990). Our results nevertheless show that soil porosity is not really needed to accurately simulate soil water content, although its absence prevents us from using the model to simulate *PET*.

We made the major assumption that soil root density decreases exponentially with depth, and from this we computed the percentage of tree transpiration extracted by the roots from each soil layer. Model predictions suggest that this new approach to modeling root distribution in soil water models is efficient. This manner of modeling root distribution also offers the opportunity to predict the amount of water extracted below the last TDR measurement point, an estimate that is often neglected (Nepstad et al., 2004; Granier et al., 2007). The water extracted at 270 cm ranged from 8 to 15% under non-stressed condition, Fig. 2, consistent with Bonal et al. (2000). However, the water extracted below 250 cm at two other Amazonian sites was estimated to be ca. 30% Markewitz et al. (2010). The difference may be due to differences in root distributions or in soil drainage which is greater at the Tapajós research site over the first 3 m than at Paracou (Guehl, 1984; Belk et al., 2007). We estimated REW by explicitly taking account of root density distribution in the soil, Eq. (9), offering the advantage of limiting the weight of the deep layers full of water that contain a negligible proportion of total roots.

Estimated permanent wilting point values are consistent with those obtained for the 0 to 160 cm soil layers in French Guiana by Guehl (1984), ranging from 10 to ca. 15%. As modeled using our DhS soil data, Guehl (1984) registered some profiles of θ_{PWP} exhibiting sharp permanent wilting point variations in less than 40 cm of soil (see Fig. 3). These variations can be explained by a red clay alloterite horizon with very different soil properties (Sabatier et al., 1997). No field measures of field capacities (θ_{FC}) have yet been made of French Guianan soils for comparisons with our estimates (from 3 to 15% of water content). But at two other tropical sites where a long-term tree growth census has been established, Barro Colorado Island (BCI, Panama) and La Selva (Costa Rica), available water capacities reported by Kursar et al. (2005) range respectively from 12 to 29% and 3 to 15% for the upper soil layers (<0.5 m depth). With regard to permanent wilting point, DhS soil showed an uncommon profile. Estimated available water capacity was less than 3% between 80 and 120 cm. This may be explained by a temporarily waterlogged watertable during the rainy season. The presence of this watertable led to no change in the water content of these soil layers, which in turn led to an extremely low extractable water value.

We adapted a Bayesian numerical method to infer model parameters, permanent wilting point θ_{PWP} and field capacity θ_{FC} , using only soil water content values obtained from a TDR probe and a mechanistic model of forest functioning. The first novelty of our approach is that θ_{PWP} and θ_{FC} estimations are entirely data driven. We believe that our approach is more realistic than previous models because we explicitly model water extraction by the forest ecosystem and we do not infer parameter values from soil water content measured at a fixed pressure commonly assumed to be less than -1.5 MPa. Kursar et al. (2009) have shown that drought tolerance differs widely for seedlings of 20 species from central Panama, and Tyree et al. (2003) determined that many woody species tolerate far lower θ_{PWP} . If we consider that each tree species has different and independent sensitivities to θ_{PWP} and θ_{FC} , the values we estimated can be interpreted as averaged θ_{PWP} and θ_{FC} at the forest ecosystem level. Uncertainties in θ_{PWP} and θ_{FC} estimates are explicitly assessed during the calibration procedure using the Bayesian framework we developed. These uncertainties are far more difficult to assess when pedotransfer functions are used, as no standard method is available (Brimelow et al., 2010).

Despite average rainfall of ca. 3000 mm per year, the Paracou site is subject to a 3-month dry season during which rainfall is less than 50 mm per month (Bonal et al., 2008). In 2006 and 2008, REW decreased to below 0.2 during this dry season, Fig. 4. In temperate forests, a REW value of 0.4 (Granier et al., 2007) has been considered as the limit below which trees experience major physiological stress. In a 1-year growth dataset obtained from the Paracou site we

also observed that diameter increments stopped when $REW < 0.4$, Fig. 5. If we apply this threshold, it is evident that the potential period of tree water stress shows marked inter-annual variability, Fig. 4, from 1.5 months in 2007 and 2009 to 3.0 months in 2008. The consequences of this interannual variability on tree functioning, growth and mortality remain to be investigated (but see Fig. 5). Near future measurements of leaf gas exchange and water potential will be used to test whether the 0.4 threshold also characterizes a significant step in leaf gas exchange. Interestingly, we noted a period of drought during the 2009 wet season with exceptionally low rainfall in May (7.2 mm d^{-1} instead of 16.6 mm d^{-1} for the 10-year average), and this led to an exceptional reduction in soil water content.

During wet seasons, an observed REW value greater than 1 is relatively frequent (Fig. 4) while the maximum predicted REW from our model remains 1 because estimated deep drainage is instantaneous and incoming water exceeding the field capacity is excluded at the daily time step. In other words, soil water content cannot mechanically exceed field capacity in the model. For most soil types during heavy rains, the model therefore does not predict reality. Moreover, lateral drainage events have been observed during heavy rains along hill slopes (Gourlet-Fleury et al., 2004) and so our model may underestimate the water entering the soil along slopes (Daws et al., 2002; Sabatier et al., 1997). Further research should improve these components of the model to take account of wet season conditions in downhill and bottomland systems.

7. Conclusions

In this study we developed, calibrated and validated a daily soil water balance model for use in tropical forests. Precipitation is the only data required with daily precision. The model works with few parameters, most of which are available in the specialized literature. We put forward a novel method to estimate the remaining site-specific parameters, θ_{FC} , θ_{PWP} and λ_{Rfd} , using TDR data only, which should facilitate calibration in other tropical forest sites. The use of a Bayesian framework is a major improvement in the modeling of soil water balance for several reasons. First, it enables us to estimate permanent wilting point (θ_{PWP}), field capacity (θ_{FC}) and their uncertainties by modeling water actually extracted by the roots (not by inferring their values by field measurements). Second, it offers the possibility to infer hierarchical models, e.g. when model parameters are estimated at different levels of integration, such as forest stand/soil types/TDR tubes. The major output of this model is soil REW , which may be the most appropriate metric for long-term analyses of tropical forest dynamics under different climatic situations. We believe the model will prove useful in deciphering the relative impact of past environmental and climatic conditions on tree growth and mortality and to explore the expected consequences on tropical forest dynamics of currently simulated future climate scenarios (IPCC, 2007).

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Appendix A. Soil drainage and characteristics, algorithm details

The model of daily water dynamics may be summed up by the following scheme:

For the top soil layer, if $Th_d \geq 0$:

$$W_{1,d} = Th_d \quad (A.1)$$

where $W_{1,d}$ is the water entering the top layer on day d . Water fills the top layer and extractable water before vegetation uptake (\widehat{EW}) is computed as follows:

$$\text{if } W_{1,d} > EW_1^{\max} - \widehat{EW}_{1,d-1} \begin{cases} W_{2,d} = W_{1,d} - (EW_1^{\max} - \widehat{EW}_{1,d}) \\ \widehat{EW}_{1,d} = EW_1^{\max} \end{cases} \quad (A.2)$$

$$\text{if } W_{1,d} < EW_1^{\max} - \widehat{EW}_{1,d-1} \begin{cases} W_{2,d} = 0 \\ \widehat{EW}_{1,d} = \widehat{EW}_{1,d-1} + W_{1,d} \end{cases} \quad (A.3)$$

While $W_{l,d} > 0$ the same process is used to fill the next layers. If any water remains after the last layer (N_{layer}), this is considered to be lost by deep drainage (Dr):

$$\text{if } W_{N_{layer}+1,d} > 0, Dr_d = W_{N_{layer}+1,d} \quad (A.4)$$

Once the water has infiltrated, part of the extractable water is absorbed by trees, and soil plus understorey evapotranspiration.

$$\widehat{EW}_{l,d} = \widehat{EW}_{l,d} - Tr_{l,d} - Eu_{l,d} \quad (A.5)$$

where $\widehat{EW}_{l,d}$ denotes extractable water, $Tr_{l,d}$ denotes tree transpiration and $Eu_{l,d}$ denotes understorey plus soil evapotranspiration, for layer l on day d .

Appendix B. Metropolis Hastings within Gibbs

Before running the algorithm, the first values of the vector of parameters are initialized.

$$\Theta^0 = \{\theta_1^0, \dots, \theta_{Npar}^0\} \quad (B.1)$$

where Θ is the vector of parameters θ and $Npar$ the number of parameters.

Then the Metropolis Hastings within Gibbs works in several steps. We give an example for an iteration n and the k th parameters of the vector of parameters.

Generation of a candidate θ_k^* and the new vector of parameters Θ^* :

$$\theta_k^* \sim \pi_{\theta}^{prop}(\theta_k^{n-1}) \quad (B.2)$$

$$\Theta^* = \{\theta_1^{n-1}, \dots, \theta_{k-1}^{n-1}, \theta_k^*, \theta_{k+1}^{n-1}, \dots, \theta_{Npar}^{n-1}\} \quad (B.3)$$

where θ_k^* is a random generation from the proposal distribution π_{θ}^{prop} which depends on θ_k^{n-1} .

Acceptation or rejection of the new candidate θ_k^* by computing the ratio of the likelihood:

$$\gamma = \underbrace{\frac{\mathcal{L}(\text{Data}|\Theta^*)}{\mathcal{L}(\text{Data}|\Theta^{n-1})}}_{\text{likelihood}} \times \underbrace{\frac{\pi_0(\theta_k^*)}{\pi_0(\theta_k^{n-1})}}_{\text{prior}} \times \underbrace{\frac{\pi_{\theta}^{prop}(\theta_k^{n-1}|\theta_k^*)}{\pi_{\theta}^{prop}(\theta_k^*|\theta_k^{n-1})}}_{\text{proposal}} \wedge 1 \quad (B.4)$$

The candidate θ_k^* is accepted or rejected as follows:

$$u^t \sim \mathcal{U}[0,1], \quad \theta_k^* \begin{cases} \theta_k^* & \text{if } \gamma \geq u^t \\ \theta_k^{n-1} & \text{if } \gamma < u^t \end{cases} \quad (B.5)$$

Proposal distribution of the forest level model, M3. The same distribution were use for M1 and M2. Here we give the proposal distribution and boundaries of the distribution.

$$\pi_{\rho}^{prop} = \mathcal{N}_T(\rho^{t-1}, 0.008); \text{ truncated on } [0, 100] \quad (B.6)$$

$$\pi_{\lambda_{Rfd}}^{prop} = \mathcal{N}_T(\lambda_{Rfd}^{t-1}, 0.001); [0, 10] \quad (B.7)$$

$$\pi_{\theta_{PWP;l,\dots,N_{layer}}}^{prop} = \mathcal{N}_T(\theta_{PWP;l,\dots,N_{layer}}^{t-1}, 0.003); [0, \theta_{FC;l,\dots,N_{layer}}^{t-1}] \quad (B.8)$$

$$\pi_{\theta_{FC;l,\dots,N_{layer}}}^{prop} = \mathcal{N}_T(\theta_{FC;l,\dots,N_{layer}}^{t-1}, 0.003); [\theta_{PWP;l,\dots,N_{layer}}^t, 1] \quad (B.9)$$

Appendix C. Quality of the soil level model's predictions

See Table C.1.

Table C.1

Root Mean Square Error of Prediction (RMSEP) between observed and predicted values of extractable water obtained using the soil level model M2 with the validation dataset (year 2006).

Soil	Tube	RMSEP
Alt	1	2.92
Alt	2	2.97
Alt	4	3.25
Alt	13	3.51
SLD	5	4.11
SLD	9	3.61
SLD	18	3.37
DhS	7	4.00
DhS	19	5.00
UHS	16	2.24

Appendix D. Nested structure of the model

See Fig. D.1.

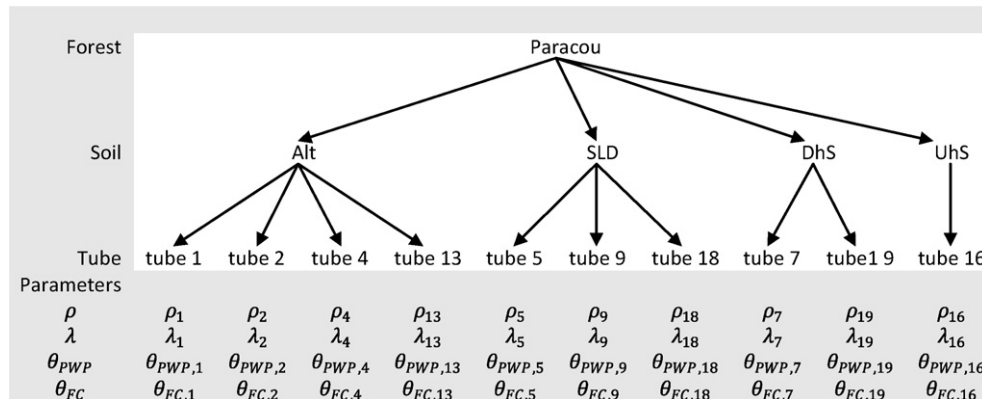


Fig. D.1. Nested structure of the model. M1, tube level: $\rho_1 = \rho_2 = \dots = \rho_{16}$; M2, soil level: $\rho_1 = \rho_2 = \dots = \rho_{16}$, $\lambda_1 = \lambda_2 = \lambda_4 = \lambda_{13}$, $\lambda_5 = \lambda_9 = \lambda_{18}$, $\lambda_7 = \lambda_{19}$, $\theta_{PWP,1} = \theta_{PWP,2} = \theta_{PWP,4} = \theta_{PWP,13}$, $\theta_{PWP,5} = \theta_{PWP,9} = \theta_{PWP,18}$, $\theta_{PWP,7} = \theta_{PWP,19}$, $\theta_{FC,1} = \theta_{FC,2} = \theta_{FC,4} = \theta_{FC,13}$, $\theta_{FC,5} = \theta_{FC,9} = \theta_{PWP,18}$, $\theta_{FC,7} = \theta_{FC,19}$; M3, forest model: $\rho_1 = \rho_2 = \dots = \rho_{16}$, $\lambda_1 = \lambda_2 = \dots = \lambda_{16}$, $\theta_{PWP,1} = \theta_{PWP,2} = \dots = \theta_{PWP,16}$, $\theta_{FC,1} = \theta_{FC,2} = \dots = \theta_{FC,16}$; Alt: alloterite at a depth of less than 1.2 m, SLD: superficial lateral drainage, DhS: downhill system, UHS: uphill system.

Appendix E. Difference of roots repartition function

See Fig. E.1.

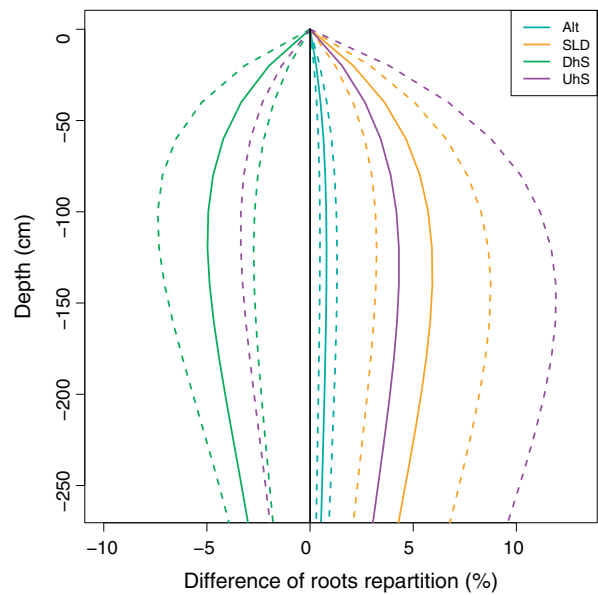


Fig. E.1. Difference of roots repartition function between the forest level model (M3, the plain vertical line) and the soil level model (M2, Alt: alloterite at a depth of less than 1.2 m, SLD: superficial lateral drainage, DhS: downhill system, UhS: uphill system). Shown are the Bayesian 95% credibility intervals.

Appendix F. Examples of extractable water profiles

See Fig. F.1.

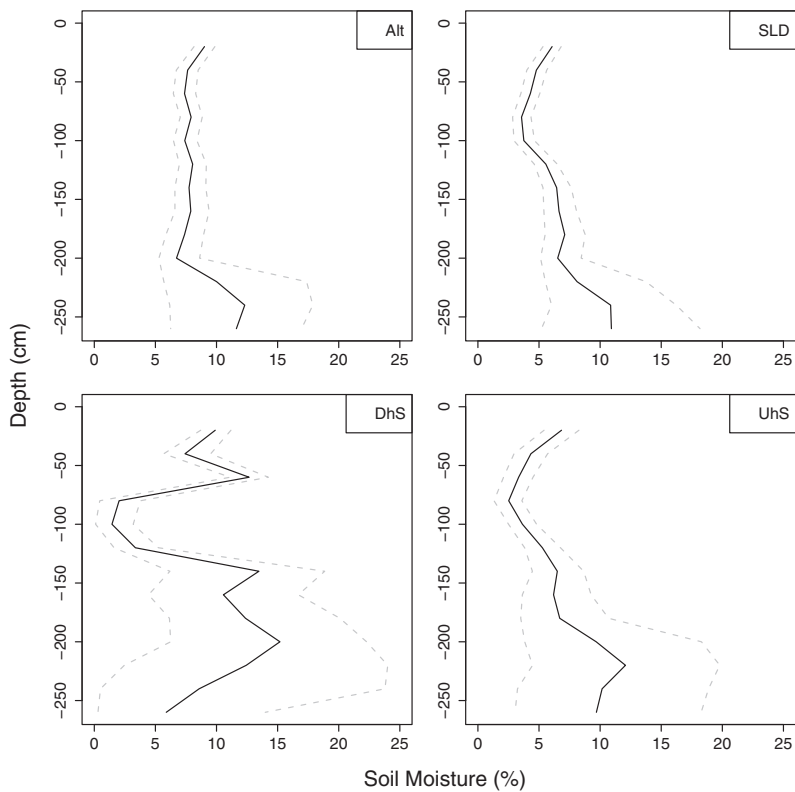


Fig. F.1. Profiles of extractable water obtained for the soil level model M2 (Alt: alloterite at a depth of less than 1.2 m, SLD: superficial lateral drainage, DhS: downhill system, UhS: uphill system). Shown are the 95% Bayesian credibility intervals.

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2 L'eau disponible dans le sol est le facteur climatique déterminant de la croissance des arbres neotropicaux

Après être parvenu à modéliser l'eau disponible pour les arbres à Paracou, nous avons analysé l'effet de cette variable, ainsi que des autres variables climatiques mesurées à un pas de temps journalier par la tour à flux du dispositif Guyaflux, sur la croissance des arbres. La plupart des dispositifs tropicaux de suivis forestiers actifs dans le monde ont des intervalles de mesures de croissance diamétrique compris entre 2 et 5 ans (Clark, 2007a). Ces données à un pas de temps pluriannuel ne permettent pas une analyse fine des variations de croissance en fonction des variations journalières/saisonnnières du climat. A Paracou, nous disposons d'un jeu de données unique pour analyser la croissance à un pas de temps fin. Les mesures de croissance de 205 arbres mesurés environ tous les 40 jours depuis 2007 avec des dendromètres dont l'erreur de mesure est inférieure à 1 mm (Stahl *et al.*, 2010). Ces données ont été mises en regard des variables climatiques avec une méthodologie statistique appropriée permettant de relier des données climatiques journalières à des croissances mesurées sur une période de plusieurs jours. Nous avons pu mettre en évidence qu'à Paracou, le climat expliquait un peu moins de 10% de la variance de la croissance, et que le déterminant climatique principal de la croissance était la disponibilité en eau. L'effet fixe de la période de mesure peut être expliqué à plus de 80% par une combinaison de 4 variables climatiques, la disponibilité en eau, la température minimale, l'irradiance et la vitesse du vent. Cette analyse permet d'expliquer les arrêts de la croissance en saison sèche mais les facteurs responsables des variations de la croissance en saison des pluies restent encore à déterminer. Ce travail est présenté dans la publication ci-après, Wagner *et al.* (soumis).

Water availability is the main climatic driver of neotropical tree growth

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Abstract

- Climate models predicted rainfall reduction in amazonian region, inducing change in water availability for trees
- Results are presented from 23 yrs of annually or bis-annually growth measurements in the forest of Paracou and the simulated daily tree water availability for this period at the site. We focused on the statistical analysis of water availability effect on tree growth through a Bayesian framework.
- Our model developed indicates that tree growth was affected by annual water availability for most of the species. Tree species have different strategies and sensibilities first, second. These strategies are linked to functional traits particularly. the remaining part of unexplained variance, c.40% may be attributed to leaf flushing phenology individual history or genetic.
- These result suggest that annual dry season have a large impact on annual tree growth and if rainfall reduction would be confirmed, tree growth will be affected

Author Summary

Introduction

Tropical forests are being threatened at an unprecedented scale by global change. The Amazon region has already experienced severe droughts recently such as in 1998 and 2005. Temperatures across Amazonia are currently increasing [1] and are expected to continue to increase with a concomitant decrease in precipitation over the next decades [2]. The HadCM3 model under updated emissions scenarios predicts severe drying events over Amazonia for the XXIth century [3,4]. Climate changes in the tropics have become an increasing concern for their potential impacts on the global carbon cycle. Indeed, tropical forests represent a major reservoir of the terrestrial carbon, accounting for half of the estimated 558 Pg of carbon stored in the vegetation [5] with 86 Pg for the Amazon basin alone [6]. Most current studies performed in tropical rain forest have highlighted three major climate drivers of forest dynamics: (i) water availability, (ii) solar irradiance and (iii) air temperature. (i) Rain or lack of rain is often implicitly viewed as the main driver of forest dynamics [7], highlighting that annual NPP generally correlates with annual amount of precipitation [8] and that rainfall seasonality plays a key role in the forest response to climate variability [9]. The relation between amount of rainfall and water availability for trees is not straightforward and determined by various soil and plant characteristics (permanent wilting point, field capacity, root distribution). Consequently, water stresses are increasingly estimated using Soil Water Balance Models [10], among which are now available some models explicitly designed for tropical forests [11]. (ii) Irradiance is obviously directly linked to the plant photosynthetic ability

through the PPFD (Photosynthetic Photon Flux Density), in turn driving carbon uptake and plant growth [12]. Through Amazonia, the occurrence of the dry season, through cloud cover reduction, was found to enhance by 25% the canopy photosynthetic capacity [13]. (iii) The effects of rising temperature on the physiology of tropical forest trees are actively debated through the scientific communities and some works suggest that although reductions in photosynthetic rate at above 30°C temperatures may occur, these are driven by reductions in stomatal conductance in response to higher leaf-to-air vapour pressure deficits [14]. Recent studies however suggest that tropical tree mortality increases significantly with increasing night-time temperature while tree growth appears surprisingly sensitive to variations in mean annual night-time temperature of 1-2°C [15]. In order to predict the potential consequences on tropical forest dynamics of currently simulated future climate scenarios (IPCC 2007), the challenge is now to rank the climate drivers and to include these drivers into forest dynamic models. With this perspective, large and long-term inventory plots with regular tree census are needed to account for variation in individual growth and in climate patterns [16]. The problem is that most of these long-term studied forests are not adapted to evaluate the climate change impacts because of multi-year census intervals [15], thus impeding our ability to compare the years with each other and to study the effect of climate seasonality. In this paper, we use of a unique dataset where bimestrial measurements of tree growth have been recorded on 205 individual trees from 54 neotropical species over a 4-year period. This paper has three objectives: (i) to find a way to include the climate variables into tree growth models when growth and climate records are not made at the same time step (ii) to quantify the proportion of observed variance in tree growth that is attributable to climatic variations, (iii) to identify (and rank) the climatic variables that most affect tree growth.

Results

Growth models with asynchronous climate and growth data

We normalized the data, growth and climate variables, by the square root of the number of days of the record periods (see method section for details). Hence we could model the link between these normalized data by linear regression. We built several models to support our analyses (i) model m_0 integrating a factorial effect *period* to assess the percentage of variance in tree growth explained by all the environmental fluctuations; (ii) univariate models $m_{varclim}$, for $varclim=REW, W, T^-, T^+, I, VPD, Patm, HR$ or Pr to assess the percentage of variance in tree growth explained by each climate variable (iii) a multivariate model, m_{BIC} , to assess the percentage of variance in tree growth explained by the best combination of variables.

Proprtion of variance in tree growth explained by climatic variation

The period effect (model m_0) explained 9 % of the tree growth variance. This means climatic variables can explain a maximum 9 % of the variance of tree growth without interactions. The tree individual effect explained 26.2 % of the tree growth variance in all the model. Remaining 64.8 % of tree growth variance can not be explain by tree effect or climatic variables effects.

Ranking of climate variables according their effects on tree growth

From the univariate analysis, REW explained a large part of the period effect on tree growth (60.0%). rainfall, wind speed, air relative humidity, atmospheric pressure, minimum temperature explained between 42.2 and 36.1 % of this period effect (respectively 42.2, 40.8, 40.5, 37.9 and 36.1). Maximum temperature, VPD and irradiance explained less than 25.7 % of period effect on the variance of growth (respectively 25.7, 5.6 and 3.8).

With the exception of atmospheric pressure, all the climatic variables were correlated above 45 % at least with one other climatic variable, Fig. 1). Minimum temperature and wind speed are moderately correlated with the other variables. Maximal temperature was well positively correlated with irradiance. Rainfall, relative extractable water and relative humidity are negatively correlated with irradiance, vapour pressure deficit and maximum temperature. The correlation circle of the PCA highlight these patterns of correlation. The first three PCA axes explained 75.9 % of the climatic daily data variance.

The first axis explained 46.7 % of the variance in the climatic data and was positively correlated with relative humidity, rainfall and REW and negatively correlated to VPD, irradiance and maximum daily temperature. The second axis explained an additional 17.4 % of variance and was positively correlated with the wind speed, minimum temperature and maximum temperature. The third axis explained a further 11.8 % of the variance and was correlated only to atmospheric pressure.

The selection procedure on the BIC kept 4 variables in the model, individual tree effect, REW, wind speed, minimum temperature and irradiance, Table 2. Proportion variance explained by each variable and parameters cannot be interpreted in the m_{BIC} model due to interaction between the climatic variables. In univariate analysis, all climatic variables have positive parameters indicating a positive effects on tree growth.

The variance of the period effect on tree growth is well explained by the climatic variables of the model m_{BIC} , 80,1 % Fig. 2.

The pattern of mean daily diameter growth have a annual frequency, Fig. 3. Diameter growth show similar patterns as REW. First, in drought season when REW decreased below 0.4, mean diameter are the smallest of the year and sometimes stopped. Second, in the start of wet season, REW and tree growth increased simultaneously. Tree growth and REW don't have the same pattern in the middle and at the end of dry season where tree growth decreased before water availability.

Prediction of the selected model

The model fail to accurately predict the growth on the c. 60 days period with a RMSEP above the mean value of growth (mean growth = $0.02630624 \text{ mm.d}^{-1}$, RMSEP = $0.03504464 \text{ mm.d}^{-1}$). The model overestimated the growth under 0.05 mm.d^{-1} and underestimated the growth above 0.1 mm.d^{-1} , Fig. 4.

Discussion

In this study we showed that no more than 9% of the observed variation in individual tree growth was attributable to fine-scale climate variations and demonstrated that water availability was the main driver of tree growth in our dataset. The individual behavior of each tree explained 26.4% of growth variation and a substantial fraction of variation in growth remains unexplained with our model. Tree growth is influenced by several non-investigated additional environmental variables (topography, light availability, etc.) and also by the unique individual history that depends on complex environmental changes occurring during the 4-year census period [17].

0.1 Soil water availability effects on tree growth

Water availability directly impacts productivity as observed in seasonal tropical forests [18,19] and as deduced from experimental forest droughts [20,21]. Our study where tree growth was linked to water availability at a daily time scale confirm some earlier studies performed at an annual scale [8,22]. In dry seasons, defined as successive months with less than 100mm [23], most trees diminish or stop their diameter growth, as previously reported for 6 dominant trees at Paracou [11]. The Paracou forest has experienced strong dry seasons during the experiment time with several months with precipitation $< 50 \text{ mm.month}^{-1}$ ($0\text{-}4 \text{ month.year}^{-1}$). During these events, the amount of available water was always below

the potential evapotranspiration which never falls below $100 \text{ mm.month}^{-1}$ in Paracou [24]. This water limitation may solely explain this slowdown of girth increment, as reported in many seasonal tropical forests [19]. However, even under strong water limitation, trees seem to be able to maintain their baseline functioning, with only a slight decrease in gross ecosystem productivity measured by a flux tower located in the Paracou forest [23]. Finally, [25] highlighted a shrinkage of stems during dry seasons. Deciphering the relative importance of shrinkage and/or decrease in diameter growth in dry seasons is beyond the scope of this work and supplementary in situ experiments are needed. During the early wet season, the strongest growth increments occurred (see Figure 4). The same pattern has already been observed at la selva leading [15] to conclude to a strong link between growth and rainfall. However we still not known whether this increment is due to sapwood growth, bark swelling or both [25]. Nutrient availability at the start of the rain season may also explain the swift diameter increment at the start of the rainy, a large pool of nutrients becoming available for trees with the first rainfall events [26].

0.2 Temperature effects on tree growth

Effect of rising temperature on the physiology of tropical forest trees are actively debated through the scientific communities [14, 27, 28]. In French Guiana, the increase mean temperature follows the general trend of Amazonia, $0.26 \pm 0.05^\circ\text{C}$ per decade [1, 29]. This increase is driven by the minimum temperatures (data not shown). Temperature variations were found to be of secondary importance at a daily time-scale. The minimal daily temperature was slightly associated with tree growth (Fig. 2) whereas maximal temperature has no effect. This is not consistent with the result of [15] who highlighted that annual growth appears sensitive to variations in mean annual night-time temperature of $1\text{-}2^\circ$. At la selva, the climate is near a-seasonal with no strong dry season. Tree diameter increment never really stopped and the night-time temperature seems to be a proxy of drought, the census with the strongest dry season being the census with the highest mean annual night-time temperature [15, 30]. In our study, we found that this seasonal effect is mostly captured by the water availability.

0.3 Irradiance effect

Amongst the climatic variables, irradiance has the smallest effect on tree growth (Fig 2). Primary production seems limited by irradiance in the Paracou forest but the critical level where irradiance becomes limiting is rarely attained ([23]). Irradiance is obviously directly linked to the plant photosynthetic ability through the PPFD (Photosynthetic Photon Flux Density), in turn driving carbon uptake and plant growth ([12]). In the final model selected by BIC, irradiance have a surprising negative effect on growth. In fact, the model used irradiance to lower growth during the strongest dry seasons. These extreme slowdowns of tree growth may be linked to the leaf fall phenology mediated by high irradiance events. In the same forest, [23] showed that the peak of litter production starts before the onset of the dry season and is at its maximum when irradiance was the highest. In French Guyana, [31] had observed that 58 of 92 tree species undergo a leaf fall in july (peak of irradiance), even if some species exhibit several periods without any leaves during the year. And throughout the Amazonian basin, irradiance has been previously reported to be the main determinant of leaf fall timing in aseasonal [32] as well as in seasonal rainforests [33, 34].

0.4 Conclusions

Globally, current IPCC scenarios predict an intensification of the dry season for the Guiana shield (IPCC 2007) during the XXI century. Our results suggest that, at least at the Paracou forest site, neotropical trees are acclimated to variable dry seasons. This dry season leads to an effective decrease in stem diameter growth but hardly affect the global annual tree growth that appears more dependent on the increment at the onset of the rain season than of the duration of dry season. In other words, six or nine

month of rain season seems to be equivalent as the highest increments occur in the first weeks of the wet season. In this context, we cannot rule out that a moderate dry season intensification will not affect average annual tree growth.

Materials and Methods

0.5 Study site

The study site is located in Paracou, French Guiana (50° 18' N, 52° 55' W), a lowland tropical rain forest near Sinnamary [35]. The climate is affected by the north/south movements of the Inter-Tropical Convergence Zone and the site receives nearly two-thirds of its annual 3041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month in September and October. The most common soils in Paracou are the shallow ferralitic soils limited in depth by a more or less transformed loamy saprolite (Gourlet-Fleury et al. 2004). The site is located approximately 40 m above sea level [35] and is made up of a succession of small hills. The forest is typical of Guianan rainforests [36]. More than 550 woody species attaining 2 cm DBH (Diameter at Breast Height, i.e. 130 cm) have been described at the site, with an estimated 160-180 species of trees > 10 cm DBH per hectare. The dominant families at the site include Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae.

0.6 Data

0.6.1 Growth measurements

Seasonal changes in trunk circumference were monitored in 205 trees from 54 species using home-made steel dendrometer bands in the Paracou site [25]. Tree growth was censused every c. 40 days from 2007 to 2010 (mean=39, sd=19.8).

0.6.2 Meteorological follow-up

In 2003, a 55 m self-supporting metallic eddy covariance flux tower, Gyaflux, was built in the Paracou forest in a natural 100 m² gap, with minimal disturbance to the upper canopy. This location covers a range of more than 1 km of forest in the direction of the prevailing winds. The top of the tower is about 20 m higher than the overall canopy and meteorological and eddy flux sensors are mounted 3 m above the tower. Full details on tower sensors are given in [23]. Description of climatic variables is given Table 1 and Fig. 5.

A soil water balance model was developed and validated for the forest of Paracou [11]. The model computes daily water fluxes (tree transpiration, understorey evapotranspiration, rainfall interception and drainage), soil water content at different layers and relative extractable water for trees for the entire soil (*REW*). *REW* is a daily value between 0 and 1, when *REW* = 1 the amount of extractable water by the tree is at its maximum and, when *REW* = 0, no water is available for trees. To investigate the association between daily climatic variables, we performed principle component analysis (PCA) on the normalized climatic dataset.

0.7 Including climate variables in growth models Data with asynchronous data

We modeled the link between tree growth and climate with linear regression. We set a factorial variable *tree* in all the models built to take into account the individual behaviors of tree growth. This individual effect was not analyzed because that was not the point of this study, we just took it into account to not bias results. First we built a reference model, m_0 , that explained the maximum variance of growth on

our data. Then we set a factorial variable *period* which integrates all the temporals effects. To handle properly that the periods had a different number of days, we had to consider a daily trees growth model:

$$Dbh_{i,d+1} - Dbh_{i,d} = tree_i + day_d + \epsilon_{i,d} \quad \text{with } \epsilon_{i,d} \sim \mathcal{N}(0, \sigma^2) \quad (1)$$

where $Dbh_{i,d}$ is the diameter at breast height for tree i the day d , $tree_i$ is the effect *tree* on growth for the tree i for one day, day_d is the effect of the day d on growth for all the trees and $\epsilon_{i,d}$ is the error of the model assumed normal. The periods consisted the successive days between two Dbh measures. The growth for the tree i over the period j starting the day d and during nd_j days was provided by summing nd_j times equations (1):

$$\underbrace{DBH_{i,d+nd_j} - DBH_{i,d}}_{Gr_{i,j}} = nd_j \times tree_i + \underbrace{day_d + \dots + day_{d+nd_j-1}}_{period_j} + \underbrace{\epsilon_{i,d} + \dots + \epsilon_{i,d+nd_j-1}}_{\tilde{\epsilon}_{i,j}} \quad (2)$$

The equation (2) simplified:

$$Gr_{i,j} = nd_j \times tree_i + period_j + \tilde{\epsilon}_{i,j} \quad \text{with } \tilde{\epsilon}_{i,j} \sim \mathcal{N}(0, nd_j \sigma^2) \quad (3)$$

where $Gr_{i,j}$ is the growth of tree i over the period j , $period_j$ is the effect *period* for period j , nd_j is the number of days of period j and $\tilde{\epsilon}_{i,j}$ is the error of the model assumed normal. The model (3) was not adapted to classical linear regression because the variances of the error terms changed over the periods. We normalized the equation (3) to get residual error variance equality, which led to the model m_0 :

$$\frac{Gr_{i,j}}{\sqrt{nd_j}} = \sqrt{nd_j} \times tree_i + \frac{period_j}{\sqrt{nd_j}} + \varepsilon_{i,j} \quad \text{with } \varepsilon_{i,j} \sim \mathcal{N}(0, \sigma^2) \quad (4)$$

where $\varepsilon_{i,j} = \tilde{\epsilon}_{i,j} / \sqrt{nd_j}$ and $Var(\varepsilon_{i,j}) = Var(\tilde{\epsilon}_{i,j}) / nd_j = \sigma^2$.

0.8 Ranking climate variables according their effect on tree growth

We assessed the capability of climate variables to explain the variance of growth by substituting them to the effect *period* in the model m_0 . First, we performed univariate analysis for each of the climate variable by considering the models $m_{varclim}$, for $varclim = REW, W, T^-, T^+, I, VPD, Patm, HR$ or Pr , defined by :

$$\frac{Gr_{i,j}}{\sqrt{nd_j}} = \sqrt{nd_j} \times tree_i + \beta_{varclim} \times \frac{varclim_j}{\sqrt{nd_j}} + \varepsilon_{i,j} \quad (5)$$

Second, we performed a multivariate analysis for all of the climate variables by considering the best model explaining the growth according the Bayesian Information Criterion (BIC), m_{BIC} (eq.6). The model m_{BIC} was obtained by an exhaustive screening of the candidate models implemented in the *glmulti* package of R.

$$\begin{aligned} \frac{1}{\sqrt{nd_j}} Gr_{i,j} &= \sqrt{nd_j} \times tree_i + \beta_{REW} \frac{REW_j}{\sqrt{nd_j}} + \beta_W \frac{W_j}{\sqrt{nd_j}} \\ &+ \beta_{T^-} \frac{T_j^-}{\sqrt{nd_j}} + \beta_I \frac{I_j}{\sqrt{nd_j}} + \varepsilon_{i,j} \end{aligned} \quad (6)$$

We compared the models through their percentage of variance explained and their predictive quality. The predictive quality was assessed by computing the root mean square errors of the predictions, *RMSEP*:

$$RMSEP = \sqrt{\frac{\sum_{i=1}^{N_{tree}} \sum_{j=1}^{N_{period}} (Gr_{i,j} - \widehat{Gr}_{i,j})^2}{N_{tree} \times N_{period}}} \quad (7)$$

where $Gr_{i,j}$ is the observed values of growth and $\widehat{Gr}_{i,j}$ is the model predictions of growth.

All analysis were performed using the R project software (<http://www.r-project.org/>).

Acknowledgments

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Figure Legends

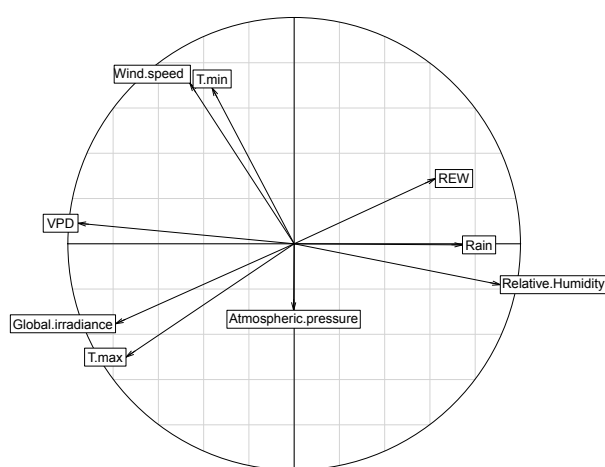


Figure 1. Principal component analysis of the climatic variables

Tables

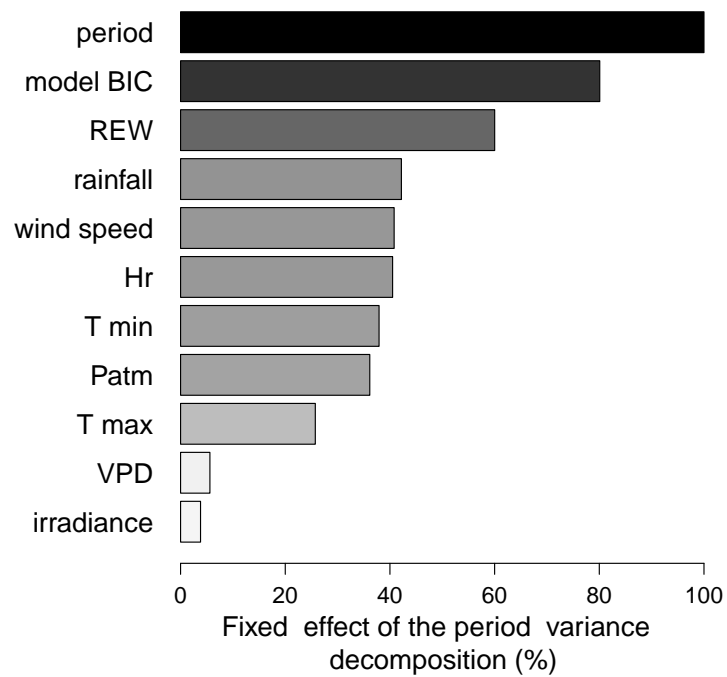


Figure 2. Part of the variance of the period effect on tree growth explained by the climatic variables and the model selected with BIC

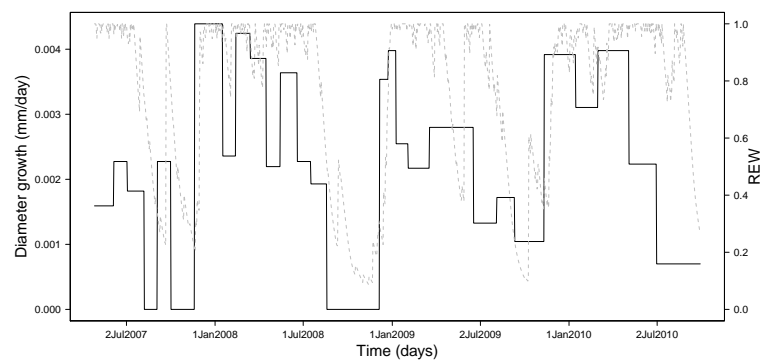


Figure 3. Mean daily diameter increments by periods of the 205 trees and water availability during the follow-up

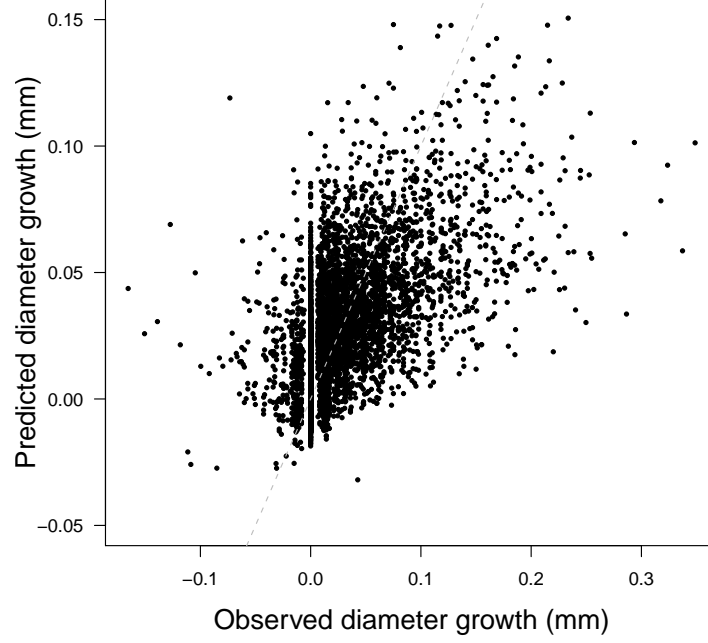


Figure 4. Growth in diameter observation versus prediction of the model m_{BIC} , the dashed line represents the line $y = x$

Table 1. Descriptive statistics of the climatic variables

variable	description	mean	SD	unit
I	global irradiance	590.34	170.17	$MJ.m^{-2}.d^{-1}$
T^-	temperature minimum	23.43	0.82	celsius degree
T^+	temperature maximum	28.37	1.35	celsius degree
REW	relative extractable water	0.77	0.28	-
VPD	vapor pressure deficit	6.05	1.68	kPa
Pr	precipitation (rain)	9.03	17.21	mm
$Patm$	atmospheric pressure	100.657	0.154	kPa
RH	relative humidity	82.58	4.34	%
W	wind speed	2.80	0.70	kn

Descriptive statistics of the climatic variables

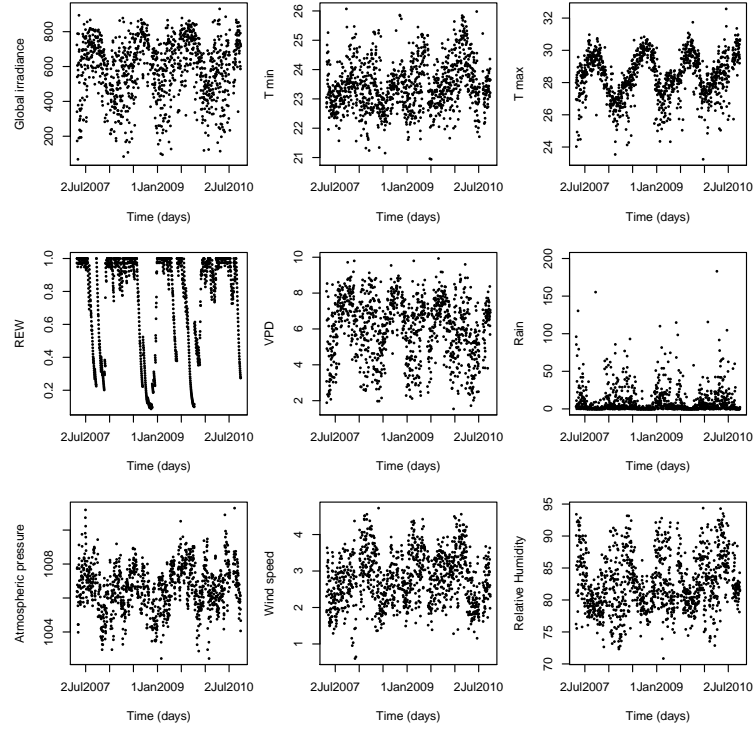


Figure 5. Variation of the climatic variables during the study period

Table 2. Climatic variable parameters of the univariate analysis and of model selected by BIC

model	climatic variable	estimate	Std. Error	t value	$Pr(> t)$
Univariate analyses	<i>REW</i>	4.658e-03	2.176e-04	21.405	< 2e-16 ***
	<i>Pr</i>	2.015e-04	1.136e-05	17.741	< 2e-16 ***
	<i>W</i>	1.571e-03	9.011e-05	17.432	< 2e-16 ***
	<i>HR</i>	6.493e-05	3.739e-06	17.366	< 2e-16 ***
	<i>T⁻</i>	2.209e-04	1.317e-05	16.774	< 2e-16 ***
	<i>Patm</i>	5.144e-06	3.144e-07	16.359	< 2e-16 ***
	<i>T⁺</i>	1.532e-04	1.117e-05	13.714	< 2e-16 ***
	<i>VPD</i>	3.028e-04	4.791e-05	6.320	2.80e-10 ***
	<i>I</i>	2.255e-06	4.330e-07	5.209	1.96e-07 ***
m_{BIC}	<i>REW</i>	1.892e-03	3.653e-04	5.179	2.30e-07 ***
	<i>W</i>	6.580e-04	2.252e-04	2.922	0.003494 **
	<i>T⁻</i>	3.251e-04	5.602e-05	5.803	6.84e-09 ***
	<i>I</i>	-1.017e-05	9.960e-07	-10.206	< 2e-16 ***

Climatic variable parameters of the univariate analysis and of model selected by BIC

3 L'effet du climat sur la croissance spécifique des arbres est expliquée par les traits fonctionnels

Un consensus des modèles de l'IPCC a montré que l'intensification de la saison sèche était probable à plus de 80% pour le bouclier des Guyanes (Malhi *et al.*, 2009). Dans ce contexte, prévoir la réponse des forêts de Guyane au changement climatique nécessite de construire des modèles *in silico* de dynamique de forêt tropicale. Les modèles de dynamique forestière sont en train d'être développés. Un des problèmes majeurs pour le paramétrage de ces modèles vient du fait que les forêts tropicales sont des communautés d'une richesse spécifique très importante (environ 1700 espèces ligneuses pour la Guyane seule), et que l'on ne dispose pas de mesures de dynamique pour toutes ces espèces. Il faut donc trouver un moyen de pouvoir prédire la croissance pour les espèces dont le diamètre n'est pas ou peu mesuré. La modélisation basée sur les traits fonctionnels semble être une approche prometteuse pour répondre à ce problème. Récemment dans notre équipe, Hérault *et al.* (2011) ont montré qu'un modèle de croissance paramétré avec seulement 4 traits fonctionnels mesurés au niveau spécifique (diamètre maximum, densité du bois, hauteur maximum et pourcentage relatif de $\delta^{13}\text{C}$) permettait de prédire la croissance des individus avec une erreur standard de prédiction relativement faible (0.51 mm par an alors que la croissance moyenne est de 1.52 mm par an). Ces modèles permettent de faire des prédictions pour la communauté avec un nombre restreint de paramètres, puisqu'on a un seul paramètre par trait fonctionnel inclus dans le modèle. Pour aller plus loin dans l'utilisation des traits fonctionnels dans la prédiction de la variabilité de la croissance, nous avons cherché si les valeurs de traits étaient associées à des stratégies particulières de croissance en réponse au climat. Pour faire cette étude, nous avons utilisé le jeu de données des dendromètres et à chaque individu a été attribué les valeurs moyennes des traits fonctionnels de son espèce (base de traits Bridge et Mariwenn). Après avoir utilisé une méthodologie nous permettant de modéliser la croissance journalière des arbres

3. L'EFFET DU CLIMAT SUR LA CROISSANCE SPÉCIFIQUE DES ARBRES EST EXPLIQUÉE PAR LES TRAITS FONCTIONNELS

en fonction de l'effet fixe de l'individu et de l'effet fixe de la période, nous avons analysé les interactions entre les valeurs de traits fonctionnels et les variables climatiques sur la croissance des arbres. Dans cette analyse, nous avons déterminé que la densité du bois, la hauteur maximum sont des traits spécifiques qui interagissent avec le climat et notamment à la sécheresse. Les arbres à fortes densités sont moins sensibles à la diminution de l'eau disponible dans le sol alors que les arbres à hauteur maximum importante montre une sensibilité importante à la sécheresse, se caractérisant par un arrêt de la croissance en diamètre. La même réaction est observée pour les arbres à gros DBH. Les espèces dont les traits foliaires sont du côté des espèces à croissance rapide du 'Leaf Economic Spectrum' (Wright *et al.*, 2004) sont plus sensibles aux variations des conditions climatiques. Ces espèces démarrent plus rapidement leur croissance diamétrique en début de saison humide et arrêtent plus rapidement leur croissance diamétrique en saison sèche .

Cette étude est présentée sous la forme d'une publication, Wagner *et al.* (in prep.).

Functional traits are involved in tropical tree responses to climate

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Abstract

- Climate models predicted rainfall reduction in the amazonian region, including change in water availability for trees
- We focused on the analysis of the climate variable/functional traits interaction effect on tree growth in a linear framework. We used data from 3 yrs of bimestrial growth measurements in the forest of Paracou, climate variables from a flux tower located near the trees and functional trait mean specific values for the 205 studied trees.
- Our results indicates that tree growth was affected by annual water availability for most of the species and tree species have different growth strategies in drought conditions. These strategies are linked to some functional traits, especially maximum height, wood density and traits

associated to the growth strategy, slow or fast growing. The later were more affected by a lack of water resource. The remaining part of unexplained variance, c. 50% may be attributed to the leaf phenology, individual history or genetic.

- These results suggest that: (i) even if trees are adapted to the dry season at Paracou, they show different responses to drought in terms of tree growth and (ii) their response appeared linked to their growth strategy. As a consequence, tropical forest dynamics would probably be affected by the expected changes of climate for the XXIst.

1. Introduction

Lower tree growth have been reported from all tropical regions in extreme El Niño events, when temperatures reach absolute records and severe droughts occur in many areas (Clark et al., 2010; Clark, 2004; McDowell et al., 2008). Over Amazonia, temperature increases have already been observed (Malhi and Wright, 2004) and climate models predicts drying for the XXIst century (Malhi et al., 2009; Burke et al., 2006; Johns et al., 2003).

The response of tropical forests to fine climate variations or to particular climatic events has been more than ever investigated during the last years (Clark et al., 2010; Brando et al., 2008; Lloyd and Farquhar, 2008; Wagner et al., 2011b), highlighting the sensitivity of tropical forest ecosystems to the climatic variables for which a change is expected, especially temperature and precipitation. But understanding the species-specific responses to

climate variations is needed to predict long-term change in forest dynamics and community assemblage. Investigating such a research question is challenging because of the high diversity of tree species in most tropical tree communities, often above 100 species.ha⁻¹.

Functional trait-based approach offer a promising way to bypass species when modeling dynamics of highly-diverse communities (Diaz et al., 2004; Lavorel and Garnier, 2002). Recently, Herault et al. (2011) had shown that the growth of 50 neotropical tree species can be accurately predicted by four functional traits only. Crossing from species to functional traits has several advantages, among which (i) strongly decreasing the number of model parameters and (ii) allowing a biological and ecological interpretation of the growth trajectory. Handling species by their shared morphological, physiological and phenological characteristics rather than by their strict phylogeny is the central theme of this approach. Several functional traits, known as the Leaf-Height-Seed strategy framework, have been proposed to reflect important functional axes that drive plant performance (Westoby, 1998; Westoby et al., 2002). An important recent breakthrough was the description of a leaf economics spectrum which reflect a trade-off between investments in productive leaves with rapid turnover versus costly physical leaf structure with a longer payback (Wright et al., 2004). Height reflects the final plant stature and its vertical position in the vegetation, and thus its access to light (Hirose and Werger, 1987). Seed mass, although not physiologically related to adult plant growth, is an important indicator of the global species life-history strat-

egy, with fast-growing pioneers tending to have smaller seeds (Moles et al., 2004). Baraloto et al. (2010) have recently highlighted that another ecological axis is shared among tropical trees the stem economics: dense wood versus high wood water content and thick bark. In the following, we detailed the interactions between climate and functional traits expected to affect tree growth (more complete definition of the studied functional traits in Cornelissen et al. (2003)). We focused on the trait/climate-growth rate interactions in adult tree only because role of functional traits toward growth changes during ontogeny (Wright et al., 2010).

Among life-history traits, maximum height reflects the adult place in the vertical profile of the canopy, a proxy of light availability (Herault et al., 2010). Poorter et al. (2008) suggested that tall trees, i.e. having crowns in the forest canopy, are exposed to dryer condition than understorey species. In other words, tall trees often fail to maintain their evaporative demand in dry periods. Granier et al. (1996), using sapflow measurements, had observed that big trees, i.e. trees having large DBH and/or DBHmax, have higher water demands. For some dominant trees, total tree sapflow reached values as high as 30 kg.h^{-1} ($250\text{-}300 \text{ kg.day}^{-1}$). Nepstad et al. (2007) used an experimental drought (60 % of incoming throughfall during each wet season reduction in rainfall) to show that after 3.2 years, the treatment resulted in a 38% increase in mortality rates. Mortality rates increased 4.5-fold among large trees ($\text{DBH} > 30\text{cm}$) and 2-fold among medium trees (10-30 cm dbh). Even if Nepstad et al. (2007) did not focus on tree growth, a diminution of

tree growth preceeding death is often observed (Monserud, 1976; Wyckoff and Clark, 2002). Earlier, Nepstad et al. (2002) highlighted a slight reduction in growth for stems <15 cm, but it remains difficult to conclude that small stems are more sensible without explicitly modeling their ontogenetic trajectory (Herault et al., 2011). In this paper, we hypothesize that species with high diameter max and height max as well as the biggest individual trees would be much sensitive to drought events and that drought will negatively affect their growth. Seed mass, even if not directly related to adult plant performance, is an important index of life-history strategy of species and fast-growing species tend to have small seeds (Moles et al., 2004; Poorter and Bongers, 2006). We hypothesize that species with small seeds could be more sensitive to drought conditions because of a less conservative resource strategy.

Among the stem economic spectrum, bark thickness as no direct link with the climate response as this trait is mainly linked to the tree defense strategy (Paine et al., 2010). But bark thickness is indirectly linked to diameter increment due to the shrinkage of stem during dry seasons (Baker et al., 2003). Trees with highest bark water contents and thicknesses displayed the strongest decreases in girth during the dry season as well as the highest increases at the start on the wet season (Stahl et al., 2010). Santiago et al. (2004) demonstrated that wood density is well-linked to hydraulic efficiency, in turn positively correlated to the photosynthetic potential. The ecological strategy 'many narrow conduits' versus 'fewer wider conduits' highlights the trade-off between the hydraulic efficiency of wide conduits and the cavitation

resistance of narrow conduits (Chave et al., 2009). This cavitation resistance is potentially great asset to the growth of species with high wood densities when the available soil water content starts to decline at the end of the wet season as species with low densities are known to be more sensitive to water availability and to have a less conservative resource strategy (Markesteijn et al., 2011). In this paper, we hypothesize that species with high wood density would be less sensitive to drought events and that drought will negatively affect the growth of softwood species.

Among the leaf economic spectrum, specific leaf area (SLA) indicates the leaf efficiency for light capture per unit biomass invested (Poorter et al., 2009). SLA is weakly or not related to the growth of large-sized trees (Poorter et al., 2008) for which leaf area and light interception are largely determined by branching patterns, the number of meristems, and tree architecture (Sterck and Bongers, 2001). Species with high SLA tends to have (i) short-lived leaves with high N and P mass content (Wright et al., 2004; Fyllas et al., 2009), (ii) high mass-based maximum photosynthetic rates (Cornelissen et al., 2003) and are usually found at the fast payback end of the leaf economic spectrum (Baraloto et al., 2010). This combination of traits is usually found at species with fast growth rates (Poorter and Bongers, 2006). At the opposite, leaf traits associated with low SLA (thick leaf blade; small, thick-walled cells) have often been interpreted as ecological adaptations to drought, i.e. allowing, at least in evergreen species, continued leaf function (or at least postponing leaf death) under very dry conditions (Wright

et al., 2004; Donovan et al., 2011). A tight correlation amongst leaf K and leaf N or P concentrations was highlighted among neotropical trees (Baraloto et al., 2010). Leaf K concentration is associated to stomatal control. K^+ concentration when stomates are open is near 10 fold superior of the K^+ concentration when stomate are closed (Roelfsema and Hedrich, 2005). Potassium limitation has been shown to have a negative effect on the ability of plants to control stomata, often leading to a reduction in water-use efficiency (Marschner, 1986; Santiago and Wright, 2007). It may be expected that species with low value of K might be more sensitive to drought as they have less flexibility to control stomata aperture, and thus less flexibility to limit the loss of water. Finally, $\delta^{13}C$ can provide a direct estimate of a tree's water use efficiency, WUE (Farquhar et al., 1989). Leaf $\delta^{13}C$ is often thought to be an integrative indicator of stomatal response to atmospheric dryness (Prentice et al., 2011; McMahon et al., 2011), and is strongly correlated with SLA, species with low water use efficiency have been found to have small SLA (Lamont et al., 2002; Fyllas et al., 2009; Baraloto et al., 2010). This trait has not been directly used by the existing coupled vegetation/climate models but would allow assignment of a key parameter for drought adaptation (Medlyn et al., 2011). In this paper, we hypothesize that drought conditions could first affect species with a high SLA (high water use efficiency).

In this paper, we addressed three specific questions: (i) Are functional traits involve in tropical tree growth response to interannual variation of climate and (ii) Which traits are linked to resistance to drought ? (iii) How

far can functional traits help predicting the future of tropical forest in term of composition toward expected changes of climate? We hypothesize that life history traits and stem economic spectrum traits, better than leaf traits, could explain the growth response to drought. Furthermore, we suspect that the tree growth response to climate is associated to the growth strategies of tropical trees, fast growing species could be more affected by fast changes of climate conditions in term of growth.

2. Methods

2.1. site

The study site is located in Paracou, French Guiana (5° 18 'N, 52° 55'W), a lowland tropical rain forest near Sinnamary (Gourlet-Fleury et al., 2004). The climate is affected by the north/south movements of the Inter-Tropical Convergence Zone and the site receives nearly two-thirds of its annual 3041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month in September and October. The most common soils in Paracou are the shallow ferralitic soils limited in depth by a more or less transformed loamy saprolithe (Gourlet-Fleury et al. 2004). The site is located approximately 40 m above sea level (Gourlet-Fleury et al., 2004) and is made up of a succession of small hills. The forest is typical of Guianan rainforests (ter Steege et al., 2006). More than 550 woody species attaining 2 cm DBH (Diameter at Breast Height, i.e. 130 cm) have been described at the site, with an estimated 160-180 species of trees > 10 cm DBH per hectare. The dominant

families at the site include Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae.

2.2. Data

First, seasonal changes in trunk circumference were monitored in 204 trees from 53 species using home-made steel dendrometer bands (Stahl et al., 2010). Tree growth was censused every c. 40 days from 2007 to 2010 (mean=39, sd=19.8). Information on 13 key functional traits (related to leaf economics, stem economics and life-history) measured on mature trees (DBH>10 cm) of the 53 focal species was extracted from a trait database of French Guianan tree species (Ollivier et al., 2007), Table 2. Details of sample collection and trait measurements are available in Baraloto et al. (2010) for the leaf and stem economic traits and in the study by Herault et al. (2010) for the life-history traits. The 95th percentile diameters was used as estimates of DBH_{max} to minimize the weight of outliers (King et al., 2006). These traits represent complementary axes of tree ecological strategies in tropical forests (table 1) and have been proposed to be important for tree performance through ontogeny (Westoby, 1998; Weiher et al., 1999; Poorter et al., 2008) and for growth responses to climate variations (McMahon et al., 2011; Chave et al., 2009; Baraloto et al., 2010). Due to a strong correlation between bark thickness and ¹³C on one hand and current tree size on the other (Paine et al., 2010), bark Thickness and ¹³C were corrected with the method given in Baraloto et al. (2010).

	roles	units	range	WET ^a	DRY ^b	references
<i>life-history</i>	dbh _{max}	architecture and structure	mm	190 – 980	+	Granier et al. (1996); Nepstad et al. (2007, 2002); Monserud (1976); Wyckoff and Clark (2002)
	height _{max}	architecture and structure	m	18 – 50	+	Poorter et al. (2008); Herault et al. (2010)
	seed mass	reproductive investment	g	<0.01 – >20	-	Moles et al. (2004); Poorter and Bongers (2006)
<i>stem economic spectrum</i>	wood density	transport structure defense	g.cm ⁻³	0.38 – 0.84	-	Santiago et al. (2004); Chave et al. (2009); Marksteijn et al. (2011)
	bark thickness	defense	mm	(-4.7) – 13	+	Stahl et al. (2010); Baker et al. (2003)
<i>leaf economic spectrum</i>	SLA	resource capture, defense	cm ² .g ⁻¹	5.41 – 16	-	Poorter et al. (2009, 2008); Sterck and Bongers (2001); Wright et al. (2004); Fyllas et al. (2009); Cornelissen et al. (2003); Poorter and Bongers (2006)
	K	resource capture	g.g ⁻¹	2×10 ⁻³ – 2×10 ⁻²	-	Roelfsema and Hedrich (2005); Marschner (1986); Santiago and Wright (2007)
	N	resource capture	g.g ⁻¹	1×10 ⁻² – 4×10 ⁻²	-	Baraloto et al. (2010); Poorter and Bongers (2006)
	P	resource capture	g.g ⁻¹	3×10 ⁻⁴ – 2×10 ⁻³	+	Baraloto et al. (2010); Poorter and Bongers (2006)
	C/N	resource capture, defense	g.g ⁻¹	13 – 34	-	Baraloto et al. (2010); Poorter and Bongers (2006)
	LTD	resource capture, defense	g.cm ⁻³	2.5×10 ⁻⁵ – 5.6×10 ⁻⁵	-	Wright et al. (2004); Donovan et al. (2011)
	chlorophyll	resource capture	μg.mm ⁻²	48 – 100	+	Wright et al. (2004); Baraloto et al. (2010); Cornelissen et al. (2003)
	toughness	defense	N	0.85–3.4	-	Wright et al. (2004); Donovan et al. (2011)
	δ15C	resource capture	‰	(-1.7) – 2.5	+	Farquhar et al. (1989); Prentice et al. (2011); Lamont et al. (2002); Fyllas et al. (2009); Baraloto et al. (2010)

^a: expected growth response to wet conditions, ^b: expected growth response to drought conditions, *: (+) trees with high values of a given functional trait are expected to grow faster. (-) trees with high values of a given functional trait are expected to grow slower.

Table 1: Functional traits used in the study, role in tree functional strategy (Baraloto et al., 2010) and range of values

Species	N	DBH _{max} mm	Height _{max} m	WdDens g cm ⁻³	Bark mm	SLA cm ² g ⁻¹	K μg g ⁻¹	N cg g ⁻¹	P μg g ⁻¹	CN g g ⁻¹	LTD g cm ⁻³	Chlo μg mm ⁻²	Tough N	δ ¹³ C ‰
<i>Apeiba glabra</i>	1	440	33	0.45	-2.6	12	0.0066	0.02	0.0086	24	3.6e-05	62	1.1	0.22
<i>Aspidosperma album</i>	2	600	43	0.67	3.6	7.3	0.0049	0.017	0.00046	28	4.1e-05	89	2.2	0.77
<i>Bocaa prouacensis</i>	4	380	37	0.84	-1.4	11	0.0026	0.025	0.00051	20	4.4e-05	63	2.4	0.35
<i>Carapa procera</i>	14	440	35	0.55	-0.5	10	0.0043	0.018	0.00064	27	3.9e-05	89	2.6	0.76
<i>Catostemma fragrans</i>	1	290	29	0.61	1.8	11	0.0017	0.023	0.00022	24	3.9e-05	68	2.5	0.91
<i>Cecropia obtusa</i>	1	300	33	0.41	-0.3	9.1	0.0086	0.028	0.0014	18	3.5e-05	66	1.8	1.8
<i>Chaetocarpius schomburgkianus</i>	4	540	33	0.77	-1.1	6	0.0018	0.013	0.00045	34	4.4e-05	100	2.7	-1.1
<i>Chinarhis turbinata</i>	1	850	40	0.61	-4.7	13	0.012	0.028	0.0011	17	2.9e-05	50	1.4	0.89
<i>Chrysophyllum pruriens</i>	4	500	33	0.8	-0.44	7.8	0.0048	0.022	0.00062	23	5.6e-05	96	2.1	1.2
<i>Chrysophyllum sanguinolentum</i>	5	560	36	0.6	3	7.2	0.0033	0.015	0.00047	33	4.9e-05	71	2.6	0.95
<i>Couepia bracteosa</i>	1	430	28	0.8	0.86	8.9	0.0044	0.015	0.00048	34	4.7e-05	59	2.4	-0.46
<i>Dicorynia guianensis</i>	10	800	50	0.65	-1.2	12	0.0037	0.024	0.00044	21	3.7e-05	77	1.7	1.5
<i>Drypetes variabilis</i>	1	500	34	0.72	0.25	9.2	0.0047	0.02	0.00078	22	3.9e-05	92	2.2	1
<i>Eperua falcata</i>	25	680	34	0.64	0.86	13	0.0038	0.021	0.00077	24	5e-05	60	1.3	2
<i>Eschweilera coriacea</i>	13	570	37	0.68	-0.57	9.9	0.0084	0.021	0.0012	24	4.9e-05	77	1.9	-0.54
<i>Eschweilera sagotiana</i>	12	530	44	0.7	0.54	7.2	0.0028	0.019	0.00045	28	4.6e-05	71	3	-0.6
<i>Goupia glabra</i>	3	830	37	0.67	1.5	13	0.0028	0.021	0.00063	24	4.9e-05	72	1.4	0.1
<i>Gustavia hexapetala</i>	1	220	35	0.62	1.8	13	0.005	0.026	4e-04	18	3.7e-05	64	1.5	0.14
<i>Hebepetalum humirifolium</i>	1	460	24	0.74	-0.065	14	0.0092	0.023	0.00064	21	3.3e-05	78	1.1	0.32
<i>Hirtella bicornis</i>	1	400	24	0.74	-0.84	15	0.0035	0.018	5e-04	26	4.3e-05	58	1.4	1.8
<i>Inga alba</i>	1	750	30	0.51	-3.8	15	0.0044	0.035	0.0012	14	4.3e-05	80	1.4	0.69
<i>Iryanthera sagotiana</i>	3	390	36	0.54	0.012	12	0.0024	0.019	0.00053	27	3.9e-05	80	0.85	-1
<i>Lacnellea aculeata</i>	1	190	18	0.54	1.6	12	0.0069	0.016	7e-04	33	3.2e-05	87	1.1	-1
<i>Laetia procera</i>	1	510	38	0.59	4.9	10	0.0035	0.025	0.001	21	4.4e-05	100	1.8	-0.26
<i>Lecythis corrugata</i>	1	410	34	0.59	-1.2	8.7	0.0041	0.019	0.00046	26	4.8e-05	64	2	-1.5
<i>Lecythis persistens</i>	4	280	38	0.69	0.36	8.1	0.0062	0.019	5e-04	27	4.2e-05	78	2.5	-0.59
<i>Lecythis poiteaui</i>	1	520	40	0.68	1.8	13	0.0046	0.028	0.00059	18	4.7e-05	54	1.3	0.47
<i>Lecythis zabucajo</i>	1	520	38	0.68	1.7	12	0.0072	0.023	0.00065	23	5.4e-05	56	1	1.2
<i>Licania alba</i>	4	440	31	0.77	-0.47	7.6	0.0043	0.014	0.00039	34	4.2e-05	60	2.7	-0.6
<i>Licania heteromorpha</i>	2	370	32	0.78	-1	8.7	0.0022	0.015	4e-04	24	4.8e-05	70	1.9	-1.6
<i>Licania membranacea</i>	9	500	42	0.8	0.049	8.2	0.0048	0.016	0.00039	30	4.8e-05	63	2	-1.6
<i>Lueheopsis rugosa</i>	1	640	28	0.52	2.1	12	0.012	0.04	0.0015	13	2.5e-05	56	1.9	2.5
<i>Macoubea guianensis</i>	1	580	39	0.43	4.9	16	0.0046	0.022	0.00069	25	3.6e-05	52	2.3	0.89
<i>Micropholis guyanensis</i>	1	650	36	0.64	-0.06	9.1	0.0051	0.021	0.00049	24	4.4e-05	64	1.5	-0.32
<i>Moronebea coccinea</i>	3	640	36	0.6	1.8	12	0.0044	0.017	0.00052	29	3.4e-05	94	0.88	0.29
<i>Oxandra asbeckii</i>	2	190	24	0.78	1.8	11	0.0034	0.02	0.00037	24	4.1e-05	84	1.8	0.53
<i>Parinari campestris</i>	1	750	33	0.7	1.1	6.8	0.0037	0.016	0.00053	29	4.5e-05	48	2.5	-0.022
<i>Platonia insignis</i>	1	960	30	0.59	13	5.4	0.0041	0.015	0.00059	31	4.1e-05	70	2.6	1.8
<i>Pouteria engleri</i>	1	570	22	0.62	2	11	0.0075	0.025	0.00053	19	5e-05	75	1.3	0.49
<i>Pouteria eugenifolia</i>	1	670	43	0.74	-1.6	8.2	0.0031	0.015	0.00044	33	5.1e-05	70	1.5	-0.29
<i>Pouteria guianensis</i>	1	570	34	0.79	-2.1	7.5	0.003	0.017	0.00046	30	5e-05	79	2	-0.99
<i>Protium giganteum</i>	1	400	27	0.44	0.58	13	0.011	0.02	0.00085	23	3.6e-05	87	2.6	-1.7
<i>Recorдохylon speciosum</i>	9	550	35	0.68	-0.46	15	0.0043	0.023	0.00082	22	3.8e-05	60	1.3	0.61
<i>Sectonia rubra</i>	2	800	50	0.47	3.2	9.4	0.0045	0.018	0.00063	29	4.3e-05	84	1.6	0.41
<i>Simaba moretii</i>	1	810	36	0.38	3	7.6	0.0061	0.019	0.00072	25	4.7e-05	71	1.7	-0.33
<i>Sterculia pruriens</i>	7	690	40	0.46	1	12	0.021	0.02	0.0019	25	3.8e-05	59	1.9	0.18
<i>Swartzia polyphylla</i>	1	980	38	0.68	-3.9	12	0.0022	0.023	0.00066	22	4.1e-05	72	1.3	-0.38
<i>Symphonia globulifera</i>	6	920	26	0.56	0.037	10	0.0065	0.02	0.00063	24	3.1e-05	91	1.3	1.1
<i>Tapirira guianensis</i>	1	420	30	0.56	-0.76	12	0.0096	0.019	0.0011	25	4.5e-05	88	1.2	0.21
<i>Tapirira obtusa</i>	1	350	25	0.44	-0.22	11	0.0035	0.019	5e-04	26	4.5e-05	69	1.1	-0.98
<i>Tapura capitulifera</i>	2	620	33	0.76	0.065	6	0.0065	0.013	0.00029	31	4.2e-05	94	3.4	0.79
<i>Tetragastris panamensis</i>	3	530	32	0.68	0.17	9	0.0047	0.016	0.00049	29	5.5e-05	74	2	-0.12
<i>Virola micheli</i>	8	520	38	0.47	0.93	11	0.0035	0.024	0.00063	22	4.8e-05	85	0.91	-1.7
<i>Viouacapoua americana</i>	17	730	42	0.69	-1.1	14	0.0073	0.026	0.0016	20	4.7e-05	56	1.5	-0.46

Table 2: Values of the 13 functional traits from 54 neotropical species used to study community response to seasonal climate variations; DBH_{max} = Maximum diameter; Height_{max} = Maximum height; WdDens = Trunk xylem density; Bark = Trunk bark thickness; SLA = Specific leaf area; K = Foliar K_m; N = Foliar N_m; P = Foliar P_m; CN = Foliar C:N; LTD = Leaf tissue density; Chlo = Laminar total chlorophyll; Tough = Laminar toughness; δ¹³C = Foliar δ¹³C composition

2.3. Meteorological Data

In 2003, a 55 m self-supporting metallic eddy covariance flux tower, Guyaflux, was built in the Paracou forest in a natural 100 m² gap, with minimal disturbance to the upper canopy. This location covers a range of more than 1 km of forest in the direction of the prevailing winds. The top of the tower is about 20 m higher than the overall canopy. Meteorological and eddy flux sensors (full details in Bonal et al. (2008)) are mounted 3 m above the tower. A large panel of climatic variables was recorded at a daily time-step (details in Table Appendix A). Most climatic variables exhibited strong seasonal changes, highlighting the north/south movements of the Inter-Tropical Convergence Zone (Fig. C.1).

We used a water balance model explicitly designed for tropical forests (Wagner et al., 2011a) in order to estimate water availability for trees. The model computes daily water fluxes (tree transpiration, understorey evapotranspiration, rainfall interception and drainage), soil water content at different layers and relative extractable water for trees for the entire soil (REW). REW is a daily value between 0 and 1, when $REW = 1$ the amount of extractable water by the tree is at its maximum and, when $REW = 0$, no water is available for trees. We create with REW a variable of water stress, SWD for soil water deficit, $SWD = 1 - REW$.

2.4. Data analysis

In a preliminary study, we investigated the association between functional traits through a principle component analysis (PCA) on the normalized

traits dataset. We modeled the link between tree growth and the functional traits/climate interactions in a linear regression framework. The model was built at a daily time step. We first include a factorial variable *tree* in the model to account for the individual behavior in tree growth. This individual effect was not analyzed furthermore because it was not the point of this study; we just took it into account to not bias our result. Next we include the factorial variable *period* which estimates a model parameter for each period. This variable captured the variance due to the climatic effect common to all individuals from all species. We then explored the interaction between functional traits and climatic variables one by one. The interaction between the current *dbh* and climate variables was also investigated to test the hypothesis of a size-mediated response to climate stress. All these interactions were successively tested in univariate models to lower multicollinearity problems associated with multivariate models. Prior to the analysis, functional traits were scaled, *i.e.* each value was divided by the trait standard error. This model was fitted with weighted least squares. The weight was calculated to correct the facts that (i) growth, climatic and traits data were summed over different period lengths and (ii) the number of studied trees changed between species.

$$Gr_{i,j} = nd_j \times tree_i + period_j + nd_j \times \theta \times (var_{trait} \times var_{clim}) + \epsilon_{i,j} \quad (1)$$

$$\epsilon_{i,j} \sim \mathcal{N}(0, weight \times \sigma^2) \quad (2)$$

$$weight = nd_j \times n_{indSp} \quad (3)$$

Where $Gr_{i,j}$ is the growth of the tree i over the period j , $tree_i$ is the individual tree effect, $period_j$ is the period effect, θ quantify the effect of the interaction between the trait value var_{trait} and the climate variable var_{clim} , and nd_j the number of day of the period j . The weight is the product of the number of day of the period, nd_j with the individual number of the species in the data, n_{indSp} .

To test the significance of each trait-climate interaction, we computed for each univariate model the Bayesian information criterion, BIC (Schwarz, 1978):

$$BIC = -2 \times \ln(L) + k \times \ln(n) \quad (4)$$

Where L is the likelihood of the model, k the number of estimated parameters and n the number of observation. The BIC measure the efficiency of the model in terms of predicting the data and penalizes the number of model parameters. A lower BIC means that the information carried by the interaction improved the model even if it added a parameter. All analyses were performed using the R project software (<http://www.r-project.org/>).

3. Results

The first axis of the principal component analysis of traits data (Fig. 1) explained 31.15 % of the variance in the trait dataset and was positively correlated with N, P, SLA, K, $\delta^{13}C$, and negatively correlated to C/N, tough-

ness, LTD and wood density. The second axis explained 12.63 % of variance and was positively correlated with bark thickness, toughness and K. The third axis explained an additional 12.09 % of variance and was negatively correlated with the Height_{max} , $\delta^{13}\text{C}$ and DBH_{max} .

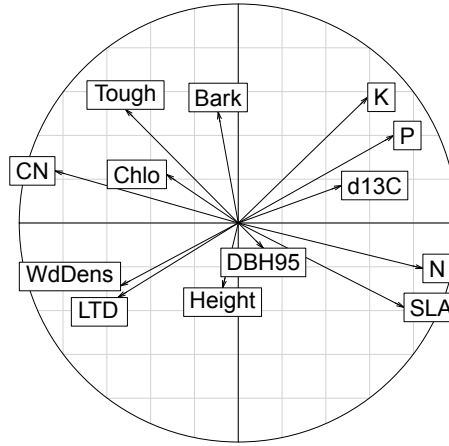


Figure 1: Correlation circle of the functional traits principal component analysis

More than 33.5 % of the observed variation in tree growth may be imputable to the individual tree behavior while the period effect explained 15.0% of the tree growth variance. This means that climate variables alone explained up to 15% of the variance of tree growth. The interaction term between a single trait and a single climate variable captured a maximum of 0.38% of the variance, Table 4. The BIC selection procedure kept 24 traits/climate interactions, Table 3. With the exception of Relative air humidity and Atmospheric pressure all the climate variables showed interactions with traits for predicting tree growth. Functional traits DBH_{max} , Bark, SLA,

K, P, and $\delta^{13}\text{C}$ are not associated to any climate variables for predicting tree growth.

3.1. Life-History

Trees with a high Height_{max} had a lesser growth when soil water deficit is high. Trees with a larger DBH had a lesser growth in drought condition (high SWD and high irradiance) and when vapour pressure was high.

3.2. Stem Economics

Trees with high wood densities and large DBH had higher growths during drought events (high SWD and high irradiance).

3.3. Leaf Economics

Trees with a high N foliar (and low CN ratio) content had a lesser growth during drought events (high SWD and high irradiance), when vapour pressure is high, temperatures and wind speed were maximum. Trees with high leaf tissue densities had higher growths in wet seasons (high REW and high precipitation), when wind speed is high, and lower growths were observed when soil water deficit was high. Trees with high leaf chlorophyll content had a higher growth in wet condition (high REW and high precipitation) and when wind speed was high. Finally, trees with high leaf toughness had a higher growth in drought condition (high SWD and high irradiance).

4. Discussion

We highlighted direct links between functional traits and growth response to climate variations, an important step to improve global vegetation models

	DBH	Height _{max}	WdDens	N	CN	LTD	Chlo	Tough
REW ^a						+	+	
Rain	+					+	+	
SWD ^b	-	-	+	-	+	-		+
Irradiance	-		+	-				+
T.max				-				
T.min				-				
Wind.speed				-		+	+	
VPD ^c	-			-	+			

^a:Relative extractable water,^b:Soil Water Deficit (1-REW),^c:Vapour Pressure Deficit

Table 3: Functional traits mediate tropical tree responses to climate variations among 54 neotropical species. (+) trees with high values of a given functional trait grown significantly faster when a given climate variable was high. (-) trees with high values of a given functional trait grown significantly slower when a given climate variable was high. Only significant interactions are shown

	DBH	Height _{max}	WdDens	N	CN	LTD	Chlo	Tough
REW ^a						0.19	0.12	
Rain	0.24					0.34	0.13	
SWD ^b	0.38	0.11	0.08	0.15	0.13	0.08		0.15
Irradiance	0.12		0.11	0.08				0.12
T.max				0.08				
T.min				0.08				
Wind.speed				0.09		0.09	0.08	
VPD ^c	0.08			0.09	0.08			

^a:Relative extractable water,^b:Soil Water Deficit (1-REW),^c:Vapour Pressure Deficit

Table 4: Functional traits mediate tropical tree responses to climate variations among 54 neotropical species. Percentages of tree growth variance explained by the interaction traits/climate in univariate analysis

in predicting tropical forest responses to global change(McMahon et al., 2011; Diaz et al., 2007). Effects of functional traits may be noticeable throughout the whole year, as found for Leaf tissue density (LTD) or current diameter

(DBH) for which interactions were significant both in wet and dry seasons, Table 3. But we need to acknowledge that most detected effects are seasonal. Positive interactions with REW and/or Rain indicated that a high value of a given trait shaped a better growth in wet seasons while positive interactions with irradiance, soil water deficit and/or vapour pressure deficit highlighted better growth in dry periods. Water (REW, SWD, Rain) and light (Irradiance) shaped the functional trait responses. Wind speed and VPD might be respectively proxy of water and light, Fig C.1. Wind speed reaches its maximum value at the start of the rain season and VPD is strongly correlated to irradiance and soil water deficit, Table B.1. Contrary to the results of (Clark et al., 2010), temperature variations caught a negligible part of growth variance. In French Guiana, temperatures are very stable through the year unlike other climate variables, figure C.1. Moreover, photosynthesis requires light and water while temperature only changes the kinetic of the reaction. Within the range of average minimum and maximum temperature (23.4 - 28.4 °C), only a minor change in photosynthesis kinetic can be expected (Lloyd and Farquhar, 2008).

4.1. Life-history traits

Big trees (DBH) were more affected by drought events than smaller ones. Big trees have higher needs in water, are more exposed to light irradiance and have their crown in more drier environments than understorey trees (Nepstad et al., 2007). Among 18 mortality studies in Amazonia, 12 have demonstrated a greater mortality rate during drought events, three found no size-related ef-

fect, and 3 indicated greater rates for small more than for large trees (Phillips et al., 2010). We also shown that taller species (Height_{max}) are more affected by drought than smaller species. However, bigger species (DBH_{max}) do not exhibit this pattern. This highlights the fact that most of our individual trees are closer to their maximum height than to their maximum diameter due to the power relationship between Height and DBH. That's also why DBH_{max} is a better index than Height_{max} for replacing a tree in its ontogenetical trajectory (Herault et al., 2011). Considering this result, DBH, and to a lesser extent Height_{max} , give an highly sensitive index of tree growth growth responses to water stress.

4.2. Stem economics

Consistently with the assumption that dense-wood species have smaller vessels that prevent them from embolism and that allow them to maintain baseline growth under drought conditions (Chave et al., 2009; Markesteijn et al., 2011), we found that, during droughts, trees having the densest wood were the less affected. On the other side of the trade-off are fast-growing species with large vessels and short life span, more reactive to resources availability but more sensitive to lack of resource. We found no relationship between bark thickness and tree growth response. Even if this trait did not mediate the tree response to drought, bark thickness is well-known as a good proxy of the resistance to fire occurrence (Paine et al., 2010). This is out the frame of this study but this trait is of primer importance if we keep in mind the most dramatic climate-change scenarios for the Amazon basin, i.e.

severe drought events and massive fires (Nepstad et al., 2004).

4.3. *Leaf economics*

Recent works suggest that leaf traits poorly contributed to shape the growth of adult trees in tropical forests (Herault et al., 2011; Poorter et al., 2008). In contrast, we highlighted that some these functional traits are implicated in tree growth response to climate (N, CN, LTD, Chlo, Tough) while others are not (SLA, K, P and $\delta^{13}\text{C}$). Species with high SLA tend to have short-lived leaves with high N and P concentrations and are usually found at the fast payback end of the 'economic spectrum' (Wright et al., 2004). On the other hand, leaf traits associated with low SLA (thick leaf blade; small, thick-walled cells) have often been interpreted as adaptations that allow continued leaf functioning (or at least postponing leaf death) under very dry conditions (Wright et al., 2004; Donovan et al., 2011). Our results are not really consistent with this hypothesis. In our dataset, N leaf concentration was, by far, more discriminant than SLA for tree growth response to drought. At a global scale, there is a strong link between N leaf content and leaf lifespan, life lifespan reaching the highest value for low concentration of leaf N (Donovan et al., 2011; Wright et al., 2004). It may be expected that trees with long-lived leaves less suffer from regular drought events while trees with short-lived leaves have lost their leaves when stressed and, consequently, stop their secondary growth, Table3, (Wang et al., 2011). Toughness, chlorophyll content and leaf tissue density are intimately correlated, Table1, but their effect seems to be associated to different seasons. In wet season, species with

high chlorophyll content and high leaf tissue densities have a better growth, Table 3. This could be linked to the capacity of species with high value of chlorophyll to have better capacity to use the lower light levels of the wet season. Leaf toughness traits are uncorrelated with relative growth rates but correlated positively with leaf lifespan (Westbrook et al., 2011; Kitajima and Poorter, 2010). Furthermore, leaf toughness is negatively correlated with the leaf traits of fast growing species (Baraloto et al., 2010). Species with a high toughness could have a higher growth in drought conditions due to their position on the leaf economic spectrum, at the opposite of fast growing species. As unexpected $\delta^{13}\text{C}$ appeared unrelated to specific growth response to climate. Foliar $\delta^{13}\text{C}$ is an indicator of leaf-level water-use efficiency reflecting a tradeoff between photosynthetic rates and stomatal conductance (Seibt et al., 2008). With the complete BRIDGE database (668 species), Baraloto et al. (2010) have found that foliar $\delta^{13}\text{C}$ was weakly correlated with LES and SES, when corrected for stature and they conclude that the sensitivity of this measure to microhabitat variation may preclude its utility as a plant functional trait at the community scale in systems with a complex vertical structure such as tropical forests. This limitation may explain why this variable is unrelated to tree growth as the measurement of $\delta^{13}\text{C}$ values are not made on the trees of our study.

4.4. Rethinking the tree growth response

We have here a unique dataset with climatic variable records and trait values at high resolution. At best our model explains 48.9% of the variance

of tree growth. Surprisingly, the interactions between traits and climate, even if some were significant and followed the general frame of the expected results, explained only a limited part of the variation in tree growth, no more than 0.4% each one. This may be a strong limiting factor for use of this modeling framework to predicting future growth in a climate change context. Supplementary researches are needed to explicit the functional link between traits and tree growth response to climate. In this paper, we only test for a linear link between both. During the 3 years of the study, climatic conditions haven't been particularly extreme for this region. This condition could be usual for the investigated trees; they may not have used those extreme strategies of survival which are assumed to be mediated by some functional traits. The majority of trees stopped their growth in dry season and we point out in this study, in dry season, which species are able to maintain their growth more days than other species, Fig 2. This response could be very different and, maybe, more linked to functional traits if a drought occurs during the wet season.

4.5. Conclusion

With the absence of extreme climatic events during our study, we can't conclude that a composition change is expected but our result join the recent finding that smaller, denser-wooded trees are able to maintain their functioning in drought condition (Phillips et al., 2010; Chave et al., 2009). In such case where climate variation is regular and imply quite thin variance explanation, using trait in analysis must be done with the traits the more close to the

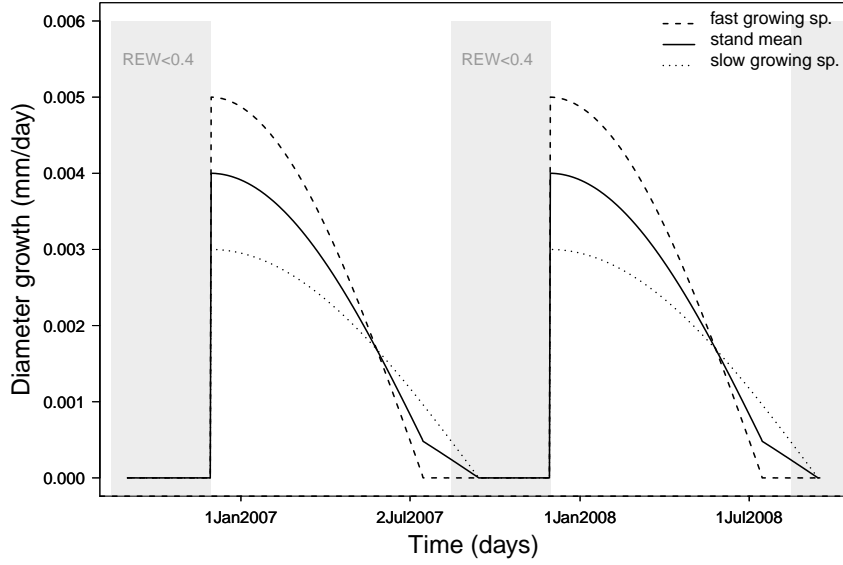


Figure 2: Tree diameter growth dynamic of the mean community (solid line), of the fast growing species (dashed line) and slow growing species (dotted line)

processus. For example, N, P, and K are very correlated but only N improve the model probably because this trait is probably the closest to the process linking tree growth and climate, as N is a proxy of the maximum photosynthetic rate and maximum growth rate (Cornelissen et al., 2003). Among the climate variables, we found no effect of trait interaction with temperature on tree growth. The mean temperature at our site is near the optimal range for photosynthesis and stable through out the year. But, if temperature follows the expected increase for the XXIst century (IPCC, 2007), temperature will impact tree growth by reducing photosynthesis kinetic (Lloyd and Farquhar, 2008).

In this study for a tree, each growth measurement is assumed to be in-

dependent of others and this is a strong assumption for growth. A single heavy rain in dry season does not have the same effect than a heavy rain in wet season. Analysing growth with dynamics models, traits based or not, is a promising way to improve tree response to climate. At the community level, in absence of extreme climate events, traits based community dynamic models of growth could help testing extreme climatic scenario. Such model approaches and experiences on unusual extreme events like drought experiments (Nepstad et al., 2002) are required to test the sensitivity of the tropical forest.

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Appendix A. Description of climate data

	mean	SD	unit
Global.irradiance	590.34	170.17	MJ.m ⁻² .d ⁻¹
T.min	23.43	0.82	celsius degree
T.max	28.37	1.35	celsius degree
REW ^a	0.77	0.28	-
SWD ^b	0.23	0.28	-
VPD ^c	6.05	1.68	kPa
Rain	9.03	17.21	mm
Atmospheric.pressure	100.657	0.154	kPa
Relative.Humidity	82.58	4.34	%
Wind.speed	2.80	0.70	kn

^a:Relative Extractable Water ,^b: Soil Water Deficit (SWD=1-REW),^c:Vapour Pressure Deficit

Table A.1: descriptive statistics of the climatic variables

Appendix B. Correlation between climate data

	irradiance	T min	T max	REW ^a	VPD ^b	Rain	P Atm ^c	H R ^d	Wind speed	SWD ^e
irradiance	1.00	0.03	0.76	-0.40	0.70	-0.52	0.11	-0.63	0.18	0.40
T min	0.03	1.00	0.06	-0.09	0.34	-0.26	-0.14	-0.34	0.45	0.09
T max	0.76	0.06	1.00	-0.60	0.62	-0.49	0.04	-0.50	-0.03	0.60
REW ^a	-0.40	-0.09	-0.60	1.00	-0.53	0.35	0.12	0.45	-0.08	-1.00
VPD ^b	0.70	0.34	0.62	-0.53	1.00	-0.64	0.02	-0.98	0.49	0.53
Rain	-0.52	-0.26	-0.49	0.35	-0.64	1.00	-0.01	0.63	-0.26	-0.35
P Atm ^c	0.11	-0.14	0.04	0.12	0.02	-0.01	1.00	-0.02	-0.07	-0.12
H R ^d	-0.63	-0.34	-0.50	0.45	-0.98	0.63	-0.02	1.00	-0.53	-0.45
Wind speed	0.18	0.45	-0.03	-0.08	0.49	-0.26	-0.07	-0.53	1.00	0.08
SWD ^e	0.40	0.09	0.60	-1.00	0.53	-0.35	-0.12	-0.45	0.08	1.00

^a:Relative Extractable Water ,^b: Vapour Pressure Deficit ,^c: Atmospheric pressure ^d:Relative Humidity,^e: Soil Water

Deficit (SWD=1-REW)

Table B.1: Correlation coefficient of the climatic variables

Appendix C. Climate variable during the study period

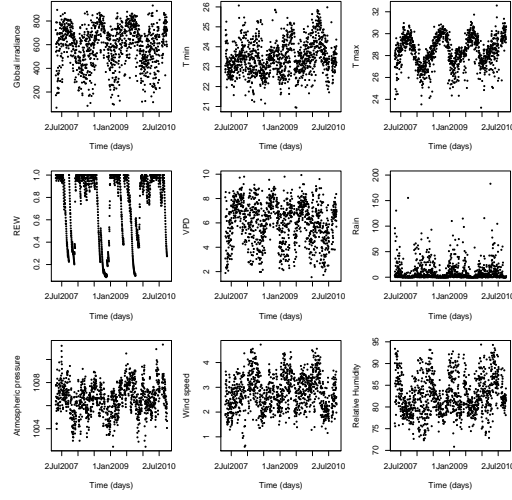


Figure C.1: Variation of the climatic variables during the study period

Synthèse et perspectives

Mieux comprendre la dynamique des arbres est un enjeu essentiel pour estimer le potentiel de réponse des forêts tropicales aux changements climatiques. Cette thèse apporte de nouveaux éléments sur la dynamique de la forêt tropicale. Premièrement, sur le stock de biomasse et les drivers des flux de carbone à Paracou. Deuxièmement, sur le lien entre climat et croissance secondaire des arbres, le processus le plus important de la fixation du carbone. Et troisièmement, sur les stratégies de réponse des espèces en terme de croissance aux variations climatiques en fonction de leurs traits fonctionnels. Dans cette synthèse, nous allons revenir sur les principaux résultats et discuter des perspectives de ce travail en 4 points : (i) Quelle est l'importance de la mortalité dans les bilans de carbone et quelles sont les perspectives pour la modélisation de ce processus ? (ii) Comment comparer l'effet du climat sur la croissance entre les dispositifs de suivi forestier permanents en régions tropicales ? (iii) Où en sommes nous sur la compréhension de la croissance secondaire des arbres des forêts tropicales ? Et pour finir, (iv) Quelles perspectives pour la forêt guyanaise ?

1 Importance de la mortalité dans les bilans de carbone

1.1 Quelles échelles spatio-temporelles d'étude ?

Dans cette thèse, nous avons mis en évidence que le dispositif de Paracou était suffisamment grand et suivi depuis assez longtemps pour donner des

estimations fiables des paramètres statiques et dynamiques de la forêt. Cinq parcelles de 6.25 ha sont nécessaires pour estimer la moyenne du taux de mortalité, sur une période 16 ans, avec un coefficient de variation de 20 % sur la moyenne. Ce travail préliminaire a permis ensuite de quantifier les flux de carbone des parcelles témoins de Paracou en tenant compte de la fiabilité de nos estimations. Suite à cette analyse, nous avons montré qu'à Paracou le bilan de carbone était positif ce qui était concordant avec les observations faites sur le reste de l'Amazonie (Phillips *et al.*, 2009). L'analyse fine des flux réalisée dans le 2^{ème} article du chapitre 1 révèle cependant que le flux est positif en l'absence d'évènement de mortalité de gros arbres. Les arbres de plus de 40 cm portent en effet 50% de la biomasse d'une parcelle de Paracou (Rutishauser *et al.*, 2010). Lorsque les bilans sont négatifs à l'échelle d'une parcelle cela s'explique par des événements ponctuels de mortalité de gros arbres. Les résultats de cette analyse vont dans le sens de l'hypothèse de la régénération après perturbation (Chave *et al.*, 2008; Korner, 2003; Muller-Landau, 2009; Wright *et al.*, 2005). Il reste encore à vérifier l'hypothèse de la fertilisation due à l'augmentation de la concentration en CO₂, mais à Paracou nous n'avons pas encore assez de recul sur les mesures de concentration atmosphérique en CO₂ pour pouvoir les lier aux accroissements des arbres (mesures uniquement depuis 2008-2009). Comprendre comment les événements de mortalité interviennent apparaît de première importance pour les bilans de biomasse. A ce jour, plusieurs études mettent en évidence que la sécheresse en forêt tropicale peut engendrer des taux de mortalité plus élevés mais les détails sur les espèces les plus touchées restent très parcellaires (Allen *et al.*, 2010; Nepstad *et al.*, 2007; Phillips *et al.*, 2009). Comprendre ces réponses spécifiques permettrait de mieux prédire la réponse des forêts tropicales aux différents scénarios climatiques attendues en terme de dynamique, de bilan de carbone et de changement de composition.

1.2 Comment modéliser la mortalité

Il existe trois causes de mortalité pour les arbres en forêt tropicale : la mort sur pied (l'arbre meurt et reste debout), la mort par chablis primaire

(l'arbre tombe) et la mort par chablis secondaire (l'arbre tombe à cause de la chute d'un autre). Respectivement, ces trois causes représentent 50%, 30% et 20% de la mortalité à Paracou. Pour les deux premières causes, d'autres individus ne sont pas à l'origine de la mort de l'arbre, pour la dernière cause, la mort est due à un autre arbre.

Certaines relations entre la topographie, les conditions édaphiques et les taux de mortalité ont déjà été mises en évidence en forêt tropicale et particulièrement en Amazonie. Les résultats de ces études montrent que le taux de chutes d'arbres, mort par chablis, est deux fois plus important sur les pentes (Ferry *et al.*, 2010). Toledo *et al.* (2011) ont observé que les taux de mortalité étaient plus élevés sur les sols fertiles (augmentation du turn-over), sur les pentes raides et sur les sols sableux dans la vallée que sur les plateaux où les sols sont bien drainés et argileux. Les effets du sol et de la topographie étaient augmentées après les orages. De plus, la relation entre type de sol, topographie et mortalité dépendrait du diamètre des arbres (Toledo *et al.*, 2011). Parmi les variables climatiques qui ont un effet sur la mortalité des arbres en forêt tropicale, on trouve le manque d'eau (Nepstad *et al.*, 2007) et le vent (Gleason *et al.*, 2008). L'effet de ce dernier est plutôt important pour les régions soumises aux cyclones.

Afin de prédire les événements de mortalité et de disposer d'un outil pour la simulation de peuplement, il reste à développer un modèle de mortalité des arbres. Dans un premier temps le modèle pourrait être au niveau spécifique et ensuite au niveau communauté en utilisant les traits fonctionnels avec la même approche que le modèle de croissance développé par Hérault *et al.* (2011). Pour l'analyse des causes de la mortalité, la principale difficulté est que la variable qui serait la plus liée à la mortalité, l'âge, est inconnue. Ceci oblige à raisonner avec la seule donnée généralement disponible, le DBH, c'est-à-dire le diamètre du tronc à 1.30 mètre du sol, de chaque individu. Il existe des modèles pour estimer l'ontogénie de l'arbre, l'endroit où il se trouve dans son développement, à partir du ratio DBH/(diamètre maximum de l'espèce) ou encore avec un modèle de croissance (Hérault *et al.*, 2011, 2010). A Paracou, on a peu de recul sur la mortalité avec un peu moins de 20% des arbres qui sont morts depuis 1984. C'est peu pour des analyses

de survie. Pour modéliser simplement la mortalité, deux options existent, soit faire un modèle basé sur un processus aléatoire (l'arbre qui meurt est tiré au hasard dans le peuplement), soit un modèle basé sur l'ontogénie (la probabilité de mourir de l'arbre varie en fonction de son âge). Pour l'instant notre hypothèse pour Paracou est que l'ontogénie est le facteur principal de mortalité, figure 13.

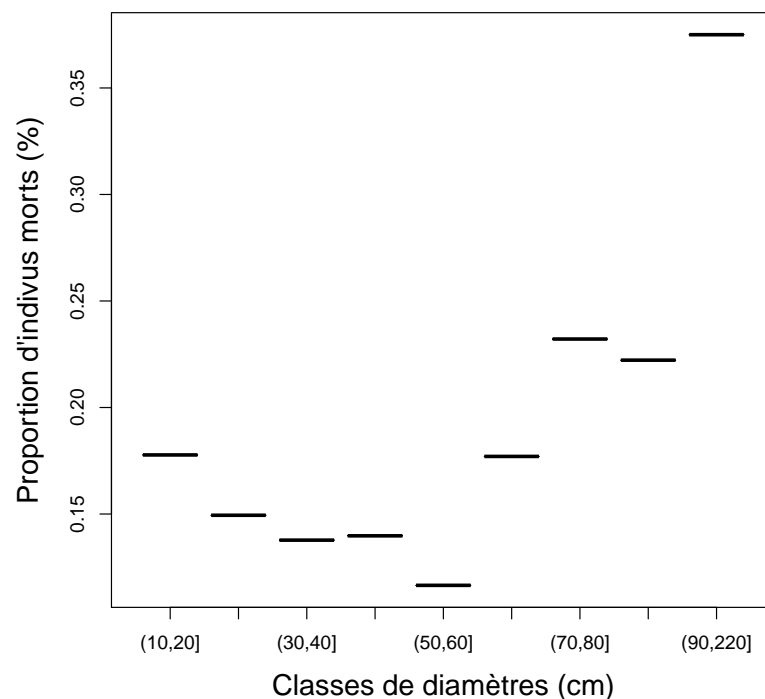


FIGURE 13 – Proportions d'arbres morts par classes de diamètres pour le dispositif de Paracou sur la période 1984-2009

Cette hypothèse est conforme avec les observations où le risque de mourir suit une courbe en forme de 'U', figure 13. Le risque, élevé à la naissance, diminue pour ensuite se stabiliser, jusqu'à ce que la sénescence intervienne, et que le risque recommence alors à augmenter. Dans la figure 13, l'ontogénie de chaque espèce n'est pas prise en compte mais on peut s'attendre à ce que chaque espèce ait sa propre courbe et il devrait être possible de modéliser

cette courbe en U pour chaque espèce en fonction des traits fonctionnels à la manière du modèle de croissance de Hérault *et al.* (2011). Plusieurs traits fonctionnels sont candidats à un rôle dans la mort de l'arbre, le diamètre, la hauteur maximum, le rapport entre le diamètre et le diamètre maximum de l'espèce (indicateurs du stade ontogénique), la densité du bois et les traits indicateurs de l'utilisation des ressources. Ces derniers sont impliqués dans la stratégie de croissance de l'espèce et cette stratégie devrait être reliée à la vigueur de l'arbre. Au final, ce modèle pourrait être intégré dans un simulateur de peuplement, pour obtenir des simulations réalistes de la dynamique forestière, dans tous les cas plus proches des données que celle produite uniquement par un processus aléatoire.

2 Comment comparer des sites ?

Pour étudier la croissance en forêts tropicales, la plupart des études utilisent un ou deux sites ce qui rend les résultats difficiles à généraliser. De plus, il est difficile d'établir les liens de causalité entre climat et croissance parce que les variables climatiques sont très corrélées en intra-sites. Chaque étude amenant un résultat sur la croissance devrait être replacée dans son contexte climatique. Un problème apparent provient de l'interprétation des résultats. Par exemple à La Selva, au Costa Rica, un mois avec moins de 50 mm de pluie est un événement exceptionnel alors qu'en Guyane, cet événement arrive tous les ans. Dans ce contexte, il semble difficile de généraliser l'effet direct de la sécheresse sans prendre en compte le fait que les arbres sont adaptés aux conditions environnementales locales. Pour illustrer ces problèmes, j'ai replacé certaines études d'Amérique du Sud et d'Amérique centrale citées dans cette thèse sur des cartes de pluviosité annuelle et du nombre de mois où les précipitations sont inférieures à 100 mm, figure 14 et figure 15.

Les recherches sur la croissance sont concentrées sur des dispositifs de suivi permanent, et qui, même s'ils sont tous en milieu tropical, montrent une forte hétérogénéité climatique. Les quantités de pluie varient de plus de 1000 mm par an, pour La Selva et Paracou par exemple, avec une saisonnalité propre à chaque endroit. Un travail de méta-analyse et la création

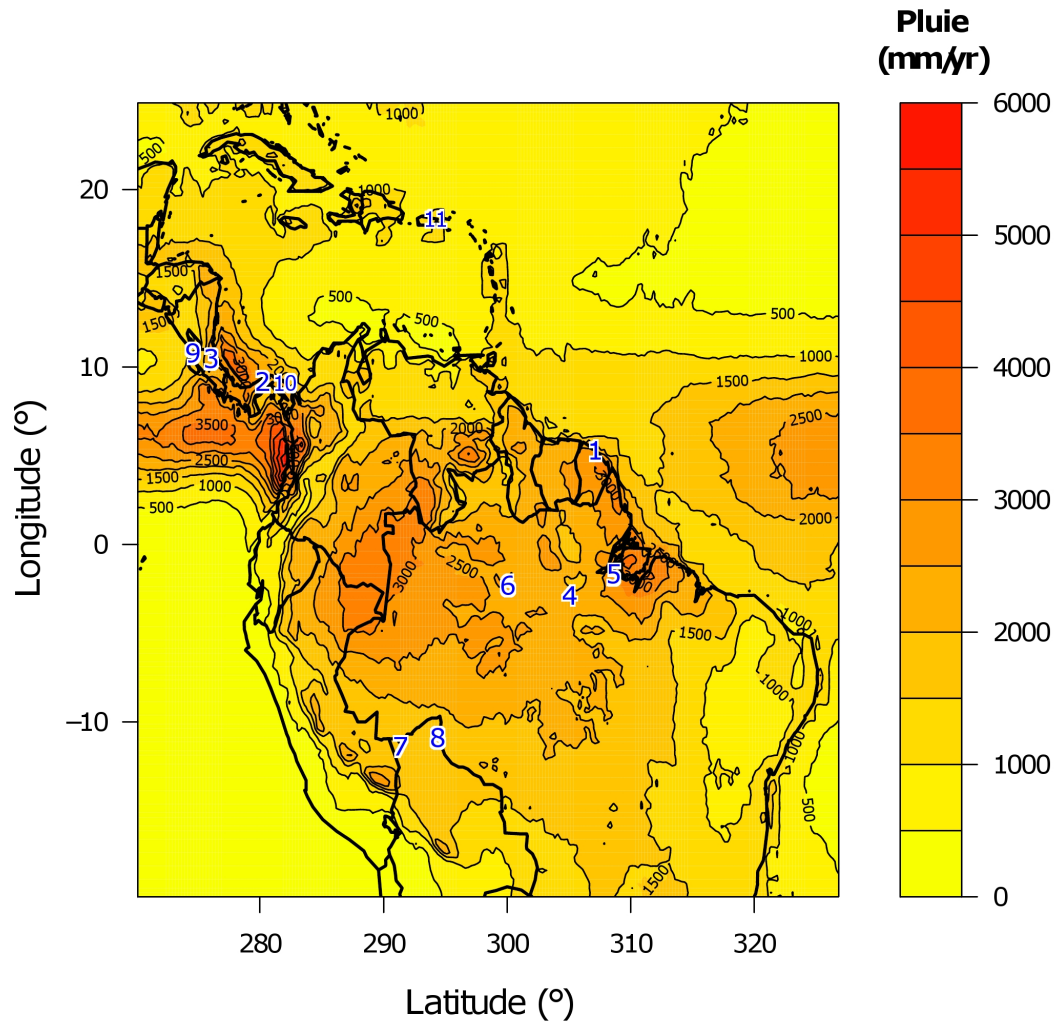


FIGURE 14 – Localisation des sites d'études sur la croissance en Amérique du Sud et Centrale, et isoclines de précipitations annuelles (données TRMM). 1 : Paracou (Guyane Française), 2 : Barro Colorado Island (BCI, Panama), 3 : La Selva (Costa Rica), 4 : Tapajós National Forest (Brésil), 5 : Caxiuanã National Forest (Brésil), 6 : Biological Dynamics of Forest Fragments Project (BDFFP, Manaus, Brésil), 7 : propriété privée Purisima (50 km de Cobija, Bolivie), 8 : concessions sylvicoles (40 km de Riberalta, Bolivie), 9 : Aire de Conservation Guanacaste (ACG, Costa Rica), 10 : Parque Natural Metropolitano (Panama), 11 : Luquillo Experimental Forest (Puerto Rico).

d'indices climatiques intégrant le fonctionnement de la plante, à la manière du REW, devraient permettre de mieux regrouper les connaissances provenant autant de données dendrochronologiques que de suivi dendrométriques. La plupart des variables climatiques sont disponibles par des mesures satellites et aujourd'hui les outils informatiques sont de moins en moins limitants pour permettre la création d'indices climatiques adaptés pour les plantes à une échelle inter-tropicale ou mondiale (Nemani *et al.*, 2003; Seneviratne *et al.*, 2006, 2010).

Les données satellitaires pourraient permettre de faire le lien entre les sites. Par exemple, l'estimation de la pluie pourrait être faite par les données de la Tropical Rainfall Measurement Mission (TRMM) et l'estimation de l'eau du sol par les données du Gravity Recovery and Climate Experiment (GRACE). Les données TRMM sont des estimations des précipitations modélisées par une combinaison de mesures satellites depuis novembre 1997. Ces données permettent d'estimer les précipitations à différents pas de temps (au minimum 3h) et par surface (la plus fine résolution est $0.25 \times 0.25^\circ$). Ces données ont servi à la réalisation des figures 14 et 15. Les deux satellites de GRACE mesurent les variations dans le temps de la gravité terrestre. Ces données permettent de cartographier les ressources en eau et leurs disponibilités. La comparaison entre les données des satellites GRACE (valeur mensuelle, données de résolution $1 \times 1^\circ$ soit 111 km de côté à l'équateur et filtrées par un filtre gaussien de 300 km de largeur) et le REW modélisé à Paracou montre des similitudes encourageantes, figure 16. La donnée pour un pixel GRACE est soustraite à la valeur moyenne du pixel sur la période, ce qui explique le centrage sur zéro. Il faudrait avoir la valeur brute pour pouvoir extrapoler à des endroits où le REW n'est pas disponible. Le REW est plus sensible en condition sèche, ceci est dû à une grande importance des couches de surface dans son calcul (Wagner *et al.*, 2011). La diminution de l'eau en saison sèche mesurée par les satellites de GRACE est beaucoup plus progressive. Pour une review récente des moyens pour estimer l'eau dans le sol à partir de ce type de données et de leurs limites, voir Seneviratne *et al.* (2010). Malgré leur résolution relativement élevée $0,25^\circ$ pour TRMM et 1° pour GRACE, ces données pourraient constituer une alternative pour accéder

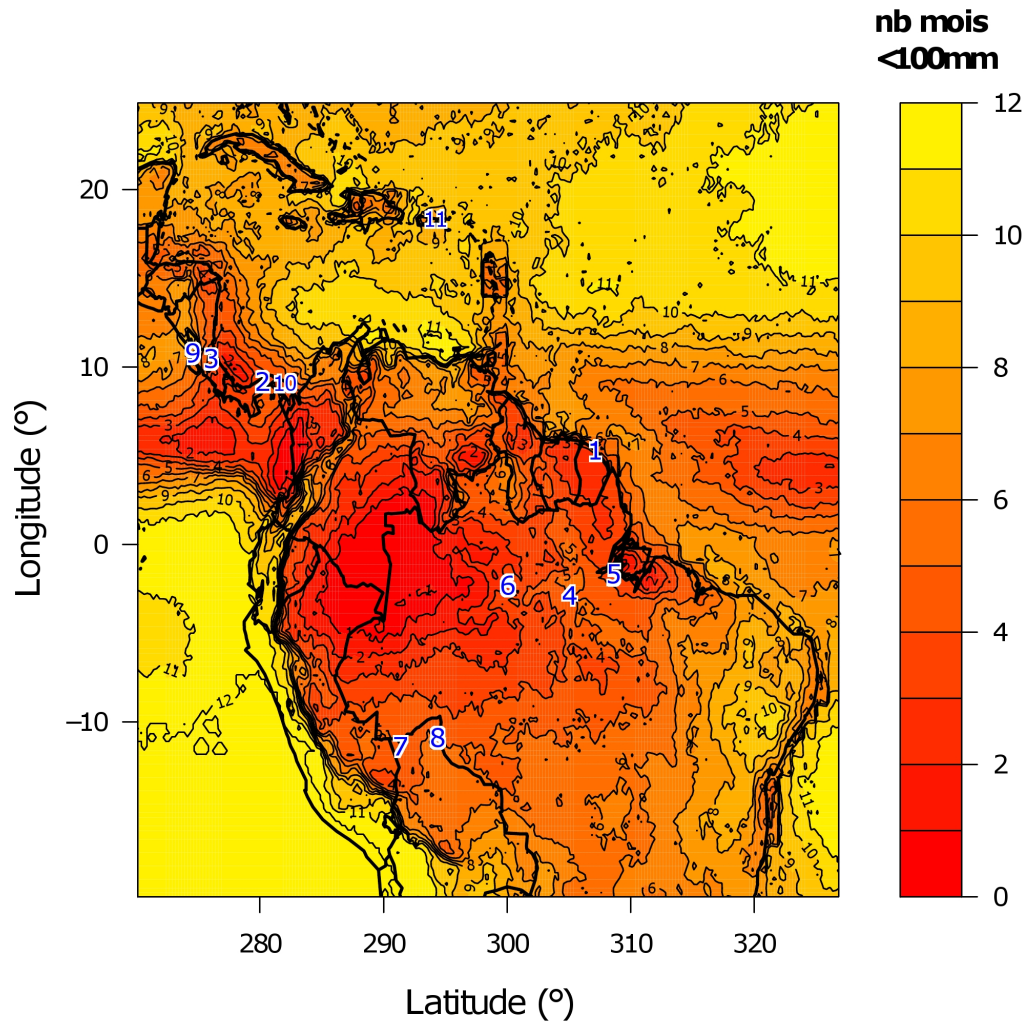


FIGURE 15 – Isoclines du nombre de mois où les précipitations sont inférieures à 100 mm (données TRMM). 1 : Paracou (Guyane Française), 2 : Barro Colorado Island (BCI, Panama), 3 : La Selva (Costa Rica), 4 : Tapajós National Forest (Brésil), 5 : Caxiuanã National Forest (Brésil), 6 : Biological Dynamics of Forest Fragments Project (BDFFP, Manaus, Brésil), 7 : propriété privée Purisima (50 km de Cobija, Bolivie), 8 : concessions sylvicoles (40 km de Riberalta, Bolivie), 9 : Aire de Conservation Guanacaste (ACG, Costa Rica), 10 : Parque Natural Metropolitano (Panama), 11 : Luquillo Experimental Forest (Puerto Rico).

à l'information sur les quantités de précipitations, la saisonnalité de ces précipitations et l'eau disponible pour les plantes dans le sol et ainsi construire des indices climatiques adaptés pour tous les sites forestiers inter-tropicaux.

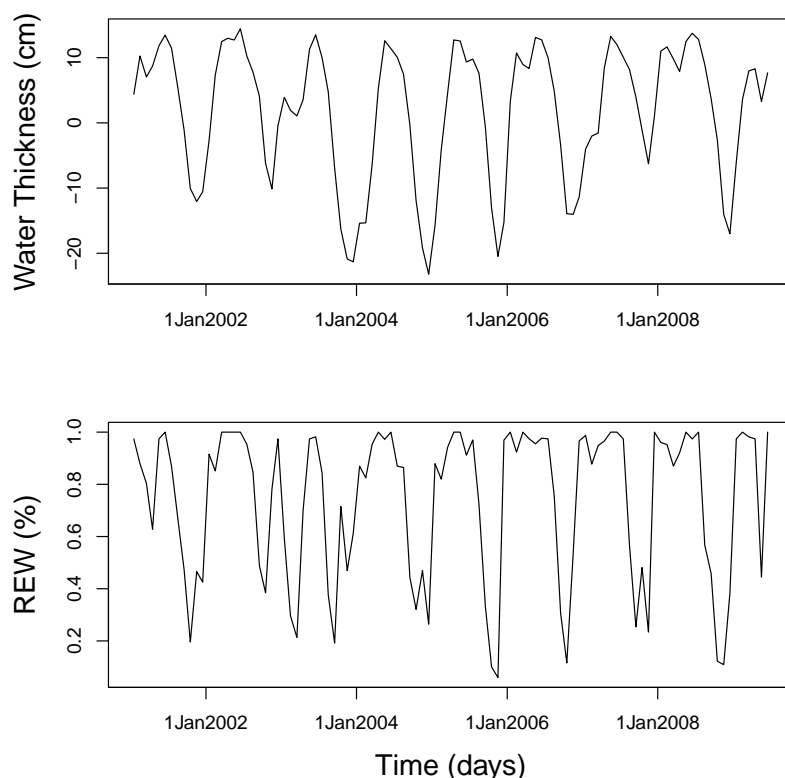


FIGURE 16 – Quantité d'eau dans le sol mesurée par les satellites de la mission GRACE et estimation de l'eau disponible pour les arbres avec le modèle de bilan hydrique (Wagner *et al.*, 2011)

3 Croissance et Climat

3.1 Où en sommes nous ?

Cette étude a mis en évidence le déroulement saisonnier de la croissance à Paracou et nous avons montré qu'une part proche de 10% de la variation observée de la croissance était due au climat. Pour les espèces étudiées, la période de croissance en diamètre des arbres s'étend de fin novembre/début

décembre à fin juillet/début août, figure 17. Pendant cette période, la quantité d'eau disponible dans le sol est toujours suffisante pour les arbres. Cette période correspond à la succession : petite saison des pluies/petit été de mars/grande saison des pluies. L'effet de la période plus sèche en mars n'est pas ressorti sur les croissances diamétriques.

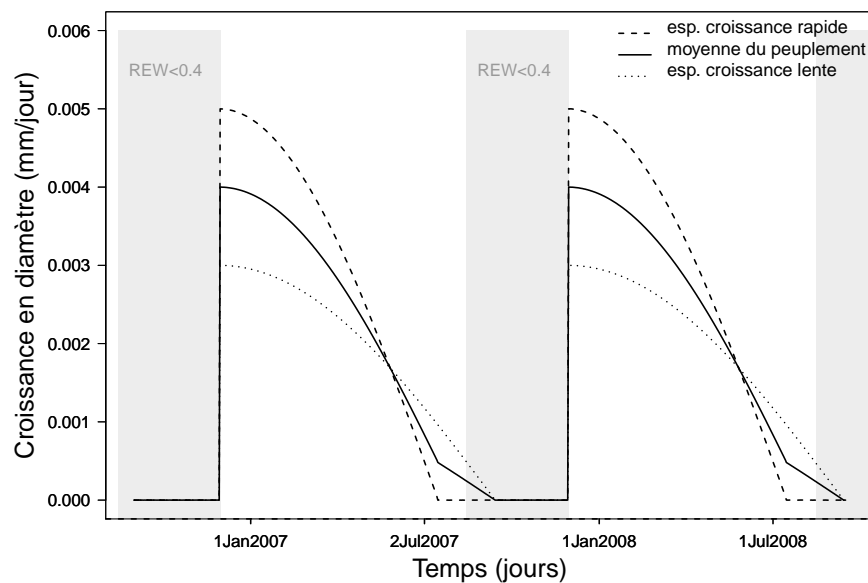


FIGURE 17 – Schéma de synthèse de la croissance en diamètre des arbres de Paracou

Facteurs climatiques de l'arrêt de croissance

La période pendant laquelle les diamètres ne montrent aucune croissance est la période où l'eau disponible dans le sol descend en dessous d'un seuil critique pour l'arbre ($REW < 0.4$). Cette période correspond à la grande saison sèche (août-novembre), lorsque la zone intertropicale de convergence (ZIC) se déplace au nord de la Guyane (Bonal *et al.*, 2008). Même en considérant un effet du gonflement ou du rétrécissement des troncs (Stahl *et al.*, 2010), la période pendant laquelle l'arbre ne grandit pas en diamètre est bien visible dans les données (Wagner *et al.*, soumis). Nous avons montré que des niveaux bas de REW constituent le principal facteur de la diminution voire de l'arrêt

de la croissance. Ce résultat montre l'influence principale de la disponibilité en eau du sol pour les arbres sur les processus biologiques associées à la croissance secondaire chez les espèces de forêts tropicales, notamment la division cellulaire du cambium. Dans une étude récente concernant quatre espèces de forêts tropicales (*Podocarpus falcatus*, *Pinus patula*, *Prunus africana* et *Celtis africana*) en Éthiopie (précipitations annuelles 1121 mm et forte saisonnalité), Krepkowski *et al.* (2011) ont montré que la saison sèche entraîne une dormance du cambium. Dans cette étude, les auteurs ont pu différencier la croissance due au gonflement des troncs et celle due à la formation des cellules puisqu'ils ont combiné des données d'anatomie du bois et des mesures avec des dendromètres automatiques. Le gonflement des tiges intervient de façon synchrone pour tous les arbres étudiés sur une période de l'ordre de quelques jours seulement. Les auteurs ont suggéré que les espèces étudiées pouvaient mettre en marche ou arrêter la croissance cellulaire du tronc en moins d'un mois.

Cet arrêt de la croissance de l'arbre en saison sèche pourrait être due à la limitation en eau du sol alors que l'évapotranspiration potentielle est toujours très élevée. Elle est supérieure à 100 mm.mois^{-1} (Roche, 1982) et elle augmente en saison sèche en lien avec le cycle solaire annuel (Hasler & Avissar, 2007). Pendant cette saison, le peuplement arrive à maintenir ses fonctions de base, la diminution de la productivité primaire brute n'est au maximum que de 20% de la productivité primaire brut observée en saison humide (Bonal *et al.*, 2008; Goulden *et al.*, 2004). Les arbres n'investiraient plus les produits de la photosynthèse dans la croissance secondaire mais plutôt dans des réserves, dans la croissance primaire (ramification et production de feuilles) et dans les organes reproductions (Kozlowski, 1992; Nepstad *et al.*, 2002). En effet, le pic de chute des feuilles intervient de juillet à septembre et la phase défeuillée dure en moyenne 20 jours par arbre. La plus grande partie de la production de nouvelles feuilles se fait pendant la saison sèche (Loubry, 1994). Dans cette dernière étude, l'auteur a observé en Guyane que la chute des feuilles précède directement le débourrement des bourgeons et qu'il n'existe pas de phase de repos végétatif.

Pourquoi la croissance varie dans le temps ?

A Paracou, la croissance en diamètre des arbres se produit entre novembre et août. La cinétique de la croissance est assez similaire à ce qui est observé pour d'autres dispositifs en forêt tropicale (Clark *et al.*, 2010; Goulden *et al.*, 2004; Nepstad *et al.*, 2002; Rice *et al.*, 2004). Elle commence par un pic de croissance les premières semaines de la saison des pluies. Nous ne savons toujours pas si ce pic de croissance est dû à une reprise de croissance cambiale ou un gonflement de l'écorce ou, ce qui est le plus probable, une combinaison des deux (Krepkowski *et al.*, 2011; Stahl *et al.*, 2010). Dans les deux cas, l'origine de ce pic est l'eau disponible. Un autre phénomène pourrait s'ajouter à l'explication de ce pic de croissance, c'est la libération d'un important pool de nutriments accumulés lors de la saison sèche et rendus disponibles par l'action des premières pluies (Anaya *et al.*, 2007).

Après les premières semaines de saison des pluies, la croissance en diamètre montre une diminution progressive alors que la disponibilité en eau est relativement constante. A la fin de la saison humide, les accroissements en diamètre diminuent fortement et parfois s'arrêtent avant que l'eau disponible n'ait atteint un seuil critique. Cette diminution au cours de la saison sèche se retrouve dans d'autres études (Goulden *et al.*, 2004; Nepstad *et al.*, 2002; Rice *et al.*, 2004). Notre hypothèse est que cette décroissance est liée à un phénomène associé à la quantité de lumière ou à la photopériode, c'est la seule variable climatique qui varie pendant cette période. Le phénomène à l'origine de cette décroissance pourrait être la phénologie. Certains auteurs suggèrent que la lumière détermine le moment de la chute des feuilles en forêt tropicale saisonnière et asaisonnière (Hutyra *et al.*, 2007; Myneni *et al.*, 2007; Zalamea & Gonzalez, 2008). A Paracou, la production de litière montre un pic vers le mois de septembre, quand l'irradiance est au maximum (Bonal *et al.*, 2008; Pennec *et al.*, 2011), bien que cette production reste élevée toute l'année (Bonal *et al.*, 2008; Chave *et al.*, 2009b). L'augmentation progressive de la chute des feuilles avant le pic de septembre pourrait expliquer la diminution progressive de la croissance et traduire un changement dans le fonctionnement de l'arbre. Des recherches sont nécessaires pour améliorer le lien entre

cette diminution de la croissance et la phénologie. En effet cette période où les feuilles tombent pourrait être interprétée comme une période où la forêt change son fonctionnement, mais c'est à cette période que sont renouvelées les feuilles et l'indice Enhanced Vegetation Index (EVI), qui reflète l'indice de surface foliaire (surface totale des feuilles par surface de sol, Leaf Area Index, LAI) atteint ses valeurs les plus fortes (Pennec *et al.*, 2011). Les variations de croissance pourraient être dues à un changement d'allocation des ressources dans l'arbre qui passe de la croissance secondaire à la croissance primaire en juillet/août pour la saison sèche et de la croissance primaire en saison sèche à la croissance secondaire lorsque les pluies reprennent. La première transition pourrait être contrôlée par la lumière/photopériode comme observé en Guyane par Loubry (1994) et la seconde transition par la disponibilité en eau. Au niveau individuel, certains facteurs environnementaux peuvent montrer des variations intra-annuelles et entraîner indirectement des modifications dans la croissance de l'arbre, c'est le cas de la compétition pour la lumière et pour les nutriments (Hérault *et al.*, 2010; Ruger *et al.*, 2011; Uriarte *et al.*, 2004). Le rôle de la température dans cette dynamique de la croissance à une échelle saisonnière n'apparaît pas comme un facteur déterminant à Paracou.

Qui pousse le mieux ? et quand ?

Certains traits fonctionnels sont associés à la réponse de la croissance au climat. La variable climatique qui ressort le mieux dans nos analyses est le stress hydrique. Cela conforte l'idée que l'eau disponible est l'élément principal de la dynamique de la croissance en diamètre. Après l'eau disponible, la lumière ressort dans ces analyses, mais dans un sens contradictoire avec le sens biologique. De fortes périodes d'insolation sont associées à une diminution de croissance. Ceci s'explique par la corrélation très importante entre la lumière et le manque d'eau dans le sol. Le lien avec la phénologie reste à confirmer. Le diamètre de l'arbre et la taille maximum de l'espèce sont des indicateurs de la réponse à la sécheresse en terme de croissance diamétrique. Plus les arbres sont grands et gros plus leur demande en eau est importante (Granier *et al.*, 1996). Lorsque ces arbres deviennent émergents, ils sont sou-

mis à des conditions plus sèches dans la canopée (Poorter *et al.*, 2008). De plus, la réponse en terme de croissance des arbres apparaît comme associée au 'leaf economic spectrum' défini par Wright *et al.* (2004). Les espèces dont la stratégie correspond à un cycle de vie rapide et à un retour rapide sur l'investissement utilisent mieux les ressources et poussent plus quand celles-ci sont disponibles, mais elles sont plus sensibles en cas de manque. À l'inverse, les espèces qui investissent les ressources sur le long terme sont moins sensibles aux variations de leurs disponibilités. Cela se traduit par une période de croissance un peu plus longue en début de saison sèche pour les espèces qui investissent sur le long terme. La stratégie de croissance des plantes reste toutefois peu explicative de la croissance bien que nos résultats soient globalement dans le sens des hypothèses *a priori*, figure 17. Ce manque d'explicativité résulte certainement de la courte période où s'exprime ces différences de stratégies, pendant les périodes de transitions entre les saisons.

3.2 Que faut-il chercher ?

En écophysiologie

En 2007, Clark (2007a) proposaient un agenda en 5 points des recherches à mener en priorité pour comprendre comment les forêts tropicales ont été affectées par les changements climatiques dans le passé et comment elles vont répondre à l'intensification vraisemblable des changements environnementaux dans le futur. Le troisième point de ce programme propose une attaque frontale sur la physiologie des plantes tropicales. L'étude de la croissance proposée dans cette thèse se place dans ce cadre en tentant de relier la croissance en diamètre et les facteurs climatiques. Cependant, ici, nous n'avons pas exploré le lien entre les variables climatiques et les processus qui se déroulent directement dans la canopée. Un autre travail de l'équipe a permis de relier certains processus physiologiques à la disponibilité en eau. Ce travail est en Annexe 1 et il a été soumis pour publication dans *Biotropica* courant octobre 2011. L'originalité de ce travail est de relier quantitativement des processus écophysiologiques avec des variables climatiques dont le REW, c'est une première en milieu tropical. Les principaux résultats de ces recherches montrent

une diminution de la photosynthèse, de -54.1% à -14.6% suivant les espèces, associée à la diminution de l'eau disponible dans le sol. Cette tendance n'est pas observée pour la respiration foliaire. Ces relations ont des implications pour les bilans de CO₂ en saison sèche. La diminution de la photosynthèse (absorption de CO₂), alors que la respiration reste constante (émission de CO₂), déséquilibre les flux et le bilan de carbone peut devenir positif en saison sèche. De plus dans cette étude, nous avons également montré une association entre la disponibilité en eau et les flux de sève. Le déterminant principal de ces flux de sève est la lumière. La disponibilité en eau est un déterminant secondaire important. Le flux de sève est diminué lorsque la disponibilité en eau diminue.

Actuellement seules des mesures de suivi des cellules du cambium permettent de mettre en évidence l'arrêt de la croissance cellulaire des troncs sans prendre en compte le gonflement de l'écorce (Krepskowski *et al.*, 2011). Ces auteurs ont montré que le gonflement intervenait de façon très similaire dans le temps chez les quatre espèces de leur étude. Dans notre analyse, le gonflement des troncs n'apparaît pas associé à l'épaisseur de l'écorce (pas d'effet significatif de l'épaisseur de l'écorce sur la croissance en début de saison humide). En faisant l'hypothèse que tous les arbres sont soumis à un gonflement/rétrécissement similaire, et uniquement lié au diamètre et à la saison, il reste à développer un modèle dépendant de la pluie pour avoir accès à cette 'vraie' croissance cambiale et confirmer nos interprétations de l'effet du climat sur la croissance en diamètre.

En Guyane, deux thèses sont actuellement en cours (Hélène Morel et Thomas Mangenet) dans lesquelles plusieurs espèces aux comportements de croissance différents font l'objet de suivis de phénologie, de croissance primaire (ramification) et de croissance secondaire (suivi de la croissance des cellules du cambium des troncs). Leurs résultats devraient permettre de mieux comprendre les stratégies d'allocation de biomasse (croissance primaire, la croissance secondaire, la ramification et la reproduction) et l'influence du climat (saisonnalité et variation inter-annuelle).

En phénologie

Nos résultats suggèrent l'existence d'un lien entre la lumière (ou la photopériode), la phénologie et la croissance secondaire. Il semblerait que la lumière puisse être le déterminant de la croissance primaire en saison sèche (Détienne & Barbier, 1988; Loubry, 1994) et jouer un rôle dans la diminution de la croissance secondaire en fin de saison humide. La phénologie est un paramètre peu précis et difficile à acquérir sur le terrain. L'apport de l'imagerie par satellite à l'analyse de la phénologie au niveau de la communauté constitue une alternative prometteuse. Récemment, Huete *et al.* (2006) ont observé une augmentation de la capacité photosynthétique du couvert en Amazonie avec un indice provenant de données satellites des capteurs Moderate Resolution Imaging Spectroradiometer (MODIS), l'Enhanced Vegetation Index (EVI) qui reflète la capacité photosynthétique du couvert. Un arrêt de la croissance secondaire est généralement observé au cours de la saison sèche (Goulden *et al.*, 2004; Rice *et al.*, 2004; Wagner *et al.*, 2010). Ceci contraste avec les prédictions des données d'EVI qui prévoient une augmentation de la productivité lors de la saison sèche. En Guyane, cet indicateur a récemment été utilisé (Pennec *et al.*, 2011). Ces auteurs ont montré que l'augmentation de la capacité photosynthétique du couvert démarrait au début de la saison sèche et se maintenait durant quelques semaines après le début de la saison des pluies, figure 18.

La phénologie en Guyane montre une rythmicité pour la chute des feuilles. Les pics de chute de litières ont lieu sur la période juillet-août-septembre (Bonal *et al.*, 2008; Loubry, 1994; Sabatier & Puig, 1986) et les feuilles sont renouvelées rapidement, généralement en moins de 20 jours (Loubry, 1994). Ce phénomène pourrait expliquer cette séparation dans le temps, avec un cycle de type croissance primaire qui commence en saison sèche suivi du démarrage de la croissance secondaire au début de la saison des pluies. Il serait intéressant de relier des données satellitaires, données de phénologie, mesures de photosynthèse du couvert et mesures diamétriques, pour améliorer la compréhension du fonctionnement de l'arbre, notamment sur la croissance primaire et la séparation dans le temps de la croissance primaire et secondaire

3. CROISSANCE ET CLIMAT

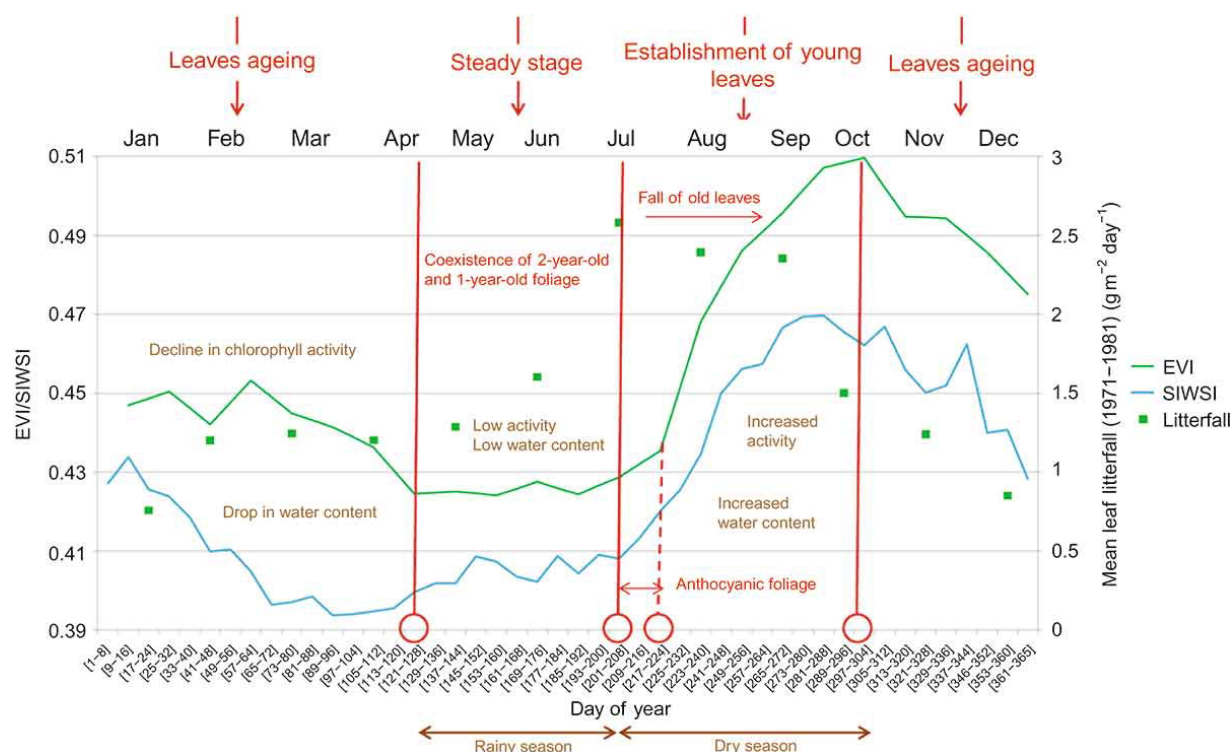


FIGURE 18 – Phénologie par mesures EVI et classes de litières des forêts de Guyane à canopée haute et régulière, du même type que Paracou (types forestiers définis dans Gond *et al.* (2009)), tiré de Pennec *et al.* (2011)

(Volland-Voigt *et al.*, 2011; Xiao *et al.*, 2006).

Sous terre

Une autre inconnue demeure : l'utilisation de l'eau par les racines. Dans le modèle d'eau disponible dans le sol, nous avons fait l'hypothèse que la capacité à extraire de l'eau est corrélée à la densité des racines. Peu d'études ont évalué la distribution verticale des racines chez les arbres de forêts tropicales mais les observations ont toutes montrées une densité de racine distribuée selon une exponentielle négative (Bonal *et al.*, 2000; Fisher *et al.*, 2007; Humbel, 1978). Les observations de diminution de l'eau dans le profil 0-260 cm à Paracou, au cours de la saison sèche, correspondent bien à cette distribution de racine. Un problème reste cependant irrésolu : en saison sèche, les observations de flux de sève montrent que certains arbres sont

encore capables d'extraire jusqu'à 250 litres d'eau par jour (Granier *et al.*, 1996). Plusieurs études ont mis en évidence des déplacements d'eau provoqués par les racines la nuit. Ces déplacements amènent de l'eau aux racines qui se trouvent dans des horizons en déficit d'eau (Lee *et al.*, 2005; Lee & Boyce, 2010; Oliveira *et al.*, 2005; Romero-Saltos *et al.*, 2005). Le déplacement vers les horizons supérieurs (remontée hydraulique ou 'hydraulic lift') a lieu en saison sèche et le déplacement vers le bas a lieu en saison humide. Ces mouvements d'eau ont été mis en évidence par des mesures d'humidité du sol et des expériences avec de l'eau marquée au deutérium (H_2). Cette remontée de l'eau permettrait à l'ensemble de l'écosystème de maintenir une transpiration et un taux de photosynthèse élevé en saison sèche. En plus de ce phénomène, il n'est pas exclu que la remontée capillaire puisse amener de l'eau aux horizons supérieurs en cas de déficit (Markewitz *et al.*, 2010). Récemment, pour le dispositif de Tapajo au Brésil, où ont été mis en évidence ces phénomènes de remontées hydrauliques, a été développé un modèle permettant de quantifier la quantité d'eau remontée par les racines (Markewitz *et al.*, 2010). Ces auteurs ont montré que l'apport des remontées hydrauliques représentait 20% de la demande en eau pour les profondeurs de 250 à 550 cm et 10% de 550 à 1150 cm en conditions sèches. Wang *et al.* (2011) ont montré que si la remontée hydraulique par les racines pouvait augmenter la croissance et la transpiration pendant les saisons sèches 'normales' en Amazonie, elle pouvait aussi réduire la transpiration et la production primaire nette lors des événements de sécheresses extrêmes comme les événements El Niño en asséchant plus rapidement le sol. La remontée hydraulique de l'eau par les racines lors des événements extrêmes provoque une accélération de la diminution de l'humidité du sol dès les premières semaines de saison sèche. La quantité d'eau disponible se rapproche plus précocement du point de flétrissement permanent pour les horizons profonds et se trouve alors réduite pour le reste de la saison. Sans ce phénomène, l'utilisation de l'eau en profondeur par la plante serait plus limitée et les stocks diminueraient moins rapidement. A Paracou, l'analyse de la profondeur d'extraction de l'eau par les racines est en cours avec une expérience basée sur l'eau marquée à l'oxygène 18 (^{18}O) et au deutérium (^2H). Les résultats devraient permettre de mieux connaître

la profondeur à laquelle l'arbre puise l'eau en saison sèche et d'amener des données pour la modélisation de ce mécanisme.

Croissance individuelle et variabilité intraspécifique

Dans cette thèse, nous nous sommes focalisés sur les variations de croissance des arbres en réponse au climat. Dans nos modèles, nous avons utilisé un effet individuel pour observer uniquement l'effet des variations intra-annuelles du climat, mais la croissance individuelle de l'arbre dépend de beaucoup d'autres facteurs environnementaux. De plus, ce type d'analyse est difficile à réaliser avec des jeux de données conséquents parce que l'on s'approche de la capacité maximale de calcul des ordinateurs. Par exemple, l'estimation d'un effet individuel avec un modèle linéaire pour le jeu de données de Paracou (≈ 28000 arbres), nécessite d'estimer 28000 paramètres et d'inverser une matrice de 28000×28000 ce qui n'est pas faisable avec un ordinateur conventionnel. Il reste encore beaucoup de recherches à mener pour comprendre les liens entre croissance et environnement avant de pouvoir modéliser la croissance individuelle. Nous avons montré que la croissance individuelle pouvait être expliquée avec les valeurs de quatre traits fonctionnels de l'arbre (Hérault *et al.*, 2011). Ruger *et al.* (2011) ont quant à eux mis en évidence un effet de l'accès à la lumière sur la croissance au niveau spécifique. Ces développements sont récents et ils permettent d'expliquer une part de la variabilité de la croissance entre 10 et 35%. Avec l'effet du climat, on peut rajouter 10% d'explication de la variance. Il reste une part importante de la variabilité qui est due à d'autres phénomènes. Une partie de la croissance pourrait être due à des processus endogènes qui ne sont pas le résultat d'une interaction avec le climat. Ces processus endogènes comprennent la fructification et la floraison, ils pourraient expliquer une partie de la variance de la croissance (Loubry, 1994; Sabatier & Puig, 1986; Wright & Cornejo, 1990).

Actuellement dans nos modèles, nous utilisons une moyenne du trait pour plusieurs individus de l'espèce. Il serait important de pouvoir conserver la variabilité individuelle des traits dans l'analyse pour prendre en compte la

plasticité phénotypique. En effet, les traits fonctionnels, même s'il est admis qu'ils renseignent sur le fonctionnement de la plante, ont des valeurs très liés à l'ontogénie de l'arbre et peuvent présenter une plasticité phénotypique importante au sein même de l'individu. Il faut de nouveaux développements pour intégrer toutes ces informations dans les modèles. Vraisemblablement, les écologues se dirigent vers des modèles de communauté basés sur les traits pour prédire la réponse des écosystèmes aux conditions climatiques (McMahon *et al.*, 2011; Reu *et al.*, 2011). L'approche bayésienne devrait être d'une grande utilité pour rendre compte des effets hiérarchiques dans ce type de modèles.

3.3 Adaptation des arbres

Les résultats de cette thèse suggèrent que les arbres de forêts tropicales sont adaptés aux changements rapides des conditions environnementales, comme observés à Paracou. La période sèche entraîne une période de diminution de l'accroissement en diamètre mais son intensité n'influence pas la croissance annuelle de l'arbre. Bien que les arbres aient une période où ils cessent de croître en diamètre, il semblerait que quelques semaines de saison humide suffisent à produire la croissance en diamètre annuelle (pic de croissance en début de saison humide). La saison sèche actuelle ne semble donc pas représenter un stress important. Les arbres ne montrent pas de repos végétatif. L'arrêt de croissance en diamètre ne serait qu'une transition vers la croissance primaire et la mise en place de nouvelles feuilles. Baker *et al.* (2008) ont montré qu'ils parvenaient à modéliser les flux nets d'échanges annuels de l'écosystème en faisant l'hypothèse qu'il existe un stock d'eau du sol pour subvenir au besoin de la transpiration accessible par les racines en saison sèche. Cette étude semble montrer que les arbres ont accès à l'eau en quantité suffisante toute l'année. La croissance annuelle apparaît sans lien avec la durée ou l'intensité de la saison sèche, pourtant, sur la période d'étude, les saisons sèches se sont montrées très variables, REW<0.4 pendant 1.5 mois en 2007 et 2009 et 3.0 mois en 2008. Sans événement extrême, il semble difficile de voir un effet de la saison sèche sur la croissance. Dans ce contexte, il

faudrait disposer de nouvelles données, par exemple par des expériences de type exclusion des pluies (Nepstad *et al.*, 2002), et pouvoir simuler *in silico* l'impact des différents scénarios climatiques de l'IPCC (Solomon *et al.*, 2007) ou d'évènements extrêmes sur la dynamique de la forêt, avant que ces évènements n'arrivent. Ce travail passe au niveau de l'arbre par la modélisation des processus de l'arbre basés sur les connaissances écophysiologiques et au niveau du peuplement par les traits fonctionnels qui traduisent pour la communauté les processus sensibles au climat (Hérault *et al.*, 2011; McMahon *et al.*, 2011; Reu *et al.*, 2011; Verbeeck *et al.*, 2011).

4 Quels risques pour les forêts de Guyane ?

La Guyane française est placée en tête des régions du monde qui ont les plus forts pourcentages de couvert forestier avec une couverture forestière estimée en 2010 à 98% (FAO, 2010). Pour cette région les risques potentiels pour la forêt sont de deux ordres, les changements climatiques et les changements d'utilisation des terres (Asner *et al.*, 2010). La Guyane française se trouve cependant dans une situation privilégiée face à ces risques. En effet, une grande partie du territoire est protégée, figure 19, la plus grande zone protégée constituant le Parc Amazonien de Guyane. Ce parc a été créé en 2007, c'est la plus grande aire protégée sur le territoire français et européen. Il recouvre 3 390 000 hectares de forêt dans le sud de la région, sur une surface recouverte par la forêt estimée à 8 083 000 d'hectares (FAO, 2010). De plus, il est uniquement accessible par voie fluviale ou aérienne. Plusieurs autres zones de la région ont des statuts de protection. Tsayem-Demaze (2008) donne tous les détails de la mise en place du parc et des zones protégées.

Risques climatiques

La Guyane se trouve dans une zone où est attendu un impact fort du climat quels que soient les scénarios envisagés (Asner *et al.*, 2010; Malhi *et al.*, 2009). En Guyane, l'IPCC prévoit pour le siècle à venir une augmentation de 3.3 °C (2.6-3.7) des températures moyennes annuelles avec une



FIGURE 19 – Principales aires protégées en Guyane française en 2007

variation plus élevée pour les mois de juin/juillet/août, 3.5 °C (2.7-3.9) (21 modèles de simulation globaux, scénario A1B (Solomon *et al.*, 2007)). Le régime des précipitations risque de varier également, avec une augmentation de la pluviométrie de 4% (0-11) pour la période décembre/janvier/février et une diminution de 3% (-10-2) pour la période juin/juillet/août (Petit & Prudent, 2008). Ces conditions plus sèches et plus chaudes vont induire un

changement dans le fonctionnement des arbres et la dynamique de la forêt. Pour la croissance, l'impact n'est pas encore connu mais des conditions plus sèches vont très probablement entraîner des taux de mortalités plus élevés, comme observé dans la plupart des biomes (Allen *et al.*, 2010). En plus d'un risque direct sur le fonctionnement des arbres, l'impact des sécheresses sur les forêts de Guyane pourrait être amplifié par le feu. Chaque année des feux sont provoqués dans les savanes du littoral. Lors d'évènements très secs où l'inflammabilité de la forêt est augmentée, ces feux de savanes pourraient se propager à la forêt (Nepstad *et al.*, 2004). Il n'est pas exclu que ces feux aient déjà eu lieu par le passé. Des charbons retrouvés dans les sols de Guyane attesteraient de ces feux de grande ampleur dont la fréquence serait d'environ 2000 ans (Charles-Dominique *et al.*, 1998). De plus, certains modèles prévoient pour la période 2075–2099 que les émissions de carbone par les feux seront les plus importantes pour l'Amérique du Sud, à cause du changement climatique et du changement démographique (Kloster *et al.*, 2011).

Risques liés au changement d'utilisation des terres

La croissance démographique de la Guyane est parmi les plus forte de l'Union Européenne, +4% par an entre 1999 et 2007 (Jean *et al.*, 2007). Ce développement va amener à revoir l'aménagement du territoire à court terme. Plusieurs phénomènes portant atteinte à la forêt ou à son fonctionnement pourraient alors apparaître ou se renforcer dans ce contexte. Plusieurs liens existent entre l'utilisation du territoire et la dégradation de la forêt. L'ouverture de route est une cause bien connue de la dégradation de la forêt (Laurance *et al.*, 2009b). Cette ouverture facilite la colonisation, l'extraction de bois et la création de zone agricole qui participe à la dégradation et la fragmentation de la forêt. La pratique de la chasse est aussi favorisée par l'ouverture de routes. La chasse a des conséquences pour la régénération de la forêt notamment pour les espèces végétales ayant recours à des animaux chassés pour la dispersion des graines. La chasse peut entraîner une limitation de la dispersion et du recrutement de nouveaux individus chez ces espèces (Forget & Jansen, 2007). La pratique de l'orpaillage, illégal ou non, entraîne

la destruction locale de l'habitat forestier. En Guyane, l'orpaillage clandestin affecte les abords des fleuves y compris à l'intérieur du parc national. Les taux sans cesse en hausse du prix de l'once d'or (plus 300% depuis 2000) ne devraient pas ralentir les chantiers clandestins. Cependant, la déforestation reste limitée pour l'instant en Guyane, malgré une surface agricole multipliée par 3 en 20 ans, elle ne représente que 23176 ha en 2007 (INSEE, 2007). Cette déforestation pourrait contribuer aux variations climatiques de la région. En effet, à l'échelle de l'Amazonie, la déforestation entraîne un changement de répartition des précipitations, une amplification de la sécheresse et de la dégradation de la forêt (Betts *et al.*, 2008). De plus, les précipitations se redistribuent à l'échelle sub-continentale, et le sud de l'Amazonie devient plus humide au dépend des régions du nord (Medvigy *et al.*, 2011)

Vers des outils prévisionnels

Pour la Guyane, les décideurs vont se retrouver face à un compromis à court terme, développer leur territoire en aménageant la forêt et préserver les services environnementaux que cette forêt rend. L'intégration de toutes les connaissances dans un simulateur est en cours de réalisation dans le cadre du projet Guyasim (PO FEDER). Cet outil d'aide à la décision devrait permettre d'optimiser l'aménagement et le développement du territoire. Concrètement, le simulateur de la Guyane devrait offrir la possibilité de visualiser l'évolution probable à différents pas de temps et d'espace des cartes de répartition des services écosystémiques (stock de carbone, la beta-biodiversité ou fonctionnement du sol) suivant les différents scénarios envisagés par les décideurs politiques. Il sera aussi possible de calculer des prévisions globales pour la Guyane de ces indicateurs et éventuellement de les relier à des valeurs financières. En attendant que les bonnes décisions soient prises.

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Annexe A

Annexe

- 1 Influence of Seasonal Variations in Soil Water Availability on Gas Exchange of Tropical Canopy Trees

LRH: Stahl, Burban, Wagner, Goret, BompY, and Bonal

RRH: Effect of drought on canopy trees

Influence of Seasonal Variations in Soil Water Availability on Gas Exchange of Tropical Canopy Trees

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Abstract

Keywords: French Guiana; photosynthesis; rainforest; respiration; soil drought; transpiration; predawn leaf water potential

SEASONAL VARIATIONS IN ENVIRONMENTAL CONDITIONS (*i.e.* SOLAR RADIATION, RAINFALL, soil water content, vapour pressure deficit, ...) influence tropical rainforest ecosystem functioning (*i.e.* gross primary productivity, respiration, evapotranspiration) (Malhi *et al.* 2002, Goulden *et al.* 2004, Hutyra *et al.* 2007, Bonal *et al.* 2008). For instance, a strong decrease in ecosystem respiration was observed during dry periods at different sites in Amazonia (Hutyra *et al.* 2007, Bonal *et al.* 2008), while variations in gross primary productivity were less affected by seasonal variations in environmental conditions. Meanwhile, evapotranspiration at the ecosystem scale usually displayed the lowest values during rainy seasons and the highest values at the onset of the dry season (Hasler & Avissar 2007, Rollenbeck & Anhof 2007). Variations in incident solar radiation are one of the main cause of seasonal variations in photosynthesis and evapotranspiration (Graham *et al.* 2003, Hasler & Avissar 2007, Bonal *et al.* 2008, Renninger & Phillips 2010), but a decrease in soil water content or an increase in atmospheric vapour pressure deficit during dry periods also induce regulation processes of most CO₂ and H₂O fluxes between the different ecosystem compartments and the atmosphere (Bonal *et al.* 2000b, Renninger & Phillips 2010, Stahl *et al.* 2011).

Periods of highly reduced soil water content, such as the exceptional droughts that occur during the El Niño Southern Oscillation events (Malhi *et al.* 2008), not only influence ecosystem CO₂ and H₂O fluxes, but can also induce large tree mortality events at the regional scale (Phillips *et al.* 2009). In the context of global climatic changes, these patterns could result in dramatic changes in tree species composition and carbon and water balance of tropical rainforest ecosystems. In order to simulate these effects and to predict these changes, functional models have been developed (*e.g.* Williams *et al.* 1998, Fisher *et al.* 2006). These models require detailed information on the functional characteristics of the tree species

present in these ecosystems, as well on their potential response to changes in environmental conditions. A huge functional diversity in carbon (net photosynthesis, leaf or trunk respiration) and water flux (leaf transpiration), as well as in the trade-off between these fluxes (water and carbon use efficiency) among trees species in FTH has already been shown (Meinzer *et al.* 1993, Bonal *et al.* 2000b, Meir & Grace 2002, Meir *et al.* 2001, Cavaleri *et al.* 2008, Baraloto *et al.* 2010, Stahl *et al.* 2011). However, little information yet exists on the range of the response of tropical rainforest canopy trees to seasonal variations in environmental conditions. Most studies published so far were conducted on seedlings in common garden or on 10-20 years old trees in plantations (Baraloto *et al.* 2005, Bonal *et al.* 2000b, Engelbrecht *et al.* 2003, Kursar *et al.* 2009), and to our knowledge, very few studies evaluated the direct influence of seasonal variations in soil water content on canopy trees functioning. A decrease in sapflow density and thus in tree transpiration during dry periods was observed for a few species in Amazonia (Rollenbeck & Anhuf 2007, Renninger & Phillips 2010), although these variations were largely explained by seasonal variations in atmospheric conditions rather by soil conditions ones. Doughty (2011) showed a slight decrease in leaf gas exchange of a few canopy trees in Tapajos, Amazonia over the dry season. In a rain exclusion experiment conducted in Amazonia (Fisher *et al.* 2006), foliar respiration of most studied trees increased when soil drought conditions increased (Metcalf *et al.* 2010). Finally, a huge inter-specific variability in the response of tree trunk respiration to seasonal soil drought was observed in tropical rainforests, even though most trees displayed a reduction or no change in trunk respiration between the wet and the dry seasons (Nepstad *et al.* 2002, Stahl *et al.* 2011).

In order to characterize the influence of seasonal variations in soil water availability on the functioning of tropical rainforest canopy trees, we conducted a set of leaf gas exchange

and transpiration measurements over two years in a tropical rainforest in French Guiana. We were able to access the sunlit leaves of 13 canopy trees using ropes attached to the trees and to the Guyaflux tower, a 55-m high tower set up in the tropical rainforest in French Guiana (Bonal *et al.* 2008). In this paper, we addressed the following specific questions:

- Do most tropical rainforest canopy trees encounter a major decrease in soil water availability during seasonal dry periods?
- When submitted to drought conditions, what is the influence of seasonal variations in soil water availability on photosynthesis, leaf respiration, stomatal conductance, and transpiration on canopy trees? How variable is this response among canopy trees?

We hypothesized that some canopy trees may not encounter a strong reduction in water status because they can access to deep soil layer that remain humid even during the dry seasons. Furthermore, for those trees which would encounter a strong reduction in soil water availability, we suspected a large variability among trees in their response to these conditions.

METHODS

SITE.—This study was conducted at Paracou, French Guiana, South America (5°16'54" N, 52°54'44" W), where the climate is controlled by the north/south movements of the Inter-Tropical Convergence Zone that causes large seasonal variation in rainfall (Fig. 1). For more information on climatic conditions at this site, refer to Bonal *et al.* (2008). This study covered a two yr period characterised by two long dry seasons with monthly rainfall lower than 100 mm. In 2007, the long dry season lasted from September to the end of November (Fig. 1) and was slightly wetter than the 10 yr average and considered to be a “La Niña” event (Fig. 1; NOAA, 2009). In 2008, the long dry season was among the most severe in the past decade and characterized by four months with less than 50 mm precipitation (Stahl *et al.* 2010). A wetter season, with monthly rainfall sums higher than 200 mm, lasted from December 2007 to mid-July 2008.

We measured daily sum of solar radiation and rainfall on top of a 55 m Gyaflux tower (see Bonal *et al.* 2008 for more details on sensors). We used relative extractable water (REW) values calculated based on a new model that we recently developed for tropical rainforests (Wagner *et al.* 2011) as an estimate of soil water available for the trees at a daily-time step to characterize the seasonal variations in soil drought conditions.

TREE SELECTION.—In order to access to sunlit leaves of canopy trees, we took benefit from the Gyaflux tower (Bonal *et al.* 2008) and used ropes securely attached to the tower by a professional climber to reach the trees surrounding the tower. Using this system, one operator was able to reach 13 canopy trees whose characteristics are described in Table 1.

GAS EXCHANGE MEASUREMENTS.—Leaf gas exchange was measured with an open-system portable infrared gas analyzer (CIRAS-1, PP-System, Hitchin, UK) equipped with a 2.5 cm² Parkinson-type leaf chamber. Measurements of photosynthesis were made under the following environmental conditions: leaf temperature: 29.1 ± 0.1°C, vapour pressure deficit: 1.06 ± 0.01 KPa, CO₂ concentration: 380 ± 3 ppm. Net photosynthesis was measured under non-limiting photosynthetic active radiation (PAR) set up to 1200 μmol/m²/sec of photons (Nepstad *et al.* 2002). All measurements were performed between 0830 and 1300 h on three or four intact mature, sunlit leaves selected on the same branch. These branches were initially tagged in order to make the measurements conducted over the two-year period on the same branch.

Measurements of foliar dark respiration were made on leaves sampled from the same branch used for photosynthesis. Detached foliage samples were transported back to the lab for dark-time respiration measurements (R_d). We conducted a pilot study to ensure the validity of measuring respiration on detached foliage. We measured foliar respiration *in situ* on 8 attached samples, detached the sampled leaves the next afternoon, and measured them again in the dark in the lab. A non-parametric Wilcoxon test clearly showed no effect of detachment (p = 0.98), confirming previous studies (Cavaleri *et al.* 2008). Respiration measurements were taken at 28.6 ± 1.6°C in lab and given the high sensitivity of leaf respiration to temperature (Atkin *et al.* 2000) data were standardized at 25°C following this equation:

$$R_d = \frac{R_{d_f}}{Q_{10}^{(T_l-25)/10}}, \quad \text{Equation 1}$$

where R_d is the foliar respiration standardized at 25°C, R_{d_f} is the foliar respiration at the leaf temperature, Q₁₀ is the change in respiration rate with 10°C change in temperature, T_l is the temperature of the leaf. We chose a Q₁₀ equal to 2.3 (Meir *et al.* 2001, Cavaleri *et al.* 2008).

In order to identify the time required for flux stabilization, we conducted a preliminary test and measured R_d every minute until 16 min on 32 leaves (10 species). The full stabilization of the flux for all leaves was reached after 5 min and this limit was then used in the following leaf respiration measurements (data not shown).

Measurements of stomatal conductance for water vapour (g_s) were made with an automatic porometer AP4 (delta T Devices, Ltd, Cambridge, UK) on four to five intact mature and sunlit leaves of the same branch than for photosynthesis. Because of equipment availability, these measurements were conducted only in 2008 and only once in each period (wet season 2008 and dry season 2008) between 1000 and 1330 h on similarly sunny days. The precise calibration of the porometer was carried out before each campaign.

WATER STATUS.—Predawn (Ψ_{pd}) (0545-0700 h) leaf water potentials were measured on one leaf per tree using a Scholander-type pressure chamber (model 1000, PMS Instruments, Corvallis, OR, USA). Ψ_{pd} was measured in the morning of each gas exchange measurements.

The sap flow density of each tree was measured with home-made, Granier-type (Granier 1987) sensors. Sap flow density sensors consist of two probes (20 mm long * 2 mm diameter) that are radially inserted in the outer xylem, the upper one being heated. The two holes (15 cm apart) were drilled into the trunk 1.5–2.5 m above the ground and any buttresses. Sap flow density is calculated by measuring the difference in temperature between the heated and the reference sensor, assuming that, at night, no sap is circulating and the temperature difference is maximal. An aluminized sheet of plastic bubble-wrap covered the probe and the tree trunk below the probe down to the ground in order to reduce any potential probe error introduced by the sun heating the trunk. Heat flux density was logged every 30 sec and the 30

min averages were converted to sap flow density ($\text{kg/dm}^2/\text{h}$) and we used the mean of the daily sapflow density (Sd). Measurements were recorded continuously on 10 trees in 2008 and in the beginning of 2009. For three other trees, measurements were conducted only at the end of the dry season in 2008 (11th November to 13th December).

DATA ANALYSIS.—A linear mixed-effects model (lme, R 2.12.1) was used to detect seasonal patterns of photosynthesis under non-limiting photosynthetic active radiation (Asat), leaf dark respiration (Rd) and the mean of the daily sapflow density (Sd), with crown exposure and sampling time as a fixed effect and tree included as a random effect. We analyse also the seasonal variation per tree with the same test. A *t*-test was realized to compare the stomatic conductance between the middle of the wet season and the end of the dry season. We used a logarithm model to analyze the relationship between leaf gas exchange (Asat and Rd) and relative extractable water (REW). In order to analyze the effect of REW on transpiration, we first analyzed the relationship between daily mean sapflow density (Sd) and daily global radiation (Rg), and then tested the effect of REW on the residuals from this previous model.

RESULTS

Seasonal variations in rainfall resulted in large seasonal variations in REW (Fig. 1). In 2007, REW strongly decreased in September and reached values below 0.4, but a strong rain event (180 mm) fully recharged the soil water. Thereafter, REW again strongly decreased down to 0.2. In 2008, the period with almost no rain lasted longer than in 2007 and the period when REW was below 0.4 lasted about 3 mo (Fig. 1).

There was a large variability among trees in the seasonal variations in predawn leaf water potential (Ψ_{pd}) (Fig. 2). Under non-limiting soil water conditions ($REW > 0.8$), Ψ_{pd} varied between -0.50 and -0.20 MPa. Under limiting conditions ($REW < 0.4$), we observed a large variability among trees in Ψ_{pd} . Some trees did not clearly show any change in Ψ_{pd} , while the values of others decreased down to -0.80 MPa for dominant and suppressed trees and below -1.20 MPa for two suppressed ones. All trees showed an increase in Ψ_{pd} at the beginning of the wet season (December). For those trees which showed lower Ψ_{pd} values during the dry season as compared to the wet ones, Ψ_{pd} was lower at the end of the dry season in 2008 as compared to 2007. Furthermore, the heavy rains in September 2007 induced a slight increase in Ψ_{pd} for most trees.

There was a huge variability in $Asat$ among trees under non-limiting water conditions (Fig. 3). These values ranged from 3.8 to 14.7 $\mu\text{mol}/\text{m}^2/\text{sec}$. There was a significant effect of time on $Asat$ for the whole population ($P < 0.001$) and for 11 trees (Dg12, Dg2, Dg4, Dg5, Gg10, Hb9, Is11, Oa7, Oa3, Va6, V1) out of the 13 trees. For those trees which showed a significant effect, 6 trees showed a significant log relationship with REW (Fig. 3, Table 2).

There was a huge variability in daily maximum sapflow density among trees under non-limiting water conditions (data not shown). There was a significant effect of time on Sd for the whole population ($P < 0.001$). There was a significant effect of Rg on daily average sapflow density (Table 3) for all trees. The residuals of this model were significantly positively correlated with REW for 9 trees (Table 3, Fig. 4) and negatively correlated with REW for one tree (Lh8). REW explained between 2.7 and 61.7 percent of variance of these residuals.

There was a huge variability in stomatal conductance among trees under non-limiting water conditions (Fig. 5). We observed three main patterns in gs between the wet and the dry season (Fig. 5). Some trees displayed no change in gs (Dg2, Dg5, Lh13, and Oa3), one increase (Lh8), and the other a decrease in gs between the wet and the dry season.

Under non-limiting soil water conditions, leaf respiration values ranged between 0.36 and 1.96 $\mu\text{mol}/\text{m}^2/\text{sec}$ (Fig. 6). There was no significant effect of time on Rd for the whole population ($P = 0.406$), but individually, for 11 trees (Dg2, Dg4, Dg5, Gg10, Hb9, Is11, Lh8, Lh13, Oa7, Oa3, Va6) out of the 13 trees showed a significant effect. For none of the trees, there was a significant relationship between Rd and REW (Fig. 6).

There was no crown exposure effect on Asat ($P = 0.220$) but a significant effect on Rd ($P = 0.006$), with dominant trees having higher values than suppressed ones.

DISCUSSION

The climatic conditions during the August to November period in both years (3 and 4 mo with < 50 mm of precipitation per month in 2007 and 2008, respectively, Fig. 1) induced a strong decrease in soil water moisture in the upper 2.6 m. This decrease was associated with a strong decrease in estimated relative extractable water for the trees (Wagner *et al.* 2011), much below the threshold that is commonly considered as inducing a clear constraint to tree and ecosystem functioning in temperate forests (*i.e.* 0.4, Granier *et al.* 2007) or to tree growth in tropical forests (Wagner *et al.* 2011). The dry period was longer and more intense in 2008 as compared to 2007, and REW reached to 0.08 in 2008.

One major result of this study was that the decrease in soil water availability in the upper 2.6 m did not result in a decrease in predawn leaf water potential for all studied trees. The root system of two trees (Lh8 and Lh13) did not encounter any decrease in soil water availability since Ψ_{pd} values did not change over the two year period (not less than -0.50 MPa). On the contrary, two trees (Oa3 and Oa7) were submitted to a strong reduction in soil water availability at the end of the dry season, with Ψ_{pd} values reaching -1.25 and -1.35 MPa, respectively. For the remaining trees, the decrease in Ψ_{pd} between the wet and the dry season was lower and ranged between -0.30 and -0.80 MPa. The absence of a general decrease in Ψ_{pd} during the dry season for the majority of our canopy trees was consistent with previous results in tropical forests (Bonal *et al.* 2000b, Fisher *et al.* 2006, Rada *et al.* 2009, Markesteijn *et al.* 2010, Stahl *et al.* 2011). Large differences in Ψ_{pd} among trees at the end of the dry period result from differences in the soil layers explored by their rooting system (morphology and structure) (Améglio *et al.* 1999). Our results suggested that the two *Licania* trees might display a deep rooting system (deeper than 2.6 m) that allows them to extract water from less

dry layers at the end of the dry period. On the contrary, the rooting system of the two *Oxandra* trees, as well as of the other trees which showed a clear decrease in Ψ_{pd} , might remain shallow (*i.e.* within the first 0.5 m of soil), or the fine roots that have the capacity to explore deeper layers might not be functional enough during dry season to be able to extract water from these humid layers. The estimation of tree root depth in forest ecosystems, and particularly in complex systems such as in tropical rainforests, is highly complicated. A few studies attempted to evaluate the vertical distribution of root biomass in tropical rainforests (Humbel 1978, Nepstad *et al.* 1994, Carvalheiro & Nepstad 1996, Bonal *et al.* 2000a) and showed an exponential decrease with depth, with only a few percentage of roots below 1 m depth, even though the maximum depth can be up to 8 m (Nepstad *et al.* 1994). Our results thus confirmed the large variability among trees in root depth at this site and further studies involving for instance a double isotope labelling of water ($^{18}\text{O}/\text{H}_2$, Romero-Saltos *et al.* 2005, Zapater *et al.* 2011) could be conducted to confirm these hypotheses and to improve our ability to model forest ecosystems response to environmental changes, such as in the context of global climate changes.

We observed that at the end of the dry season, a large proportion of the studied trees (9 over 13) were highly sensitive to the rain events (a total of 42.6 mm rain fell between the 20th of November and the 5th of December 2008). These trees showed a clear increase in Ψ_{pd} (*i.e.* less negative values) (Fig. 2) right after these events, *i.e.* far before the deep soil layers could be recharged (data not shown). Thus, whether these trees use water from deep or shallow soil layers during dry periods, our observations confirm that they develop efficient shallow fine root systems on which they can rely on for transpiration when soil moisture in the upper layers increases (Cao 2000). This is not surprising as in tropical rainforests the strategy of

having shallow fine roots is also associated with nutrient acquisition as most nutrients are mainly concentrated in the soil upper layers (Yavitt & Wright 2001).

Interestingly, the two *Oxandra* trees were the smallest trees accessible from the tower that we studied and they showed the strongest decrease in Ψ_{pd} . Whether a clear correlation between tree size and rooting depth of tropical rainforest tree species exists is still unknown. No correlation between tree size and Ψ_{pd} at the end of the dry season was found for the trees studied here or in previous studies (Fisher *et al.* 2006, Stahl *et al.* 2011). Furthermore, it is interesting to note that the different seasonal patterns of Ψ_{pd} were not associated with differences in wood density among trees, whereas a high wood density has been associated with higher drought tolerance in tropical dry forests (Markesteijn *et al.* 2011).

The range of carbon assimilation or respiration under non-limiting water conditions (*i.e.* wet season) in our study (Fig. 3, 6) was similar to previous observations made in tropical rainforest ecosystems (Bonal *et al.* 2000b, Lerdau & Throop 2000, Meir *et al.* 2001, Cavaleri *et al.* 2008, Doughty 2011) and confirmed the large interspecific variability in functional characteristics observed to date for Neotropical rainforest species at the leaf and stem level (Baraloto *et al.* 2010). Furthermore, from the end of the wet season to the end of the dry season, we observed a large variability among trees in the response in their leaf gas exchange and transpiration to the changing environmental conditions. We distinguish hereafter whether these variations occurred in association with a strong decrease in Ψ_{pd} or not.

Among the trees that encountered a clear decrease in Ψ_{pd} during the dry season, the two *Oxandra* trees (Oa3 and Oa7) displayed the strongest negative response of A_{sat} , g_s , and S_d to the decrease in REW (Fig. 3, 4, 5; Table 2, 3). These results show a direct negative

effect of soil water availability on the functioning of these trees, pointing to a high sensitivity to soil drought conditions. Furthermore, these two trees showed a concomitant decrease in Ψ_{pd} and g_s (Fig. 2, 5), thus suggesting a control of leaf transpiration close to the anisohydric behaviour (Tardieu & Simonneau 1998). No studies so far addressed a direct negative influence of soil drought on leaf gas exchange of tropical rainforest canopy trees, with repeated leaf gas exchange measurements during wet and dry seasons. However, a similar decrease in leaf gas exchange was observed between the wet and the dry seasons in Mato Grosso, Brazil (Miranda *et al.* 2005) and Doughty (2011) also observed a slight decrease in leaf gas exchange measurements for its control (normal temperature) leaves over the dry season in Para, Brazil.

Seasonal patterns of leaf gas exchange of the other trees which showed a slight decrease in Ψ_{pd} were highly variable, even though the general trend was a decrease in photosynthesis (-54.1% to -14.6%) and g_s (-81.9% to -12.0%) between the wet and the dry seasons. Seasonal variations in photosynthesis were significantly correlated with REW for four trees (Dg12, Gg10, Hb9, V1), but not clearly for the other trees (Dg2, Dg4, Is11, Va6) (Table 2). Furthermore, seasonal variations in S_d were strongly explained by solar radiation (Table 3), and the residues from this relationship were positively correlated with REW, with the exception for Hb9 and Va6. The absence of highly negative Ψ_{pd} for these trees, beside the fact they could partly access to humid soil layers, suggested that stomatal regulation early during the dry season, when REW started to decrease (Fig. 1), was efficient enough to avoid major water loss thru transpiration. Nevertheless, even though this strategy leads to reduced photosynthesis and potentially reduced secondary growth, it is rather conservative and can prevent these trees, for instance, to reach hydraulic thresholds when xylem cavitation might occur as previously shown by Markesteijn *et al.* (2011) for tropical dry trees. The origin of

this stomatal regulation is probably mediated by chemical messengers (*e.g.* ABA) (Tyree & Yang 1990) that may have been synthesised by fine roots mainly located in the soil surface and that encountered a rapid decrease in soil water content at the onset of the dry periods. We were not able to test for any seasonal change in the synthesis of such hormonal signals during this experiment, but further studies should be conducted in order to disentangle their effect from that of hydraulic signals.

In contrast with Asat and Sd, we did not observe any clear seasonal changes in Rd for any tree, whether Ψ_{pd} strongly decreased or not, and seasonal variations in Rd were not significantly correlated with variations in REW. These results were consistent with the absence of clear seasonal variations in Rd observed so far in the Amazon basin (Metcalf *et al.* 2010), but in contradiction with experimental studies on the influence of soil drought on Rd (*e.g.* Ayub *et al.* 2011). Increasing drought conditions could indeed result in a decrease in Rd by (i) decreasing the supply of substrate to mitochondria as a result of reduced photosynthesis; (ii) decreasing the demand for respiratory energy to support cellular metabolism; (iii) decreasing the abundance, structure, and composition of individual mitochondria (Lawlor & Fock 1977, Atkin & Macherel 2009, Rodriguez-Calcerrada *et al.* 2011). The absence of clear seasonal changes in Rd for the studied trees thus suggests either that these processes were not strong enough to be detected by our measurements, or that tropical rainforest tree species display peculiar characteristics allowing maintaining rather constant respiration values. The inconstancy between seasonal patterns in Asat and Rd, as previously observed (*e.g.* Gimeno *et al.* 2010), suggests a balance between the negative effect of decreased supply of substrates to mitochondria (reduced Asat) and increased demand for respiratory ATP under soil drought conditions (Atkin & Macherel 2009). Furthermore, it

points to major changes in carbon balance at the leaf level for these tropical trees during dry periods.

Among the trees that did not display a significant decrease in Ψ_{pd} during the dry season, the two *Licania* trees (Lh8 and Lh13) clearly did not show major variations in leaf gas exchange during the dry periods. For these trees, there was no significant relationship between Asat or Sd and REW. Furthermore, these two trees were the only one to display higher gs values at the end of the dry season as compared to the end of the wet season (Fig. 5). This increase was not related to any peculiar change in phenological status for these trees (data not shown), but probably to the warmer and slightly drier atmospheric conditions during the dry periods. These two trees illustrate that in spite of large seasonal variations in soil water conditions during the dry period, some tropical canopy tree clearly do not encounter the strong decrease in soil water availability in the upper soil layers (*i.e.* absence of a decrease in Ψ_{pd}), and these variations have only little influence on their global functioning. However, our study does not preclude that these trees might not be sensitive to soil drought. Indeed, we were not able to test the influence of soil drought on their leaf gas exchange and transpiration as they just did not encounter soil drought. The soil drought in 2008 was much stronger than in 2007, and REW decreased far below 0.4 in 2008, but still it was not strong enough to induce for these trees a strong reduction in water availability. However, whether the intensity of future drought periods, as expected in the context of global climate changes, will lead to the down regulation of the gas exchange of these trees is a worthy question?

With the exception of the two *Oxandra* trees, the response of the studied trees to seasonal variations in REW was not related to their crown exposure index or their diameter (Table 1). These results are consistent with the fact that understory or emergent trees can

either have shallow or very deep roots (Sternberg *et al.* 1998). The lack of association between these characteristics clearly increases the complexity for models to predict the response of tropical trees to soil drought conditions.

Conclusions

Our study underline that the high species diversity in FTH is associated with a high heterogeneity of the response of canopy trees to soil drought conditions. These results have important applications in modelling approaches because it makes necessary a precise evaluation of these response patterns and a potential grouping of these patterns before any tree-based functional models would efficiently describe the response of tropical forest ecosystems to future environmental conditions changes. Our data indicate that only a small proportion of the studied canopy trees really faced strong soil water depletion during seasonal dry periods. Those trees encountering soil drought displayed a wide range of leaf gas exchange response to soil water depletion. Finally, our results point to the strong need for a better characterisation of the rooting depth of canopy tropical rainforest tree species and the depth at which these trees preferentially extract water under varying environmental constraints.

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TABLE 1. Characteristics of the trees that were sampled from the Guyaflux tower.

Tree species and family; trees code; crown exposure code: D: dominant, S: suppressed; tree Dawkins index; diameter at breast height (DBH); phenology: e: evergreen, d: deciduous; total height of the tree; height of leaf gas exchange measurements and wood density.

Species	Family	Tree code	Crown exposure	Dawkins index	DBH (cm)	Phenology	Total height (m)	Measurement height (m)	Wood density (g/cm ³)
<i>Dicorynia guianensis</i>	Caesalpiniaceae	Dg2	D	4	39.9	d	26	23	0.77
<i>Dicorynia guianensis</i>	Caesalpiniaceae	Dg4	D	4	33.0	d	30	28	0.67
<i>Dicorynia guianensis</i>	Caesalpiniaceae	Dg5	S	3	23.2	d	28	27	0.69
<i>Dicorynia guianensis</i>	Caesalpiniaceae	Dg12	D	5	41.1	d	36	31	0.71
<i>Goupia glabra</i>	Celastraceae	Gg10	D	4	79.9	e	35	29	0.75
<i>Hirtella bicornis</i>	Chrysobalanaceae	Hb9	S	3	14.5	e	25	23	0.88
<i>Iryanthera sagotiana</i>	Myristicaceae	Is11	S	2	24.6	e	27	23	0.63
<i>Licania heteromorpha</i>	Chrysobalanaceae	Lh8	D	4	22.8	e	26	23	0.92
<i>Licania heteromorpha</i>	Chrysobalanaceae	Lh13	S	3	16.8	e	25	23	0.89
<i>Oxandra asbecki</i>	Annonaceae	Oa3	S	3	16.7	e	20	18	0.92
<i>Oxandra asbecki</i>	Annonaceae	Oa7	S	3	10.6	e	19	18	0.95
<i>Vantanea sp.</i>	Humiriaceae	V1	D	5	40.7	e	34	30	0.94
<i>Vouacapoua americana</i>	Caesalpiniaceae	Va6	D	4	28.3	d	28	27	0.82

TABLE 2. Statistical results from the relationship between saturated net photosynthesis (Asat) and relative extractable water (REW). The model used here was $Asat = f(\log REW)$.

Tree code	R^2	P value	rmsep
Dg2	0.38	0.057	1.72
Dg4	0.35	0.094	1.35
Dg5	0.38	0.192	1.69
Dg12	0.80	0.001	1.08
Gg10	0.79	0.001	1.52
Hb9	0.82	0.002	0.76
Is11	0.49	0.051	0.94
Lh8	0.28	0.094	1.12
Lh13	0.02	0.768	0.98
Oa3	0.82	0.002	0.47
Oa7	0.60	0.040	0.86
V1	0.64	0.003	1.77
Va6	0.39	0.053	1.60

Table 3. Left: Statistical results from the relationship between daily mean sapflow density and global radiation (Rg). Right: Statistical results from the relationship between the residues of the previous model and relative extractable water (REW).

Tree code	Rg		REW	
	<i>P</i> value	% variance	<i>P</i> value	% variance
Dg2	< 0.001	67.0	< 0.001	16.9
Dg4	< 0.001	63.6	< 0.001	14.3
Dg5	< 0.001	6.2	0.222	0.8
Dg12	0.003	3.3	< 0.001	67.1
Gg10	< 0.001	60.0	< 0.001	23.5
Hb9	< 0.001	43.3	0.455	0.7
Is11	< 0.001	52.1	< 0.001	27.9
Lh8	< 0.001	60.6	< 0.001	11.2
Lh13	< 0.001	62.3	0.005	6.0
Oa7	< 0.001	47.0	< 0.001	31.5
Oa3	< 0.001	58.0	< 0.001	7.7
V1	< 0.001	79.5	< 0.001	2.7
Va6	< 0.001	62.1	0.310	0.9

FIGURE 1. Daily sum of rainfall (solid line) and daily relative extractable water (dotted line) over the two years of experimentation. The arrows correspond to the long dry seasons in 2007 and 2008.

FIGURE 2. Seasonal variation of predawn leaf water potential (MPa) for (A) dominant trees and (B) suppressed trees around eddy flux tower. Dg2 (open circle), Dg4 (open triangle down), Dg5 (filled triangle down), Dg12 (filled circle), Gg10 (open square), Hb9 (filled square), Is11 (semi-filled right square), Lh8 (filled diamond), Lh13 (open diamond), Ox3 (open triangle up), Ox7 (filled triangle up), V1 (thin X) and Va6 (filled triangle up with a plus). The arrows correspond to the long dry seasons in 2007 and 2008. For species abbreviations see Table 1.

FIGURE 3. Relationship between photosynthesis under non-limiting radiation (A_{sat} , $\mu\text{mol}/\text{m}^2/\text{s}$) (mean \pm SE) and the relative extractable water (REW) for each tree. Significance levels: solid line: $P < 0.05$. Stars denote significant seasonal effect ($* = P < 0.05$)

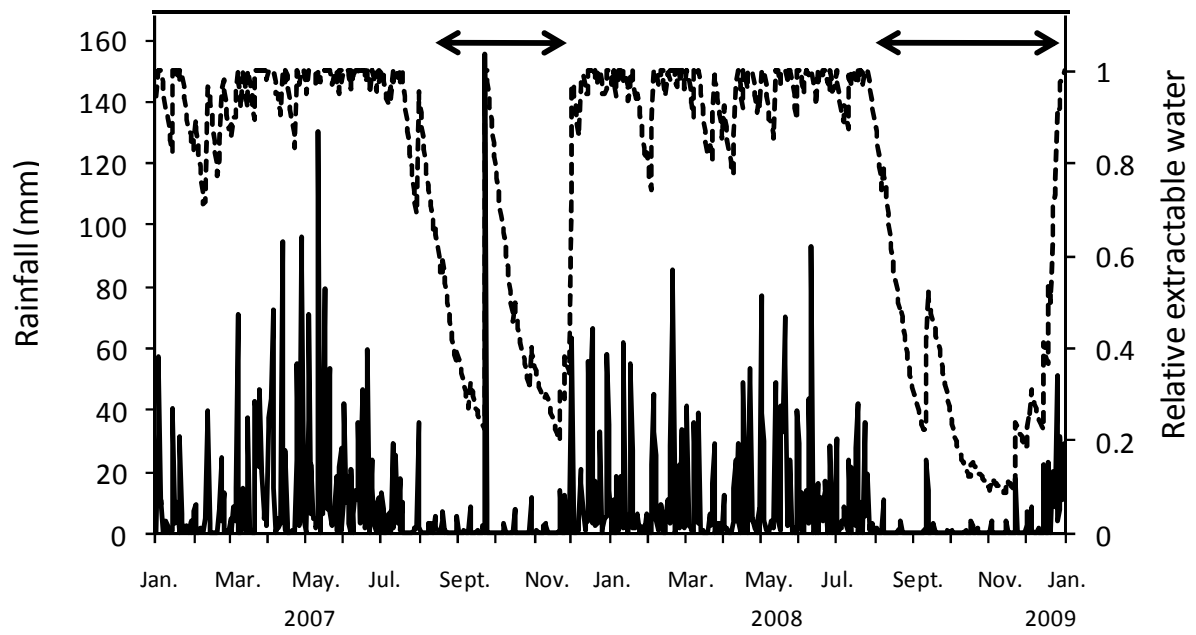
FIGURE 4. Relationship between the residuals of daily mean sapflow density (S_d) and the relative extractable water (REW) for each tree. Stars denote significant relationship ($** = P < 0.05$; $* = P < 0.001$)

FIGURE 5. Stomatal conductance (g_s , $\text{mmol}/\text{m}^2/\text{s}$) during the middle of wet season and the end of dry season 2008. Stars denote significant differences between the two seasons ($* = P < 0.05$). For symbol correspondence see Fig. 2. For more clarity the mean are indicated without SE.

FIGURE 6. Relationship between foliar dark respiration (R_d , $\mu\text{mol m}^{-2} \text{s}^{-1}$) (mean \pm SE) and the relative extractable water (REW) for each tree. Stars denote significant seasonal effect ($* = P < 0.05$)

1 FIGURE 1.

2



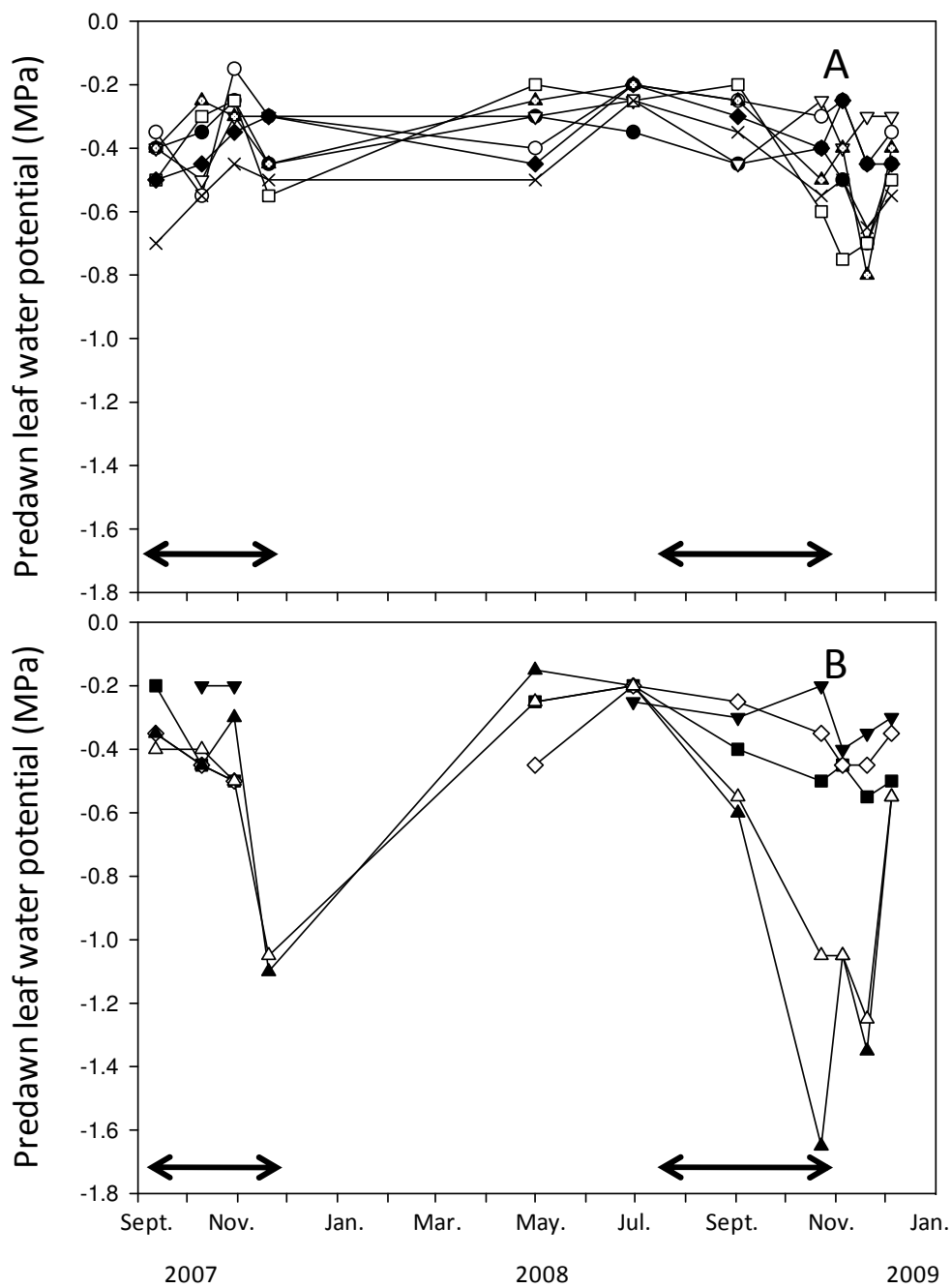
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1 FIGURE 2.

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FIGURE 3.

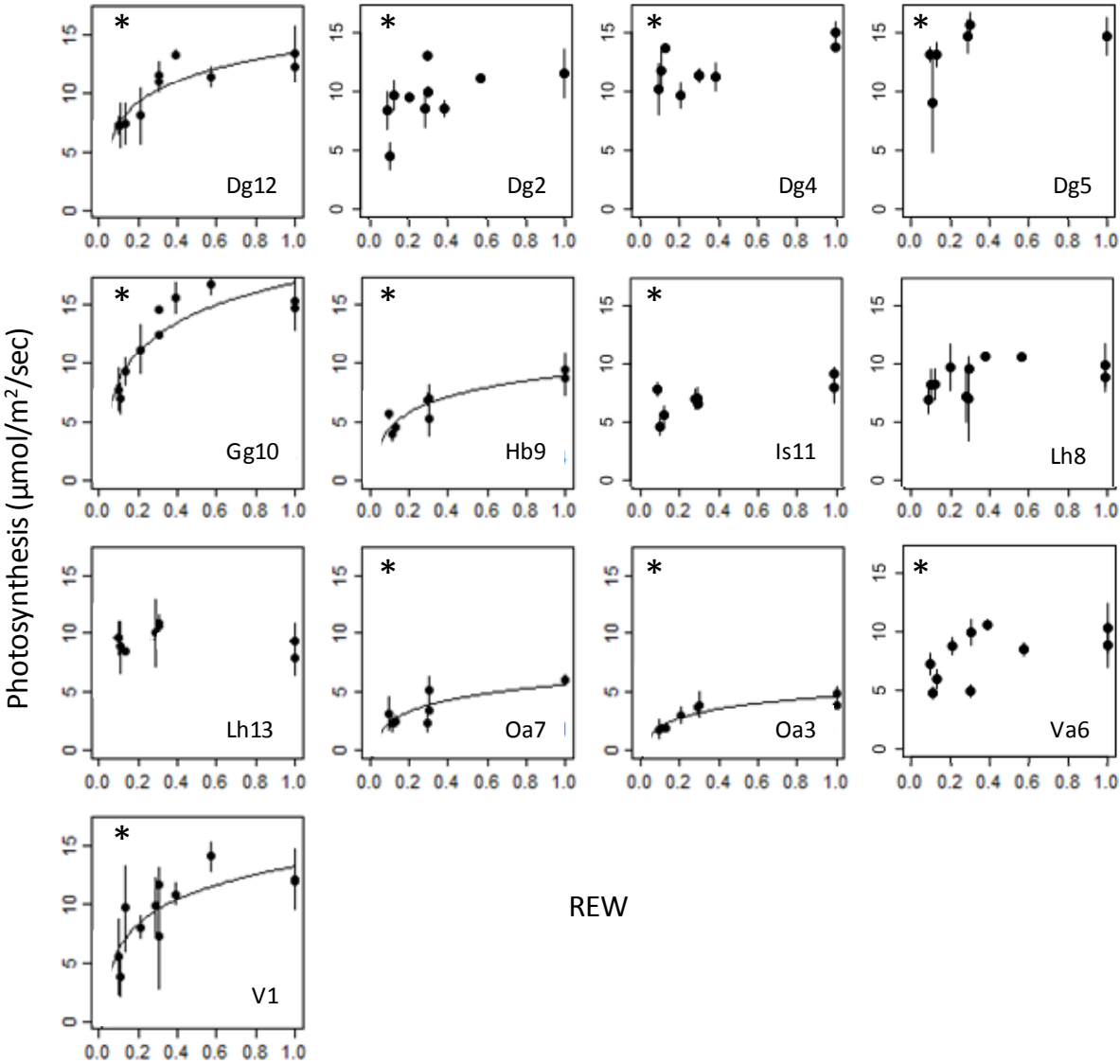


FIGURE 4.

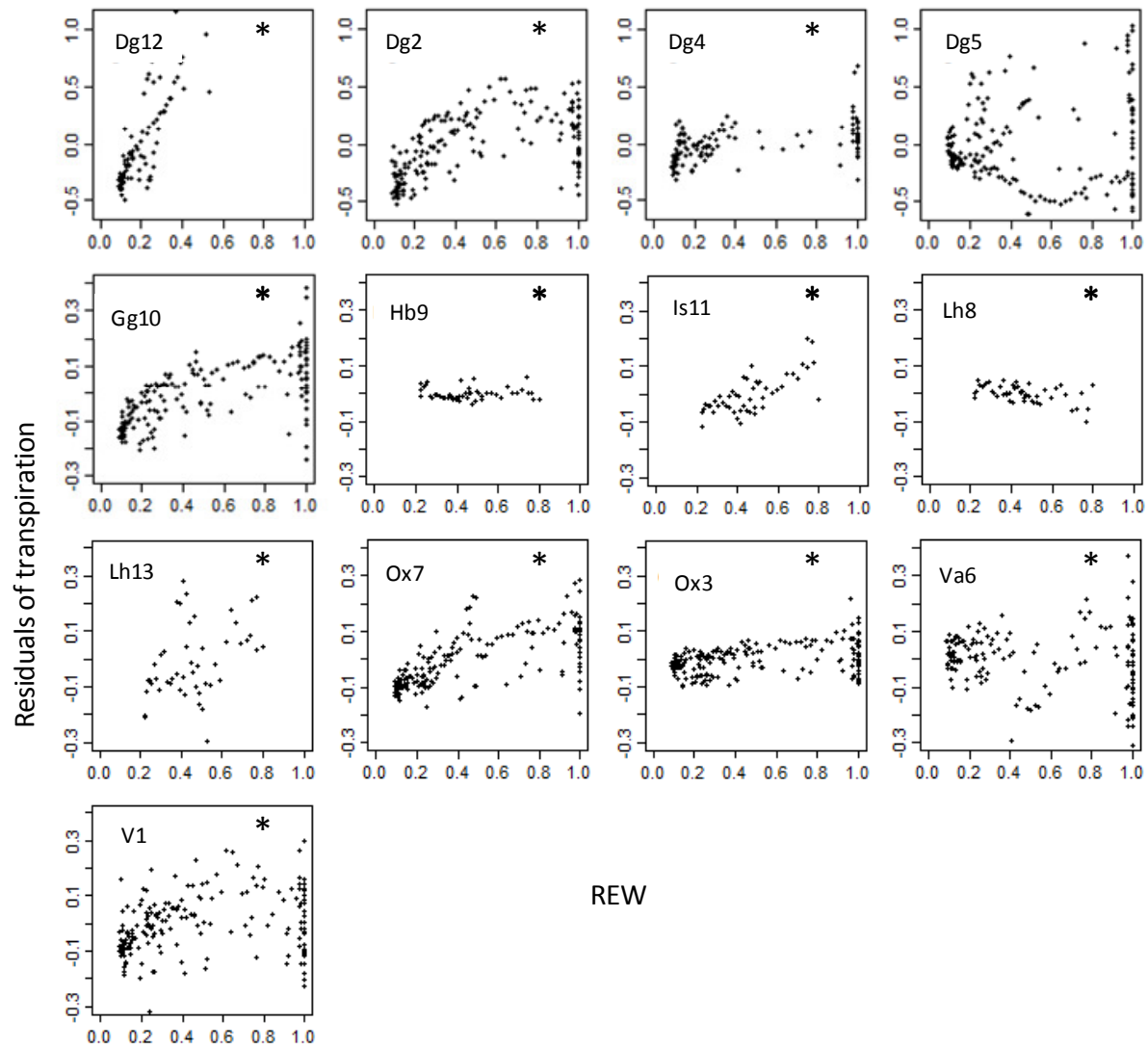


FIGURE 5.

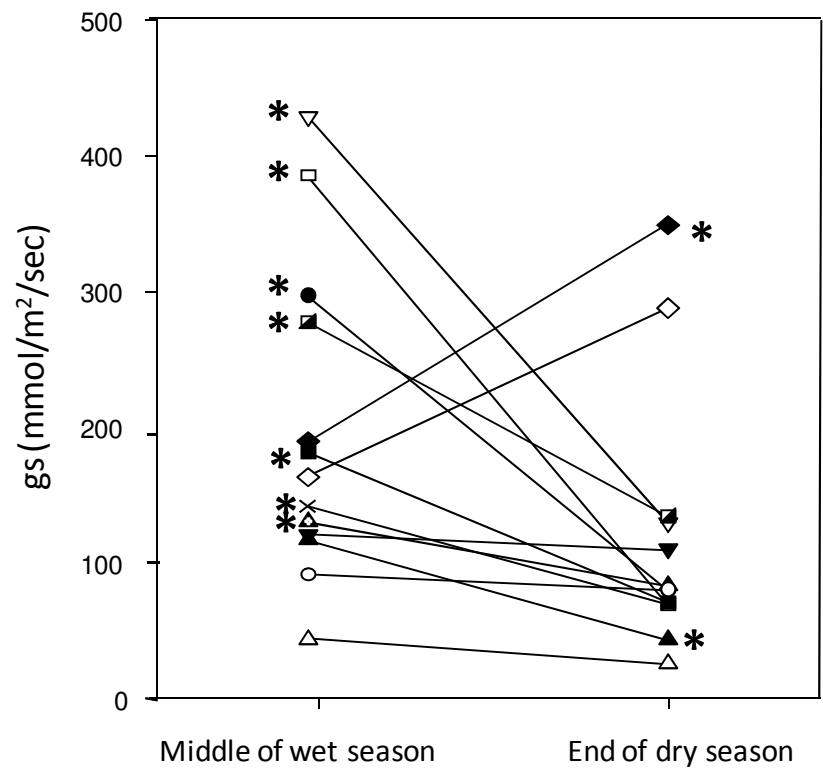


FIGURE 6.

