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Quelle sera la réponse des forêts tropicales humides à l'augmentation des températures et aux changements de pluviométrie? Modéliser la dynamique forestière pour identifier les processus sensibles en Guyane Française

Méline Aubry-Kientz

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UNIVERSITE DES ANTILLES ET DE LA GUYANE
Faculté des sciences exactes et naturelles
École doctorale pluridisciplinaire
Thèse pour le doctorat en physiologie et biologie des organismes,
populations, interactions

Mélaine Aubry-Kientz

**Quelle sera la réponse des forêts tropicales humides à
l'augmentation des températures et aux changements de
pluviométrie ?**

Modéliser la dynamique forestière pour identifier les processus
sensibles en Guyane Française.

Sous la direction de Bruno Hérault et de Vivien Rossi
Soutenue le 04 décembre 2014 à Kourou

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Résumé

En 2013, Le Groupe d'experts intergouvernemental sur l'évolution du climat (GIEC) publie son cinquième rapport concernant les changements climatiques. Il y est souligné que le réchauffement climatique est sans équivoque, et que de nouvelles émissions de gaz à effet de serre impliqueront une poursuite du réchauffement et des changements affectant toutes les composantes du système climatique. En région tropicale, une hausse de la température, ainsi qu'une intensification des événements de sécheresse et de pluviométrie extrêmes sont à prévoir. C'est dans ce contexte que s'inscrit ce travail, dont le but est d'étudier la réponse de la forêt tropicale à ces changements climatiques prédits en Guyane Française. Pour ce faire, j'ai utilisé les données du dispositif de suivi forestier de Paracou pour construire un modèle de dynamique individuel basé sur les traits fonctionnels des arbres. Un modèle de mortalité a d'abord été réalisé puis couplé à un modèle de croissance. Le modèle couplé ainsi construit permet de modéliser la croissance et la mortalité des arbres sur un pas de temps de 2 ans tout en tenant compte de leur ontogénie et de leurs traits fonctionnels. Ce modèle a d'abord été appliqué aux essences commerciales de Guyane Française en forêt naturelle et exploitée en y ajoutant un indice de stress hydrique. Ceci permet de montrer que le stress hydrique fait baisser la croissance et augmenter la mortalité, tandis que l'exploitation a l'effet inverse. Malgré le signal commun, différentes réponses sont observées selon les espèces. Le modèle a ensuite été appliqué à la communauté en forêt naturelle pour identifier les drivers climatiques et les processus impactés. Il ressort que la croissance est impactée par le stress hydrique et la température, et que la mortalité est impactée par le stress hydrique et la pluviométrie totale. Ces résultats ont enfin permis de construire un modèle complet de dynamique forestière climat dépendant, et de simuler l'évolution d'une communauté pendant un siècle selon différents scénarios correspondant aux prédictions du GIEC. Les simulations mettent en évidence une très forte diminution de la croissance, ainsi qu'une plus faible diminution de la mortalité. Ceci entraîne une diminution notable de la surface terrière, du diamètre quadratique et de la biomasse fraîche. Une analyse de sensibilité montre que ces changements sont principalement dus à l'augmentation sévère des températures prédites pour le siècle à venir. Des pistes de réflexion sur les enjeux de modélisation et les échelles considérées sont proposées en discussion de ce travail.

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1 Les forêts tropicales

Les forêts tropicales recouvrent environ 17 millions de km² sur trois continents, en Amérique latine, en Afrique et en Asie (Roy *et al.*, 2001). Ces forêts sont au centre d'intérêts majeurs, notamment car elles contiennent un stock de 471 ± 93 Pg de carbone, soit 55% du carbone présent dans la forêt sur Terre (Pan *et al.*, 2011).

1.1 Carbone et biodiversité

A l'heure actuelle, la forêt amazonienne est encore souvent considérée par le grand public comme le poumon de la planète. Elles jouent le rôle d'un puits de carbone (Phillips, 1998; Nemani *et al.*, 2003; Baker *et al.*, 2004; Lewis *et al.*, 2004; Ichii *et al.*, 2005) mais ce rôle est controversé et notre compréhension du rôle de la forêt tropicale dans le cycle du carbone reste partielle. Certes, les forêts tropicales participent activement au stockage du carbone terrestre (Pan *et al.*, 2011), mais ce stock est dynamique : du carbone est absorbé par les végétaux lors de la photosynthèse, et du carbone est rejeté dans l'atmosphère via la respiration de la biomasse vivante et la décomposition de la biomasse morte. Les incertitudes restent grandes quant à l'estimation des flux de carbone en forêts tropicales (Phillips and Lewis, 2013), les données disponibles ne permettent ni de trancher définitivement sur la question ni d'estimer avec précision les changements de stock (Phillips and Lewis, 2013). Une erreur, telle qu'une détection de tendance à court terme ne reflétant pas le processus à plus long terme, peut être vite com-

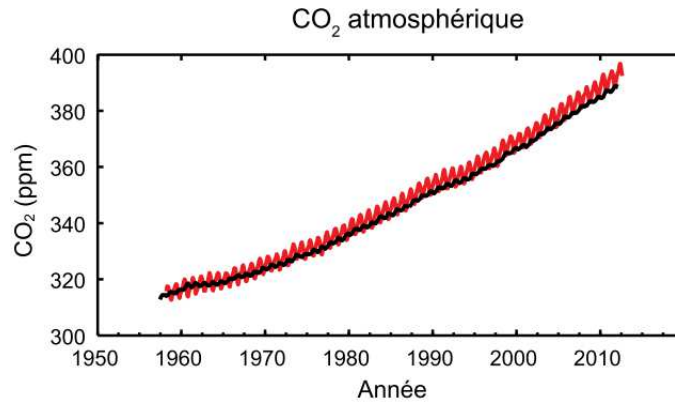


FIGURE 1 – **Evolution du CO₂**. Mesures des concentrations atmosphériques de dioxyde de carbone (CO₂) effectuées à Mauna Loa (19°32'N, 155°34' O en rouge) et au pôle Sud (89°59' S, 24°48' O en noir) depuis 1958 (Stocker *et al.*, 2013).

mise, notamment car le temps de mesure est limité au regard des processus étudiés. En effet, si un arbre stocke indubitablement du carbone lors de sa croissance, la mort d'un gros arbre est responsable d'un rejet de carbone important dans l'atmosphère, rejet qui va s'étaler sur plusieurs années voire parfois plusieurs décennies (Hérault *et al.*, 2010). Un phénomène ponctuel, la mortalité, prend alors toute son importance, soulignant ainsi l'importance de considérer différentes échelles de temps, mais aussi d'espaces, lors des travaux d'étude de l'évolution des stocks de carbone.

Le débat à propos du carbone est à l'origine de nombreux travaux de recherche et projets scientifiques, car le CO₂ est un des gaz à effet de serre impliqués dans les processus responsables des changements climatiques globaux. La concentration de dioxyde de carbone dans l'atmosphère a augmenté de 40% depuis l'époque préindustrielle (Figure 1). Cette augmentation s'explique en premier lieu par l'utilisation de combustibles fossiles, et en second lieu par le bilan des émissions dues aux changements d'utilisation des sols (IPCC, 2013).

Bien que le stock de carbone en forêt tropicale soit peu conséquent comparativement au stock de carbone dans les océans (38 000 milliards de tonnes) ou dans le sol (2 011 milliards de tonnes), ce stock (212 milliards de tonnes dans la végétation des forêts tropicales, IPCC (2000)) est celui sur lequel l'homme est le plus à même d'agir via, par exemple, la déforestation ou la

mise en oeuvre de politiques de protection. En outre, les flux de carbone peuvent changer sous l'impulsion des changements climatiques, et participer ainsi à ces changements, créant des effets de feedback qui sont difficiles à prévoir et à quantifier.

1.2 Diversité spécifique et fonctionnelle en forêt tropicale

La forêt tropicale n'est pas uniquement un stock de carbone, mais aussi un réservoir de biodiversité. Avec entre 50 et 70 % des espèces vivantes en milieu terrestres sur seulement 7 % des terres émergées, les forêts tropicales peuvent être considérées comme une formidable machine à créer et maintenir de la biodiversité. Cette diversité, notamment des espèces d'arbres, est telle que les écologues cherchent à comprendre comment ces espèces coexistent (Chesson, 2000; Hubbell, 2001; Webb *et al.*, 2002; Wright, 2002).

Les espèces ont souvent été regroupées de façon à distinguer par exemple les espèces pionnières des espèces à croissance lente (Favrichon, 1998). Ces regroupements peuvent parfois se baser sur (i) des distances phylogénétiques qui permettent de regrouper les espèces par genre ou par famille ou (ii) sur la distance fonctionnelle entre espèces, distance qui n'était pas facilement quantifiable avant la récolte systématique d'un grand nombre de traits fonctionnels. Ces traits fonctionnels peuvent être relatifs au bois, à la feuille, ou à l'architecture de l'arbre, et sont autant d'indicateurs des stratégies d'allocation des ressources des différentes espèces. Un effort collectif important a été fourni, ces dernières années, par la communauté scientifique pour créer des bases de données de traits (Baraloto *et al.*, 2010a,b; Chave *et al.*, 2009; Wright *et al.*, 2004) selon des protocoles standardisés (Cornelissen *et al.*, 2003).

Ces bases de données de traits fonctionnels ont permis d'étudier la variabilité inter- et intra-spécifique des traits et de tester l'existence d'éventuels compromis fonctionnels. Ces études montrent que des axes orthogonaux peuvent être créés, chaque axe pouvant être décrit par un certain nombre de traits, et représentant un gradient continu de stratégies écologiques. Différents axes ont donc été mis en avant, d'abord par Westoby *et al.* (2002), qui identifie des traits relatifs aux feuilles, à la tige, et à la structure générale de l'arbre. La portée mondiale de l'axe relatif aux feuilles a été mise en avant par Wright *et al.* (2004) (LES : leaf economics spectrum). Plus récemment un axe relatif au bois a été identifié (Chave *et al.*, 2009) (SES : stem economics spectrum). Ces deux axes sont orthogonaux chez les arbres tropicaux (Baraloto *et al.*, 2010b). Le LES reflète un gradient d'investissement des ressources partant d'espèces ayant une production de feuilles à fort

taux de renouvellement d'un côté vers, à l'autre extrémité du gradient, des espèces caractérisées par la production de feuilles plus robustes à renouvellement plus rares, qui se défendent ainsi mieux contre les ennemis (Coley and Barone, 1996). Le SES reflète un gradient de stratégies similaires au niveau du tronc, avec d'un côté des bois denses, relativement coûteux à construire mais plus résistants aux pathogènes, et de l'autre des bois riches en eau et des écorces plus fines (Chave *et al.*, 2009).

Les traits fonctionnels sont donc des outils puissants d'analyse pour mieux comprendre les différentes stratégies des différentes espèces coexistant en forêts tropicales. D'autre part, certains traits sont également des indicateurs de l'efficacité de l'utilisation des ressources. En fonction de leurs traits, les arbres peuvent avoir des comportements différents vis à vis des stress auxquels ils sont soumis (exploitation, sécheresse). C'est pourquoi l'utilité de ces traits dans des modèles de dynamique de peuplement forestier me semble judicieuse.

1.3 La dynamique forestière

Les différentes stratégies fonctionnelles des espèces et la grande diversité en forêt tropicale se traduisent en différences du point de vue de la dynamique démographique. C'est notamment ce qui fait une grande différence entre espèces pionnières à croissance rapide et espèces à croissance plus lente. La dynamique des forêts tropicales à l'échelle d'une communauté est donc un mélange de comportements individuels d'arbres qui cohabitent. Cette dynamique est importante car elle peut être actrice de changements. La dynamique forestière est classiquement structurée en trois processus fondamentaux : le recrutement, la croissance et la mortalité. Ces trois processus peuvent être étudiés séparément car ils sont en théorie bien distincts.

1.3.1 Le recrutement

Le recrutement peut être défini de façon très large, de la synthèse de graines par l'arbre, à la dissémination de ces graines grâce à différents agents, biotiques ou abiotiques, puis à la germination de ces graines, à l'apparition d'une plantule et enfin, à la croissance de la plantule jusqu'à un diamètre seuil (10 cm dans notre cas). On distingue 4 stades chez les arbres des forêts tropicales humides : les graines, les semis (seedlings), les juvéniles (saplings) et les adultes. Ces stades diffèrent par leurs morphologies, mais aussi par leurs caractéristiques écologiques, comme l'héliophilie par exemple (Porter and Rose, 2005). En forêt tropicale, où la diversité est considérable, cette

variabilité additionnelle ne permet pas de connaître avec précision le comportement de chaque stade de chaque espèce. En l'absence de perturbation, de nombreux modélisateurs préfèrent souvent considérer le recrutement comme un processus aléatoire respectant les proportions des différentes espèces présentes (Moravie *et al.*, 1997).

1.3.2 La croissance

La croissance peut être de deux types, la croissance primaire concerne la taille tandis que la croissance secondaire concerne le diamètre. Il est difficile de mesurer la taille d'un arbre en forêt, et les forestiers s'intéressent en général à la croissance en diamètre. Des modèles d'allométrie permettent éventuellement de passer du diamètre à la taille (Molto *et al.*, 2014), même si ces modèles fournissent des prédictions entachées de grandes incertitudes (Molto *et al.*, 2013). La croissance en diamètre est, par conséquent, un sujet relativement bien traité dans la littérature des forêts tropicales humides, et ceci notamment grâce aux dispositifs de suivi forestier comme Paracou en Guyane française, La Selva au Costa Rica, ou BCI au Panama (Barro Colorado Island). Ce type de dispositif permet de suivre la croissance d'arbres de différentes espèces sur plusieurs dizaines d'hectares et de façon régulière dans le temps sur plusieurs décennies. La croissance secondaire peut être mise en relation avec différents traits fonctionnels, et ainsi être associée à différentes stratégies écologiques. Deux comportements extrêmes se distinguent avec, d'une part, les arbres pionniers dont la croissance est rapide, le bois peu dense, et le cycle de vie court. Ces espèces sont héliophiles et le *Cécropia* en est un représentant emblématique en Guyane Française. Un grand nombre d'individus de cette espèce se retrouve dans les trouées ou au bord des routes. Cette espèce est donc souvent observée en forêt secondaire. A l'ombre de ces espèces pionnières, d'autres espèces peuvent se développer et croître de façon plus lente. Ces espèces sont souvent caractérisées par des bois plus denses. La croissance peut aussi considérablement varier entre les individus d'une même espèce. Cette variabilité intra-spécifique peut être liée à des facteurs environnementaux exogènes (climat, lumière...), biotiques exogènes (compétition, prédation, facilitation...) et endogènes (génétique). Enfin, les arbres grandissent à des vitesses différentes en fonction de leur stade ontogénique (Héroult *et al.*, 2011), ce qui ajoute une variabilité intra-individuelle.

1.3.3 La mortalité

La mortalité est un processus plus difficile à observer que la croissance et ses causes sont, de fait, moins comprises. La mortalité peut être de plusieurs

types : sur pied, ou par chablis primaire ou secondaire. La mortalité est un processus ponctuel, observable uniquement lors de suivis réguliers dans le temps. Pourtant les processus impliqués dans la mortalité peuvent être longs de plusieurs décennies. La complexité du processus de mortalité provient également de notre incapacité à détecter précisément l'occurrence du phénomène. Un arbre peut être pris pour mort une année, puis vivant l'année suivante, le processus peut en effet toucher une partie de l'arbre uniquement. La mortalité est très importante, car elle peut être à l'origine d'un chablis et d'une trouée, qui ouvrira la canopée pour laisser les rayons du soleil atteindre le sous-bois. C'est suite à la mort des arbres que d'autres plus jeunes prennent la place libre, la mortalité est donc le moteur à part entière de la dynamique.

La probabilité de mourir n'est pas la même en fonction du stade ontogénique de l'arbre. Les arbres très jeunes ont des taux de mortalité élevés, dus à la très forte compétition régnant parmi les jeunes plantules. Les petits arbres sont en effet soumis à une forte pression de sélection, et seul un petit nombre d'entre eux parviendront à une taille adulte. Le taux de mortalité est aussi plus élevé pour les vieux arbres, ceci est dû à la sénescence. Comme c'est le cas pour la croissance, d'autres facteurs entrent en jeu. Les arbres peuvent être soumis à différentes contraintes (herbivorie, événements climatiques extrêmes...) et ne pas se remettre des dégâts causés. Une faiblesse causée par une sécheresse pourra, par exemple, être fatale à un arbre des années plus tard, lors d'une seconde sécheresse moins importante (Dobbertin, 2005).

1.3.4 La compétition pour les ressources

Il est difficile de décrire la dynamique forestière sans faire intervenir la notion de compétition. Il s'agit de la compétition pour les ressources, à savoir la lumière, l'eau et les nutriments et ions nécessaires à la croissance et au maintien de l'arbre. L'idée de compétition est omniprésente et a une longue tradition en écologie dès que plusieurs organismes sont en présence (Lotka, 1925; Volterra, 1926; Gause, 1932; Tilman, 1981), elle est intimement liée à l'idée de la sélection, qui ne conserve, à long terme, que les individus qui ont les meilleures valeurs sélectives. En forêt, les arbres sont soumis à une forte compétition pour la lumière, qui les fera grandir le plus vite et le plus haut possible, et à une compétition pour l'eau, qui les obligera à former un système racinaire adapté.

Pour quantifier cette compétition pour la ressource, de nombreux indices de compétition ont été créés. Les indices indépendants de la distance prennent en compte le nombre de voisins et/ou leurs tailles (Gourlet-Fleury,

1998; Stoll and Newbery, 2005). Les indices dépendants de la distance ajoutent à cela la distance entre les arbres (Canham *et al.*, 2004; Uriarte *et al.*, 2010; Thorpe *et al.*, 2010). Plus rares, certains indices se basent sur les diagrammes de Voronoi, pour lesquels la disponibilité de la ressource est dépendante de l'agencement spatial des voisins. Les diagrammes de Voronoi permettent de partitionner la surface étudiée en autant de polygones que d'arbres, chaque polygone représente alors un espace disponible pour l'arbre et l'aire du polygone est utilisée comme indice de compétition pour l'arbre associé (Aakala *et al.*, 2013). Certains indices dépendent aussi de la taille de l'arbre considéré. Par exemple, le nombre total d'arbres qui se trouvent au voisinage de l'arbre d'intérêt et qui sont plus gros que ce dernier. Dans un modèle de croissance dépendant du diamètre, de tels indices sont difficilement utilisables, car ils sont directement liés au diamètre de l'arbre, et covarient de façon évidente avec ce diamètre. Ils sont donc à proscrire pour inclure de la compétition dans un modèle de croissance, pour ne pas avoir de confusion d'effets entre ontogénie et compétition. En forêt tempérée, les relations inter-spécifiques de compétition sont parfois très bien décrites et peuvent être correctement, c'est à dire une à une, prise en compte dans la construction des indices de compétition, ce qui rend l'indice encore plus puissant. En forêt tropicale, il est compliqué d'envisager une telle complexité, au vu du nombre d'espèces. En forêts exploitées, les gradients liés à la compétition sont importants, l'intensité d'exploitation étant très hétérogène dans l'espace, ce qui justifie l'utilisation de ces indices de compétition. En forêt naturelle, ces gradients existent aussi grâce aux chablis naturels. Ceci dit, très peu d'individus sont finalement en situation de faible compétition si bien que les gradients de compétition ne semblent pas expliquer une part importante de la variabilité de la croissance observée (Gaspard, 2014). Il est difficile de trouver un estimateur de compétition sans inclure dans cet estimateur les effets à expliquer. Par exemple, une fois que la variance liée à l'ontogénie est correctement prise en compte, la variance résiduelle expliquée par la compétition est finalement très faible. La compétition n'est donc pas traitée dans ce manuscrit et n'a pas été incluse dans les modèles utilisés. Toutefois il faut garder en tête que celle-ci s'avérerait nécessaire pour étendre nos modèles à des forêts exploitées, ce dont il sera question dans le chapitre 4.

1.4 Plus particulièrement en Guyane Française

La Guyane française est située entre le Suriname à l'Ouest, le Brésil au Sud-Ouest, et l'océan Atlantique au Nord. La Guyane française est le plus grand



FIGURE 2 – La Guyane française.

département français avec ses 83 846 km², mais c'est aussi le département le plus boisé car la forêt tropicale recouvre 95% du territoire (Figure 2). Seul territoire européen situé sur le continent sud-américain, à 7000 km de la France métropolitaine, la Guyane est, de fait, le seul territoire amazonien de l'Union Européenne.

1.4.1 L'environnement physique

Le massif forestier de Guyane française appartient au bouclier des Guyanes, entité géologique qui s'étend de la province brésilienne d'Amapa au Sud-Est jusqu'au delta de l'Orénoque (Venezuela) au Nord-Ouest. Les roches sont datées du Paléoproterozoïque. Les roches les plus anciennes se sont formées il y a plus de 2 milliards d'années et proviennent de l'ouverture d'un océan ayant séparé les boucliers archéens d'Amazonie et d'Afrique de l'Ouest. C'est durant cet épisode de l'histoire de la Terre que se sont formées la quasi-totalité des roches de Guyane. Son relief se caractérise par une alternance de collines (entre 20 et 50 m d'altitude) et de vallées peu profondes et humides (Epron *et al.*, 2006). Ses sols sont principalement de type acrisol (FAO, 1998).

1.4.2 L'environnement biologique

En Guyane française, la forêt est équatoriale sempervirente ombrophile de plaine. La biodiversité rencontrée en Guyane est considérable. Plus de 7000 espèces végétales (champignons exclus) sont recensées dont 5600 de plantes supérieures incluant 1500 espèces d'arbres. Plus de 9 espèces végétales sur 10 sont des espèces forestières. La faune est également très riche. A titre d'exemple, si la France métropolitaine recense 77 espèces de poissons d'eau douce, quasiment 500 sont répertoriées en Guyane. Qui plus est, un tiers de ces poissons sont, à l'heure actuelle, endémiques de Guyane. A ce jour, 190 espèces de mammifères, 740 d'oiseaux, 160 de reptiles, 110 d'amphibiens sont relativement bien connus alors qu'on estime à 400 000 le nombre d'espèces d'invertébrés peuplant les forêts guyanaises (de Noter, 2008). Une grande partie de cette biodiversité a pu se maintenir en Guyane grâce à une densité de population extrêmement faible à l'intérieur des terres.

1.4.3 La population

La population guyanaise estimée en 2013 était de 250 109 hab, ce qui fait de la Guyane un département de très faible densité démographique. Mais cette densité est en forte augmentation et les prédictions pour 2030 sont de 425 000 hab (INSEE, 2013). Cette augmentation provient d'une démographie très dynamique et d'une forte immigration des pays voisins. L'exploitation forestière en Guyane française est réglementée et réduite au domaine forestier permanent, ce qui fait de la forêt un espace relativement protégé. Mais d'ici 2030, la demande en bois de construction augmentera fortement, ainsi, probablement, que la demande en bois énergie pour suppléer au barrage de Petit-Saut.

1.4.4 Le climat

La Guyane, "terre d'eaux abondantes" en Arawak, porte bien son nom. Comme c'est souvent le cas en climat tropical, le climat est plus influencé par le régime des pluies que par les variations saisonnières de températures. Les précipitations moyennes sont comprises entre 2000 et 4000 mm par an et montrent une très grande variabilité spatiale et temporelle (Figures 3, 5 et 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 proches de 1500 mm pour certaines stations à l'ouest du département. La variabilité saisonnière des précipitations est importante en Guyane. Ces variations sont dues au déplacement de la zone intertropicale de

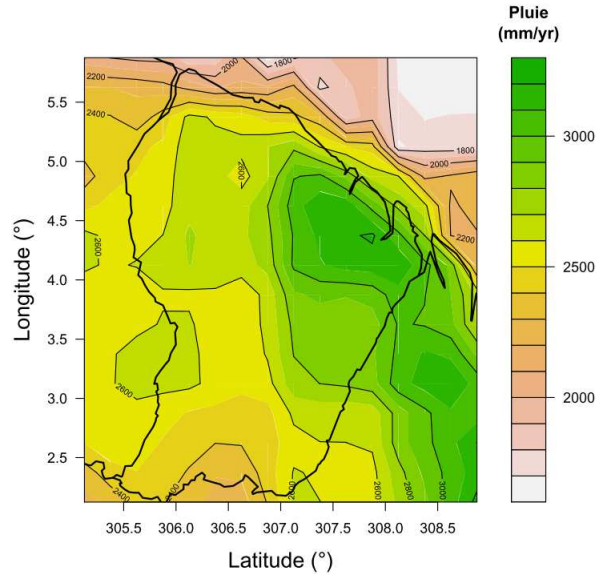


FIGURE 3 – **Carte des précipitations moyennes annuelles en Guyane.** Carte réalisée à partir des données satellites TRMM (Tropical Rainfall Measurements Mission) mensuelles sur la période 1998-2011 (<http://disc.gsfc.nasa.gov/precipitation/>).

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. Lorsque la ZIC est au-dessus de la Guyane, elle provoque des épisodes pluvieux. Les saisons se décomposent en une longue saison humide d'avril à mi-juillet suivie d'une saison sèche avec des mois où les précipitations sont inférieures à 50 mm de mi-juillet à mi-novembre. 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 événements El Niño et/ou l'augmentation des températures de surface du nord de l'océan Atlantique sont associés à l'intensité de la saison sèche en Amazonie. La température quant à elle présente très peu de variation 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.

La variabilité intra-annuelle du climat en Guyane française est impor-

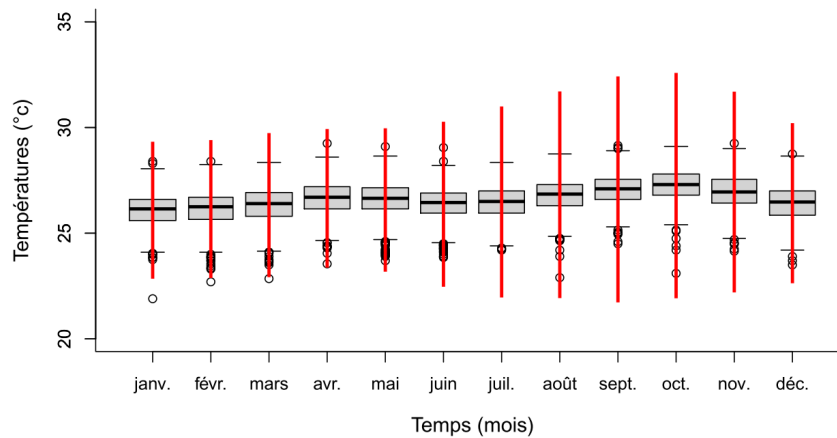


FIGURE 4 – **Évolution saisonnière des températures mensuelles.** Évolution mesurées à la station de Pointe-Combi (15km à l’ouest du site de Paracou) sur la période 1981-2011. L’amplitude de température est plus importante en saison sèche (août-novembre).

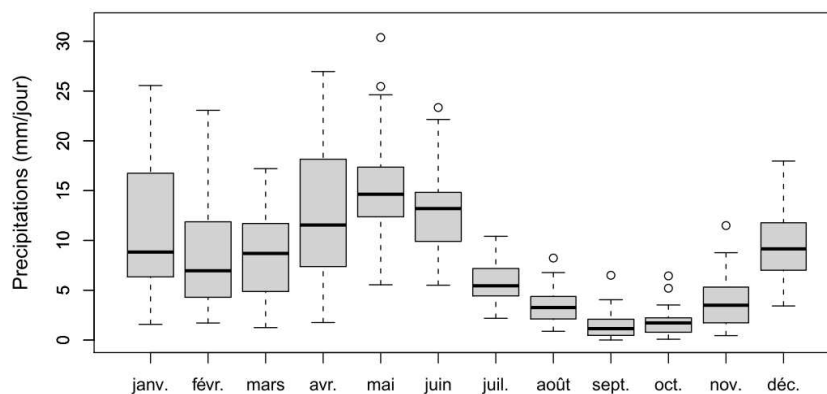


FIGURE 5 – **Évolution saisonnière de la pluviométrie mensuelle.** Évolution mesurée à la station de Pointe-Combi (15 km à l’ouest du site de Paracou) sur la période 1981-2011.

tante, de par la différence de précipitation entre la saison sèche et la saison des pluies, cette variabilité est donc bien connue. La variabilité inter-annuelle, qui est moins facile à appréhender, est aussi moins connue. Des changements climatiques considérables sont attendus dans le futur et la question de l’avenir de la forêt tropicale humide en climats incertains est fondamentale.

1.5 Le site de Paracou

1.5.1 Le site expérimental

Le site expérimental de Paracou est installé sur la commune de Sinnamary depuis 1984, il est constitué de 15 parcelles de 6.25 hectares chacune et d'une parcelle de 25 hectares (Figure 6). Certaines de ces parcelles ont été soumises à des traitements d'exploitation forestière, il existe trois traitements différents, correspondant à une exploitation plus ou moins intense. Les autres parcelles ont été laissées en contrôle pour servir de témoins (parcelles 1,6,11, Figure 6). Les parcelles 13,14,15 et 16 ont été ajoutées au dispositif en 1990. Le site était initialement conçu pour étudier l'impact de l'exploitation forestière, et répondre à des questions de sylviculture. Cette problématique initiale s'est peu à peu diversifiée, et aujourd'hui le site de Paracou est utilisé pour étudier la dynamique des écosystèmes forestiers guyanais en général. La forêt du site de Paracou comprend plus de 700 espèces d'arbres de DBH supérieur à 10cm. Les familles dominantes sont les *Fabaceae*, les *Chrysobalanaceae*, les *Lecythydaceae* et les *Sapotaceae*.

1.5.2 Les données disponibles

Chaque année, pendant la saison sèche (à partir du mois de juillet), l'inventaire des parcelles 1 à 15 du site de Paracou a lieu. Pendant cet inventaire, tous les arbres dont le diamètre à 1.30m (DBH : diameter at breast height) est supérieur à 10cm sont mesurés, avec une précision de 0.5cm. Les arbres recrutés, qui n'étaient pas dans l'inventaire l'année précédente, sont ajoutés avec leurs coordonnées, les arbres morts sont notés morts, et le type de mort est relevé (sur pied, chablis primaire ou secondaire). Lorsqu'un arbre a de trop gros contreforts ou un tronc de forme particulière, la mesure du diamètre est rehaussée, ou estimée. Cet inventaire annuel permet donc de suivre la dynamique individuelle des arbres depuis l'installation du site en 1984 ou depuis 1990 pour les parcelles les plus récentes.

Le travail réalisé sur le site de Paracou et les données qu'il génère sont à l'origine de nombreuses études qui ont permis et permettent encore de mieux comprendre l'écosystème forestier guyanais, c'est un travail titanesque qu'il convient de saluer et d'apprécier à sa juste valeur.

1.5.3 L'identification taxonomique

L'identification taxonomique de tous les arbres des parcelles témoins du site de Paracou est finalisée depuis 2012. Avant cette date, les arbres étaient

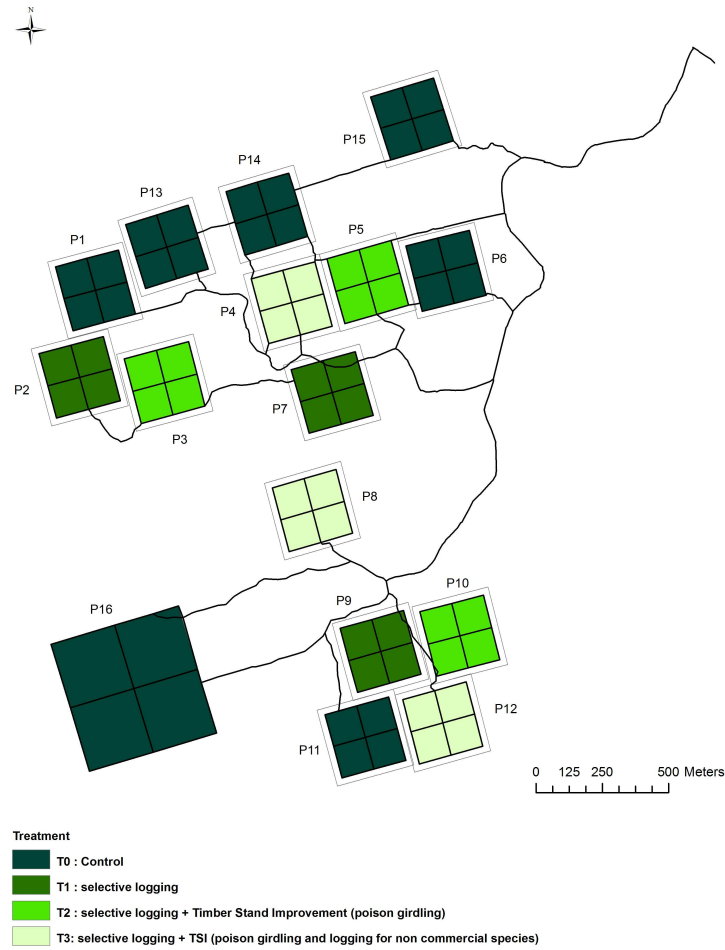


FIGURE 6 – Les parcelles du site expérimental de Paracou. Le site expérimental de Paracou est situé en Guyane Française, près de Sinnamary. Il a été créé en 1984 et depuis, les parcelles 1 à 12 sont suivies. Les parcelles 13 à 16 ont été ajoutées en 1990. Différentes intensités de traitements sylvicoles ont été appliquées sur les parcelles, et certaines parcelles n'ont pas été traitées pour servir de témoins.

identifiés grâce à leurs noms vernaculaires. Des numéros étaient associés à ces noms vernaculaires et chaque arbre était associé à un numéro lors de son recrutement, c'est-à-dire son entrée dans la base de donnée. Or, ces noms vernaculaires n'ont pas une grande précision taxonomique, certains noms vernaculaires correspondent à plusieurs espèces, et les correspondances sont parfois beaucoup moins claires qu'attendues. Il a donc été décidé d'identifier tous les arbres de Paracou, grâce à l'expertise de botanistes, avec l'aide de l'herbier de Cayenne lorsque c'était nécessaire.

2 Les changements climatiques

Le 21/09/2014, la marche mondiale pour le climat a mobilisé des centaines de milliers de personnes dans plus de 2500 endroits du globe. A Cayenne, en Guyane Française, seule une cinquantaine de personnes ont défilé. Pourtant cette région du monde ne sera pas épargnée par les changements prévus par le groupe d'experts intergouvernemental sur l'évolution du climat (GIEC).

2.1 Les changements globaux

Les changements climatiques sont au cœur de plusieurs milliers de publications chaque année. Leurs impacts sur les écosystèmes sont une des préoccupations au cœur des débats. Les climatosceptiques sont de plus en plus rares, et les rapports fournis par le GIEC sont maintenant reconnus comme une base de travaux extrêmement fiable.

Le GIEC a été créé en 1988 sous l'impulsion de l'organisation météorologique mondiale (OMM) et du Programme des Nations Unies pour l'Environnement (PNUE). L'une des principales activités du GIEC consiste à procéder, à intervalles réguliers, à une évaluation de l'état des connaissances relatives au changement climatique. Dans le rapport du GIEC intitulé "Changements climatiques 2013, les éléments scientifiques", et comme le montre la Figure 8, le GIEC souligne que le réchauffement du système climatique est sans équivoque et que, depuis les années 1950, beaucoup de changements observés sont sans précédent depuis des décennies voire des millénaires (IPCC, 2013). L'atmosphère et l'océan se sont réchauffés, les couvertures de neige et de glace ont diminué, le niveau des mers s'est élevé et les concentrations des gaz à effet de serre ont augmenté.

Pour tirer ses conclusions sur les futurs climats probables, le GIEC utilise des scénarios dits RCP (Representative Concentration Pathway) plus ou moins optimistes. Ces scénarios permettent d'envisager le futur en fonction des décisions prises et des émissions de gaz à effet de serre, tels que le CO₂.

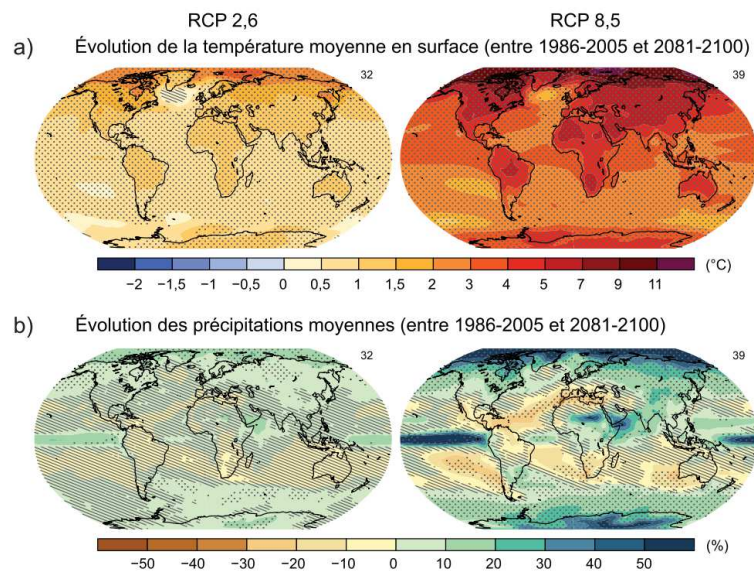


FIGURE 7 – Cartes des moyennes multi-modèles CMIP5 pour les scénarios RCP2,6 et RCP8,5 sur la période 2081-2100. a) évolution de la température moyenne annuelle en surface, b) évolution moyenne en pourcentage des précipitations moyennes annuelles. Tiré de IPCC (2013).

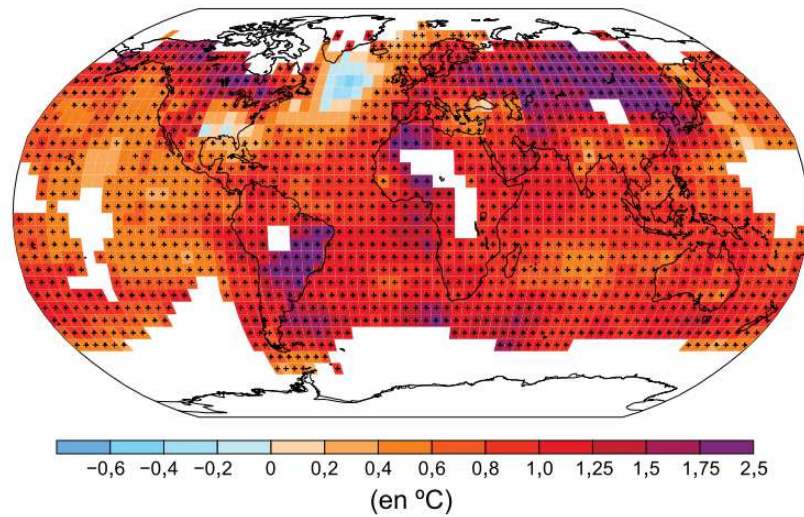


FIGURE 8 – **Évolution de la température en surface observée entre 1901 et 2012.** Carte de l'évolution des températures en surface observée entre 1901 et 2012, dérivée des tendances de températures déterminées par régression linéaire d'un ensemble de données. Les tendances ont été calculées uniquement pour les régions où la disponibilité des données permet une estimation robuste (c'est-à-dire, uniquement pour les mailles présentant des relevés complets à plus de 70 % et plus de 20 % de données disponibles dans les 10 premiers et 10 derniers % de la période temporelle). Les autres régions sont en blanc. Les mailles pour lesquelles la tendance est significative au niveau de 10 % sont indiquées par le signe +. Tiré de IPCC (2013).

Dans son dernier rapport, le GIEC propose 4 scénarios, dont les noms correspondent aux forçages radiatifs en $W.m^2$. Le plus optimiste des scénarios est le RCP2.6, le plus pessimiste est le RCP8.5. Deux scénarios intermédiaires, le RCP4.5 et le RCP6.0 sont aussi disponibles. Jusqu'aujourd'hui, ce sont les scénarios les plus pessimistes proposés par le GIEC qui ont été suivis par l'humanité.

- RCP 2.6 : le scénario de faibles émissions appelé "peak and decay" : le forçage radiatif atteint un maximum au milieu du XXI^{ème} siècle, avant de décroître vers une valeur de $2.6W.m^{-2}$,
- RCP 4.5 : un scénario intermédiaire, le forçage radiatif se stabilise à une valeur de $4.5W.m^{-2}$,
- RCP 6.0 : un scénario intermédiaire, le forçage radiatif se stabilise à une valeur de $6W.m^{-2}$,
- RCP 8.5 : le scénario d'émissions fortes ($8.5W.m^{-2}$), le "pire" des scénarios, aussi appelé "business as usual".

Concernant le futur, le GIEC met en garde les décideurs. De nouvelles émissions de gaz à effet de serre impliqueront une poursuite du réchauffement et des changements affectant toutes les composantes du système climatique. À la fin du XXI^{ème} siècle, l'augmentation de la température à la surface du globe sera probablement supérieure à $1.5^{\circ}C$ par rapport à l'époque allant de 1850 à 1900, pour tous les RCP sauf le RCP2.6. Il est probable qu'elle dépassera $2^{\circ}C$ selon les RCP6.0 et RCP8.5, et il est plus probable qu'improbable qu'elle dépassera $2^{\circ}C$ selon le RCP4.5. Dans tous les RCP envisagés à l'exception du RCP2.6, le réchauffement se poursuivra après 2100. Il continuera à présenter une variabilité inter-annuelle à décennale et ne sera pas uniforme d'une région à l'autre. Les changements concernant le cycle mondial de l'eau en réponse au réchauffement au cours du XXI^{ème} siècle ne seront pas uniformes. Le contraste des précipitations entre régions humides et régions sèches ainsi qu'entre saisons humides et saisons sèches augmentera, bien qu'il puisse exister des exceptions régionales (Figure 7). Les événements de précipitation ou de sécheresse seront très probablement plus intenses et plus longs, notamment sous les tropiques.

2.2 Les modèles du GIEC

Les modèles utilisés par le GIEC pour établir ses prédictions sont principalement des "General Circulation Models" (GCMs), des modèles climatiques

basés sur la combinaison de modèles biogéochimiques, géographiques et de perturbations climatiques, et qui permettent de modéliser les différents flux sur la surface terrestre ainsi que l'impact des changements climatiques sur la végétation et sur les cycles de carbone et d'eau associés. Leur utilisation n'est pas aisée, et les sorties des modèles ne sont pas présentées de façon à pouvoir être directement utilisées pour étudier l'impact des changements climatiques sur d'autres systèmes dynamiques (Jones *et al.*, 2009). Les sorties des GCMs doivent être réduites pour obtenir des données journalières à un endroit donné de la planète. Différentes méthodes existent pour réduire les données, les méthodes les plus grossières sont en général aussi les plus mauvaises, tandis que des méthodes plus précises auront de meilleurs résultats mais nécessiteront des données additionnelles pour permettre de calibrer les sorties des modèles.

Différents outils sont actuellement développés pour réaliser des descentes d'échelles. C'est le cas de MarkSim, ce logiciel permet de simuler des données à partir de 17 modèles pour les années 2010 à 2095, et il est mis à disposition sur internet (gisweb.ciat.cgiar.org/MarkSimGCM/). Le logiciel MarkSim est calibré grâce aux données climatiques de plus de 10 000 stations météorologiques dans le monde. D'autre part, une descente d'échelle a été réalisée pour la France (métropole, mais aussi DOM-TOM) pour le modèle Arpege-V4.6 de Météo-France (non disponible dans MarkSim), qui est disponible en ligne sur la plateforme DRIAS (<http://www.drias-climat.fr/>). Cet outil permet entre autres d'avoir des prédictions précises pour la Guyane (Figures 9 et 10). Ces descentes d'échelles sont d'un grand intérêt car (i) elles permettent d'utiliser des données précises et de les intégrer dans des modèles pour les appliquer à des processus climat-dépendants et (ii) la mise à disposition de ces données spatiales permet à tout un chacun de se faire une idée des climats attendus dans une région d'intérêts, et de mieux prendre conscience des changements climatiques en cours.

2.3 Les climats futurs en forêts tropicales

D'après le dernier rapport du GIEC (IPCC, 2013), des augmentations des températures moyennes saisonnières et annuelles importantes sont prévues. Les épisodes de précipitations extrêmes deviendront très probablement plus intenses et fréquents sur les continents des moyennes latitudes et dans les régions tropicales humides d'ici la fin de ce siècle, en lien avec l'augmentation de la température moyenne en surface. Les modèles utilisés pour construire les prédictions du GIEC sont nombreux et issus de laboratoires différents, répartis partout dans le monde. A l'échelle amazonienne, un consensus semble

2. LES CHANGEMENTS CLIMATIQUES

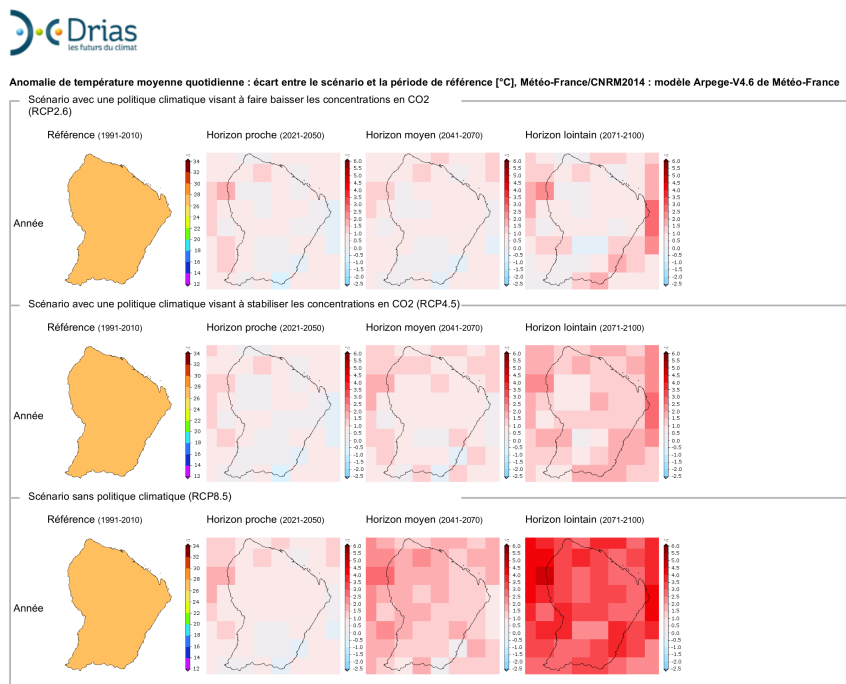


FIGURE 9 – Anomalies de température moyenne quotidienne avec **DRIAS**. Écart avec le scénario de référence (°C), le modèle utilisé est celui de Météo-France/CNRM2014 : Arpege-V4.6. L'augmentation de la température est à horizon lointain (2071-2100) et varie entre -0.5 et 3°C pour le RCP2.6, entre 1.5 et 5°C pour le RCP8.5.



Anomalie du cumul de précipitations : écart entre le scénario et la période de référence [mm], Météo-France/CNRM2014 : modèle Arpege-V4.6 de Météo-France

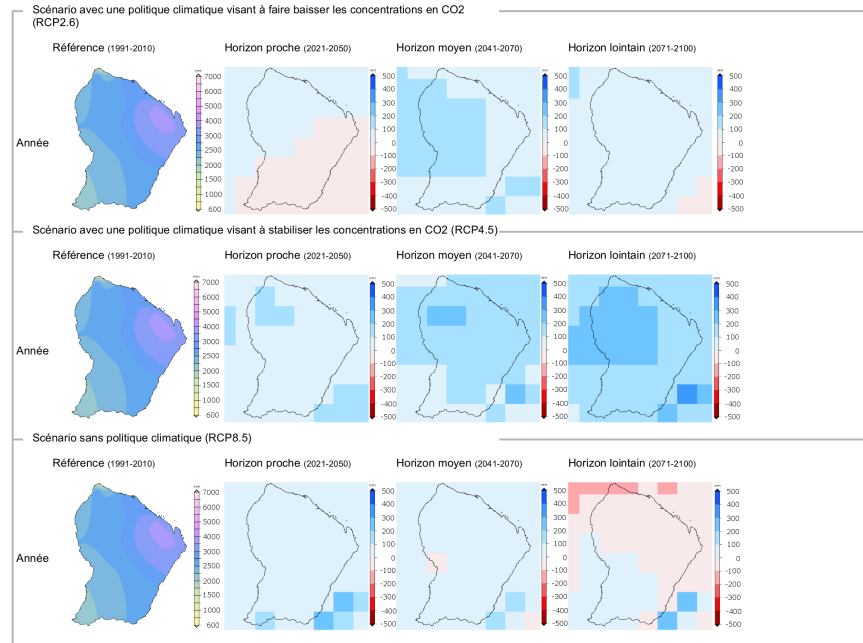


FIGURE 10 – Anomalies du cumul de précipitations avec DRIAS. Écart avec le scénario de référence (mm), le modèle utilisé est celui de Météo-France/CNRM2014 : Arpege-V4.6. Peu d’anomalies sont observées à horizon lointain pour le RCP 2.6. Pour le RCP 8.5, des anomalies négatives (jusqu’à -200mm) sont observées dans le Nord de la Guyane, et des anomalies positives (jusqu’à +200mm) sont observées dans le Sud.

émerger des modèles du rapport IPCC AR5 et suggère un renforcement (en durée et en intensité) des saisons sèches (Joetzjer *et al.*, 2013). Toutefois, il est à noter que les différents modèles ont des sorties différentes et que l'unique consensus qu'il est possible d'établir est bien cette prolongation de la saison sèche, particulièrement dans la partie Est du bassin Amazonien. De tous les modèles utilisés, seul celui de l'IPSL (ipsl-sm5a-lr) prévoit une diminution de la longueur de la saison sèche, tandis que 6 modèles (CCCMA, CNRM, MOHC, MPI, MRI et NCAR) prévoient une augmentation significative de la longueur de la saison sèche (Joetzjer *et al.*, 2013).

Les variations de température à la surface de l'océan Pacifique, principalement causées par le phénomène El Niño-Southern Oscillation (ENSO), jouent un rôle important dans le renforcement de la saison sèche. En effet, les événements El Niño sont responsables de climats plus chauds et plus secs pour le bassin amazonien (Malhi *et al.*, 2008; Li *et al.*, 2006). De plus, une augmentation des gradients de température à la surface de l'océan (sea surface temperature SST) du Nord-Ouest de l'Atlantique est prévue par les GCMs. Ceci peut déplacer la ZIC et modifier les gradients pluviométriques à l'échelle intra-annuelle mais aussi modifier le système de circulation des cellules de Hadley, ce qui impliquerait un renforcement des saisons sèches sur une échelle de temps plus longue (Christensen *et al.*, 2007). Les modèles utilisés par l'IPCC 5AR ne sont pas capables de bien modéliser ces changements de longueur de saisons sèches (Fu *et al.*, 2013), ce qui laisse présager des augmentations plus drastiques que celles qui sont annoncées.

Le logiciel MarkSim m'a permis de construire un jeu de données climatique pour le site de Paracou. Les modèles disponibles ne sont pas les mêmes que dans Joetzjer *et al.* (2013), et je me suis demandée si le même consensus est observable. En effectuant 99 itérations de MarkSim pour chacun des 17 modèles disponibles, l'augmentation de la période sèche n'est pas si consensuelle, que ce soit en regardant le nombre de jours ou le nombre de mois. Aucune conclusion ne peut être tirée concernant l'évolution du régime pluviométrique. Par contre, l'augmentation de la température est unanime pour tous les modèles et pour tous les scénarios. Il faut garder en tête qu'il est toujours plus difficile d'avoir confiance en une prédiction très spatialisée que de dégager des tendances communes, à l'échelle du bassin amazonien.

Sous la plateforme DRIAS, une forte augmentation de la température est observée, notamment pour le scénario 8.5 (Figure 9). L'évolution de la pluviométrie est moins marquée, avec toutefois une diminution de la pluviométrie prévue pour le scénario 8.5 dans le Nord-Ouest de la Guyane (Figure 10), or cette région est déjà la région qui reçoit le moins d'eau ($< 2000\text{mm}$). Le seuil d'évapotranspiration nécessaire en forêt tropicale humide est de 1500mm

(Roche, 1982), ce qui signifie qu'au minimum 1500mm doivent entrer dans le système. Si la pluviométrie diminue trop et finit par être inférieure à ce seuil, le fonctionnement des forêts tropicales humides sera profondément bouleversé.

2.4 Effets attendus des changements climatiques sur la forêt tropicale

Le régime pluviométrique et la température en forêt tropicale amazonienne risquent d'être modifiés. Ces changements impacteront-ils la dynamique forestière dans ces forêts, et si oui, comment ? Pour comprendre cela, il faut commencer par comprendre les relations qui existent entre le climat et le fonctionnement écophysologique de l'arbre, mais il faut aussi comprendre comment ces relations se retranscrivent à l'échelle de la dynamique de la communauté, ce changement d'échelle est important car il convient de correctement prendre en compte la diversité de comportements individuels.

2.4.1 A l'échelle de l'arbre

La hausse de la température a un effet non linéaire sur le fonctionnement de l'arbre. La température joue un rôle dans les réactions chimiques ; une augmentation de la température peut causer une augmentation de la vitesse des réactions, notamment de la photosynthèse. Toutefois, si la température augmente trop, la structure tertiaire des enzymes responsables des réactions peut être endommagée (Fitter and Hay, 2001). Les réactions enzymatiques se font alors plus difficilement, voire plus du tout. La combinaison de ces deux principes conduit à la Figure 11, où la croissance est représentée en fonction de la température. Cette courbe prend la forme d'une cloche. En fonction de la température actuelle, une augmentation de la température peut avoir un impact positif sur la croissance. Ou bien, si la température est élevée, comme cela semble être le cas en forêt tropicale (Clark *et al.*, 2003), une augmentation de la température aura un impact négatif sur la croissance.

L'augmentation de la longueur et de l'intensité des saisons sèches prévue sur la bassin amazonien aura probablement aussi des conséquences à l'échelle individuelle. Lorsqu'un arbre manque d'eau, la pression au niveau de ses racines diminue, la différence de pression nécessaire pour la montée de la sève dans le xylème diminue alors elle aussi, ce qui peut ralentir cette montée, et avec elle tout le métabolisme de l'arbre. Si la sécheresse continue, la pression trop faible sera cause de cavitation, des bulles d'air se formeront dans les vaisseaux, ce qui peut conduire à l'embolisme, au mauvais fonctionnement de

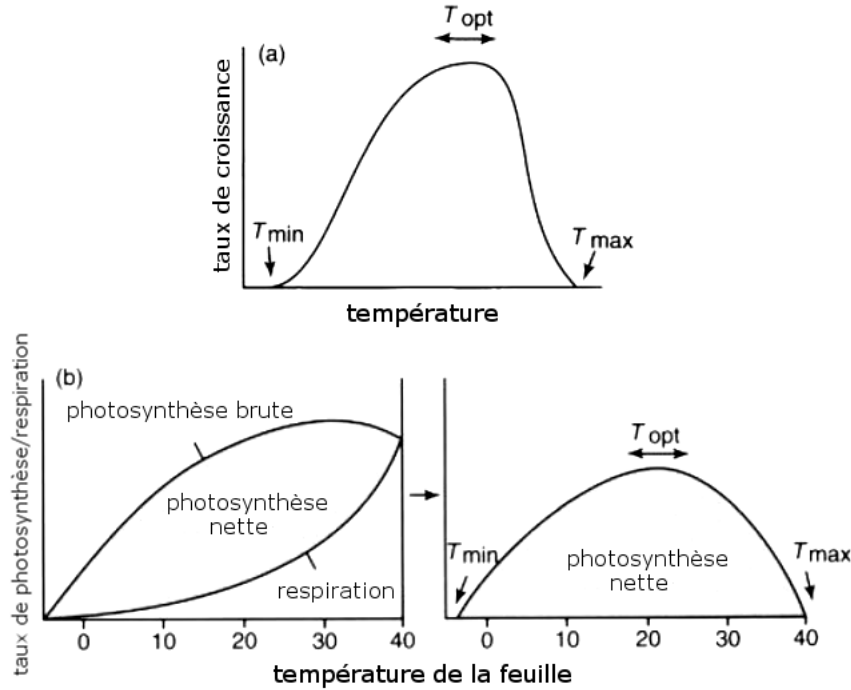


FIGURE 11 – **Relation entre croissance et température.** (a) Réponse de la croissance des plantes à la température, représentation de la température minimale (T_{min}), de la température maximale (T_{max}) et de l'intervalle de températures optimales (T_{opt}). (b) Influence de la température sur la photosynthèse brute et la respiration. Inspiré de Fitter and Hay (2001).

certaines vaisseaux, voire à leur destruction. L'arbre aura alors des difficultés pour se développer et pour survivre. Pour estimer la tolérance à la sécheresse de l'arbre, le point de perte de turgescence est un indicateur facile à mesurer (Bartlett *et al.*, 2012) qui permet d'estimer la capacité d'un arbre à maintenir une forte turgescence, c'est-à-dire une forte pression, et donc à éviter la cavitation.

L'augmentation du CO_2 permet quant-à-elle d'augmenter l'efficacité d'utilisation de l'eau lors de la photosynthèse (Chambers and Silver, 2004). La conductance des stomates ainsi que la transpiration sont réduites, donc une quantité plus importante de carbone peut être assimilée pour un même taux de transpiration.

Les interactions entre certaines variables climatiques et la physiologie d'un arbre peuvent être mesurées expérimentalement sur les feuilles (Doughty,

2011), ou sur un arbre (Wullschleger *et al.*, 1998). Toutefois, pour passer à l'échelle de la forêt, les extrapolations ne sont pas forcément simples.

2.4.2 A l'échelle de la forêt

De façon générale, bien que les processus qui agissent au niveau de la feuille soient assez bien connus, les réactions de la forêt tropicale aux changements climatiques à l'échelle de la communauté restent inconnues.

Concernant la température, les conséquences d'une augmentation de température à l'échelle de la communauté sont inconnues. En effet, les températures en forêt tropicales sont relativement peu variables, et aucune expérience de réchauffement n'a été réalisée pour simuler le réchauffement des prochaines décennies.

Pour étudier l'effet de la sécheresse sur la forêt, les études se sont basées sur la dynamique forestière observée suite aux sécheresses importantes de 2005 et de 2010 (Phillips *et al.*, 2009; Lewis *et al.*, 2011). Ces travaux ont montré que la disponibilité en eau avait un effet important sur la dynamique forestière, en augmentant notamment le taux de mortalité annuel. De façon générale, la sécheresse augmente la vulnérabilité des plantes (McDowell *et al.*, 2008; Allen *et al.*, 2010; Choat *et al.*, 2012). D'autre part, il a été possible de mettre en place des expériences d'exclusion en recouvrant la forêt pour empêcher la pluie de venir irriguer le sol (da Costa *et al.*, 2010; Nepstad *et al.*, 2007; Brando *et al.*, 2008). Ces expériences appelées TFE (throughfall exclusion) ont permis de mettre en évidence, une fois encore, une augmentation de la mortalité, notamment de la mortalité des gros arbres. Toutefois, ces expériences ne reflètent pas vraiment l'évolution continue vers un potentiel climat futur, mais un changement drastique et brutal de la disponibilité en eau. Les modèles inter-annuels actuels de dynamique forestière ne permettent pas encore de prédire de façon correcte les conséquences des sécheresses futures (McDowell *et al.*, 2013). A l'échelle saisonnière toutefois, la disponibilité en eau est le déterminant majeur de la dynamique de la forêt tropicale (Wagner *et al.*, 2012, 2014).

Tout comme la température, l'effet de la concentration de CO₂ sur la dynamique est controversé. L'augmentation du CO₂ a été mise en relation avec une augmentation du recrutement et de la croissance en Amazonie (Lewis *et al.*, 2004), mais il a été argumenté que la hausse de la concentration du CO₂ ne pouvait avoir impacté aussi rapidement la croissance (Chambers and Silver, 2004), dont l'augmentation doit être plutôt causée par d'autres facteurs environnementaux dont les effets sont plus instantanés, comme l'irradiance ou encore des perturbations environnementales anciennes (Chambers and

Silver, 2004). L'augmentation des concentrations de CO₂ atmosphérique est linéaire dans le temps, il est donc difficile de bien différencier les effets dus à cette augmentation de CO₂ d'effets purement temporels liés à l'évolution de la forêt dans le temps.

3 La modélisation

Pour mieux comprendre la dynamique des arbres en forêt tropicale, ainsi que les impacts que peuvent avoir les changements climatiques sur cette dynamique, la modélisation est un outil incontournable. La modélisation permet en effet de schématiser des systèmes complexes, en ne gardant que les processus sur lesquels porte l'étude. De par l'incessante croissance des capacités de nos ordinateurs, la modélisation est devenue une discipline à part entière et des méthodes de modélisation ont vu le jour, qui ne sont plus limitées par les temps de calcul ou la place en mémoire. Dans cette thèse, je cherche à modéliser la dynamique de la forêt tropicale à Paracou, et plus particulièrement les effets des variations climatiques inter-annuelles sur cette dynamique. La construction et l'utilisation d'un tel modèle me permettent (i) de mettre au point une méthodologie transposable dans d'autres sites d'études, (ii) si les réponses sont suffisamment génériques, d'établir les grandes lignes de scénarios possibles pour l'évolution de la dynamique des forêts tropicales.

3.1 Les modèles de dynamique forestière

Les trois processus de recrutement, croissance et mortalité peuvent être modélisés séparément ou conjointement. Les modèles de croissance sont les plus nombreux, car la croissance est souvent liée à la productivité de la forêt et au stockage du carbone, ce qui intéresse particulièrement les exploitants et différents acteurs de la gestion forestière.

Différentes classifications ont été proposées en fonction de l'architecture des modèles proposés. Ces différentes classifications font référence à différentes classes de modèles, Porté en propose une en 2002 que je vais brièvement décrire ici (Figure 12). Il faut garder en tête que d'autres classifications existent et que cette présentation me permettra essentiellement de passer en revue les différents modèles existants.

3.1.1 Stand models

Dans les stand models, la forêt est représentée comme une mosaïque de sous-forêts (plots). Cette classe de modèles se divise en deux groupes, en fonction

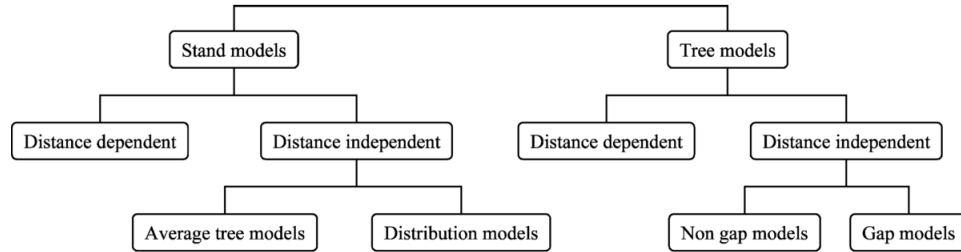


FIGURE 12 – **Classification des modèles selon Porté and Bartelink (2002).**

de la façon dont les plots sont gérés.

- Les "distance-dependant stand models"

Les plots sont décrits (distribution des DBH, composition spécifique) et spatialisés. Les interactions entre plots se font à plus ou moins grande échelle en fonction des processus étudiés. Ces modèles sont peu utilisés pour les forêts mixtes, et seul le modèle FORMIX2 est utilisé en forêt tropicale.

- Les "distance-independent stand models"

Ces modèles peuvent être de deux types : "average tree model", où chaque plot a ses propres caractéristiques environnementales et est décrit (surface terrière, nombre d'arbres dans le plot...) en fonction de ces caractéristiques. La dynamique des plots est décrite par un système d'équations différentielles, et ces modèles sont souvent utilisés pour calculer la production d'une forêt. L'autre type, celui des "distribution models", permet de prendre en compte plus facilement l'hétérogénéité spécifique d'un plot. Ces modèles ont été développés dans les années 1980-1990. L'évolution des processus se fait de façon discrète grâce à des modèles matriciels ou de façon continue grâce à des régressions.

3.1.2 Tree models

Les modèles basés sur les arbres comme individus sont plus récents, comme tous les modèles individus-centrés en général, car ils se sont développés en même temps que la puissance des ordinateurs. Il est en effet possible de résoudre certaines équations à la main, mais souvent impossible de suivre les trajectoires de chaque arbre indépendamment.

On distingue encore différentes sortes de modèles, en fonction de la gestion ou non de l'espace :

- les "distance-dependent tree models"

On modélise chaque arbre individuellement, en prenant en compte sa place dans l'espace. La plupart des modèles ne se contentent pas de représenter la croissance, mais aussi souvent la mortalité, et parfois le recrutement, et se basent sur des régressions multivariées pour calculer la croissance individuelle. Plus rarement, ils utilisent une approche plus mécaniste et fonctionnelle basée sur la production primaire et secondaire. La prise en compte de la distance entre les arbres permet d'inclure des indices de compétition comme prédicteurs dans les régressions.

- les "distance independent tree models"

Certains modèles ne prennent pas en compte la position de l'arbre, ceux-ci sont pour la plupart des gap-models. Les gap-models s'inspirent de JABOWA, développé par Botkin *et al.* (1972), les gap sont des morceaux de forêt de taille variable et caractérisés par une liste d'individus. Ces gaps ont des conditions environnementales homogènes et la dynamique de chaque arbre à l'intérieur de chaque gap est calculée de façon individuelle. Les gap models calculent le recrutement, la croissance et la mortalité, en prenant en compte la quantité de lumière disponible pour chaque arbre dans chaque gap, qui est l'un des paramètres les plus importants intervenant dans ce type de modèle. Les "distance independent tree models" qui ne sont pas des gap models sont plutôt rares, et se basent sur des fonctions empiriques.

Le Tableau 1 permet de synthétiser les avantages et inconvénient liés à la construction et à l'utilisation des différents modèles.

3.2 Les enjeux de modélisation en forêts tropicales

La plupart des forêts mondiales sont constituées de plusieurs espèces d'arbres qui cohabitent, et sont appelées "mixed forests". Tous les modèles de dynamique présentés précédemment ne sont pas forcément adaptés (Porté and Bartelink, 2002). En forêt tropicale, le nombre très important d'espèces rend impossible la paramétrisation de modèles spécifiques à chaque espèce. Des stratégies doivent donc être mises en place pour prendre cette diversité en compte tout en la synthétisant. Ainsi, parmi les classes de modèles présentées plus tôt, certaines très utilisées en climat tempéré peuvent s'avérer peu

transposables en forêt tropicale. Historiquement, dans les ditribution-models, des groupes d'espèces ont été créés pour gérer l'hyper-diversité en forêt tropicale (Vanclay, 1989; Alder, 1995; Favrichon, 1998). Plus récemment, dans les "distance-dependant tree models", ces groupes ont de nouveau été utilisés, parfois de manière plus affinée, en fonction du besoin en lumière des espèces (Chave *et al.*, 1999), ou de leur position dans la canopée (Moravie *et al.*, 1997; Liu and Ashton, 1998). Les "stand-models" n'ont pas été très utilisés en forêt tropicale, d'une part car de trop nombreuses données sont nécessaires pour construire ce genre de modèle, et d'autre part car ils sont peu adaptés pour gérer un grand nombre d'espèces.

TABLE 1 – **Les avantages et les inconvénients des différents types de modèles.** Classification développée dans (Porté and Bartelink, 2002), avantages et inconvénients des différentes approches pour modéliser la dynamique forestière.

Modèles	Avantages	Inconvénients
Distance dependent stands models	Spatialisation simple	Pas de diversité
	Précision des indicateurs	Besoin de beaucoup de données
Average tree models	Indicateurs précis	Pas de diversité
	Simple d'utilisation	Validation limitées
	Peu de paramètres	Pas de prédiction
Distribution models	Diversité prise en compte	Relations empiriques
	Validation à long terme	(peu de sens biologique)
	Précision des indicateurs	Beaucoup de données nécessaires
Tree distance dependent models	Spatialisation	Beaucoup de données nécessaires
	Trajectoires individuelles	
	Diversité prise en compte	
Tree distance independent models	Trajectoires individuelles	Relations empiriques
		(peu de sens biologique)
Gap models	Trajectoires individuelles	Relations empiriques
	Spatialisation	(peu de sens biologique)
		Caractéristiques du gap
		Pas de relation entre proches

3.2.1 L'approche groupes fonctionnels

Des groupes d'espèces ont couramment été créés pour gérer le grand nombre d'espèces en forêts tropicales. Les critères de groupement diffèrent en fonction des objectifs à atteindre, ces critères sont par exemple souvent relatifs à la place de l'arbre dans la canopée (Chave *et al.*, 1999), qui est considérée comme un indicateur de la lumière disponible pour l'arbre. Le rapprochement des espèces en groupes fonctionnels est un outil qui peut aussi être utilisé pour étudier la coexistence des espèces et la redondance des fonctions écologiques de ces espèces.

Les groupes peuvent également être créés en s'appuyant directement sur les processus étudiés, ce qui demande une méthodologie appropriée (Ouedraogo *et al.*, 2013). Les groupes sont alors formés pendant le processus de modélisation et n'ont pas forcément de signification biologique. Certains algorithmes peuvent notamment chercher le nombre de groupes le plus approprié, ce qui résout la question épineuse du nombre de groupes (Mortier *et al.*, 2013). Les méthodes développées sont alors des méthodes d'optimisation combinatoires, et des heuristiques doivent être utilisées (Picard *et al.*, 2002).

In fine, l'idée des groupes fonctionnels est de rassembler les espèces par type de comportements. Ces groupes permettent donc de prendre toute la variabilité des stratégies observées, d'un comportement extrême à l'autre. Toutefois, ces groupes peuvent sembler artificiels, les limites arbitraires et le choix du nombre de groupes subjectif d'autant qu'il n'y a pas de consensus sur les critères de regroupement importants.

3.2.2 L'approche traits fonctionnels

L'approche par les traits fonctionnels permet de mieux prendre en compte le continuum entre les différentes stratégies. En effet, bien que différents comportements soient observés en forêt tropicale, la création de groupes bien distincts est parfois artificielle. Les traits fonctionnels sont considérés comme des proxys des différentes stratégies sur les différents axes de variations possibles : le leaf economics spectrum, le wood economics spectrum et le life-history spectrum. Un nombre restreint de traits qui ont un rôle prépondérant dans les stratégies de recrutement/croissance/mortalité peuvent être choisis comme variables à inclure dans les différents modèles pour les différents processus démographiques. Cette approche permet de chercher, d'une part, un signal commun à tous les arbres, et d'autre part de prendre en compte la variabilité de chaque espèce, sans avoir à gérer un trop grand nombre de

paramètres. De plus, contrairement à des groupes qui peuvent paraître artificiels et vides de fondements biologiques, les traits fonctionnels permettent de baser nos modèles sur des hypothèses éco-physiologiques.

Contrairement à l'approche par groupes, l'utilisation des traits fonctionnels n'est pas adaptée pour prendre facilement en compte les comportements extrêmes. De plus, les traits fonctionnels disponibles sont des traits dits "soft" qui ne sont que des indicateurs des traits "hard". Les traits "hard" sont mécaniquement plus liés aux performances des arbres, mais sont difficiles à mesurer, ce qui limite fortement leur utilisation.

3.3 Les enjeux actuels

Actuellement, des modèles basés sur les traits fonctionnels permettent de prendre en compte l'immense diversité présente en forêt tropicale. Ceci permet de manipuler cette diversité avec un nombre restreint de paramètres et de construire des modèles de dynamique individu-centrés. De plus, les données climatiques disponibles permettent d'inclure des variables climatiques dans ces modèles, il devient dès lors indispensable de construire des simulateurs qui permettent d'explorer les différents scénarios possibles, en utilisant les prédictions issues de modèles climatiques. Ces prédictions permettent de se faire une meilleure idée de la façon dont la forêt tropicale peut répondre à l'augmentation des températures et aux changements de régimes pluviométriques.

3.4 L'inférence bayésienne

Les modèles utilisés au cours de la thèse ont été calibrés par des méthodes bayésiennes. Ces méthodes permettent l'inférence de modèles intégrant de l'information *a priori* dans une structure hiérarchique. C'est le cas de la méthode développée dans le premier chapitre pour attribuer des traits fonctionnels à tous les arbres du jeu de données. L'expertise des forestiers sur la correspondance entre noms vernaculaires et noms scientifiques correspond à une connaissance *a priori*. Tout au long de la thèse, l'incertitude taxonomique est prise en compte grâce aux distributions *a posteriori* obtenues dans le premier chapitre. Les méthodes bayésiennes sont très souples et permettent d'inférer des modèles complexes, tout en propageant bien les incertitudes. C'est notamment ce qui a permis de calibrer un modèle de croissance et de mortalité conjointement dans cette thèse.

4 Plan

Dans cette thèse, j’apporterai des éléments de réponse et de réflexion sur la réaction des forêts tropicales aux changements climatiques. Le document est articulé en cinq chapitres, qui prennent la forme d’articles publiés, soumis, ou en phase finale de rédaction.

- Dans le premier chapitre, je présenterai une méthode de gestion de l’incertitude taxonomique, qui permet d’attribuer des traits fonctionnels à tous les arbres d’une communauté quel que soit leur niveau d’identification taxonomique, et qui sera utilisée dans la suite de mon travail. Cette méthode a permis de prendre en compte l’ensemble des arbres morts avant que leur identification botanique ne soit faite pour construire un modèle de mortalité à l’échelle de la communauté.
- Dans le second chapitre, ce modèle de mortalité est couplé avec un modèle de croissance. Le couplage fait intervenir la vigueur individuelle des arbres. Pour estimer cette vigueur, la croissance observée sur le terrain est comparée à la croissance prévue par le modèle de croissance. La vigueur ainsi estimée est un très bon prédicteur de la probabilité de mourir, les arbres qui grandissent plus que prévu ont une probabilité plus faible de mourir.
- Dans le troisième chapitre, je présenterai les résultats obtenus lorsque ce modèle joint est paramétré spécifiquement pour les espèces commerciales de Guyane française. Deux variables sont ajoutées dans les modèles pour tenir compte de l’intensité d’exploitation et du stress hydrique. Ces modèles permettent d’observer un gradient de réponses au stress hydrique chez les essences commerciales. L’exploitation a tendance à diminuer la compétition et ainsi à augmenter la croissance et diminuer la mortalité, tandis que le stress hydrique a l’effet inverse. Malgré cette réponse commune, des profils de susceptibilité différents sont observés pour chaque essence commerciale, ce qui permet d’identifier des essences particulièrement sensibles, et d’autres plus résistantes.
- Dans le quatrième chapitre, je présenterai l’introduction de variables climatiques dans le modèle joint à l’échelle de la communauté, en forêt naturelle. Ce chapitre met en évidence l’impact du stress hydrique, de la température, et de la saturation du sol en eau. Le stress hydrique a un impact négatif sur la croissance et la mortalité, la température a un impact négatif sur la croissance, et la saturation du sol en eau augmente la taux de mortalité.

- Dans le cinquième et dernier chapitre, le modèle climat dépendant est implémenté dans le simulateur de forêt SELVA, et différents scénarios climatiques correspondant aux simulations du GIEC sont testés pour le siècle prochain sur la communauté d'arbres actuelle de Paracou. Les sorties montrent que les hausses de température à venir peuvent être responsables d'un ralentissement de la croissance et d'une diminution substantielle de la surface terrière, du diamètre quadratique et de la biomasse.

Des pistes de réflexion sur les enjeux de modélisation et les échelles considérées sont proposées en discussion de ce travail.

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CHAPITRE 1

TOWARD TRAIT-BASED MORTALITY MODELS FOR TROPICAL FORESTS

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La mortalité est un processus moteur de la dynamique forestière. Les arbres qui meurent laissent leurs places à de nouveaux arbres, plus jeunes, parfois d'espèces différentes, et qui formeront la forêt quelques années plus tard. Lors de la mort de gros arbres, des trouées de plusieurs dizaines de m² se forment, où pourront pousser des espèces héliophiles qui ne pouvaient se développer dans l'ombre du sous-bois. Mais la mortalité est aussi un processus complexe. Bien que ce soit un processus binaire et ponctuel, il faut parfois connaître l'histoire de vie d'un arbre dans sa totalité pour comprendre les causes de sa mort et parfois, elles restent inconnues.

Dans ce premier chapitre, nous proposons une méthode de modélisation de la mortalité des arbres en forêt tropicale qui fait intervenir les traits fonctionnels et le stade ontogénique de l'arbre pour calculer une probabilité individuelle de mourir. Nous nous plongeons dans les méthodes bayésiennes qui permettent d'inférer des modèles tout en tenant compte des incertitudes sur les prédicteurs. Ceci nous permet notamment d'attribuer des traits fonctionnels aux arbres qui sont morts sans avoir été identifiés.

Ce premier chapitre nous permet donc de modéliser le processus fondamental de la mortalité en forêt tropicale, à l'échelle de la communauté, tout en tenant compte des caractéristiques de chaque individu.

1 Abstract

- Tree mortality in tropical forests is a complex ecological process for which modelling approaches need to be improved to better understand, and then predict, the evolution of tree mortality in response to global change. The mortality model introduced here computes an individual probability of dying for each tree in a community.
- The mortality model uses the ontogenetic stage of the tree because youngest and oldest trees are more likely to die. Functional traits are integrated as proxies of the ecological strategies of the trees to permit generalization among all species in the community. Data used to parametrize the model were collected at Paracou study site, a tropical rain forest in French Guiana, where 20,408 trees have been censused for 18 years.
- A Bayesian framework was used to select useful covariates and to estimate the model parameters. This framework was developed to deal with sources of uncertainty, including the complexity of the mortality process itself and the field data, especially historical data for which taxonomic determinations were uncertain. Uncertainty about the functional traits was also considered, to maximize the information they contain.
- Four functional traits were strong predictors of tree mortality : wood density, maximum height, laminar toughness and stem and branch orientation, which together distinguished the light-demanding, fast-growing trees from slow-growing trees with lower mortality rates.
- Our modelling approach formalizes a complex ecological problem and offers a relevant mathematical framework for tropical ecologists to process similar uncertain data at the community level.

2 Introduction

The dynamics of tree populations in tropical rain forests is a complex ecological process, involving biotic and abiotic interactions between diverse tree species and their environment. Three demographic processes are motors of tree dynamics : recruitment, growth and mortality. Tree recruitment is often defined as recruitment above a minimum DBH (diameter at breast height)

(Alder and Silva, 2000). Recruitment depends, on the one hand, on species characteristics related to regeneration (seed mass, dispersal ability ...) (Moles and Westoby, 2004; Baraloto *et al.*, 2005; Baraloto and Forget, 2007; Poorter and Rose, 2005) and, on the other, on diverse environmental variables such as competition for light (Gourlet-Fleury *et al.*, 2005) or soil fertility (Ferry *et al.*, 2010). Tree growth first depends on the species' own life-history strategy (Gourlet-Fleury, 1999), from fast-growing pioneer species to light-wooded understorey species (Wright *et al.*, 2010). In addition, tree growth is mediated by climate (Wagner *et al.*, 2012), environment (light, soil moisture) and competition (Uriarte *et al.*, 2004) drivers (Poorter, 1999). Mortality is the least-documented process for diverse reasons. Standing death may occur due to intrinsic senescence (Carey *et al.*, 1994) or extrinsic agents such as drought or natural enemies. Trees may fall (alone or together) or die standing but may also be broken by wind, rain, or by other falling trees, sometimes causing cascading treefall events (Jansen *et al.*, 2008). Finally, dominant modes of death may differ in different regions (Chao *et al.*, 2009). As a result, tree mortality is a complex phenomenon that hampers the development of robust and predictive forest dynamics models on a large scale.

Mortality is a punctual phenomenon and, moreover, uncommon (rarely exceeding 2 or 3% y^{-1} in tropical rain forests all over the world (Carey *et al.*, 1994; Condit *et al.*, 1995)). Like any phenomenon of this kind, difficulty in observing the event renders problematic the understanding of its determinants and, ultimately, its modelling. In this context, mortality modelling has often focused on mortality rates and contrasted these rates between DBH (diameter at breast height) classes (Bohlman and Pacala, 2012; Condit *et al.*, 2004) or between species groups (Alder and Silva, 2000). However, recent studies suggest that mortality rates are very hard to accurately estimate (Wagner *et al.*, 2010), their value being particularly sensitive to the time between forest censuses (Sheil and May, 1996; Lewis *et al.*, 2004). For example, an inaccurate modelling of mortality processes prevents accurate simulation of the spatial variations in above-ground biomass (Delbart *et al.*, 2010). An alternative strategy is to model the probability of dying at the individual tree level (Phillips *et al.*, 2004), taking species' ecological strategies into account, in addition to local environmental factors affecting each individual. Such models take advantage of individual tree characteristics, such as past tree growth, neighbouring basal area or current DBH (Phillips *et al.*, 2004; Gourlet-Fleury *et al.*, 2005), and of the local environment, including competition, climatic variables or soil characteristics. To date, the ecological strategy of each species and the individual vigour of each tree has not been integrated in these approaches. As a starting point, we can suppose that each species

has its own ecological strategy, resulting in a unique determinism of the mortality behavior of each species. But the parameterization of such mortality models in mega-diverse communities such as tropical forests poses several problems. First, assuming that it is technically feasible, what interpretation is ecologically meaningful without making the effort to link these behaviours to their biological determinism, i.e. to their functional traits? A second problem is model surparameterization. Indeed, if one wishes to estimate as many model parameters as species, the amount of data to be acquired to obtain robust species estimators is prohibitive. A promising way to solve these two problems simultaneously is to integrate the tree ecological strategy into mortality models through the explicit inclusion of functional traits in the model core, a goal recently achieved for growth models of tropical trees (Hérault *et al.*, 2011; Rüger *et al.*, 2012). A central goal of ecology is to understand how variation in the biological properties, i.e. functional traits, of species relates to differences in population dynamics, which, in turn, shape the spatial distribution and temporal fluctuation of communities (McGill *et al.*, 2006). Among community ecologists, a consensus is emerging on the existence of different orthogonal axes related to the characteristics of the leaves, wood, seeds and life-history (Westoby, 1998; Baraloto *et al.*, 2010b). The leaf economics spectrum opposes inexpensive, short-lived leaves with rapid returns on investments to long-lived leaves with delayed payback times (Wright *et al.*, 2004). Wood density is emerging as a core plant functional trait for woody species (Chave *et al.*, 2009), because it is related to stem construction costs, biomechanics and hydraulic constraints. Seed mass, although not directly related to rates of population dynamics, is an important indicator of the life-history strategy of species, with fast-growing species tending to have small seeds that are easily dispersed (Moles and Westoby, 2004). Given that large trait databases on tropical trees are now emerging (Chave *et al.*, 2009; Baraloto *et al.*, 2010a), demonstrating the ability of functional traits to accurately predict mortality behaviour could have important implications for developing robust mortality models in tropical forests. The paper has three objectives :

- to present a new community mortality model based on functional traits,
- to present an original statistical method used to select the variables and to parameterize the model in a Bayesian framework
- to highlight how species functional traits shape individual tree mortality.

3 Materials and Methods

3.1 Data collection

The study was conducted using data from the Paracou experimental site (5°18'N, 52°55'W), a lowland tropical rain forest near Sinnamary, in French Guiana. The forest is typical of Guianan rain forests, with dominant tree families including *Fabaceae*, *Chrysobalanaceae*, *Lecythidaceae* and *Sapotaceae*, and with more than 500 woody species attaining 10 cm DBH found at the site. Mean annual precipitation averages 2980 mm (30-y period) with a long dry season from mid-August to mid-November and a short dry season in March (Wagner *et al.*, 2011). Soils are mostly Acrisols, limited in depth by a transformed loamy saprolite (≤ 1 m deep), which has a low permeability and leads to lateral drainage during heavy rains (Ferry *et al.*, 2010).

Two data sets are used in the study. The first data set is an inventory of all trees >10 cm DBH in 6 natural forest plots of 6.25 ha. Forest inventories were conducted since 1991. Censuses of mortality, recruitment and diameter growth have been conducted every year until 1995 and every 2 years thereafter. We used mortality inventories between 1992 and 2010. The whole data set contained 20,408 individual trees, among which 17,450 were alive in 2010. For each tree in each year, we know the location, DBH, vernacular name and status (dead or alive). The vernacular name is the name used by local treespotter. Botanical determination of the trees was completed in 2012, following extensive inventories with voucher collection and determination at regional and international herbaria. Hence, a large part of the trees that died during the period studied (1992-2010) have no botanical determination, but only a vernacular name.

The second data set is a collection of 15 functional traits of 335 Guianan tree species that occur at the Paracou site. Traits are related to leaf economics, stem economics and life history (see Table 1.1) and are extracted from a large database (Baraloto *et al.*, 2010a,b; Hérault *et al.*, 2010b, 2011).

TABLE 1.1 – **The 15 functional traits used in the study.** Variable names, units, % of species for which the value of this trait is known in our data set, % of individuals for which the value of this trait is known in our data set, range of the value and results of the Kuo-Mallick (KM) algorithm for variable selection. We chose to use a value of 90% as threshold for accepting the trait for inclusion in the final model.

Variable	Units	known species	known indiv.	Range	KM
Leaf economics					
Foliar $\delta^{13}C$ composition ($\delta^{13}C$)	‰	75%	79%	[-36.13 ; -26.2]	0.044
Foliar $C : N$ (CN)	cg g^{-1}	75%	79%	[10.8 ; 46.7]	0.38
Foliar Km (K)	mg g^{-1}	47%	70%	[0.00122 ; 0.223]	0.47
Foliar Nm (N)	cg g^{-1}	75%	79%	[0.108 ; 0.0451]	0.25
Foliar Pm (P)	mg g^{-1}	47%	70%	[0.00029 ; 0.00216]	0.34
Leaf tissue density (LTD)	g cm^{-3}	80%	79%	[1.6 10 ⁻⁵ ; 1.4 10 ⁻⁴]	0.31
Laminar total chlorophyll ($chloro$)	$\mu\text{g mm}^{-2}$	80%	79%	[20.8 ; 149]	0.13
Laminar toughness ($tough$)	N	79%	79%	[0.22 ; 11.4]	1
Specific leaf area (SLA)	$\text{cm}^2 \text{g}^{-1}$	81%	79%	[4.01 ; 37.6]	0.28
Life history					
Maximum height (H_{max})	m	66%	77%	[8 ; 56]	1
Maximum diameter (DBH_{max})	mm	69%	79%	[132 ; 1110]	0.29
Seed mass ($seed$)	g	42%	64%	[0.01 ; 20]	0.14
Stem and branch orientation ($ortho$)	ortho (1) plagio (0)	46%	64%	0/1	0.91
Stem economics					
Trunk wood moisture content (WM)		72%	75%	[0.26 ; 1.8]	0.37
Trunk xylem density (WD)	g cm^{-3}	80%	79%	[0.28 ; 0.91]	1

3.2 Addressing uncertainties in botanical determination

The traits data set is complete for 51% of individuals, and our goal was to attribute functional traits to all trees in the database. This is not feasible directly for three cases :

- (i) the tree species is known but some trait values of the species are not available ;
- (ii) the tree species is not determined at the species level, but only at the family or genus level ;
- (iii) the tree is dead before being identified and only its vernacular name is available.

The trees falling in this third case cannot be excluded because they represent 85% of dead trees.

An intuitive approach is to use a weighted mean of the traits for the missing data. But this approach has some disadvantages. First, some traits are qualitative ; attributing a mean value to these traits is not feasible. Most importantly, it could be dangerous to use mean traits. As shown in Figure 1.1, using means instead of the true values may create an artificial signal in the process we want to model. For instance, if trees of species A and B are well determined but trees of species C and D are not and share the same vernacular name. Using a standard ‘mean-trait’ approach, the mean trait value will be associated with individuals of species C and D, and a false signal may be detected. A final reason for using our method is the uncertainty. If mean traits are used, their values will not be permitted to vary. Then, it will be impossible to propagate the inherent uncertainty of the trait values when observing the uncertainty of the model outputs. Results of the covariates selection using weighted means of the traits and using our method are compared in Figure 1.2. These results clearly show that using a weighted mean approach would have led to a false trait-based mortality model.

We addressed the cases (i) and (ii) with one relationship model and the case (iii) with a second relationship model (Figure 1.3). We describe below these relationship models for a single trait T , but the same relationship models were used independently for all traits.

The starting point was a set of n_T species $\{s_1, \dots, s_{n_T}\}$ for which we have the associated set of values $\{t_1, \dots, t_{n_T}\}$ for the trait T . For any tree of a species $s \in \{s_1, \dots, s_{n_T}\}$, the trait value was set to t_s . For the other trees, the value of the trait was modelled by a multinomial distribution on the

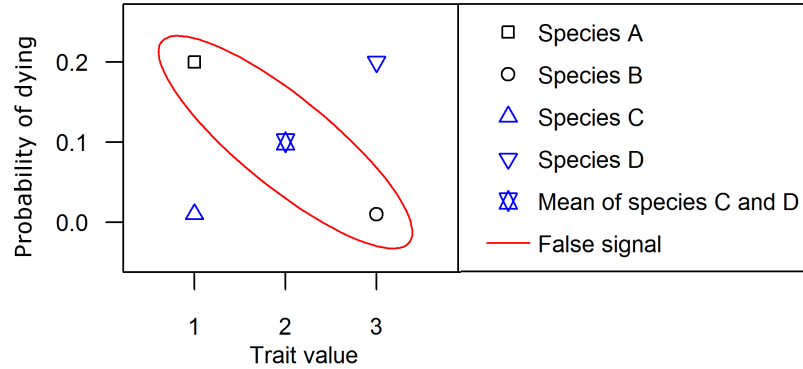


FIGURE 1.1 – **The use of mean traits may produce false signals.** Trees of species A and B are botanically well-determined. Trees of species C and D are not, but share the same vernacular name. Using a standard ‘mean-trait’ approach, the mean trait value will be associated with individuals of species C and D, and a false signal may be detected.

values $\{t_1, \dots, t_{n_T}\}$ with the associated probabilities computed differently according to the cases (i), (ii) and (iii). The different attribution rules of the trait value are described in the following sections.

3.2.1 Attributing trait values to trees of species without known trait values or to trees determined at genus/family levels : Cases (i) and (ii)

Cases (i) and (ii) deal with attributing trait values to tree without known trait values or to trees determined at genus/family levels. The studied functional traits are phylogenetically conserved within many families, so taxonomic substitution can be used (Baraloto *et al.*, 2012). This information can be used to fill the gaps of the functional trait data set. For any tree of a species $s \notin \{s_1, \dots, s_{n_T}\}$ or any tree determined only at the genus/family level, the distribution of trait values was assumed as a multinomial distribution $\mathcal{M}((\tilde{t}_1, \dots, \tilde{t}_{g_T}), (\nu_1, \dots, \nu_{g_T}))$. Where $(\tilde{t}_1, \dots, \tilde{t}_{g_T})$ is a subset of $\{t_1, \dots, t_{n_T}\}$ for which the associated species have the same family/genus as the tree; $\nu_i = \frac{N_i}{N}$, N_i number of trees which have the same family/genus as the tree and have the trait \tilde{t}_i ; N total number of tree which have the same family/genus as the tree.

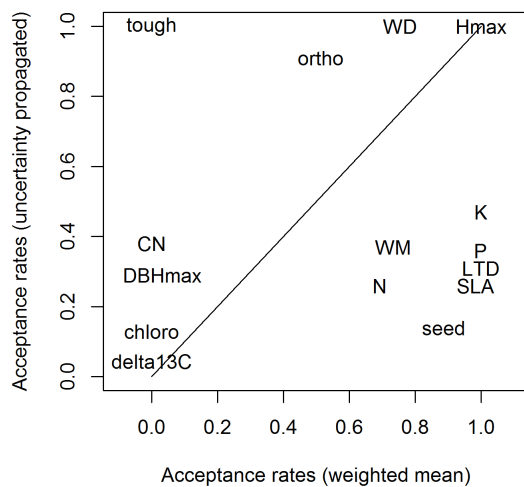


FIGURE 1.2 – **The use of mean traits may produce false signals.** Results of the Kuo-Mallick algorithm for parameter selection using weighted means of trait values are different from what we obtain when we correctly propagate uncertainty.

3.2.2 Attributing trait values to trees having only vernacular names : Case (iii)

Case (iii) deals with attributing trait values to tree having only vernacular names. For any tree with a vernacular name v , the distribution of trait values was assumed as a multinomial distribution $\mathcal{M}((t_1, \dots, t_{n_T}), (\alpha_1, \dots, \alpha_{n_T}))$. Determination of the probabilities $\alpha^v = (\alpha_1, \dots, \alpha_{n_T})$ was made using the Bayesian relationship model between the vernacular names and the species determination.

The vernacular name of all trees is known, and therefore can be used as a basis for attributing species. We collected two types of information linking vernacular names to species determination : expert field botanist knowledge linking qualitatively vernacular names to species determination ; and field data from the recent inventories, from which we could calculate the frequency with which pairs of vernacular and species names occurred. We then used a Bayesian framework to include these two types of information in the relationship model. The expert knowledge was included as prior in-

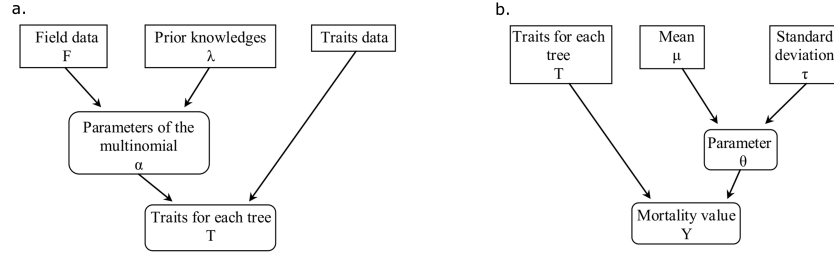


FIGURE 1.3 – **Two steps of model construction.** **a** : The functional traits are uncertain variables. The contingency matrix F and the prior information λ are used in the Dirichlet law to compute the trait variables T for each tree. **b** : Parameters θ of the model are estimated using a Metropolis-Hastings algorithm with proposal law $\theta^{prop} \sim \mathcal{N}(\mu, \tau)$. Parameters θ and traits T are then used in the final model to compute the mortality measure y for each tree.

formation ; it informs on which vernacular names are used for which species. For a vernacular name v , this information can be summed up by a vector $\lambda^v = (\lambda_1, \dots, \lambda_{n_T})$ where $\lambda_i = \frac{1}{m_v}$ if the link between the species s_i and the vernacular name v is established by the experts, with m_v being the number of species linked by the experts with the vernacular name v ; and $\lambda_i = \frac{\varepsilon}{n_T - m_v}$ if the link between the species s_i and the vernacular name v is not established by the experts, with ε allowing for a small background noise, and n_T the total number of species in the inventory data.

The field data was included to update the prior information. Trees (alive or dead) for which both the vernacular name and the species name are known allowed us to build for each vernacular name the vector of frequencies belonging to each species. In particular, for the vernacular name v , $f^v = (f_1, \dots, f_{n_T})$ where f_i is the number of times a tree with the vernacular name v was determinate of species i .

With these data, λ^v and f^v , a Multinomial-Dirichlet scheme was used (Robert and Casella, 2004). The expert knowledge, λ^v , was used as hyperparameters for the prior distribution on θ^v : $[\alpha^v] = \text{Dirichlet}(\lambda^v)$. We assumed a multinomial distribution for f^v conditionally to α^v . As Multinomial and Dirichlet are conjugate distributions (Robert and Casella, 2004), the posterior distribution of α^v was a Dirichlet distribution $[\alpha^v | f^v, \lambda^v] = \text{Dirichlet}(f^v + \lambda^v)$.

3.3 Modelling tree mortality

We modelled tree mortality with a generalized linear model (GLM) using a logit link function (McCullagh and Nelder, 1989). Tree mortality is a binary variable equal to 0 if the tree remained alive between 1992 and 2010, else equal to 1. The probability of dying for each tree is the logit of a linear combination of a set of covariates : 15 functional trait covariates and 2 ontogenetic covariates $\frac{DBH}{DBH_{max}}$ and $\left(\frac{DBH}{DBH_{max}}\right)^2$. DBH is the diameter of the tree at breast height and DBH_{max} is computed as the 95th percentile of the observed DBH for each species. The ratio $\frac{DBH}{DBH_{max}}$ is then used as a proxy of the ontogenetic stage of the tree. As it is well-known that the curve linking mortality probability to ontogenetic stage is U-shaped, we also introduced $\left(\frac{DBH}{DBH_{max}}\right)^2$ as a covariate. The originality of the model is that the trait covariates are uncertain for some trees and certain for the other trees. We used the method proposed by Kuo and Mallick (1998) to select the trait covariates useful to explain mortality. The method consists in multiplying each trait covariate by an indicator. This indicator can be 0 if its covariate is not included in the model or 1 if its covariate is included in the model. We developed a Gibbs algorithm to attribute either 1 or 0 to the indicators and a Metropolis-Hastings within Gibbs algorithm to estimate the coefficients of the covariates. We included a trait covariate in the final model if the expectation of its indicator, given by the Kuo-Mallick method, was between 0.9 and 1 (Figure 1.4). We chose the threshold 0.9 after considering the histogram of the expectations of the trait covariate indicators (Figure 1.4). Once the final model was defined, the coefficients of the covariates selected were estimated using the Metropolis-Hastings algorithm. To test the convergence of the chain, we run several chains from diverse initial values and inspect the chains to verify they all converge on the same value after some iterations. The autocorrelation is computed to ensure the chain is mixing adequately. The autocorrelation must decrease to zero when we increase the lag value. The methodology of model building is shown in Figure 1.3. See Appendices for further information.

All of the algorithms and statistical treatments were implemented with R software (R Development Core Team, 2010).

3.4 Model validation

To validate our mortality model, we split our data into a calibration data set, which contains data between 1992 and 2001, and a validation data set,

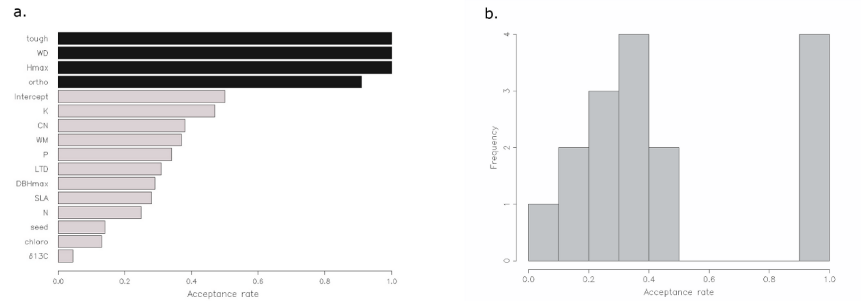


FIGURE 1.4 – **Results of the Kuo-Mallick algorithm for parameter selection.** **a** : Mean of the distribution for each variable ; variables are included in the final model if the mean value exceeds 90%. Variables included in the final models are : stem and branch orientation (*ortho*), maximum height (H_{max}), wood density (WD) and laminar toughness (*tough*). **b** : Histogram of the results of the Kuo-Mallick algorithm for parameter selection. Acceptance rates showed a gap from 0.5 to 0.9, and variables with results above 0.9 were selected for the final model.

which contains data between 2001 and 2010. The calibration data set was used to estimate the model parameters. Next, we predicted mortality rates for the validation data set. These rates were computed for different classes of trees binned across the distribution of each functional trait.

4 Results

The probability of dying showed a U-shaped pattern, i.e. $(\frac{DBH}{DBH_{max}})^2$ is positively linked and $\frac{DBH}{DBH_{max}}$ is negatively linked with the mortality probability. This means that the probability of dying first decreased with DBH, was minimum for a DBH ratio close to 0.15 and, then, increased sharply (Figure 1.5).

The histogram resulting from the Kuo-Mallick selection procedure showed a large break with no values between 0.5 and 0.9 (Figure 1.4). Predictive functional traits having values above the 0.9 threshold were thus included in the final mortality model (Figure 1.4) : maximum height (H_{max}), orthotropic orientation (*ortho*), wood density (WD) and laminar toughness (*tough*). Trees with orthotropic orientation had a lower probability of dying and the other three traits were negatively correlated with the individual probability of dying (Table 1.2). This means that the probability of dying is even higher

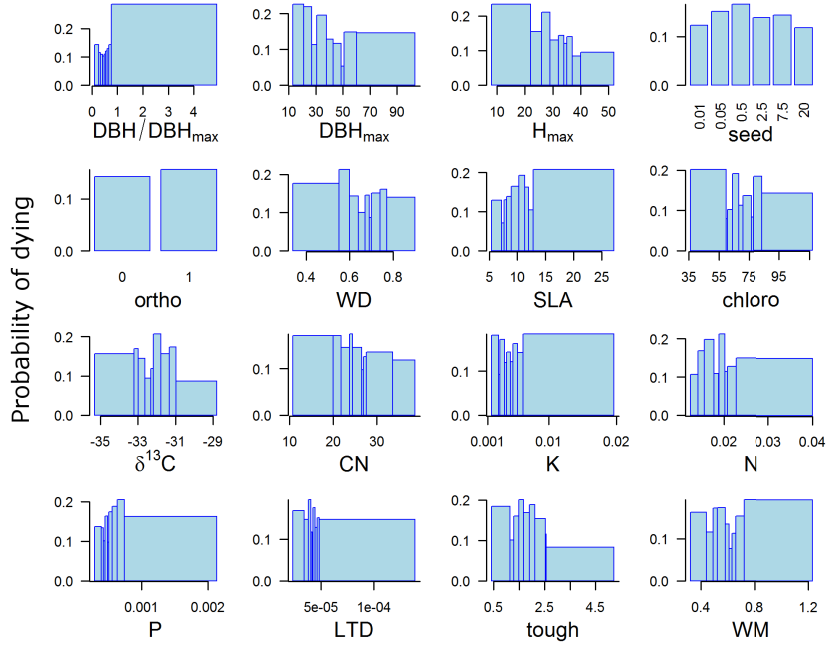


FIGURE 1.5 – **Effects of ontogenetic stage and functional traits on mortality rates.** Mortality rates were computed for each class of tree based on distribution deciles and plotted in the form of a histogram. In most cases, trait values are not evenly distributed, and this explains why the size of the bins is not regular. On the top-left histogram, we can see the U-shaped pattern for the ontogenetic variable.

when the tree is small, it has orthotropic branches, it has a low density of wood, or it has fragile leaves (Figure 1.6). Note that functional traits do not modify the shape of the curve linking DBH_i to the dying probability, but functional traits drive the value of this probability in the way that they induce a translation of the curve (Figure 1.6).

Results of the model validation procedure are presented in Figure 1.7. For the five covariables, we plotted the predicted rates of tree mortality versus the observed rates of tree mortality. The model, overall, overpredicts the probability of dying (7.6% of observed dead trees versus 8.1% of predicted dead trees) in the prediction data set. The ontogenetic signal has the best fit, especially for high values of $\frac{DBH}{DBH_{max}}$. Predictions for H_{max} and *tough*

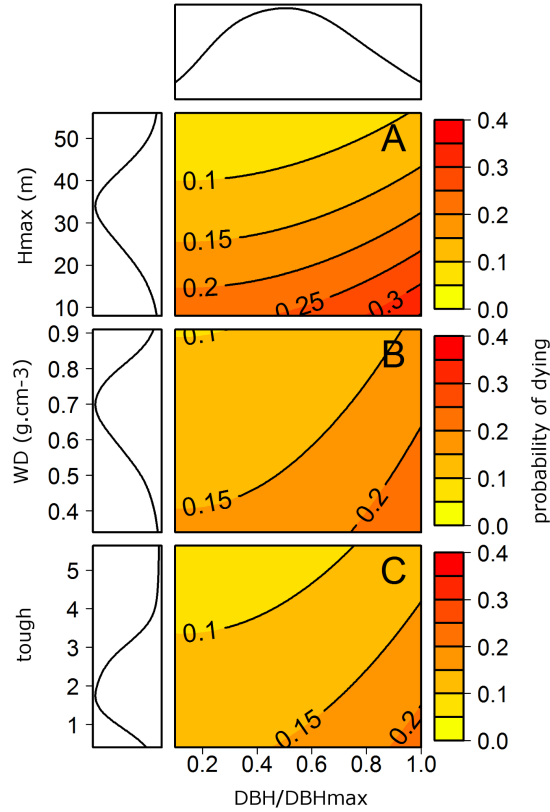


FIGURE 1.6 – The probability of dying depends on the individual ontogenetic stage and on tree functional traits : the maximum height, H_{max} ; the wood density, WD ; and the laminar toughness, **tough**. Simulation of the probability of dying versus the ontogenetic stage ($\frac{DBH}{DBH_{max}}$) of the tree, with variation of the three continuous functional traits selected in the final model : **A** the maximum height, **B** the wood density and **C** the laminar toughness. Marginal densities are plotted for each trait and for $\frac{DBH}{DBH_{max}}$, with a bandwidth equal to 10% of the amplitude. Density for laminar toughness (**C**) shows that maximal values (above 3) are rare; variation of mortality due to this trait is not as strong as the variation due to the maximal height.

TABLE 1.2 – **Results of the Metropolis-Hastings algorithm for parameter estimation.** Median and 90% credibility intervals of the posterior distribution for the selected parameters.

Variable	Estimates	90% credibility intervals
$\frac{DBH}{DBH_{max}}$	-0.23	[-0.71 ; 0.26]
$(\frac{DBH}{DBH_{max}})^2$	0.78	[0.44 ; 1.1]
H_{max}	-0.028	[-0.035 ; -0.022]
<i>ortho</i>	-0.19	[-0.33 ; -0.045]
<i>WD</i>	-0.87	[-1.1 ; -0.55]
<i>tough</i>	-0.15	[-0.21 ; -0.078]

are correct. For *WD*, the variability over the observed mortality rates is only slightly represented in the simulated rates. Quite the opposite, for *ortho*, the variability is higher in the predicted rates than in the observation.

5 Discussion

This study introduces a new method to design mortality models in tropical forests. Tree ontogenetic stage had an obvious effect on tree mortality, resulting in a somewhat typical U-shaped mortality curve (Muller-Landau *et al.*, 2006; Coomes and Allen, 2007). In other words, young trees and old trees die more frequently (Rüger *et al.*, 2011), probably because of intense competition among the youngest and due to senescence for the oldest. We used functional traits as uncertain covariates of a generalized linear model to predict tree mortality in a tropical rain forest in French Guiana. The results of our study showed that some functional traits are very useful covariates to compute the individual probability of dying for each tree in the forest community. Other parameters, mostly environmental or edaphic, have also been demonstrated to explain the probability of dying (Stephenson *et al.*, 2011; Toledo *et al.*, 2011; Rüger *et al.*, 2011). Our study provides a foundation for coupling both individual characteristics and environmental variables, which we believe will be a promising way to better understand tree mortality and model the consequences of global change on tropical forests.

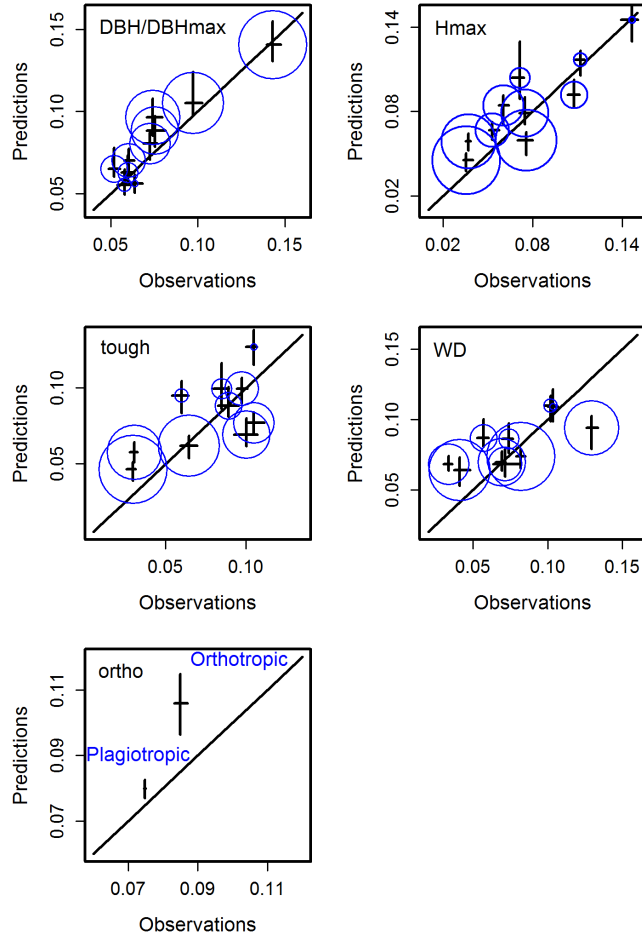


FIGURE 1.7 – **Model validation : the model was calibrated using data from 1992 to 2001 and applied to a validation data set (2001-2010).** For each covariate of the mortality model, we binned individuals into ten bins of equal size, corresponding to the deciles of the covariate distribution. Mortality rates were then computed for each bin using the validation data set (2001-2010). Predictions were plotted against observed rates. Moreover, the size of the blue circle is proportional to the value of the median of each bin.

5.1 Functional Traits

We used an original selection procedure to evaluate which tree functional traits shape the mortality curves. In doing so, we formally incorporated tree functional diversity into forest dynamics modelling without the necessity to build any functional groups. All in all, only four functional traits were robust predictors of the mortality probability. Most of the numerous measured traits related to leaf economics ($\delta^{13}C$, $K...$) were not included in the final model, instead traits related to life history or stem economics were largely selected.

First, wood density was expected to be a good predictor of mortality rates, since Chao *et al.* (2008); Kraft *et al.* (2010) reported a robust negative correlation between wood density and tree mortality in Amazonian forests. Moreover, King *et al.* (2006) also highlighted the importance of wood density in the trade-off between resource acquisition and investment in survival. In a nutshell, trees with low density are light-demanding trees with rapid bole expansion, leading to a higher mortality probability. High wood density is known to shape resistance to water-stress embolism (Jacobsen *et al.*, 2005), mechanical breakage or attack by pathogens (Chave *et al.*, 2009; Zanne *et al.*, 2010). This finding is in line with Chao's hypothesis that species with high mortality rates would create more canopy gaps that, in turn, favor low wood-density species and vice-versa. This means that the mortality regime in tropical forests may be both a cause and an effect of floristic composition (Chao *et al.*, 2008).

H_{max} was predicted to be negatively linked to mortality probability (Figure 1.5), as reported by Wright *et al.* (2010). We know that H_{max} captures a major variation in functional traits found among tropical rain forest tree species, and in combination with light-demand, it provides a rough but straightforward model to understand niche differentiation in tropical forests (Poorter *et al.*, 2006). H_{max} is predicted to be small for light-demanding species with rapid growth and mortality and large for shade-tolerant species with slow growth and mortality (Wright *et al.*, 2010).

Light-demanding tropical trees are characterized by orthotropic stems and branches, large leaves, and a monolayer leaf arrangement (Poorter *et al.*, 2006). They are known to realize an efficient height growth through formation of narrow, shallow crowns (Poorter *et al.*, 2006). Species with orthotropic architecture are therefore expected to be fast-growing and light demanding (Poorter *et al.*, 2003) and, thus, to have higher mortality rates than plagiotropic species. Surprisingly, our model parameters suggest that orthotropic trees have lower mortality rates than plagiotropic trees. We believe this is due to the combined effect of wood density and maximum height, that over-

estimated the effect of both traits on mortality. In other words, orthotropic species indeed have higher mortality rates than plagiotropic trees, but the trait model over-predicts this rate for individuals that are small or have a low wood density.

Finally, shade-tolerant plant species have tough leaves because of the high cost of leaf replacement in shade relative to potential carbon gain (Westbrook *et al.*, 2011). Leaf toughness (resistance to fracture per unit fracture area) was the only trait from the leaf economic spectrum to be retained in the mortality model. Leaf toughness was a good candidate because, for some tree saplings, Kitajima and Poorter (2010) showed that fracture toughness correlated positively with leaf lifespan and survival. Recently, Westbrook *et al.* (2011) also showed that mortality rates of individuals 1-10 cm in stem diameter were negatively correlated with material toughness and lamina density but were independent of structural toughness and cell-wall fiber content. We extend this finding to adult trees, highlighting the importance of plant-defense traits in shaping individual tree survival.

5.2 Toward new community models of population dynamics ?

In a context of global change, the long-term response of tropical forests to climate change cannot be predicted without using forest simulators or Dynamic Vegetation Models that incorporate both growth and mortality processes. Although tropical forests are known to have very different dynamics regimes, it has been shown that past tree growth is an accurate predictor of tree mortality (Chao *et al.*, 2008). The problem with such a result is that it is difficult to use past tree growth per se in a predictive model. Indeed, it only postpones the prediction problem, as it restricts one to predicting events of low growth in the life of a given tree, a goal very hard to achieve across the forest community for at least two reasons. First, most ecological works have focused on the average growth rates (Wright *et al.*, 2010), as predicting outliers is something extremely complicated in statistical modelling. Second, a tree's death linked to a decline in vigour appears predictable by its growth pattern before mortality, but tree death caused by disturbance, such as wind, is far from predictable (Chao *et al.*, 2008). In this context, we choose to decouple, at first, the growth determinants (Héroult *et al.*, 2011) from the mortality determinants and, then, we hope to find the right ways to combine both processes into a single modelling framework.

The community growth model developed in Héroult *et al.* (2011) is based on individual growth computed with the functional traits of trees as covariates. We used the same strategies to build a mortality model, but in our

study, we also have to deal with uncertainty of the process of death on the one hand, and with incomplete species information on the other. The strategy of using functional traits does add some uncertainty to the model. The methodology developed in this study handles the uncertainty of the covariates, due both to missing information about the functional traits and to different levels of botanical identification. This kind of incomplete information is common in many tropical forest inventory data sets with high variability in the levels of botanical determination of the trees (Réjou-Mechain *et al.*, 2011). We used the maximum available information about the trees (species, vernacular name, family/genus) to attribute trait values, under the assumption that functional traits are strongly conserved between species of the same genus and/or the same vernacular name. Although there is some support for this assumption in French Guianan trees (Baraloto *et al.*, 2012), the method necessarily involves a loss of some trait information.

Variable selection in nonlinear models remains a complex issue. In our study, the unconventional uncertainties about trait covariates complicated the issue even further. To select the covariates, usual frequentist criteria based on the penalized likelihood, like AIC, BIC, . . . , were unusable. Bayesian methods were better adapted because they naturally support different sources of uncertainties in the models. However, using the Bayesian versions of penalized likelihood criteria, such DIC, AIC_m, . . . , over all combinations of the trait covariates would have required too much computation time. Therefore, we developed a Bayesian algorithm that explores all combinations of trait covariates while calibrating the parameters. There were two possible approaches : Kuo and Mallick (Kuo and Mallick, 1998) or the reversible jump (Richardson and Green, 1997). We chose the Kuo and Mallick approach because it performs better in cases of correlated covariates. Furthermore, its interpretation and implementation are more intuitive because the dimension of the model is not variable, as in the reversible jump approach.

5.3 Conclusion

Our aim in this study was to model tree mortality in a tropical rain forest using functional traits. Considering first the complexity of the mortality process, and second the uncertainty due to the data, the model needed to be developed with particular attention to the methodology. We used a Bayesian framework, on the one hand to use all data about the tree and functional traits at our disposal, and on the other hand, to build the most accurate model using this data. This approach can be generalized to many similar studies about tropical forest dynamics, because more and more data are col-

lected about tree dynamics, but frameworks are missing to correctly process this data. Indeed, ecologists are often limited in their research when working with data from old inventories. Our method should permit increased use of data from old inventories to examine tree mortality. This is particularly interesting for conducting meta-analyses, which are generally based on data with widely varying levels of accuracy.

Tree mortality plays a key-role in the carbon cycle (Rutishauser *et al.*, 2010; Hérault *et al.*, 2010a) and is intimately linked to forest productivity (e.g. Stephenson *et al.* (2011)). Global changes, and associated increases in the frequency, duration and/or severity of drought events and heat stress already could have amplified natural tree mortality and potentially will continue to in the future (Phillips *et al.*, 2010; Allen *et al.*, 2010; Condit *et al.*, 1995), altering tropical forest dynamics and other ecosystem services (Corlett, 2011; Lewis, 2006; Condit *et al.*, 1996). Based on a long-term forest data set, in this study, we developed mortality models suitable for species-rich tropical forest communities, using functional traits as surrogates for taxon-level models. Methods used in this study allow us to model the tree community as a continuum, connecting functional traits to the mortality probability without collapsing species into functional groups.

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1.A Mortality model equation

Tree mortality is a binary variable y_i equal to 0 if tree i is alive, else equal to 1. The mortality model is a generalized linear model, which computes a tree-individual probability of dying. The probability of dying p_i for tree i is calculated with a logit function :

$$p_i = \text{logit}^{-1}(LC_i) = \frac{LC_i}{1 + \exp(LC_i)}$$

where LC_i is a linear combination of the covariates associated with the tree i . The covariates are 15 functional traits of tree i and two ontogenetic variables $\left(\frac{DBH_i}{DBH_{max,i}}$ and $\left(\frac{DBH_i}{DBH_{max,i}}\right)^2\right)$, included to estimate the ontogenetic stage of tree i (Hérault *et al.*, 2011) :

$$LC_i = \theta_0 + \theta_1 \frac{DBH_i}{DBH_{max,i}} + \theta_2 \left(\frac{DBH_i}{DBH_{max,i}}\right)^2 + \theta_3 \delta^{13}C_i + \theta_4 CN_i + \dots$$

where $\theta = \theta_0, \theta_1, \theta_2, \dots, \theta_m$ is a vector of parameters to be estimated. The mortality value y_i for tree i is then $y_i \sim \text{Bern}(p_i)$.

1.B Algorithms

1.B.1 Algorithms for sampling traits value for undetermined trees

We sampled the trait values using different algorithms, according to the level of determination of the trees. (i) If the tree species is known but some trait values of the species are not attributed, we used the algorithm 1 to sample the missing trait values.

```

for each determined tree, with some unattributed trait values
do
  for each trait T with unattributed value for the tree do
    - let  $n_T$  the number of species in the same genus with
      the value of trait  $T$  attributed :  $t_1, \dots, t_{n_T}$ ;
    - for  $i = 1, \dots, n_T$ , let  $\nu_i = \frac{N_i}{N}$  with  $N_i$  the number of
      trees in the genus with the trait value  $t_i$  and  $N$  the
      number of trees in the genus ;
    - sample  $\tilde{t} \sim \mathcal{M}((t_1, \dots, t_{n_T}), (\nu_1, \dots, \nu_{n_T}))$ , the value
      for the trait  $T$  for the tree;
  end
end

```

Algorithm 1: Multinomial algorithm for sampling traits values - case (i)

For the trees determined at the genus/family level we used the following algorithm 2.

```

for each tree determined at the genus/family level do
  for each traits T do
    - let  $n_T$  the number of species in the same genus/family
      with the value of trait  $T$  attributed :  $t_1, \dots, t_{n_T}$ ;
    - for  $i = 1, \dots, n_T$ , let  $\nu_i = \frac{N_i}{N}$  with  $N_i$  the number of
      trees in the genus/family with the trait value  $t_i$  and  $N$ 
      the number of trees in the genus ;
    - sample  $\tilde{t} \sim \mathcal{M}((t_1, \dots, t_{n_T}), (\nu_1, \dots, \nu_{n_T}))$ , the value
      for the trait  $T$  for the tree;
  end
end

```

Algorithm 2: Multinomial algorithm for sampling traits values - case (ii)

For the trees with only a vernacular name we used the algorithm 3.

```

for each tree with only a vernacular name do
  let  $v$  the vernacular name of the tree;
  for each traits  $T$  do
    - let  $n_T$  the number of species with the value of trait  $T$ 
      attributed :  $t_1, \dots, t_{n_T}$ ;
    - let  $f^v = (f_1, \dots, f_{n_T})$  the number of trees with
      vernacular name  $v$  which were determined among these
      species;
    - let  $m_v$  the number of species among the  $n_T$  for which
      the expert confirmed a link with the vernacular name  $v$ ;
    - let  $\lambda^v = (\lambda_1, \dots, \lambda_{n_T})$  with
      
$$\lambda_i = \begin{cases} \frac{1}{m_v} & \text{if the link is confirmed} \\ \frac{\varepsilon}{n_T - m_v} & \text{otherwise} \end{cases} ;$$

    - sample  $(\tilde{\alpha}_1, \dots, \tilde{\alpha}_{n_T}) \sim \text{Dir}(f^v + \lambda^v)$  ;
    - sample  $\tilde{t} \sim \mathcal{M}((t_1, \dots, t_{n_T}), (\tilde{\alpha}_1, \dots, \tilde{\alpha}_{n_T}))$ , the value
      for the trait  $T$  for the tree;
  end
end

```

Algorithm 3: Multinomial algorithm for sampling traits values - case (iii)

Practically, to implement the algorithm 3 on our case study we used $\varepsilon = 0.1$.

1.B.2 Algorithm for estimating parameters in a classical logit model

First, let us assume that the covariates (the 15 functional traits) are completely known for all the trees. The model is :

$$y_i \sim \text{Bern}(\text{logit}(\theta_0 + \theta_1 x_{i1} + \theta_2 x_{i2} + \dots + \theta_m x_{im})).$$

The likelihood function is :

$$\mathcal{L}(Y|X, \theta) = \prod_{i=1}^n \frac{\exp((\theta_0 + \theta_1 x_{i1} + \dots + \theta_m x_{im}) y_i)}{1 + \exp(\theta_0 + \theta_1 x_{i1} + \dots + \theta_m x_{im})}$$

where

- $Y = y_1, y_2, \dots, y_n$ is the vector of mortality values for all trees,

- $X = x_{i1}, x_{i2}, \dots, x_{im}$ is the vector of covariates for tree i (ontogenetic variables and traits),
- $\theta = \theta_1, \theta_2, \dots, \theta_m$ is the vector of parameters of the model.

The estimation of parameters θ in the Bayesian framework consists in estimating the posterior distribution of the parameters $\pi_{\theta|Y,X}$. From the Bayesian formula we have $\pi_{\theta|Y,X}(\theta) \propto \mathcal{L}(Y|X, \theta)\pi_{\theta}^0(\theta)$ where π_{θ}^0 is the prior distribution set by the user on θ . To estimate the posterior distribution $\pi_{\theta|Y,X}$ we can use a Monte Carlo Markov Chain algorithm, like Metropolis-Hastings (cf. algorithm 4). Such algorithm only requires a proposal distribution π^{prop} to sample possible values for θ and this values are kept or not in the chain according to their likelihoods.

```

Initialisation :  $t = 1, \theta^t \sim \pi_{\theta}^0$ ;
repeat
  Sample  $\theta^* \sim \pi^{prop}$  ;
  Sample  $u \sim Unif[0, 1]$  ;
  Compute  $\rho(\theta^t, \theta^*) = \frac{\mathcal{L}(Y|X, \theta^*)\pi_{\theta}^0(\theta^*)}{\mathcal{L}(Y|X, \theta^t)\pi_{\theta}^0(\theta^t)} \frac{\pi^{prop}(\theta^t)}{\pi^{prop}(\theta^*)}$ ;
  if  $u < \rho(\theta^t, \theta^*)$  then
    |  $\theta^{t+1} = \theta^*$ 
  else
    |  $\theta^{t+1} = \theta^t$ 
  end
   $t=t+1$ 
until the chain  $(\theta^t)_{t=1, \dots}$  reaches its stationary state;
Algorithm 4: Metropolis-Hastings

```

1.B.3 Algorithm for estimating parameters in a logit model with random covariates

However, in our case study, the covariates are not completely known for all the trees. In the paper we built models of knowledge for the traits, thus, the covariates become random for some trees. Let us note $\pi_{X|i}$ the distribution of the covariate values for the tree i as defined by the algorithm described in the section 1.B.1. For a tree i , for which all traits values are known, $\pi_{X|i}$ is a Dirac measure on its traits values i.e. sampling from $\pi_{X|i}$ always return the traits values of the tree.

Thanks to the Bayesian framework, we could take the randomness on X into account while estimating θ . We must add a Monte-Carlo step into the

Metropolis-Hastings algorithm. Practically, we run the Metropolis-Algorithm and new values for the covariates are sampled at each iteration (cf. Algorithm 5).

```

Initialisation :  $t = 1, \theta^t \sim \pi_\theta^0$ ;
repeat
  Sample covariate values for each individual  $i : \tilde{X}_i \sim \pi_{X,i}$ ;
  Sample  $\theta^* \sim \pi^{prop}$  ;
  Sample  $u \sim Unif[0, 1]$  ;
  Compute  $\rho(\theta^t, \theta^*) = \frac{\mathcal{L}(Y|\tilde{X}, \theta^*)\pi_\theta^0(\theta^*)}{\mathcal{L}(Y|\tilde{X}, \theta^t)\pi_\theta^0(\theta^t)}$ ;
  if  $u < \rho(\theta^t, \theta^*)$  then
    |  $\theta^{t+1} = \theta^*$ 
  else
    |  $\theta^{t+1} = \theta^t$ 
  end
   $t=t+1$ 
until the chain  $(\theta^t)_{t=1,\dots}$  reaches its stationary state;
Algorithm 5: Monte Carlo within Metropolis-Hastings for a model
with random explicative variables

```

1.B.4 Algorithm for estimating parameters and selecting covariates in a logit model with random covariates

The last methodological point of the paper was to select useful covariates to explain the mortality while taking their randomness into account. We used a method proposed by Kuo and Mallick (1998) which consists in adding an indicator for each covariate :

$$y_i \sim Bern(\text{logit}(\theta_0 + \theta_1 I_1 x_{i1} + \theta_2 I_2 x_{i2} + \dots + \theta_m I_m x_{im})).$$

These indicators, I_1, \dots, I_m , are considered as unknown parameters. This parameters have to be estimates in addition to θ . We added some steps, inspired from Kuo and Mallick (1998), in the algorithm 5 to estimate the posterior distribution of the indicators while taking into account the randomness of the covariates (cf. algorithm (Kuo and Mallick, 1998)). The idea of that method is that if the posterior distribution of the indicator I_j has its mode close to 1, then the covariate j must be kept in the model, otherwise the covariate j must be discarded.

```

Initialisation :  $t = 1, \theta^t \sim \pi_\theta^0, I_j^{(t)} \sim \text{Ber}(0.5)$  for
 $j = 1, \dots, m$  ;
repeat
  Sample covariates values for each individual  $i : \tilde{X}_i \sim \pi_{X,i}$ ;
  for each covariate  $j$  (selected in a random order) do
    Update  $\theta_j$ 
    |  $\theta^* = \theta^t$  ;
    | Sample  $\theta_j^* \sim \pi_{\theta_j|I^{(t)}}^{prop}$  ;
    | Sample  $u \sim \text{Unif}[0, 1]$  ;
    | Compute  $\rho(\theta^t, \theta^*) = \frac{\mathcal{L}(Y|\tilde{X}, \theta^*)\pi_\theta^0(\theta^*)}{\mathcal{L}(Y|\tilde{X}, \theta^t)\pi_\theta^0(\theta^t)}$  ;
    | if  $u < \rho(\theta^t, \theta^*)$  then
    | |  $\theta_j^t = \theta_j^*$ 
    | end
    Update  $I_j$ 
    | Compute  $\rho = \frac{1}{1 + \frac{\mathcal{L}(Y|\tilde{X}, \theta^t, I_j=0, I_{-j}^t)}{\mathcal{L}(Y|\tilde{X}, \theta^t, I_j=1, I_{-j}^t)}}$  ;
    | Sample  $I_j^{(t+1)} \sim \text{Bern}(\rho)$  ;
  end
   $\theta^{t+1} = \theta^t$ ;
   $t = t + 1$ ;
until the chain  $(\theta^t)_{t=1, \dots}$  reach its stationary state;

```

Algorithm 6: Kuo-Mallick method : Gibbs algorithm to determine the indicators I

Practically, to implement the algorithm of Kuo and Mallick (1998) on our case study we used :

- a low informative prior distribution on the parameters, $\pi_\theta^0 = \mathcal{N}(0, 10^6)$.
- a normal proposal distribution, $\pi^{prop} = \mathcal{N}(\hat{\theta}, \tau^2 I^{-1}(\hat{\theta}|Y))$, where :
 - $\tau = 2$, this parameter is chosen to change the scale of the algorithm steps and have a good acceptance rate.
 - $\hat{\theta}$ is the maximum likelihood estimate,
 - $I^{-1}(\theta|Y)$ is the Fisher matrix information :

$$I(\theta|Y) = \mathbb{E} \left[-\frac{\partial^2 \ell(\theta|Y)}{\partial \theta \partial \theta^t} \right], \text{ with } \ell(Y|X, \theta) = \log(\mathcal{L}(Y|X, \theta)).$$

This proposal distribution was used for a similar problem in one dimension by A. Altaieb and C. Robert (Altaieb and Robert, 2001).

CHAPITRE 2

TREE VIGOUR IS A KEY COMPONENT OF TROPICAL FOREST DYNAMICS

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Une fois le processus de mortalité modélisé, je souhaitais l'intégrer dans un simulateur, avec un modèle de croissance et un modèle de recrutement. Mais lorsque j'ai simplement concaténé un modèle de croissance et un modèle de mortalité dans le simulateur SELVA, la dynamique résultante n'était pas satisfaisante et ne reproduisait pas ce qui est observé en forêt naturelle. Pour mieux modéliser la dynamique, il faut comprendre comment les processus de croissance et de mortalité s'articulent entre eux. Dans ce deuxième chapitre, il est donc question de coupler les deux processus dans un seul et même modèle, et de prendre en compte l'impact de la croissance sur la mortalité. En effet, ces deux processus ne sont pas indépendants l'un de l'autre, et un arbre qui pousse vite a une plus faible probabilité de mourir. Pour prendre cette idée en compte dans notre modèle, j'introduis la notion de vigueur. Cette quantité est décrite comme la capacité d'un arbre à pousser plus que ce que prédisent ses traits fonctionnels et son stade ontogénique. Lorsque cette vigueur est ajoutée comme prédicteur de la probabilité de mourir, le modèle de mortalité est sensiblement amélioré. La méthodologie développée dans ce chapitre permet de créer un modèle de croissance et de mortalité pour la communauté, tout en introduisant la vigueur, une composante essentielle de la dynamique en forêt tropicale.

1 Abstract

- Tree vigour is often mentioned when tree mortality is predicated from tree growth, but it is rarely clearly defined. We propose a way to quantify tree vigour at the community level, based on the difference between expected and observed growth.
- The available methods to join non-linear tree growth and mortality processes are not commonly used by forest ecologists. We develop an inference methodology based on an MCMC approach, allowing us to sample the parameters of the growth and mortality model according to their posterior distribution by using the joint model likelihood.
- We apply our framework to a set of data on the 20-year dynamics of a forest in Paracou, French Guiana, taking advantage of functional-trait based growth and mortality models already developed independently.
- Our results showed that growth and mortality are intimately linked and that the vigour estimator is the main negative predictor of mortality, highlighting that trees growing by more than expected have a lower probability of dying. Our joint model methodology is sufficiently generic to be used to join two longitudinal and punctual linked processes and thus may be applied to a wide range of growth and mortality models.
- In the context of global, at the community level, such joint models are urgently needed in tropical forests to analyse, and then predict, the effects of the ongoing changes on the dynamics of hyperdiverse tropical forests.

2 Introduction

The biological processes responsible for tree mortality involve a combination of environmental stresses, but early warning signs can be detected by looking at the behaviour of tree growth (Pedersen, 1998; Dobbertin, 2005). Indeed, it is widely acknowledged that trees exhibiting the highest growth rates have a better chance to stay alive, while trees with lower than expected growth rates are more likely to die before their expected size at maturity (Chao *et al.*, 2008). This phenomenon is often called tree vigour. However, although the concept of tree vigour is often used, or suggested, it has been rarely precisely defined. Nevertheless, this vigour is a good starting point from which to build

coupled models of growth and mortality that explicitly take into account the demographical link between these two processes. Tree population dynamics result from three demographic processes : recruitment, growth, and mortality. In tropical forests, tree recruitment is a complex ecological process that in forest simulators is often assumed to be species neutral (Hubbell, 2001) because of its ‘lottery’ nature (Busing and Brokaw, 2002). In contrast, modelling individual tree growth in tropical forests is a well-documented task (Gourlet-Fleury, 1999; Hérault *et al.*, 2011), while modelling mortality has received considerable attention in recent years (Aubry-Kientz *et al.*, 2013; Kraft *et al.*, 2010; Rüger *et al.*, 2011). However, once models for these two demographical processes are developed, coupling them in a single framework is a delicate issue that is harder to achieve than a simple concatenation. The two processes are obviously not independent. Few studies have proposed a clear quantification of vigour, which is a concept rather than a measurable quantity. Shigo (2004) proposed a definition of tree vigour as ‘the capacity to resist strain ; a genetic factor, a potential force against any threats to survival’ and distinguished between vigour and vitality : ‘the ability to grow under the conditions present’. Most studies have not distinguished between these two views, and tree vigour has been generally related to high survival or high growth rates. Indeed, on the one hand, this concept may be related to tree mortality, as a loss of vigour is expected to imply a higher susceptibility to stresses (Manion, 1981). On the other hand, vigour may be linked with growth, and most studies using the term vigour have described this quantity as the diameter growth rate (Buchman *et al.*, 1983; Rosso and Hansen, 1998). A more complex estimator of vigour based on growth is the stem growth per unit of leaf area, which was used in Waring *et al.* (1980) as an estimator of the proportion of carbon allocated to stem wood production. Based on growth rates, this kind of vigour estimator may then be linked with mortality, and past growth may be included as a predictor in mortality models (Chao *et al.*, 2008; Bigler *et al.*, 2004).

Vigour may be related to the pressure undergone in tree dynamics, such as competition and environmental stress. Vigour is then sometimes related to the cause and not to the consequences (growth). For instance, vigour may be defined as competitive vigour, the quality of how a tree is able to compete for resources, or it may also be used as capability to react to environmental stresses.

One can consider that tree vigour is an individual property that describes the health of the tree and its capacity to maintain this healthy state, independent of not only the processes observed (growth, mortality, competition, etc.), but also the species strategies and the ontogeny. Indeed in tropical forests where

species diversity is high growth strategies highly differ between species. Pioneer species have high growth rates, while many other species grow slowly. A good vigour estimator has to be independent of the species identity, in the knowledge that an individual having a low growth may effectively have very low vigour if it belongs to a species that normally grows growing fast, but a normal vigour value if it belongs to a slow-growing species. Moreover, growth is highly dependent on the ontogenetic stage. Most species attained the maximum growth rate at 60% of their maximum diameter and showed hump-shaped ontogenetic growth trajectories (Hérault *et al.*, 2011). The probability of mortality is also strongly dependent on ontogenetic stages. Young trees and old trees die more frequently, because of the intense competition among the youngest and senescence of the oldest (Muller-Landau *et al.*, 2006; King *et al.*, 2006). Thus, a good vigour estimator also has to be independent of the ontogenetic stage.

In this paper, we present (i) a quantification of tree individual vigour ; (ii) improvement of a mortality model using this vigour estimator ; and (iii) a way to bind growth and mortality in a model of tropical tree dynamics using the results of our investigation of vigour. We then discuss the possibilities that such a methodology offers, as well as limitations and possible improvements.

To achieve this goal, we need to build growth and mortality models of tropical trees. A wide range of linear models is used to describe the tree growth process because linear models are easy to implement and infer using user friendly available tools. However, as our knowledge on the growth process has improved, diverse non-linear models are being developed in order to take into account the size-dependent growth trajectory (Paine *et al.*, 2012). Non-linear growth models have a long history (Hunter, 1982), and it is generally acknowledged that most tropical tree species attain maximal absolute growth rates at intermediate sizes (Hérault *et al.*, 2011), leading to a typical hump-backed, growth-diameter relationship. During the early stages of tree growth, the growth curve of the tree size may accelerate rapidly because taller trees have better access to light and a larger photosynthetic area (Sterck *et al.*, 2003), while the growth rates of mature and old trees often decline because of (i) resource reallocation towards reproduction (Thomas, 1996), (ii) respiration costs of roots and stems becoming too high (Ryan and Yoder, 1997), or (iii) trees beginning to senesce. Non-linear models have to be inferred using likelihood maximization or Bayesian Monte-Carlo Markov chain (MCMC) methods, implying that building a sophisticated non-linear model requires more computational effort for parametrization (e.g., Rüger *et al.* (2012)). Paradoxically, while the biological determinants of mortality seem less well known than those of growth, mortality modelling may be sim-

pler because it is a binary process that is well captured by logistic models (Brando *et al.*, 2012; Monserud and Sterba, 1999; Ruiz-Benito *et al.*, 2013). In this study, we used a community growth model and a community mortality model, both of which use functional traits and ontogenetic stage as predictors of tree dynamics.

3 Materials and methods

3.1 Data

The study was conducted using data from the Paracou experimental site ($5^{\circ}18'N, 52^{\circ}55'W$), a lowland tropical rain forest near Sinnamary, French Guiana. The forest is typical of Guianan rain forests, with dominant tree families including *Fabaceae*, *Chrysobalanaceae*, *Lecythidaceae*, and *Sapotaceae* and with more than 500 woody species attaining 10 cm diameter at breast height (DBH). Mean annual precipitation averages 2980 mm (30-year period), with a long dry season from mid-August to mid-November and a short dry season in March (Wagner *et al.*, 2011).

Two data sets were used in the study. The first data set is a 20-year inventory of all trees >10 cm DBH in six natural forest plots of 6.25 ha. Censuses of mortality and diameter growth were conducted every 10 years. DBH was calculated from precise measurements of circumferences at 0.5 cm. We excluded individuals with buttresses or other problems that required an increase in measurement because we were unsure about the height of the initial points of measurement on these trees. The data set contained 17,151 trees. For each tree every 10 years, we know the location, DBH, vernacular name, and status (dead or alive). The vernacular name is the name used by local tree spotters. The botanical determination of the trees was completed in 2012, following extensive inventories with voucher collections and determination at regional and international herbaria. Hence, a large number of the trees that died during the study period (1991–2011) have no botanical determination, only a vernacular name.

The second data set was a collection of six functional traits of the 335 Guianan tree species that occur at the Paracou site (Table 2.1). Traits are related to leaf economics, stem economics, and life history and are extracted from a large database (Baraloto *et al.*, 2010a,b). Some of these functional traits are accurate proxies of growth trajectories (Hérault *et al.*, 2010, 2011) and mortality rates (Aubry-Kientz *et al.*, 2013). The set of data on traits is not complete for all individuals because all trees were not determined at the species level, and some trait values were not available for all species.

We used the method of Aubry-Kientz *et al.* (2013) to compute the posterior distribution of the traits for each individual.

TABLE 2.1 – **The six functional traits used in the study.** For each functional trait, variable name, unit, abbreviation used in the article, and range of values.

Functional traits	Abbreviation	Range
Maximum diameter (m)	<i>DBHmax</i>	[0.13;1.11]
Maximum height (dm)	<i>Hmax</i>	[0.8;5.6]
Stem and branch orientation (orthotropic (1);plagiotropic (0))	<i>Ortho</i>	-
Trunk xylem density (g.cm ⁻³)	<i>WD</i>	[0.28;0.91]
Laminar toughness (N)	<i>Tough</i>	[0.22;11.4]
Foliar $\delta^{13}C$ composition (‰)	$\delta^{13}C$	[-3.61;-2.62]

3.2 Growth and mortality models

The growth individual-based model is a non-linear model developed by Héroult *et al.* (2011) where functional traits and ontogenetic stages of the trees are explicit predictors of the growth trajectory.

$$\begin{aligned} \log(\widehat{AGR}_{i,s,t-1} + 1) = & (\theta_1 * DBH95_s + \theta_2 * WD_s + \theta_3 * Hmax_s \\ & + \theta_4 * \delta^{13}C_s) \\ & * \exp \left(-\frac{1}{2} \left(\frac{\log \left(\frac{DBH_{i,t-2}}{\theta_5 * DBH95_s} \right)}{\theta_6 * WD_s} \right)^2 \right), \end{aligned}$$

and

$$\log(AGR_{i,s,t-1} + 1) = \log(\widehat{AGR}_{i,s,t-1} + 1) + \varepsilon_i,$$

with

$$\varepsilon_i \sim \mathcal{N}(0, \theta_7).$$

$\widehat{AGR}_{i,s,t-1}$ is the predicted growth between time $t - 2$ and time $t - 1$; $DBH95_s$, $Hmax_s$, $Tough_s$ and $\delta^{13}C_s$ are functional traits of species s to which tree i belongs (Table 2.1); $\theta_1, \theta_2, \dots, \theta_7$ are the parameters to be estimated; and ε_i is an individual error term following a normal distribution.

The mortality individual-based model was developed by Aubry-Kientz *et al.* (2013) to compute the individual probability of dying at each time step. At each time step, a tree i of species s may die with probability $p_{i,s,t}$.

$$p_{i,s,t} = \text{logit}^{-1} \left(\beta_1 * \frac{DBH_{i,s,t-1}}{DBH95_s} + \beta_2 * \left(\frac{DBH_{i,s,t-1}}{DBH95_s} \right)^2 + \beta_3 * Hmax_s + \beta_4 * Ortho_s + \beta_5 * WD_s + \beta_6 * Tough_s \right)$$

$DBH95_s$, $Hmax_s$, $Ortho_s$, WD_s , and $Tough_s$ are functional traits of species s to which tree i belongs (Table 2.1); $\beta_1, \beta_2, \dots, \beta_6$ are the parameters to be estimated.

3.3 Vigour quantification

The vigour estimator must be independent from the ontogenetic stage and from the species ecological strategies. These two factors are included in the growth model. The ontogenetic stage is $\frac{DBH_{i,s,t-1}}{DBH95_s}$, and the functional traits allow taking into account the specific ecological strategies. Thus, we used the growth model to compute four possible vigour estimator. Vigour is described as the difference between the computed expected growth and the growth observed in the field. The four estimators postioned are : $AGR_{i,t} - \widehat{AGR}_{i,t}$; $\frac{AGR_{i,t}}{\widehat{AGR}_{i,t}}$; $\log \left(\frac{AGR_{i,t} + 1}{\widehat{AGR}_{i,t} + 1} \right)$; and $\frac{\log(AGR_{i,t} + 1)}{\log(\widehat{AGR}_{i,t} + 1)}$, where $AGR_{i,t}$ is the observed growth between time $t - 1$ and time t for tree i , and $\widehat{AGR}_{i,t}$ is the predicted growth between time $t - 1$ and time t for tree i using a growth model.

3.4 Coupling growth and mortality

The growth and mortality processes were linked through tree vigour and are parametrized simultaneously. If tree i stays alive, it grows at a growth rate $AGR_{i,s,t}$, and its diameter $D_{i,t-1}$ becomes $D_{i,t}$. The joint model likelihood is then

- $\prod_{t=1}^n f(D_{i,t}|D_{i,t-1}) * (1 - p_{i,s,t})$ if tree i stays alive during the length of the study period,
- $p_{i,s,k} * \prod_{t=1}^{k-1} (f(D_{i,t}|D_{i,t-1}) * (1 - p_{i,s,t}))$ if tree i dies between time $k-1$ and time k

where

- $f(D_{i,t}|D_{i,t-1})$ is the probability density for a tree with diameter $D_{i,t-1}$ at time $t - 1$ to have a diameter $D_{i,t}$ at time t ; this quantity is used to compute the vigour estimator
- $p_{i,s,t}$ is the probability of dying between time $t - 1$ and time t , which depends on the vigour estimator, added as a new predictor in the mortality model by multiplying the vigour estimator by β_0 .

The model computes the mortality probability $p_{i,s,t}$ and the predicted growth rate $\widehat{AGR}_{i,s,t}$. In this study, these two demographical parameters are computed using a joint model inspired by the studies of Hérault *et al.* (2011) and Aubry-Kientz *et al.* (2013), as described in the previous subsection on the growth and mortality models. However, this coupling methodology can be used with all other growth and mortality models.

3.5 Estimation and selection

We implemented a MCMC algorithm to estimate the parameters (Robert and Casella, 2004). A random walk was used as proposal distribution to sample new values of parameters that were or were not selected, using the Metropolis-Hastings ratio. Only standard deviation θ_7 was sampled in an inverse-gamma posterior distribution, using a Gibbs sampler. The functional traits used as demographical predictors were uncertain because botanical determination was incomplete for the older censuses, and not all values of functional traits were available for all species. We used the method developed in Aubry-Kientz *et al.* (2013) to handle these uncertainties. Because the growth and mortality models were created separately, some functional traits were independently selected in the two processes. We used the method proposed by Kuo-Mallick (Kuo and Mallick, 1998) to select the most useful predictors in the joint model. The method then was applied to eight predictors : *Hmax*, *Ortho*, *WD*, and *Tough* of the mortality process and *DBH95*, *WD*, *Hmax*, and $\delta^{13}C$ of the growth process.

All algorithms and statistical treatments were implemented using R software (Team, 2013). The R codes developed in this study are available in the Appendix 2.B.

4 Results

4.1 Quantification of vigour

Distributions of the four investigated vigour estimators are plotted in Figure 2.4. The first one, $AGR_{i,t} - \widehat{AGR}_{i,t}$ is not symmetric because few trees grew faster than predicted. The same problem was observed with the second estimator $\frac{AGR_{i,t}}{\widehat{AGR}_{i,t}}$, but with the additional problem that this estimator had no value lower than 0. To avoid this long-tailed distribution of vigour, we introduced a logarithm. The third estimator was $\log\left(\frac{AGR_{i,t} + 1}{\widehat{AGR}_{i,t} + 1}\right)$ and was more symmetric. This distribution corresponded to the error of the growth model. The last estimator $\frac{\log(AGR_{i,t} + 1)}{\log(\widehat{AGR}_{i,t} + 1)}$ was highly bimodal and thus less appropriate. We retained $\log\left(\frac{AGR_{i,t} + 1}{\widehat{AGR}_{i,t} + 1}\right)$.

4.2 Tree vigour and mortality

When vigour was included in the mortality model, the values of parameter β_0 were around -0.4 (Table 2.2), implying that a tree with a higher past growth than expected would have a lower probability of dying (Figure 2.1). The BIC of the mortality model without vigour was 11,215, and with vigour was 10,987. The adjusted pseudo-r² of Mac Fadden without vigour was 0.0288 and 0.0492 with vigour. If we computed the adjusted pseudo-R² with the reference model set as the model without vigour, we obtained 0.0209.

4.3 Model coupling

Starting from the values of the parameters found in Hérault *et al.* (2011) and Aubry-Kientz *et al.* (2013), we realized 2000 iterations of the Metropolis-Hastings algorithm. We used a burning of 1000 iterations and a thinning of 10 to achieve a satisfying autocorrelation. The histogram resulting from the Kuo-Mallick selection procedure showed a large break with no values between 0.4 and 0.8 (Figure 2.2). The 0.4 value was the indicator associated with orthotropic orientation (*Ortho*). Therefore, this predictor was not included in the final coupled model.

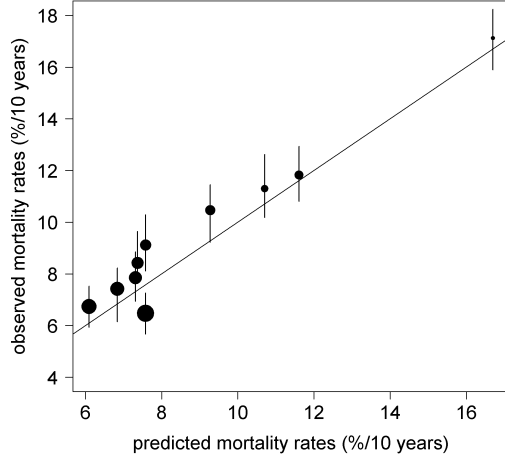


FIGURE 2.1 – **Mortality depends on tree vigour.** Predicted mortality rates versus observed mortality rates. Trees were regrouped into 10 groups depending on the value of the vigour estimate. Circle sizes are proportional to the averaged vigour of the groups. As mortality is a stochastic process, 100 simulations were realized and predicted values are plotted. Segments correspond to the 90% credibility interval.

5 Discussion

5.1 Quantifying tree vigour

Growth was finally included in the mortality processes using the vigour estimator $\log\left(\frac{AGR_{i,s,t-1} + 1}{\widehat{AGR}_{i,s,t-1} + 1}\right)$. The ‘easiest-to-implement’ approach is to use directly the observed growth as a predictor in the mortality submodel (Chao *et al.*, 2008; Metcalf *et al.*, 2009; Rüger *et al.*, 2011). However, this approach would not take into account the growth potential inherent in each species (Héroult *et al.*, 2010, 2011). For instance, a low observed growth may be either due to a slow-growing species (in this case the vigour will be close to 0) or, alternatively, to a slowdown in the growth of a fast-growing species due to an external force (in this case the vigour will be negative). The parameter θ_0 associated with this vigour estimator was easily estimated, and all Markov chains converged quickly around -0.4 . This demographical link between growth and mortality rates has already been well accepted (Chao

TABLE 2.2 – **Results of the estimation method.** For each parameter of the model, median, and 90% credibility interval of the posterior distribution. Note that β_4 does not appear in the final model because *Ortho* was not selected by the selection procedure.

Parameter	predictor	median	90% credibility interval
β_0	$\log\left(\frac{AGR_{i,s,t-1+1}}{AGR_{i,s,t-1+1}}\right)$	-0.403	[-0.446 ; -0.359]
β_1	$\frac{DBH_{i,s,t-1}}{DBH95_s}$	0.140	[-0.430 ; 0.625]
β_2	$\left(\frac{DBH_{i,s,t-1}}{DBH95_s}\right)^2$	0.502	[0.175 ; 0.905]
β_3	$Hmax_s$	-0.414	[-0.463 ; -0.365]
β_5	WD_s	-0.951	[-1.24 ; -0.622]
β_6	$Tough_s$	-0.327	[-0.397 ; -0.254]
θ_1	$DBH95_s$	2.43	[1.98 ; 2.92]
θ_2	WD_s	-0.384	[-0.545 ; -0.246]
θ_3	$Hmax_s$	0.0318	[-0.0435 ; 0.103]
θ_4	$\delta 13C_s$	-0.403	[-0.467 ; -0.333]
θ_5	$DBH95_s$	1.59	[0.866 ; 3.304]
θ_6	WD_s	4.81	[3.422 ; 6.67]
θ_7	ε	27.5	[27.0 ; 28.0]

et al., 2008; Dobbertin, 2005) and is mainly related to changes in the carbon allocation of trees. Under environmental stress, trees are supposed to place higher priority on new foliage or new roots and lower priority on radial growth (Wunder *et al.*, 2008). Slow-growing trees are thus likely to be unhealthy, exhibit physiological stress, and be prone to infection or death (Bigler *et al.*, 2004; Van Mantgem *et al.*, 2003). Most temperate-zone studies confirmed that tree vigour is a good indicator of mortality (Yao *et al.*, 2001). In our framework, an additive error describes the vigour of each tree individually, regardless of its species or ontogenetic stage. This individual error is normally distributed and centred around 0 with standard deviation θ_{14} .

This error corresponded to the third estimator presented in this study. We choose this estimator to compute vigour after considering the observed density of the four alternative estimators. Indeed, the two first estimators,

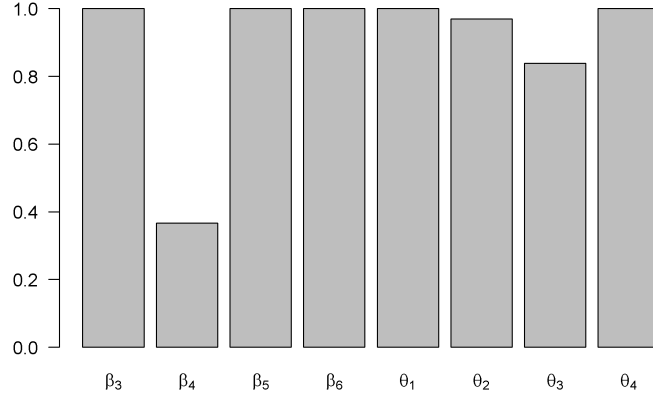


FIGURE 2.2 – **Results of the Kuo-Mallick algorithm for parameter selection.** Median of the distribution for each variable ; variables are included in the final model if the median value is inferior as 0.8. A gap with no value between 0.4 and 0.8 is observed, and the variable associated with *Ortho* (β_4) takes value 0.4, which is why *Ortho* is not included in the final model. Variables included are : *Hmax* (β_3), *WD* (β_5), *Tough* (β_6) in the mortality process ; and *DBH95* (θ_1), *WD* (θ_2), *Hmax* (θ_3), $\delta 13C$ (θ_4) in the growth process.

$AGR_{i,t} - \widehat{AGR}_{i,t}$, and $\frac{AGR_{i,t}}{\widehat{AGR}_{i,t}}$, were not selected because they were not symmetric. The last estimator, $\frac{\log(AGR_{i,t} + 1)}{\log(\widehat{AGR}_{i,t} + 1)}$, was bimodal with most values equal to 0 because of the high number of observed growth values equal to 0. We selected the third estimator because its density is almost normal. Tree vigour is expected to be due to a large number of biotic and abiotic variables, as genetic factors or environmental conditions. Thus, as vigour may be considered as the resultant process of the sum of this numerous variables, this quantity may be expected to be normally distributed.

The vigour estimator was then exactly the error of the growth model. This means that the posterior distribution of θ_{14} could be directly used to predict the probability of dying. In other words, the error in the growth process directly gave the vigour estimator of the mortality process. For example,

a tree with high value of the vigour estimator deterministically would have a higher growth rate and a smaller probability of dying. However, this is questionable when we want to use this joint model in a forest simulator. Roughly, there are two possibilities. Either an error is sampled at each time step, or each individual tree has its own vigour, which does not change throughout its life. This is an important choice in the simulation, and it is clear that the reality may be more nuanced. Even if the vigour of a tree may change during its life because of biotic or abiotic factors (Moravie *et al.*, 1999), there is also increasing forestry evidence of strong observed temporal dependence (Woollons and Norton, 1990). Some studies indicated that the inclusion of temporal dependence in stochastic dynamic models results in outputs that are similar to those of deterministic models (Kangas, 1997, 1998), but the theoretical and ecological basis of the stochastic model is clearly superior to that of the deterministic model (Fox *et al.*, 2001). A more realist alternative could thus be to sample a new vigour estimator at each time t , depending on the vigour estimator at time $t - 1$, such as in an autoregressive model (Suarez *et al.*, 2004).

5.2 Improvement of the mortality model

Building a vigour estimator and including it in the mortality model allowed us to take into account individual variability, which previously was not possible. The introduction of vigour into the mortality model improved the prediction and highlighted that vigour is a key driver of mortality (Figures 2.1, 2.3). The Mac Fadden's adjusted pseudo-R² can be interpreted as the ratio of the estimated information gain when the model is used in comparison with the null model in order to estimate the information potentially recoverable by including all possible explanatory variables (Shtatland *et al.*, 2002). In our case, the R² was almost double when vigour was included, which implies that the goodness-of-fit would be almost double if the vigour estimator were included. Thus, past tree growth, independent of ontogeny and species ecological strategies, was by far the first predictor of tree mortality. Reduced radial growth is often linked to increased mortality rates (Wunder *et al.*, 2008), but as Dobbertin (2005) asserted, 'important for any potential vitality indicator is the comparison with a suitable reference'. This reference may be the difference or residual of tree growth against mean growth or modelled growth (Dobbertin, 2005).

Our definition of vigour includes vigour and vitality according to Shigo (2004), where vigour is defined as 'the capacity to resist strain ; a genetic factor, a potential force against any threats to survival', and vitality is defined

as ‘the ability to grow under the conditions present’ (Shigo, 2004). Indeed, the individual part of vigour, because of genetic or environmentally constant pressures, will be the same during the entire life of the tree. While punctual stresses may induce a loss of vigour (or vitality according to Shigo (2004)), followed by a restitution phase, until reaching either a lower vigour, identical vigour, or a vigour higher than before (Dobbertin, 2005; Manion, 1981; Kozłowski and Pallardy, 2002).

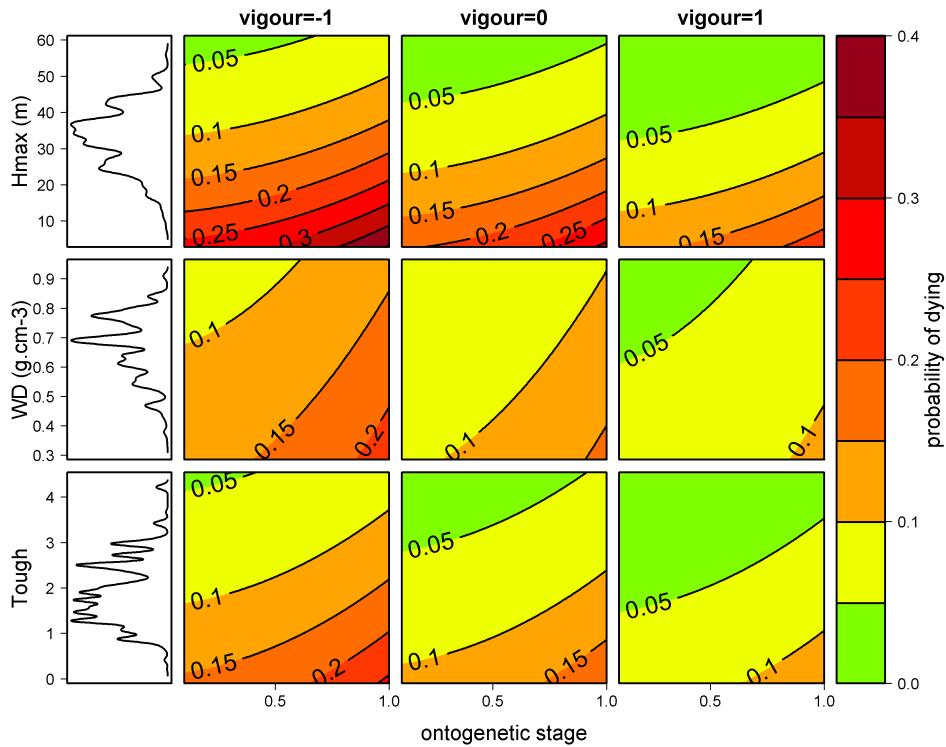


FIGURE 2.3 – **Tree vigour is a predictor of mortality.** Simulations using the final mortality model. Tree lines corresponds to tree functional traits used as predictors : H_{max} , WD and $Tough$. The three columns corresponds to tree vigour : -1, 0 and 1. Probability of dying is plotted, depending on the ontogenetic stage estimated by $\frac{DBH_i}{DBH95_s}$ where DBH_i is the diameter of tree i and $DBH95_s$ is the maximum diameter for species s to which tree i belongs to.

5.3 Coupling tree growth and mortality

The available methods of combining non-linear tree growth and mortality processes are not commonly used by forest ecologists. Our inference methodology is based on an MCMC approach, which allowed us to sample the model parameters according to their posterior distribution, using the joint model likelihood. This likelihood takes growth and mortality forest dynamic processes into account at each step of the algorithm. Hence, growth and mortality parameters are estimated simultaneously until stabilization. The joint model parameters were sampled individually to increase convergence speed. When the sampled parameter concerned the mortality process only, the growth process did not change and only the term of the likelihood linked to the growth process ($f(D_{i,t}|D_{i,t-1})$) was updated. When the estimated parameter concerned the growth process, as the growth process is plugged into the mortality process, all terms of the likelihood were affected : $f(D_{i,s,t}|D_{i,s,t-1})$ and $p_{i,s,t}$. In practical terms, the parameters involved in the mortality process converged more easily than parameters involved in the growth process. Indeed, tree growth is strongly shaped by many additional environmental variables (*e.g.*, topography, light availability, etc.) (Héroult *et al.*, 2010) and by local competition (Uriarte *et al.*, 2004); however, neither factor was investigated in the present methodological study. Nevertheless, our methodology succeeded in binding the two processes, and the selection method allowed keeping only the useful variables as the parameters in the final model. Thus, the collinearity of the two processes was managed.

6 Conclusion

In this paper, we present a method of estimating tree vigour and a flexible methodology for building a growth–mortality joint model using this vigour estimator. The vigour estimator, based on the difference between observed and predicted growth, significantly improved the mortality model. This result confirmed that the individual behaviour of trees is of great importance in the processes of growth and mortality and therefore should be considered in the study of forest dynamics. We successfully applied our conceptual framework to a complex hyperdiverse tropical forest community, taking into account different sources of data uncertainties, and confirming the link between growth and mortality in a tropical forest. Our joint model methodology may be used with a wide range of growth and mortality models. Indeed, the inference process needs only one growth model that computes $\widehat{AGR}_{i,s,t}$ and a mortality model that computes $p_{i,s,t}$. Once computed, these two sets of values

are used to calculate the global likelihood and to estimate posterior distributions. The growth model may be more straightforward (e.g. a linear model) or more complex (e.g. random species effects). This joint model approach provides an interesting framework for including other predicting variables possibly linked with tree dynamics, such as environmental and climatic variables. In the context of climate change, proper methodological frameworks are needed both to model the effect of climate variations on the dynamics of hyperdiverse tropical forest communities (Choat *et al.*, 2012; Feeley *et al.*, 2012; Wagner *et al.*, 2011) and to include these climate-explicit models into forest simulators in order to test their resilience to future expected changes.

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2.A Vigour estimator

We want to use an estimator of the tree vigour, depending on the observed growth and the predicted growth. The estimator finally chosen to introduce the vigour of trees in the mortality process is $\log\left(\frac{AGR_{i,s,t} + 1}{\widehat{AGR}_{i,s,t} + 1}\right)$ where $AGR_{i,s,t}$ is the observed growth between time $t - 1$ and time t for tree i of species s (in mm); and $\widehat{AGR}_{i,s,t}$ is the mean predicted growth between time $t - 1$ and time t for tree i of species s (in mm) using the growth sub-model (see Figure 2.4).

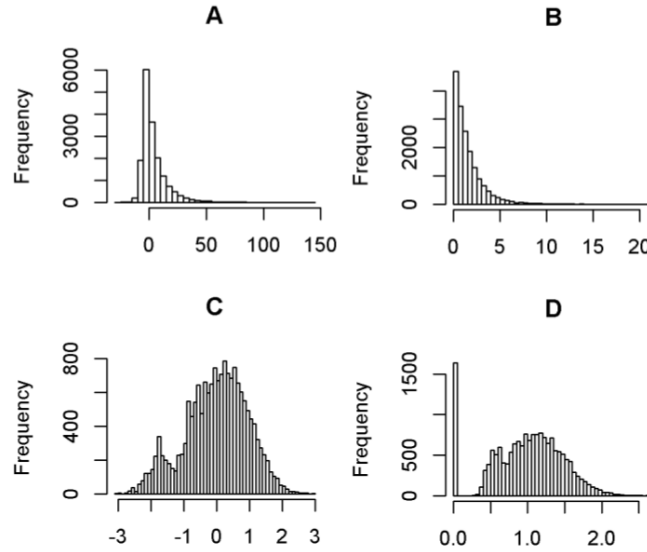


FIGURE 2.4 – **Distributions of the vigour estimators.** The four estimators are : $AGR_{i,t} - \widehat{AGR}_{i,t}$ (A), $\frac{AGR_{i,t}}{\widehat{AGR}_{i,t}}$ (B), $\log\left(\frac{AGR_{i,t} + 1}{\widehat{AGR}_{i,t} + 1}\right)$ (C), $\frac{\log(AGR_{i,t} + 1)}{\log(\widehat{AGR}_{i,t} + 1)}$ (D), where $AGR_{i,t}$ is the observed growth between time $t - 1$ and time t for tree i ; and $\widehat{AGR}_{i,t}$ is the predicted growth between time $t - 1$ and time t for tree i using a growth model.

2.B R codes

We developed functions to allow an easy use of the computational method used in our study.

- *growth model* : a function specifying the growth model to be estimated.
- *mortality model* : a function specifying the mortality model to be estimated.
- *loglikelihood growth* : a function computing the part of the loglikelihood depending of the growth process.
- *loglikelihood mortality* : a function computing the part of the loglikelihood depending of the mortality process.
- *prep data* : a function to formalized the data create tables that will be used in the estimation process.
- *chain building* : a function to create the Markov chains for each parameter of the model.
- *plot function* : a function to plot the chains.
- *creation data* : a function to create simulated data.

The two models used in the articles are implemented and the simplest one can be tested easily with simulated data using the provided script.

```
#### script to test

# example of predictors for virtual data
predictors <- matrix(rnorm(2000*2,c(420,0.68),c(80,0.1)),ncol=2,byrow=T)
data <- creation_data(NbTree = 2000,predictors = predictors)
data_tree <- prep_data(data[, -1])

# example of initiation of the parameters
nb_iterations <- 1000
nb_param <- 6
nb_sample_traits <- 10
theta <- c(0.01,0.1,4,0.01,-0.002,-10)
theta <- matrix(theta,nrow=nb_param,ncol=nb_sample_traits,byrow=F)
step <- c(0.001,0.2,0.1,0,0.001,2)
A0 <- 0.1
B0 <- 0.1
mean_prior <- 0.5
```

```

sd_prior <- 500
model <- 1
id_sigma <- 4

# creation of the MCMC chains
test <- chain_building(model,id_sigma,nb_iterations,nb_param,theta,
nb_sample_traits,step,traits,data_tree,A0,B0,mean_prior,sd_prior)

# plot the results
plot_function(test,burn=0,thin=1)

####

#### functions

growth_model <- function(theta,traits,data_DBH)
{
  lAGR_pred <- t(theta[1,] * traits[,,'DBH95']*10 *
  exp(-0.5 *
  ((log( (data_DBH[,2])/(theta[2,]*traits[,,'DBH95']*10) )
  / ( theta[3,] * traits[,,'WD'] ) )^-2)))
  return(lAGR_pred)
}

growth_model <- function(theta,traits,data_DBH)
{
  lAGR_pred <- t(t(theta[1,] * t(traits[,,'DBH95']/100) +
  theta[2,] * t(traits[,,'WD']) + theta[3,] * t(traits[,,'Height']/10) +
  theta[4,] * t(traits[,,'Delta13C']/10) ) *
  exp( -0.5 * ((log((data_DBH[,2])/t(theta[5,]*t(traits[,,'DBH95']*10)))
  / (t(theta[6,]*t(traits[,,'WD'])))^-2)))
  return(lAGR_pred)
}

mortality_model <- function(theta,rate,traits,data_DBH,nb_sample_traits)
{
  logit_p <- t(theta[5,] *
  traits[(1:nb_sample_traits),IdTrees,'DBH95']*10 +
  theta[6,] * t(rate))
  return(logit_p)
}

mortality_model <- function(theta,rate,traits,data_DBH,nb_sample_traits)
{
  logit_p <- t(theta[8,] * t(rate)) + t(theta[9,] *
  t((data_DBH[,3]/10)/t(traits[(1:nb_sample_traits),IdTrees,'DBH95']))) +
  t(theta[10,] *

```

```

t(((data_DBH[,3]/10)/t(traits[(1:nb_sample_traits) ,IdTrees,'DBH95']))^2))+
t(theta[11,] * (traits[(1:nb_sample_traits),IdTrees,'Height']/10)) +
t(theta[12,] * (traits[(1:nb_sample_traits),IdTrees,'Ortho'])) +
t(theta[13,] * (traits[(1:nb_sample_traits),IdTrees,'WD'])) +
t(theta[14,] * (traits[(1:nb_sample_traits),IdTrees,'Tough']))
return(logit_p)
}

loglikelihood_growth <- function(theta_sigma,AGR_obs,lAGR_pred,data1_unique,
rep,nb_sample_traits)
{
  ll_growth <- dnorm(log(AGR_obs+1),mean=lAGR_pred,
  sd=matrix(theta_sigma,ncol=nb_sample_traits,nrow=length(AGR_obs),byrow=T),
  log=TRUE)
  rownames(ll_growth) <- rownames(data1_unique)

  ll_growth_tot <- colSums(ll_growth * as.double(rep))
  return(ll_growth_tot)
}

loglikelihood_mortality <-
function(theta,AGR_obs2,AGR_obs3,lAGR_pred2,lAGR_pred3,data2_unique,data3,
nb_sample_traits,rep2)
{
  # living trees:
  rate1 <- log(AGR_obs2 + 1) - lAGR_pred2
  ll_morta_alive <- - log( 1 +
  exp( mortality_model(theta,rate1,traits,data2_unique,nb_sample_traits) ))
  ll_morta_alive_tot <- colSums(as.double(rep2[rownames(data2_unique)]) *
  ll_morta_alive)

  # dead trees:
  rate2 <- log(AGR_obs3 + 1) - lAGR_pred3
  ll_morta_dead <- - log( 1 +
  exp( - ( mortality_model(theta,rate2,traits,data3,nb_sample_traits) )))
  ll_morta_dead_tot <- colSums(ll_morta_dead)

  return(ll_morta_alive_tot+ll_morta_dead_tot)
}

prep_data <- function(data,CheckArguments = TRUE)
{
  if (CheckArguments)
  {
    check_arguments()
  }
}

```



```

#### Creation of data1:
## DBH for living trees, used in the growth model

#### Creation of data2:
## DBH for living trees, used in the mortality model

#### Creation of data3:
## DBH for died trees, used in the mortality model

id_alive <- rownames(data)[which(!is.na((rowSums(data))))]
id_dead <- rownames(data)[which(is.na(data[,3]) & !is.na(data[,2]))]

data1 <- data[as.character(id_alive),c(2,3)]
data2 <- data[as.character(id_alive),c(1,2)]
data3 <- data[as.character(id_dead),c(1,2)]

for (i in 3:(ncol(data)-1))
{
  data1 <- rbind(data1,data[as.character(id_alive),c(i,i+1)])
  data2 <- rbind(data2,data[as.character(id_alive),c((i-1),i)])

  id <- rownames(data)[which(is.na(data[,i+1]) & !is.na(data[,i]))]

  data3 <- rbind(data3,data[as.character(id),c(i-1,i)])

  for (j in 2:(i-1))
  {
    data1 <- rbind(data1,data[as.character(id),c(j,(j+1))])
    data2 <- rbind(data2,data[as.character(id),c((j-1),j)])
  }
}

data1 <- cbind(as.numeric(rownames(data1)),data1)
data2 <- cbind(as.numeric(rownames(data2)),data2)
data3 <- cbind(as.numeric(rownames(data3)),data3)

return(list(data1=data1,data2=data2,data3=data3))
}

chain_building <- function(model,id_sigma,nb_iterations,nb_param,theta,
nb_sample_traits,step,traits,data_tree,A0,B0,mean_prior,
sd_prior,CheckArguments = TRUE)
{
  if (CheckArguments)
  {

```

```

    check_arguments()
  }
  source(paste('growth_model_',model,'.R',sep=''))
  source(paste('mortality_model_',model,'.R',sep=''))

  source('loglikelihood_growth.R')
  source('loglikelihood_mortality.R')

  data1_unique <- unique(data_tree$data1)
  data2_unique <- unique(data_tree$data2)
  data3 <- data_tree$data3

  names1 <- unique(paste(as.character(data_tree$data1[,1]),
    as.character(data_tree$data1[,2]),as.character(data_tree$data1[,3]),sep='_'))
  rownames(data1_unique) <- names1
  rep <- table(paste(as.character(data_tree$data1[,1]),
    as.character(data_tree$data1[,2]),as.character(data_tree$data1[,3]),sep='_'))

  names2 <- unique(paste(as.character(data_tree$data2[,1]),
    as.character(data_tree$data2[,2]),as.character(data_tree$data2[,3]),sep='_'))
  rownames(data2_unique) <- names2
  rep2 <- table(paste(as.character(data_tree$data2[,1]),
    as.character(data_tree$data2[,2]),as.character(data_tree$data2[,3]),sep='_'))

  names3 <- paste(as.character(data3[,1]),as.character(data3[,2]),
    as.character(data3[,3]),sep='_')
  rownames(data3) <- names3

  names2_ok <- names2[which(names2%in%names1)]
  names3_ok <- names3[which(names3%in%names1)]

  AGR_obs <- apply(data1_unique[,c(2,3)],1,diff)
  AGR_obs[AGR_obs<0] <- 0

  AGR_obs2 <- apply(data2_unique[,c(2,3)],1,diff)
  AGR_obs2[AGR_obs2<0] <- 0

  AGR_obs3 <- apply(data3[,c(2,3)],1,diff)
  AGR_obs3[AGR_obs3<0] <- 0

  traits1 <- traits[(1:nb_sample_traits),as.character(data1_unique[,1]),]

  lAGR_pred <- growth_model(theta,traits1,data1_unique)
  rownames(lAGR_pred) <- names1

  lAGR_pred2 <- matrix(NA,nrow=nrow(data2_unique),ncol=nb_sample_traits)
  rownames(lAGR_pred2) <- names2
  lAGR_pred2[names2_ok,] <- lAGR_pred[names2_ok,]
  num2 <- which(is.na(lAGR_pred2[,1]))

```

```

traits2 <- traits[(1:nb_sample_traits),as.character(data2_unique[num2,1]),]
lAGR_pred2[num2,] <- growth_model(theta,traits2,data2_unique[num2,])

lAGR_pred3 <- matrix(NA,nrow=nrow(data3),ncol=nb_sample_traits)
rownames(lAGR_pred3) <- names3
lAGR_pred3[names3_ok,] <- lAGR_pred[names3_ok,]
num3 <- which(is.na(lAGR_pred3[,1]))
traits3 <- traits[(1:nb_sample_traits),as.character(data3[num3,1]),]
lAGR_pred3[num3,] <- growth_model(theta,traits3,data3[num3,])

llG <- loglikelihood_growth
  (theta[id_sigma,],AGR_obs,lAGR_pred,data1_unique,rep,nb_sample_traits)

llM <- loglikelihood_mortality(theta,AGR_obs2,AGR_obs3,
  lAGR_pred2,lAGR_pred3,data2_unique,data3,nb_sample_traits,rep2)

res <- array(dim=c(nb_iterations+1,nb_param,nb_sample_traits))
res[1,,] <- theta

for (compt in 1:nb_iterations)
{
  ordre <- sample(1:nb_param)

  for (i in ordre)
  {
    theta_new <- theta

    if (i<id_sigma)
    {
      theta_new[i,] <- rnorm(nb_sample_traits,theta[i,],step[i])

      lAGR_pred_new <- growth_model(theta_new,traits1,data1_unique)
      rownames(lAGR_pred_new) <- names1

      lAGR_pred2_new <- matrix(NA,nrow=nrow(data2_unique),
        ncol=nb_sample_traits)
      rownames(lAGR_pred2_new) <- names2
      lAGR_pred2_new[names2_ok,] <- lAGR_pred_new[names2_ok,]
      lAGR_pred2_new[num2,] <-
        growth_model(theta_new,traits2,data2_unique[num2,])

      lAGR_pred3_new <- matrix(NA,nrow=nrow(data3),ncol=nb_sample_traits)
      rownames(lAGR_pred3_new) <- names3
      lAGR_pred3_new[names3_ok,] <- lAGR_pred_new[names3_ok,]
      lAGR_pred3_new[num3,] <- growth_model(theta_new,traits3,data3[num3,])
    }
  }
}

```

```

llG_new <- loglikelihood_growth(theta_new[id_sigma,],
  AGR_obs,lAGR_pred_new,data1_unique,rep,nb_sample_traits)

llM_new <- loglikelihood_mortality(theta_new,AGR_obs2,AGR_obs3,
  lAGR_pred2_new,lAGR_pred3_new, data2_unique,data3,nb_sample_traits,rep2)

logr <- llM_new + llG_new - llG - llM +
  dnorm(theta[i,],theta_new[i,],step[i],log=T) -
  dnorm(theta_new[i,],theta[i,],step[i],log=T) +
  dnorm(theta_new[i,], mean_prior, sd_prior, log=T) -
  dnorm(theta[i,], mean_prior, sd_prior, log=T)

r <- exp(logr)

nb_ok <- which(!is.na(r))
r_ok <- na.omit(r)

accepte <- nb_ok[(runif(length(r_ok),min=0,max=1) < r_ok)]

theta[,accepte] <- theta_new[,accepte]

llG[accepte] <- llG_new[accepte]
llM[accepte] <- llM_new[accepte]

lAGR_pred[,accepte] <- lAGR_pred_new[,accepte]
lAGR_pred2[,accepte] <- lAGR_pred2_new[,accepte]
lAGR_pred3[,accepte] <- lAGR_pred3_new[,accepte]
}

if (i==id_sigma)
{
  theta[i,] <- rgamma(nb_sample_traits, A0+nrow(lAGR_pred)/2,
    (sum((log(AGR_obs+1)-lAGR_pred)^2))*0.5+B0)

  llG <- loglikelihood_growth(theta[id_sigma,],AGR_obs,lAGR_pred,
    data1_unique,rep,nb_sample_traits)
}

if (i>id_sigma)
{
  theta_new[i,] <- rnorm(nb_sample_traits,theta[i,],step[i])

  llG_new <- llG

```

```

llM_new <- loglikelihood_mortality(theta_new,AGR_obs2,AGR_obs3,
  lAGR_pred2,lAGR_pred3,data2_unique,data3,nb_sample_traits,rep2)

logr <- llM_new + llG_new - llG - llM +
  dnorm(theta[i,],theta_new[i,],step[i],log=T) -
  dnorm(theta_new[i,],theta[i,],step[i],log=T) +
  dnorm(theta_new[i,], mean_prior, sd_prior, log=T) -
  dnorm(theta[i,], mean_prior, sd_prior, log=T)

r <- exp(logr)

nb_ok <- which(!is.na(r))
r_ok <- na.omit(r)

accepte <- nb_ok[(runif(length(r_ok),min=0,max=1) < r_ok)]

theta[,accepte] <- theta_new[,accepte]

llM[accepte] <- llM_new[accepte]

}

}

res[compt+1,,] <- theta

}

return(res)

}

plot_function <- function(result,burn,thin)
{
  nb <- dim(result)[2]
  l <- dim(result)[1]
  nb2 <- dim(result)[3]

  r <- nb%%3

  r2 <- 1
  if (r == 0)
    {r2 <- 0}

  a <- layout(matrix(c(1:(2*nb),rep(0,2*(3-r))),

```

```

ncol = 2*((nb\%/\%3)+r2),nrow=3,byrow=T), heights=rep(1,3),
widths = rep(c(1,0.2),((nb\%/\%3)+r2)))

for (i in 1:nb)
{
  par(mar=c(2,2,2,0.5))
  plot(result[seq(from=burn,to=1,by=thin),i,1],type='l',main=paste('theta',i))
  for (j in 2:nb2 )
  {
    lines(result[seq(from=burn,to=1,by=thin),i,j],col=j)
  }

  par(mar=c(2,0,2,1))
  plot(density(na.omit(result[seq(from=burn,to=1,by=thin),i,1]))\$y,
       density(na.omit(result[seq(from=burn,to=1,by=thin),i,1]))\$x,
       type='l',yaxt='n',xaxt='n')
  for (j in 2:nb2)
  {
    lines(density(na.omit(result[seq(from=burn,to=1,by=thin),i,j]))\$y,
         density(na.omit(result[seq(from=burn,to=1,by=thin),i,j]))\$x,
         type='l',col=j)
  }
}

}

creation_data <- function(NbTree, NbYears , param, param_sd , predictors)
{
  epsilon <- rnorm(NbTree,0, param[4])
  DBH <- matrix(rnorm(NbTree,15,0.2))

  ID <- 1 : NbTree
  names(epsilon) <- ID
  rownames(predictors) <- ID
  rownames(DBH) <- ID

  dat <- DBH

  DBH <- cbind(ID,DBH)

  # growth function
  growth_model <- function(id)
  {
    lAGR_pred <- rnorm(1,param[1],param_sd[1]) *
    predictors[as.character(id),1] *
    exp( -0.5 * (( log( DBH[as.character(id),2]))/
    (rnorm(1,param[2],param_sd[2]) * predictors[as.character(id),1]) )/

```

```

    ( rnorm(1,param[3],param_sd[3]) * predictors[as.character(id),2] ) ^2 )
  return(lAGR_pred)
}

# mortality function
mortality_model <- function(id)
{
  logit_p <- rnorm(1,param[5],param_sd[5]) *
  predictors[as.character(id),1] + rnorm(1,param[6],param_sd[6]) * epsilon
  return(logit_p)
}

# first year:
LC <- mortality_model(ID)
p_death <- 1/( 1+exp(-LC))
dead <- rbinom(NbTree,1,p_death)
res <- rep(NA,NbTree)
id_alive <- DBH[dead==0,1]
lAGR_pred <- growth_model(id_alive)
lAGR_sim <- lAGR_pred + epsilon[id_alive]
res[dead==0] <- DBH[id_alive,2] + (exp(lAGR_sim)-1)
dat <- cbind(DBH,res)

for (i in 1:(NbYears-2))
{
  dead <- rbinom(NbTree,1,p_death)
  res <- rep(NA,NbTree)
  names(res) <- rownames(dat)
  id_alive <- DBH[dead == 0 & !is.na(dat[,i+2]),1]
  lAGR_pred <- growth_model(id_alive)
  lAGR_sim <- lAGR_pred + epsilon[id_alive]
  res[id_alive] <- dat[id_alive,i+2] + (exp(lAGR_sim) - 1)
  dat <- cbind(dat,res)
}

dat <- dat[!is.na(dat[,2]),]

return(dat)
}

```

CHAPITRE 3

VULNERABILITY OF COMMERCIAL TREE SPECIES TO WATER STRESS IN FRENCH GUIANA

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La méthode de couplage développée dans le chapitre précédent peut être utilisée pour répondre à des questions de foresterie. Dans le cadre du stage d'Hélène Fargeon, nous avons cherché à appliquer cette méthode pour créer des modèles de croissance-mortalité pour 14 espèces d'intérêt commercial en Guyane Française. Les modèles intègrent un indice d'intensité d'exploitation et un indice de stress hydrique. En effet, selon les prédictions du GIEC, les périodes sèches vont augmenter en intensité et en durée dans les régions tropicales, ce qui augmentera le stress hydrique auquel seront soumises les forêts. Nos résultats montrent un comportement communs aux différentes essences étudiées : le stress hydrique diminue la croissance et augmente la mortalité, tandis que l'exploitation augmente la croissance et diminue la mortalité. Malgré cette réponse commune, des profils de susceptibilité différents sont observés et permettent d'identifier des essences particulièrement sensibles et d'autres plus résistantes. Les résultats de cette étude nous interpellent sur la nécessité de bien définir le rôle de l'exploitation en terme de gestion durable des forêts tropicales humides.

1 Abstract

- Although the rate of global deforestation has decreased slightly in the last decade, the future of tropical managed forests is threatened by climate change, a new phenomenon that is the indirect result of human activity. In anticipation of the changes in rainfall patterns and the increase in frequency of water stress episodes predicted by climatic models for intertropical regions, it is essential to study commercial trees' resilience and vulnerability to water stress by identifying potential interaction effects between stress caused by logging and stress due to a lack of water.
- Focusing on 14 species presenting a potential or acknowledged interest for the timber industry in the Guiana Shield, a joint model coupling growth and mortality processes for each species was parametrized, including a climatic variable related to water stress and an estimator of the intensity of logging : the quantity of aboveground biomass lost after logging. Moreover, we looked for any interaction effects between the two predictors.
- For the vast majority of the species, water stress had a negative impact on growth rate, while the impact of logging was positive. The opposite results were observed for the mortality process. Some groups may be extrapolated from the combined results of the two processes, generating their vulnerability profiles and ranking from species apparently quite resistant to water stress (*Balata pomme*, *Goupi*, *Gonfolo Rose*), even under logging pressure, to highly vulnerable species (*Kobe*).
- In light of our results, the timber industry may want to conduct a conservation strategy of the most vulnerable species, leading to a diversification of the logged species. Conservation of the already-adapted species may also be considered as the most certain way to protect the tropical forests under future climates. Scientists and foresters have to define the role of silviculture in forest conservation, and the timber industry will necessarily have to adapt to changes expected under future climates.

2 Introduction

Half of standing primary tropical forests, up to 400 million hectares, are designated by national forest services for timber production (Blaser, 2011). In

this context, clarifying the role of tree harvesting in forest management is essential. Recently, selective logging has been recognized as one of the less disturbing land-use changes (Gibson *et al.*, 2011). As a result, sustainable logging through reduced-impact rules is often promoted as the best way to both develop local economy and to preserve large rainforest areas. However, this "middle-way" between deforestation and integral conservation is politically charged, and sustainability remains poorly defined (Putz *et al.*, 2012).

Presently, the extension of production areas is particularly rapid, even in the most sparsely populated rainforests such as Guiana Shield (Hammond, 2005). For example, in Suriname production, areas dropped from 2.5 M to 4.0 M ha in the last twenty years and timber production dropped from 200,000 to 400,000 m³ in the last three years. In French Guiana, forests areas managed for production also increased by 2.2 M ha in the last twenty years, but mean annual timber production is still limited to about 75,000 m³, with a very low logging rate of 1 to 6 trees.ha⁻¹ (Guitet *et al.*, 2012). It is expected that the timber demand will increase, as demographic projections forecast a doubling of the Guianan population before 2030. In both countries, timber selection is concentrated on a few species : *Dicorynia guianensis* (common name : Angélique) and *Qualea rosea* (Gongolo rose) constitute 60% of the wood logged in French Guiana and 35% of the wood logged in Suriname.

Numerous studies about the sustainability of logging have been conducted, and even forest management's striving for sustainability appears to be questioned (Zimmerman and Kormos, 2012). Logging unavoidably causes timber and carbon loss (Asner *et al.*, 2005), and logging impacts on biodiversity, which are more difficult to quantify (Clark and Covey, 2012). Concerning forest dynamics, forest logging decreases resource competition between trees immediately after exploitation and promotes rapid growth of residual trees (Silva *et al.*, 1995; Dwyer *et al.*, 2010; D'Amato *et al.*, 2011). In Northern French Guiana, an increase from 1.2 mm.years⁻¹ to 2.2 mm.year⁻¹ was observed by Guitet *et al.* (2009) and Herault *et al.* (2010) the years following logging. This growth increase is still observable more than eight years after logging in 7 neotropical forests sites resumed in Blanc *et al.* (2009). At the same time, the effects of logging on tree mortality switches from high mortality rates of damaged trees straight after logging to no impact several years after logging (Blanc *et al.*, 2009; Silva *et al.*, 1995).

It is well accepted by the scientific community that climate change will have a serious impact on tropical forests, particularly in the Amazon Basin, resulting in a change in rainfall patterns and, as a result, increased water stress (GIEC, 2013). A consensus emerged on the lengthening and streng-

thening of the drought periods regarding precipitation predicted by models of the intergovernmental panel on climate change (IPCC) (Joetzjer *et al.*, 2013), even if these models potentially underestimate the variability of the dry season length in Amazonia (Fu *et al.*, 2013). Recent studies have tried to understand the potential impact of this increase in water stress on tropical forests (Malhi and Phillips, 2004; Allen *et al.*, 2010; Choat *et al.*, 2012). A consensus about higher mortality due to high drought emerged, thanks to the large number of studies on the effect of the intense droughts of 2005 and 2010 in Amazonia (Phillips *et al.*, 2009; Lewis *et al.*, 2011) and to results of experimental droughts in Brasil (Nepstad *et al.*, 2007; Brando *et al.*, 2008). Recently, Coomes *et al.* (2014) showed that the response of wood production to anthropogenic climate change not only depends on the physiological responses of individual trees, but is also highly contingent on whether forests adjust in composition and structure. Some studies have shown that mortality results from interactions between climate and competition on an individual scale (Clark *et al.*, 2014), but competition is hard to estimate and is consequently seldom included in models of forest response to climate change. It is remarkable, then, to see how few studies include the possible interaction between water stress and logging activities, since logging is expected to reduce competition.

Concerning the interaction between water stress and exploitation, two theoretical hypotheses are debated in the current literature. Logging is known to punctually modify the floristic composition of the forest, for example, in logging gaps where the installation of pioneer species is highly favoured (Baraloto *et al.*, 2012). Logging could, as a result, have a negative effect on the global ecosystem resistance to water stress because these pioneer species, which allocate their resources for a fast growth, are less resistant to water stress (Ouedraogo *et al.*, 2013). Logging might also have a beneficial impact on the resilience of tropical rainforests to water stress by reducing the competition for resources like water and light, and thereby reducing (i) water-stress induced mortality, and (ii) growth slowing.

Studies about the possible interactions between climate and logging on forest dynamics are hampered by data availability (Clark *et al.*, 2014). The intervals between censuses are often long, and climatic variables need to be aggregated over these long periods, erasing exceptionally wet or dry seasons' effects. Moreover, not only the data, but also the models may be unable to catch the interaction effects. As tree dynamics is drawn by two processes, growth and mortality, these processes and the relations linking these processes together have to be accurately modelled. In this study, we took advantage of two opportunities : (i) a 75ha forest dynamic dataset from a long-term

TABLE 3.1 – **List of the commercial species taken into account for the study.** The current level of exploitation was calculated as a relative percentage of the 20 main commercial species logged during the last 25 years. Column 3 indicates the abundance of the species in the study site of Paracou, French Guiana.

Common name	Taxonomic identification	Trees in Paracou	Current exploitation level (% in volume)
Angélique	<i>Dicorynia guianensis</i>	647	41.63%
Balata franc	<i>Manilkara bidentata</i>	138	2.28%
Balata pomme	<i>Chrysophyllum spp.</i>	205	0.04%
Boco	<i>Bocoa prouacensis</i>	1135	0.01%
Carapa	<i>Carapa surinamensis</i>	702	0.04%
Gonfolo gris	<i>Ruizterania albiflora</i>	73	1.43%
Gonfolo rose	<i>Qualea rosea</i>	669	21.12%
Goupi	<i>Goupia glabra</i>	291	1.89%
Grignon franc	<i>Sextonia rubra</i>	188	8.94%
Kobe	<i>Sterculia spp.</i>	460	<0.0003%
Manil marécage	<i>Symphonia spp.</i>	69	<0.0003%
Wacapou	<i>Vouacapoua americana</i>	874	1.29%
Wapa	<i>Eperua falcata</i>	2628	0.49%
Yayamadou montagne	<i>Virola michelii</i>	344	0.26%

logging experiment, where all trees with $DBH > 10\text{cm}$ were censused every 2yr over a 20yr post-logging period, and (ii) a joint growth-mortality model recently developed (chapter 2). Fourteen forest species (see Table 3.1) were identified, together with forest managers, as potentially interesting for the Guianan timber industry using criteria including natural abundance, current level of exploitation or future logging potential. We tackled two questions :

- How will these commercial species respond, in terms of demographical rates, to the increase in water stress induced by climate change ?
- Will logging and water stress interact, making some species more fragile than others ?

3 Materials and Methods

3.1 Study site

The study was conducted using data from the Paracou experimental site (5°18'N, 52°55'W), a lowland tropical rain forest near Sinnamary, French Guiana. It is typical of Northern Guianan rain forests (Rutishauser *et al.*, 2010; ter Steege *et al.*, 2006), with a high species diversity (more than 500 woody species attaining 10 cm Diameter at Breast Height DBH found at the site) and dominant tree families including *Fabaceae*, *Chrysobalanaceae*, *Lecythidaceae*, *Sapotaceae* and *Burseraceae*. Nearly two-thirds of the annual 3040 mm of precipitation between mid-March and mid-June, followed by a long dry season from mid-August to mid-November (Wagner *et al.*, 2011). Most common soils in Paracou are Acrisol, limited in depth by a transformed loamy saprolite (≤ 1 m deep), which has a low permeability and leads to lateral drainage during heavy rains (Ferry *et al.*, 2010).

3.2 Data

Twelve plots of 6.25 ha each were established in 1984 for a complete annual inventory of all trees > 10 cm of DBH. These plots underwent 3 different logging treatments between October 1986 and May 1987, with 3 plots assigned as controls. An average of 10 trees ≥ 50 cm DBH (treatment 1), 32 trees ≥ 40 cm DBH (treatment 2) and 40 trees ≥ 40 cm DBH (treatment 3) were removed per hectare. Three new additional control plots of 6.25 ha were established in 1990. Forest inventories have been conducted since 1991. Censuses of mortality, recruitment and diameter growth were conducted every year until 1995 and every 2 years thereafter. DBH was calculated from circumference measures made to a precision of 0.5 cm. We used data from 1991 to 2011. For each tree we know the location, DBH, name and status (dead or alive).

3.3 Model

The joint model used is based on 2 sub-models. The first one is a non-linear growth model developed in Hérault *et al.* (2011) in which the growth trajectory depends on 3 parameters : G_{max} (the maximum growth rate), D_{opt} (the diameter at maximum growth) and K (the kurtosis of the curve defining the shape of the ontogenetic variation in growth rate).

The second one is a mortality model developed by Aubry-Kientz *et al.* (2013), computing the individual probability of dying at each time step.

These 2 processes are interdependent, insofar as past tree growth has an impact on the individual probability of dying (Chao *et al.*, 2008; Metcalf *et al.*, 2009), and similar ecological predictors can be simultaneously implied in the two processes. To address the delicate issue of coupling both processes, we used tree vigour to link growth and mortality. Tree vigour is estimated with $\log\left(\frac{AGR_{i,t} + 1}{\widehat{AGR}_{i,t} + 1}\right)$, where $AGR_{i,t}$ is the observed absolute growth rate between time $t-1$ and time t for individual tree i , and $\widehat{AGR}_{i,t}$ is the predicted absolute growth rate between time $t-1$ and time t for individual tree i using the growth sub-model. At each time step, an individual tree i may die with probability $p_{i,t}$. If tree i stays alive, it grows at a growth rate $AGR_{i,t}$, and its diameter $D_{i,t-1}$ becomes $D_{i,t}$. The joint model likelihood is then :

- $\prod_{t=1}^n f(D_{i,t}|D_{i,t-1}) * (1 - p_{i,s,t})$ if tree i stays alive during the length of the studied period,
- $p_{i,s,k} * \prod_{t=1}^{k-1} (f(D_{i,t}|D_{i,t-1}) * (1 - p_{i,s,t}))$ if tree i dies between time $k-1$ and time k ,

where $f(D_{i,t}|D_{i,t-1})$ is the probability density for a tree with diameter $D_{i,t-1}$ at time $t-1$ to grow to diameter $D_{i,t}$ at time t , and $p_{i,t}$ is the probability of dying between time $t-1$ and time t . This probability is computed by the model :

$$p_{i,t} = \text{logit}^{-1}\left(\theta_1 * \log\left(\frac{AGR_{i,t-1} + 1}{\widehat{AGR}_{i,t-1} + 1}\right) + \theta_2 * D_{i,t-1} + \theta_3 * (D_{i,t-1})^2 + \theta_4 * Water_t + \theta_5 * AGBL_i + \theta_6 * Water_t * AGBL_i\right)$$

$Water_t$ is here a covariate related to the water stress undergone by trees at time t . We chose, as the water stress indicator, an estimator computed using the relative extractable water index (REW) (Wagner *et al.*, 2011), that is the area over the REW curve and under the threshold of 0.4 defined as critical by Wagner *et al.* (2012). To include the logging impact in the model, we quantified it by the above-ground biomass (AGB.ha⁻¹) loss measured, at the 6.25ha plot level, right after the logging. This value varies from 0 to 225 t.ha⁻¹, which is the covariate indicated by $AGBL_i$ in the equation. To compare, mean AGBL in current harvested blocks in French Guiana is estimated between 20% and 35% that correspond to 70-100 tMS.ha⁻¹ (Guitet *et al.*, 2012). We expect θ_2 to be negative and θ_3 to be positive in the probability

of dying, leading to a U-shape mortality curve. This means that a tree has higher risks of dying when it is young and small, or large and old, than when it has an intermediate DBH, a phenomenon that we can explain by intense competition among the youngest and by senescence for the oldest (Aubry-Kientz *et al.*, 2013). Growth rates are predicted with the following model, also including a water stress effect ($Water_t$), a logging effect ($AGBL_i$) and an interaction between those two effects :

$$\begin{aligned} \log(\widehat{AGR}_{i,t-1} + 1) &= (\theta_1 + \theta_4 * Water_{t-1} + \theta_5 * AGBL_i \\ &\quad + \theta_6 * Water_{t-1} * AGBL_i) \\ &\quad * \exp\left(-\frac{1}{2} \left(\frac{\log\left(\frac{D_{i,t-2}}{\theta_2}\right)}{\theta_3}\right)^2\right) \\ \log(AGR_{i,t-1} + 1) &= \log(\widehat{AGR}_{i,t-1} + 1) + \varepsilon \\ &\quad \text{with } \varepsilon \sim N(0, \theta_7) \end{aligned}$$

In these equations, θ are all unknown parameters that we will infer. ε is an error term following a normal distribution.

3.4 Inference and Selection Method

A Bayesian Monte-Carlo Markov Chain (MCMC) method was implemented to estimate the parameters (Dellaportas *et al.*, 2002). A random walk was used as proposal distribution to sample new values of parameters that were or were not selected, using the ratio of Metropolis-Hastings. The only parameter that was not sampled this way was the standard deviation of the growth model θ_7 , for which an inverse-gamma posterior distribution with a Gibbs sampler was used. Since values of vigour change as predicted growth changes, growth and mortality processes were parametrized simultaneously. The growth model is taken into account through the vigour estimate when mortality parameters are estimated. All parameters are sampled one by one at each step, and the global likelihood is computed. Three thousand iterations of Metropolis-Hastings were done for each parameter. All the algorithms and statistical treatments were implemented using R software RCoreTeam (2014).

We used the selection method proposed by Kuo and Mallick (1998) to determine whether it was significant to include an interaction between climate and water stress in the growth model or in the mortality model. The

method consists of multiplying each interaction term we want to test by an indicator, whose value will be either 1 (term included in the model) or 0 (term not included). A Gibbs algorithm was used to attribute either 1 or 0 to the indicator, and a Metropolis-Hastings within Gibbs algorithm was used to estimate the value of the parameters. We decided to include the interaction effect when the expectation of the indicator given by the Kuo-Mallick method was above 0.8.

3.5 Quantification of the impacts of water stress on growth and mortality

The water stress effect, represented by the covariate ($Water_t$), has the same range for all the species. The parametrization of the joint model for each species gives us a value of parameter θ_4 multiplying this covariate, but to quantify a standardized (*i.e.*, comparable between species) impact of water stress on the two processes, further calculations were necessary.

3.5.1 Impact on growth

For the growth process, the water stress is added to other terms in equation (2), so that we weight it with θ_1 , a parameter related with the maximum growth rate of the species. In order to have access to an index of water stress impact on growth comparable between the species, we considered a value of water stress of 1 and a value of above-ground biomass loss ($AGBL$) corresponding to the logging treatment 3, and we calculated :

$$\text{Impact on growth} = \frac{\theta_4 + \theta_6 * AGBL}{\theta_1}.$$

This index describes the proportional decrease of growth rates observed with water stress. No impact of water stress on the growth of the tree species considered corresponds to a value of 0. If an interaction between water stress and logging is selected for a species, then θ_6 is not null to take this interaction into account.

3.5.2 Impact on mortality

For the mortality process, the calculations used were more complicated due to the logit function in equation (1). We calculated a medium basal signal relating the ontogeny of the tree with the probability of dying and included a water stress effect :

$$\text{Basal signal} = \theta_2 * \text{median}(DBH) + \theta_3 * (\text{median}(DBH))^2.$$

The probabilities of dying with and without water stress were then calculated :

$$proba_{\text{without water stress}} = \text{logit}^{-1}(\text{basal signal});$$

$$proba_{\text{with water stress}} = \text{logit}^{-1}(\text{basal signal} + \theta_4 + \theta_6 * AGBL).$$

We considered again a standard value of water stress of 1. The impact was

$$\text{Impact on Mortality} = proba_{\text{with water stress}} / proba_{\text{without water stress}}.$$

This index describes as a result the increase in probability of dying observed with water stress. No impact of water stress on the mortality of the tree species considered corresponds to a value of 1. If an interaction between water stress and logging is selected for a species, then θ_6 is not null to take this interaction into account.

4 Results

4.1 Variable selection

The histograms resulting from the Kuo-Mallick procedure showed clear results, bringing out 4 species for which an interaction had to be included in the model to improve the likelihood (see Figure 3.1). The final growth model included, as a result, an interaction term for 3 species : Carapa, Manil marécage and Wapa. The selection rate was above 99% for all selected species. Regarding the mortality model, an interaction term was only selected for the Grignon Franc, with a selection rate of 86%.

4.2 Response to the combined effects of logging and water stress

In order to visualize the combined effects of logging and water stress on growth and mortality rates for each species, we simulated growth and mortality rates with varying logging and water stress. Only a few representative curves are presented here in order to present an overview of the response profiles. All simulations of growth and mortality rates for the species not presented in this part are available in the Appendices.

4.2.1 Growth

A general signal was common to all species (Figure 3.2a). The tendency observed corresponds to what was expected : growth rate is lower when the

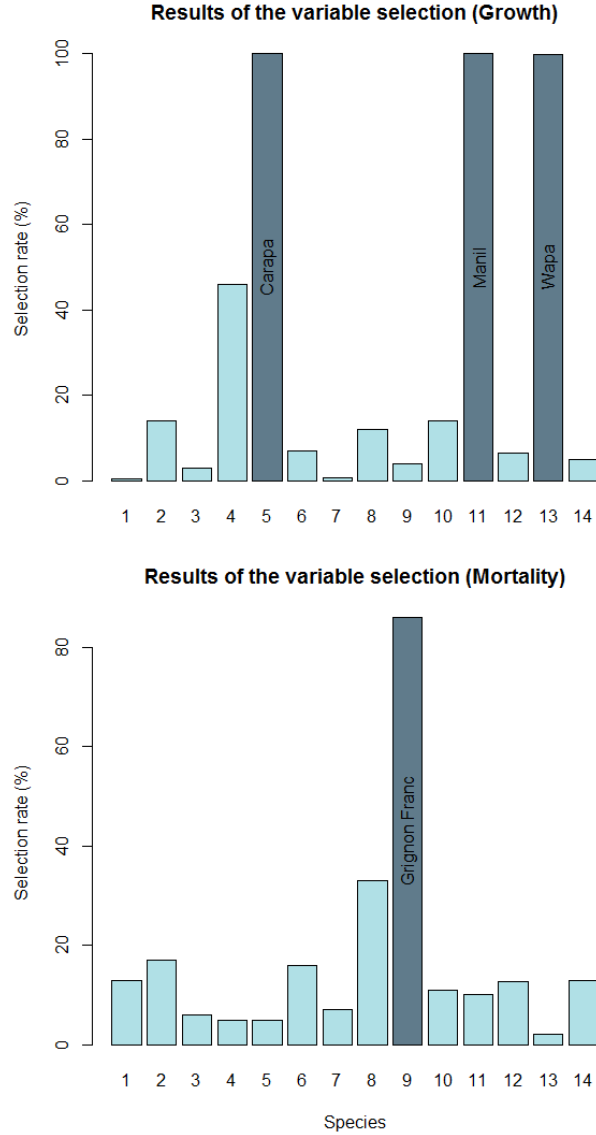


FIGURE 3.1 – Histograms presenting the selection rate of the interaction term $Water_t * AGBL_i$ in the growth (left) and mortality (right) models resulting from the Kuo-Mallick selection method. Three species revealed an interaction effect in the growth model, whereas only the Grignon Franc showed an interaction effect in the mortality model. 1 : Angélique, 2 : Balata franc, 3 : Balata pomme, 4 : Boco, 5 : Carapa, 6 : Gongolo gris, 7 : Gonfolo rose, 8 : Goupi, 9 : Grignon franc, 10 : Kobe, 11 : Manil marécage, 12 : Wacapou, 13 : Wapa, 14 : Yayamadou montagne.

tree is exposed to an important water stress, but exploitation has an opposite effect insofar as it decreases competition among trees for common resources such as light and water in the soil.

Besides this common pattern, important differences between species can be pointed out. All the species are distributed along a gradient, as illustrated in Figure 3.2. Some of them are well resistant to water stress (like the Balata Pomme) and show nearly horizontal isoclines. Other tree species appear more affected by the lack of water, though exploitation seems to play an offsetting role (Angélique). For these species, the isoclines tend to be more vertical. Finally, the Manil marécage illustrates how the interaction between logging and water stress can twist the curves and lead to a low growth rate when the water stress becomes too significant, even with logging.

4.2.2 Mortality

For the probability of dying, no pattern was shared by all the species. However, the majority of them (12 species out of 14) showed a common scheme (see Figure 3.3). The tendency observed is again in agreement with what was expected : probability of dying is higher when the tree is exposed to an important water stress, but exploitation has an opposite effect by decreasing competition, and therefore, exploitation reduces mortality rates. All the species sharing this tendency (*i.e.*, all except Grignon Franc and Yayamadou) are distributed along the same kind of gradient as shown in the section labeled "growth" above ; this gradient is illustrated in Figure 3.3.

Some of them are well resistant to water stress. That is the case for the Wacapou, whose isoclines are horizontal. Other tree species appear less resistant to the lack of water, though exploitation could play an offsetting role to a certain extent. The Boco, as well as a lot of other species like the Goupi or the Gonfolo Gris, match this profile. Some species have isoclines that tend to be vertical, conveying an impact of water stress on the probability of dying which may or may not be strong but which is observed with or without exploitation. That is the case of the Kobe, but also of the Carapa.

A completely different profile was observed for 2 residual species : the Yayamadou and the Grignon Franc. The isoclines of the Grignon Franc are a little confused, likely due to the small number of trees in the database (73 ; see Table 3.1). The interaction effect was difficult to interpret for the same reason. The profile of the Grignon Franc is quite similar to the Yayamadou insofar as we consider that we have a basal mortality rate for standard conditions (high water stress only, intense exploitation only, or a combination of low water stress and light exploitation). The combination of high water stress

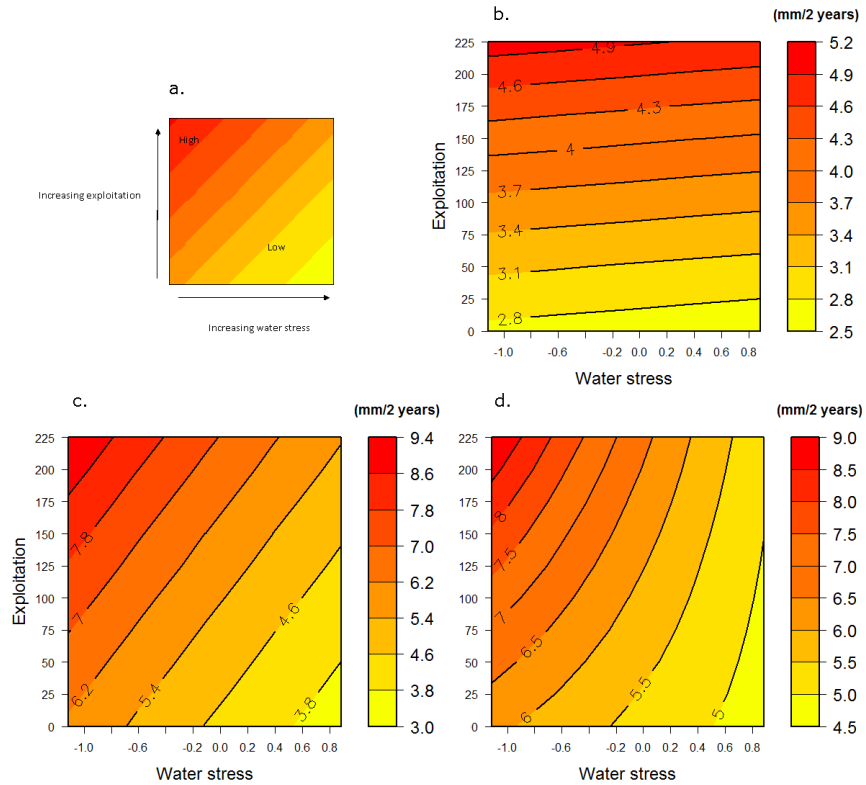


FIGURE 3.2 – Common pattern (a), and simulation of growth rates under different water stress and logging for the Balata Pomme (b), the Angélique (c) and the Manil marécage (d). These 3 species enable a good visualization of the gradient along which all the species are distributed. Some are well resistant to water stress (like the Balata Pomme), others are more affected by the exploitation (Angélique) and finally, the Manil marécage illustrates how the interaction between logging and water stress can twist the curves and lead to a low growth rate when the water stress becomes too significant, even with logging.

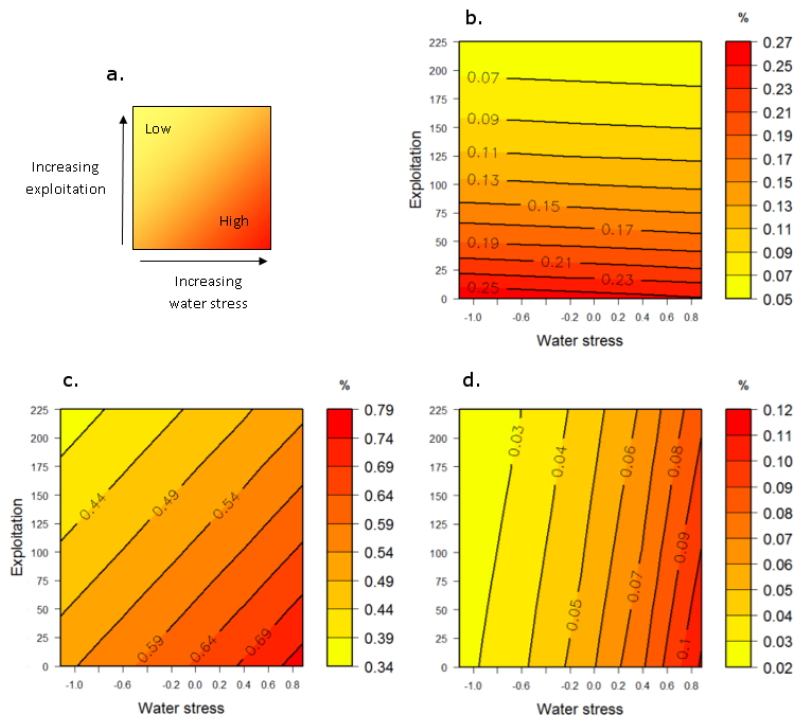


FIGURE 3.3 – Common pattern (a), and simulation of probabilities of dying under different water stress and exploitation intensity for the Wacapou (b), the Boco (c) and the Kobe (d). These 3 species illustrate the gradient along which the majority of tree species are distributed, though some species differ notably. The Wacapou is quite resistant to water stress, while other species are more affected. Some of them have the same profile as the Boco, which means that for them, logging plays an offsetting role, but for species like the Kobe or the Carapa, water stress is the dominant factor of mortality, and exploitation cannot change the tendency.

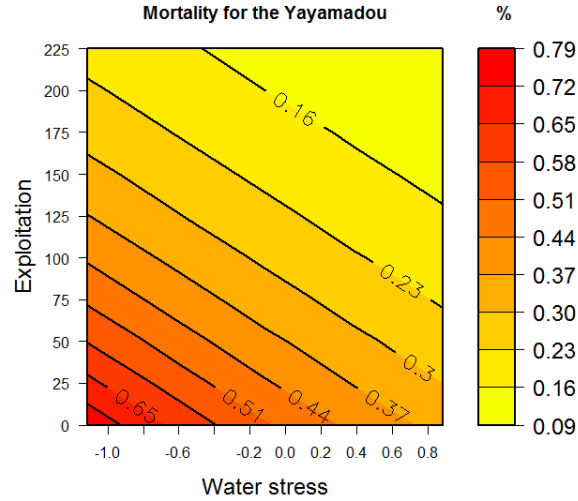


FIGURE 3.4 – **Simulation of probabilities of dying for the Yayamadou.** This simulation differs notably from the global pattern. The lowest mortality rate is observed in conditions of high water stress and intense logging.

and intense logging is the most beneficial for the Grignon franc, as for the Yayamadou, leading to the pattern visible on Figure 3.4, with the lowest mortality rate observed.

4.3 Response profiles observed

In order to synthesize the influence of water stress on both processes, the impacts on growth and mortality were illustrated in one graph (see Figure 3.5). A common pattern emerges, as the vast majority of species appear to be in the right lower quadrant delimited by the 2 ‘no impact’ blue dashed lines. For most species in this study, water stress has a negative effect on growth rates and increases the probability of dying.

Three groups of species are encircled in green, orange and red dashed lines. The green line encircles the species that appear quite resistant to water stress. The Balata Pomme is emblematic of this profile, where water stress only slightly increased the probability of dying, and the decrease in growth rate appears limited compared to other species. The orange line encircles other species that are more affected by water stress, with a gradient of differing responses, from (i) species that manage to reduce their growth in

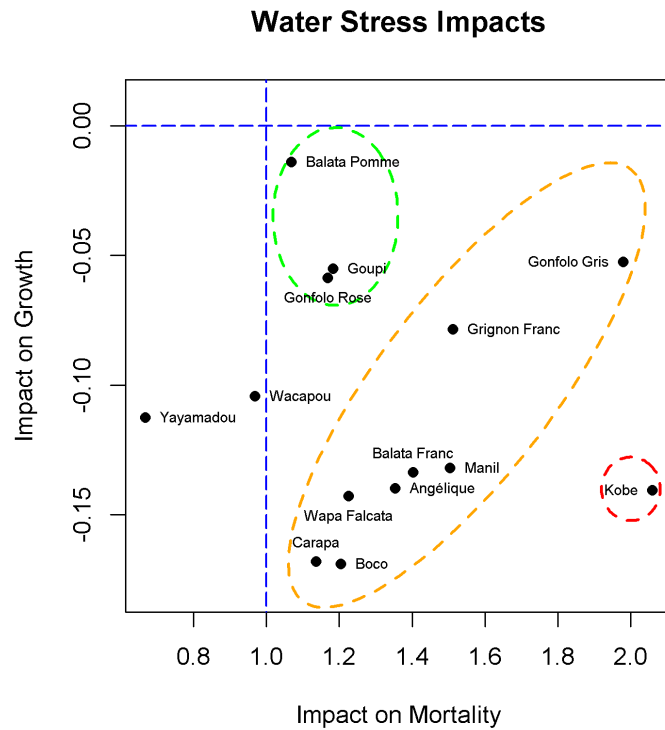


FIGURE 3.5 – **Water stress impacts on growth and mortality.** The climate parameter of the growth model is weighted by the intercept (related to the maximum growth rate of the species), giving the proportional decrease of growth rate observed with water stress. No impact corresponds to a value of 0 and is represented by the horizontal blue dashed line. The climate parameter of the mortality model is weighted with an artificial intercept (calculated with the distribution of diameters for the tree species considered) and included in the logit function. Impact is calculated by dividing probability of dying with water stress by probability of dying without. No impact corresponds therefore to a value of 1 and is visualized with a vertical blue dashed line. Three groups of species were made, and are represented with green, orange and red dashed lines. To account for interactions between water stress and logging, interaction terms are added when selected, and the *AGBL* value is set at the maximal value of logging. This concerns the growth of the Carapa, the Manil and the Wapa, as well as the mortality of the Grignon franc.

order to resist water stress, maintaining a probability of dying close to the norm (like the Boco), to (ii) species in which no significant growth reduction is observed, but water stress leads to an important increase in mortality rates (like the Gonfolo Gris). Finally, the red line encircles a unique species, the Kobe, which appears highly vulnerable to water stress. Its probability of dying is indeed particularly increasing with water stress and its growth rate is also significantly reduced.

If an interaction is observed, the interaction term is added and the value of *AGBL* is set at the maximum value of logging. This is the case for the growth of the Carapa, the Manil and the Wapa, and for the mortality of the Grignon franc. If the effects of water stress are computed without interaction for the Carapa, the Manil or the Wapa, the growth reductions are lower, switching these species from the orange susceptible group to the green resistant group (see Figure 3.5).

5 Discussion

The aim of this study was to quantify the vulnerability of commercial tree species in French Guiana to a combination of exploitation and water stress. Joint models for growth and mortality were successfully parametrized for 14 species; parameters included climate and logging effects. An interaction effect appeared necessary for several species, confirming the necessity of including competition (through logging) and water stress in forest models for the prediction of managed forests' responses to climate change (Clark *et al.*, 2014). Some common patterns were noticeable in our results. For the vast majority of species, water stress had a negative impact on growth rates, while the impact of logging was positive. The opposite results were observed for mortality.

5.1 Exploitation impacts

Logging, by removing mature trees using resources like water, soil nutrients and light, reduces competition among remaining trees, allowing them to grow faster. Positive effects of logging on growth last more than 8 years (Blanc *et al.*, 2009) and may be increased by the use of silvicultural treatments (Peña Claros *et al.*, 2008; Guitet *et al.*, 2009). This increased growth is of particular importance considering the large live tree carbon increment. Although reducing the competition through logging may counterbalance the impacts of water stress, the effects are not strong enough to totally compensate for it, and some significant interaction terms showed us that these

effects of reduced competition may be partly attenuated in cases of water stress (see Figures 3.2 and 3.3).

5.2 Water stress impacts

Plant performance under drought is a well-documented phenomenon (Choat *et al.*, 2012; Allen *et al.*, 2010; Phillips *et al.*, 2009). Water stress leads to a drop in soil water potential, resulting in a decrease of the leaf water potential of the plant. This triggers a reduction in stomatal conductance, enabling the plant to reduce excessive transpiration but also limiting the carbon assimilation. In the case of prolonged drought, this reduction in stomatal conductance may lead to a continued decline of assimilation and thus a noticeable growth reduction. Under extreme drought events, an increased number of xylem vessels run the risk of cavitation, because water transported through the xylem is under negative pressure (Choat *et al.*, 2012). The resultant air embolism blocks xylem conduits and reduces the plant's ability to move water from soil to sites of photosynthesis, with vessels becoming completely dysfunctional. A series of events such as loss of plant hydraulic conductivity, stomatal closure and finally the abscission of leaves, shoots and branches will sometimes lead to plant death (Choat *et al.*, 2012; Markesteijn, 2010). If water became insufficient, the competition for these resource will increase and the most adapted trees will be favoured ; indeed, it has been shown that drought kills selectively (Phillips *et al.*, 2009). Reducing this competition by logging may have different impacts on the water budget available for the remaining trees.

5.3 From tree vulnerability to timber logging strategy

Our results draw our attention to the problem that the timber industry will face in the next century : if some tree species are more vulnerable, or will become vulnerable, how should the timber industry react or prepare ?

In view of forest sustainability, some arguments may suggest a conservation strategy of the most vulnerable species. As 3 species (Carapa, Manil marécage and Wapa) are particularly fragile under logging (negative θ_6), the exploitation of these species may be avoided. It is then noticeable that the Angélique, the first tree species logged in French Guiana, appears quite vulnerable to climate change. It might be worth trying to encourage the timber industry to reduce the logging pressure on Angélique, should water stress intensify drastically in the coming decades. This diversification should lead to a preferential exploitation of species like the Balata Pomme, the Goupi or the Gonfolo Rose, which are more resilient to water stress. It also appears

necessary to alleviate the pressure on species like the Kobe, the Gonfolo Gris or the Boco, as they were revealed vulnerable to water stress by our study. With minimal logging pressure for the most vulnerable species, we enable the conservation of a larger genetic pool, trusting in the adaptative potential of these species to drier conditions by natural selection of the most resistant individuals. Moreover, the diversification of logged species has other benefits ; Putz *et al.* (2012) showed that if the same species continue to be harvested, only 35% of the original timber stock will be available for the second cut, compared to 54% if other species are harvested in the same time.

Another strategy could be defended : at similar logging intensities, protecting the vulnerable species highlighted in this study will occur to the detriment of other better-adapted species. One could argue that the conservation of these already-adapted species may be considered the most assured way to protect the tropical forests under the future climates and to guarantee a larger genetic pool of species that are likely to be resistant. Sensitive species that are vulnerable to climate changes may be condemned, and their protection for some time is, in any case, doomed to failure in the long run. Our results highlight many questions that need to be asked. Indeed, the tropical forest and its dynamics are a complex system that may be drastically impacted by climate changes and by logging practices, and consequences of logging practices have to be considered before action is taken. Scientists and foresters have to define the role of silviculture in forest conservation. Sustainable logging in the tropics involves many trade-offs.

6 Conclusion and Prospects

Our results allowed a species-centered interpretation of the influence of logging and climate on growth and mortality, the fundamental processes of forest dynamics. They enabled to point out some global trends on the response of the tree species studied for each process : (i) growth rates increase with logging and decrease with water stress while (ii) probabilities of dying have the exact opposite pattern. Resistant species were identified, like the Balata Pomme ; on the contrary, the Kobe or the Angélique stood out as more vulnerable. Forest plots are sometimes dominated by one species and population are rarely homogeneous. This is the case for the Angélique, which is extremely abundant in some areas. Some future studies need to address this population, to study the potential amplification feedbacks effects. Indeed, as the Angélique appears vulnerable to water stress, increased mortality of areas dominated by this species will likely experience a drastic loss of bio-

mass and other changes for the remaining trees. As suggested by Coomes *et al.* (2014), the forests's structure will potentially condition the response to climate changes. Even if the species studied here are somewhat representative of commercial species founded in Amazon (ter Steege *et al.*, 2006), studying forests that are under different climatic conditions is urgent.

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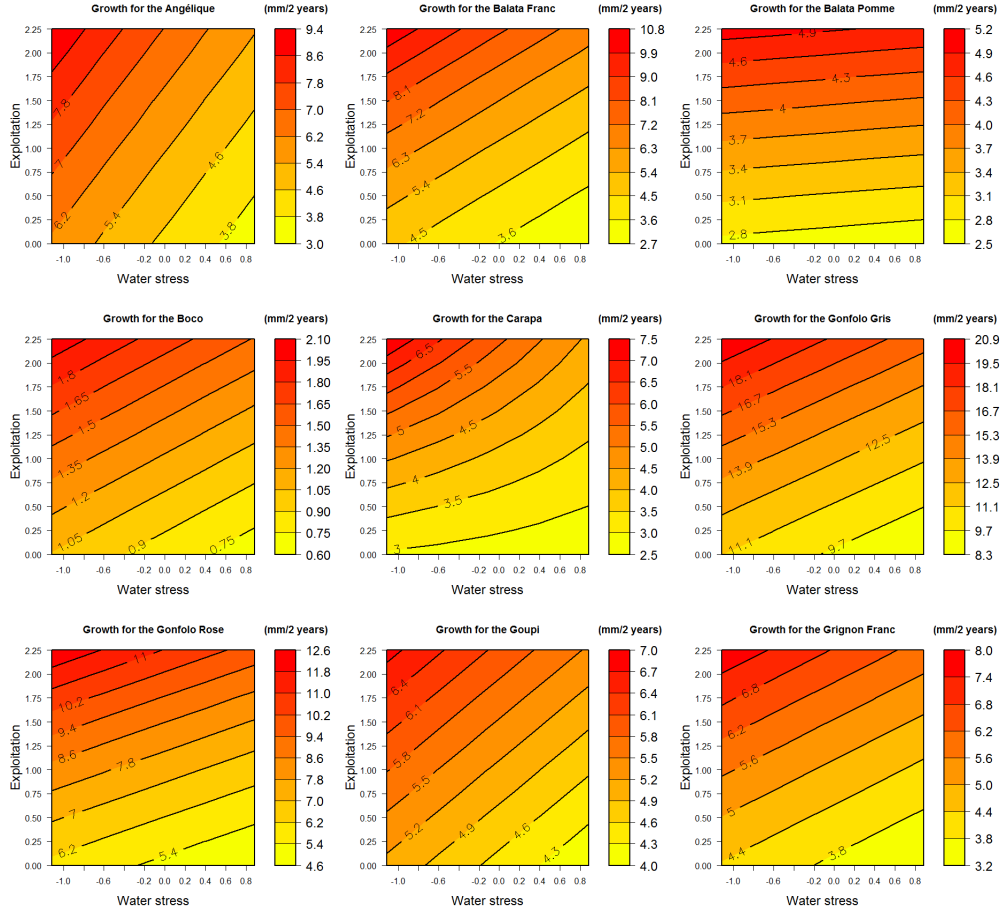
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3.A Simulations of growth



3.A. SIMULATIONS OF GROWTH

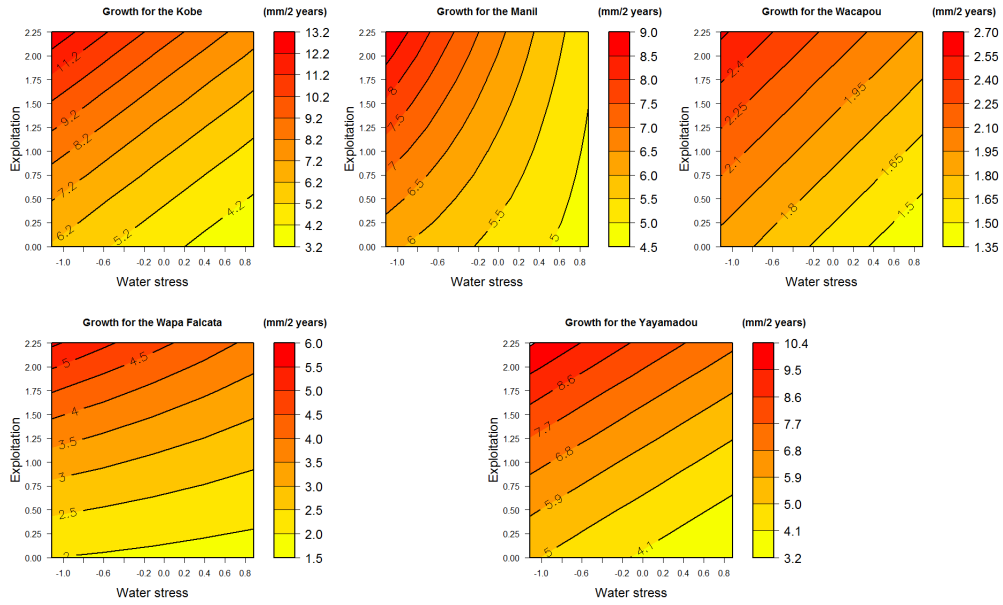
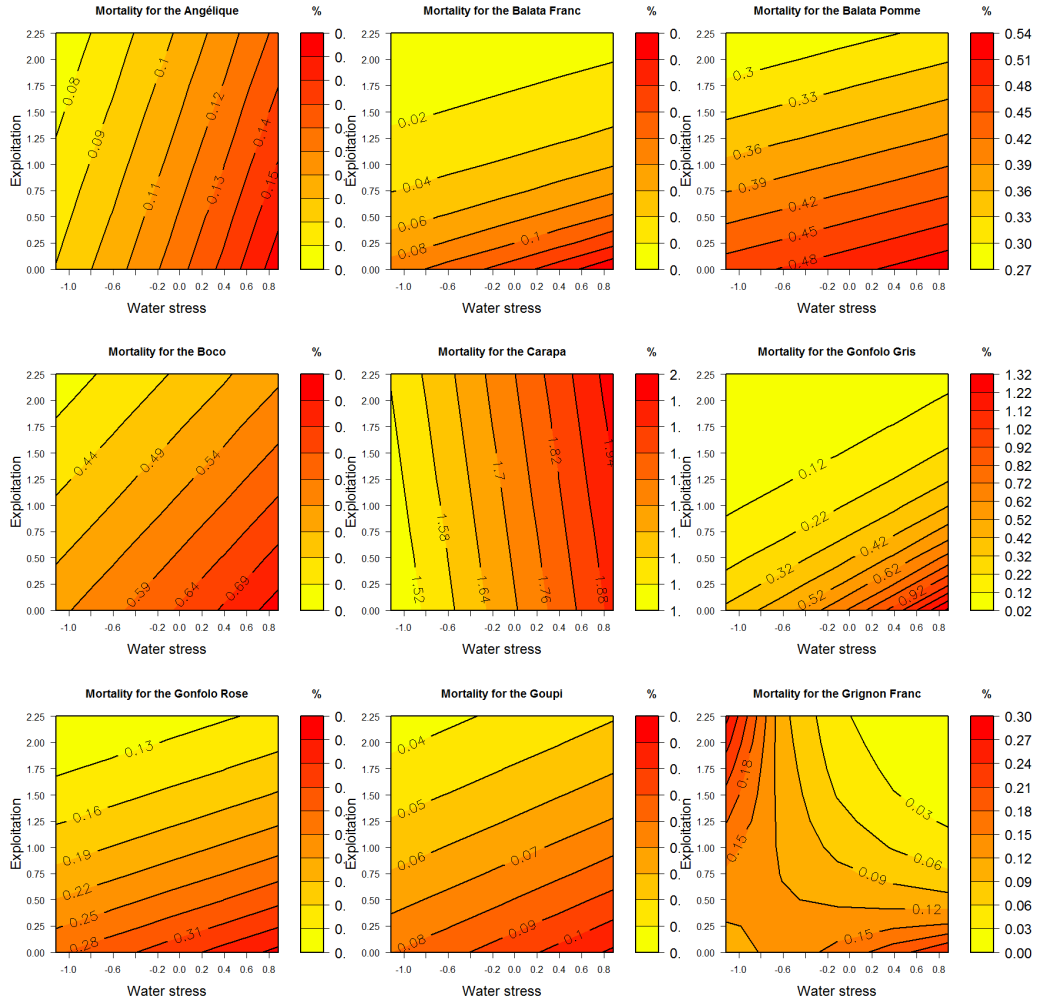


FIGURE 3.6 – Simulation of growth rates under different water stress and logging. Simulations for the 14 species studied.

3.B Simulations of mortality



3.B. SIMULATIONS OF MORTALITY

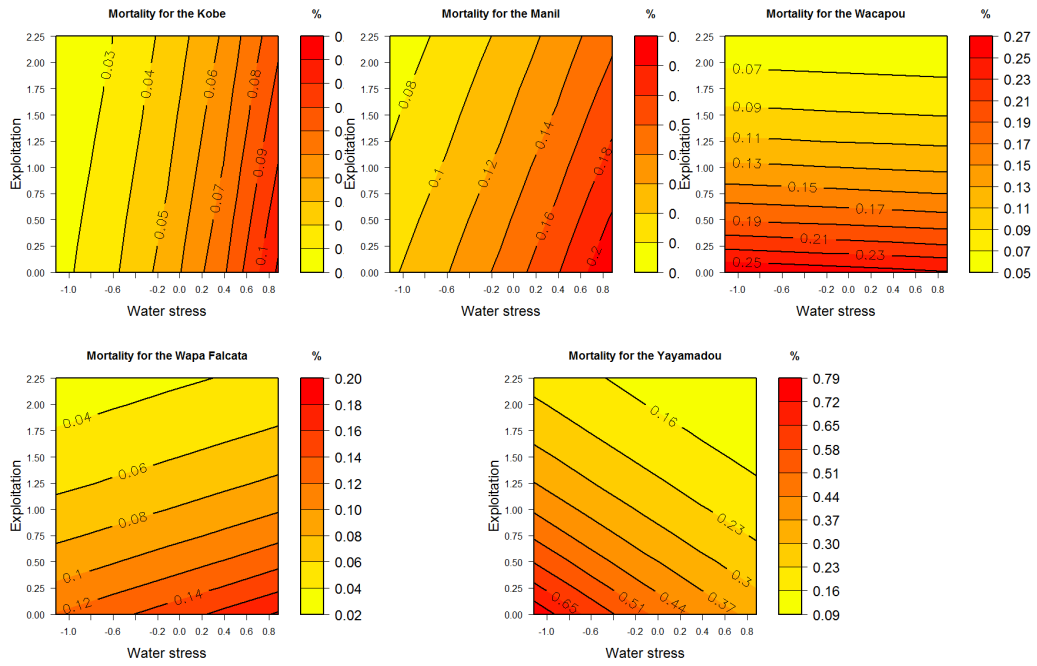


FIGURE 3.7 – Simulation of probability of dying under different water stress and logging. Simulations for the 14 species studied.

CHAPITRE 4

IDENTIFYING CLIMATIC DRIVERS OF TROPICAL FOREST DYNAMICS USING A GROWTH-MORTALITY MODEL

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Dans le chapitre précédent, l'introduction du climat s'est faite par l'estimation du stress hydrique. Mais d'autres changements sont prévus par le GIEC, notamment une augmentation marquée de la température. Pour mieux prendre en compte le climat dans notre modèle, les variables climatiques qui ont un rôle dans la croissance et/ou la mortalité doivent être attentivement sélectionnées. Dans ce chapitre, je cherche à identifier ces variables. Pour commencer, une analyse multivariée permet de mettre en évidence des axes relatif à la température, au stress hydrique, et à la saturation du sol en eau. Ensuite, l'ajout des variables climatiques sélectionnées dans le modèle montre que le stress hydrique a un impact négatif sur la croissance et la mortalité, que la température a un impact négatif sur la croissance, et que la saturation du sol en eau augmente le taux de mortalité. Une interaction entre la densité du bois et le stress hydrique est ajoutée dans le processus de croissance, et montre que les arbres à bois dense sont plus résistants à la sécheresse. De même, une interaction entre le diamètre de l'arbre et le stress hydrique montre que les arbres les plus gros sont aussi les plus sensibles à la sécheresse. Les variables climatiques et les interactions mises en évidence sont ajoutées dans le modèle développé dans le chapitre 2, ce qui permet de construire un modèle de croissance et de mortalité climat-explicite pour la communauté.

1 Abstract

- In the context of climate changes, identifying and then predicting the impacts of climatic drivers on tropical forest dynamics is becoming a matter of urgency.
- We used a coupled model of tropical tree growth and mortality, calibrated with forest dynamic data from the 20-year study site of Paracou, French Guiana, in order to introduce and test a set of climatic variables.
- Three major climatic drivers were identified through the variable selection procedure : drought, water saturation and temperature. Drought decreased annual growth and mortality rates, high precipitation increased mortality rates and high temperature decreased growth. Interactions between key functional traits, stature and climatic variables were investigated, showing best resistance to drought for trees with high wood density and for trees with small current diameters.
- Our results highlighted strong long-term impacts of climate variables on tropical forest dynamics, suggesting potential deep impacts of climate changes during the next century.

2 Introduction

In French Guianan forests, the intra-annual climate variability is strongly structured by the occurrence of the dry seasons : a long dry season from mid-August to mid-November, and a short one in March. Such a seasonality is typical in many tropical forest areas, and implies various changes of the availability of resources, such as water and light, necessary to tree development and to forest functioning. The seasonality of tree growth and tree mortality is consequently highly studied in tropical forests, with demonstrable success in the past (Wagner *et al.*, 2012; Grogan and Schulze, 2012; Brando *et al.*, 2010). Tree growth is mainly related to water availability, resulting in growth during the wet months and static or even contracted states during the dry season months (Grogan and Schulze, 2012). The use of a convenient water availability estimator like the relative extractable water (REW) (Wagner *et al.*, 2011) shows that low levels of REW rather than lack of rainfall *per se* are the key drivers of the decrease in growth rate, or even of the stop, at a seasonal time step. (Wagner *et al.*, 2012).

At another time scale, long-term forest dynamic changes may also be related to exceptional climate events. Effects of unusual dry periods on tree

growth and mortality may enlighten us about the long-term processes linking water availability and tree dynamics. After the intense 2005 drought in Amazonia, the forest suffered an additional mortality, leading to a huge loss of alive tree biomass (Phillips *et al.*, 2009). A consensus about higher mortality due to severe drought events has recently emerged (Choat *et al.*, 2012; Allen *et al.*, 2010). Experimental droughts in Brazil provide results in line with this consensus (Nepstad *et al.*, 2007; da Costa *et al.*, 2010; Brando *et al.*, 2008).

Besides exceptional events and the intra-annual seasonal rhythmicity, there is a gap in our research knowledge on an inter-annual scale investigating the potential links between inter-annual climate variations and forest dynamics from a long-term perspective. This gap is partly due to the weak magnitude of variation of the demographic rates when compared to what is observed from a seasonal point of view or from some spectacular events. This gap is also due to the lack of sites in tropical forests where annual regular inventories of tree growth and death are performed and where climatic data on the same time-scale are available. Convenient tools are needed to process these data. A modelling approach may help to tackle these questions (Zuidema *et al.*, 2013) because models can mechanistically link climate conditions, resource acquisition, allocation, and functional plant traits to tree growth and survival. Functional traits have been recently used to include functional diversity in models of tree growth (Hérault *et al.*, 2011; Rüger *et al.*, 2012; Wagner *et al.*, 2014) and tree mortality (Aubry-Kientz *et al.*, 2013). Such models need to start from potential underlying physiological processes, helping to articulate hypotheses that will serve as the basis for building the models.

Some climatic variables are expected to play a role in forest dynamics regarding the tree's physiological processes. Water stress due to drought is well documented (Phillips *et al.*, 2009; Allen *et al.*, 2010). Water insufficiency leads generally to higher mortality rates and lower growth (Choat *et al.*, 2012). Water stress needs to be estimated, and diverse estimators may be found in the literature (Wagner *et al.*, 2011; Toledo *et al.*, 2011; Aragão *et al.*, 2007; Malhi *et al.*, 2009). The length of the dry season seems to be the simplest estimator. The REW described in the study of Wagner *et al.* (2011) was computed using the daily rainfall and gave an estimate of the quantity of water available for tree development. This indicator is already related to intra-annual forest dynamics in Wagner *et al.* (2012). Although water availability is expected to reduce growth and increase mortality, these impacts have to be investigated on an inter-annual time-scale.

Rain may also be responsible for water saturation, a phenomenon that

is far less studied but that can have an effect on tree mortality or growth. For instance, Ferry *et al.* (2010) underlined a higher mortality rate in waterlogged areas. Inter-annual variations of rain quantities can lead to more or less waterlogged soils, independent of their topographical location, implying instability that can cause cascading tree-falls.

The effects of temperature are less consensual; some studies suggested that tropical forests can be near a high temperature threshold and that these systems may be more vulnerable to climate change than previously believed (Clark *et al.*, 2003). For instance, Clark *et al.* (2003) showed a negative correlation between 16-year diameter increments and annual means of daily minimal temperature in La Selva, Costa Rica, while Toledo *et al.* (2011) found a positive correlation between annual diameter growth and temperature in Bolivia. An explanation for such apparently conflicting results was proposed by Dong *et al.* (2012), that the effects of variability in solar radiation and daily minimum temperature on tree growth appear to be largely independent.

In this study, we first explore the potential relationships existing between climate variables computed on two-year time step and forest dynamics. We identify independent variable responsible for the inter-annual variation of growth and mortality rates. These variables are then included in a coupled growth-mortality model to test their multivariate effects. Finally, we include in the model some interactions between functional traits and the climate predictors to test for a potential differentiated response depending on the individual functional identity.

3 Materials and Methods

3.1 Data Collection

The study was conducted using three datasets. The major dataset comes from the Paracou experimental site ($5^{\circ}18'N, 52^{\circ}55'W$), a lowland tropical rain forest near Sinnamary, French Guiana. The forest is typical of Guianan rain forests, with dominant tree families including *Fabaceae*, *Chrysobalanaceae*, *Lecythidaceae*, and *Sapotaceae* and with more than 700 woody species attaining 10 cm diameter at breast height (DBH). Mean annual precipitation averages 2980 mm (30-year period), with a long dry season from mid-August to mid-November and a short dry season in March (Wagner *et al.*, 2011).

3.1.1 Tree dynamic

The first data set is an inventory of all trees >10 cm DBH in six natural forest plots of 6.25 ha between 1991 and 2011. Censuses of mortality and diameter growth have been conducted every two years. DBH was calculated from circumference measures made to a precision of 0.5 cm. We excluded individuals with buttresses or other problems that required an increase in measurement because we were unsure about the height of the initial points of measurement for these trees. The data set contained 20,340 trees. For each tree and every two years, we know the location, DBH, vernacular name, status (dead or alive), and the mode of death for dead trees (tree-fall or standing death). The vernacular name is the name used by local tree spotters. Botanical determination of the trees was completed in 2012, following extensive inventories with voucher collections and determination at regional and international herbaria. Hence, a large part of the trees that died during the study period (1991–2011) have no botanical determination but only a vernacular name. The method of Aubry-Kientz *et al.* (2013) is used to handle this uncertainty and to integrate the information on botanical determination contained in the vernacular names of trees that were not identified.

3.1.2 Functional traits

The second data set was a collection of five functional traits of 335 Guianan tree species that occur at the Paracou site (see Table 4.1). Traits are related to leaf economics, stem economics and life history and are extracted from a large database (Baraloto *et al.*, 2010a,b). The leaf economics reflects a trade-off between investments in productive leaves with rapid turnover versus costly physical leaf structure with a longer playback. The stem economics defines a similar trade-off at the stem level : dense wood versus high wood water content and thick bark (Baraloto *et al.*, 2010b). Life-history strategies describe how trees allocate resources to different organs and how these allocation translate into a species' ability to compete for resources and finally to grow, survive, reproduce and disperse (Rüger *et al.*, 2012).

3.1.3 Climate

The third data set consists of climate data (Table 4.2). Six variables were provided by the Climatic Research Unit (CRU) at the University of East Anglia (Mitchell and Jones, 2005), consisting in month-by-month variations in climate over the last century calculated on high-resolution grids (0.5*0.5 degree) (Mitchell and Jones, 2005). We used the aggregated variables (mean

TABLE 4.1 – **The five functional traits used in the growth-mortality model.** Descriptions of the traits, abbreviations used in this study and ranges observed in our data set.

Functional traits	Abbreviation	Range
Maximum diameter (m)	<i>DBHmax</i>	[0.13 ;1.11]
Maximum height (dm)	<i>Hmax</i>	[0.8 ;5.6]
Trunk xylem density (g.cm ⁻³)	<i>WD</i>	[0.28 ;0.91]
Laminar toughness (N)	<i>Tough</i>	[0.22 ;11.4]
Foliar $\delta^{13}C$ composition (‰)	$\delta^{13}C$	[-3.61 ; -2.62]

or sum, depending of the nature of the observed process) for two years, from July to July, to include the dry season (mid-August to mid-November). Selected variables that may have an impact on forest dynamics are the cloud cover (*Cld*), the potential evapo-transpiration (*Pet*), the precipitation (*Pre*), the daily mean temperature (*Tmp*), the vapour pressure (*Vap*) and the wet day frequency (*Wet*).

Three other climate variables are computed using the REW computed with a model developed by Wagner *et al.* (2011); this REW index takes values between 0 and 1 at our study site, corresponding to the available water for trees. This REW index is used to compute Nb_{under} , the number of days under a REW threshold of 0.4, which is the threshold recommended in Wagner *et al.* (2011); A_{under} , the area over the REW curve and under the threshold of 0.4; and A_{over} , the area situated under the REW curve and over the threshold of 0.95. Nb_{under} and A_{under} are built to be indicators of drought, while A_{over} is related to soil water saturation. All climate variables are centred to allow an easier interpretation of the results.

TABLE 4.2 – **The climate variables included in the growth-mortality model.** Descriptions of the climate variables, abbreviations used in this study, ranges observed in our data set, and sources used to compute the variables : CRU means that the variable is provided by the Climate Research Unit (Mitchell and Jones, 2005), and REW means that the variable is computed from the water balance model of Wagner *et al.* (2011).

Variable	Abbreviation	Range	Source
Cloud cover (%)	<i>Cld</i>	[56.85417 ; 60.70833]	CRU
Potential evapotranspiration (mm)	<i>Pet</i>	[80.4 ; 84.4]	CRU
Precipitation (mm)	<i>Pre</i>	[5486.3 ; 6207.3]	CRU
Daily mean temperature (° C)	<i>Tmp</i>	[26.12917 ; 26.91667]	CRU
Vapour pressure (HPA)	<i>Vap</i>	[705.7 ; 724.7]	CRU
Wet day frequency (days)	<i>Wet</i>	[385.23 ; 432.12]	CRU
Number of days with REW <0.4	<i>Nb_{under}</i>	[89 ; 170]	REW
Area over REW and <0.4	<i>A_{under}</i>	[9.05203 ; 32.96535]	REW
Area under REW and >0.95	<i>A_{over}</i>	[8.274586 ; 12.485895]	REW

3.2 Model

The model used in this study was developed in chapter 2. It consists of a model coupling growth and mortality processes at the whole community scale. The likelihood is computed using the distribution probability of mortality and the computed growth rate, as detailed in the Appendix 4.A. A vigour index is added into the mortality process, taking the past growth into account. We added the climate variables into the two processes to highlight the links between some climate drivers and one particular process.

$$p_{i,s,t} = \text{logit}^{-1} \left(\gamma_1 \times \text{clim}_1 + \theta_1 \times \text{Vigour}_{i,s,t} + \theta_2 \times \frac{\text{DBH}_{i,s,t-1}}{\text{DBHmax}_s} + \theta_3 \times \left(\frac{\text{DBH}_{i,s,t-1}}{\text{DBHmax}_s} \right)^2 + \theta_4 \times \text{Hmax}_s + \theta_5 \times \text{WD}_s + \theta_6 \times \text{Tough}_s \right)$$

with

$$\text{Vigour}_{i,s,t} = \log \left(\frac{\text{AGR}_{i,s,t-1} + 1}{\widehat{\text{AGR}}_{i,s,t-1} + 1} \right),$$

and

$$\begin{aligned} \log(\widehat{\text{AGR}}_{i,s,t-1} + 1) &= (\gamma_2 \times \text{clim}_2 + \theta_7 \times \text{DBHmax}_s \\ &+ \theta_8 \times \text{WD}_s + \theta_9 \times \text{Hmax}_s + \theta_{10} \times \delta 13C_s) \\ &* \exp \left(-\frac{1}{2} \left(\frac{\log \left(\frac{\text{DBH}_{i,t-2}}{\theta_{11} \times \text{DBHmax}_s} \right)}{\theta_{12} \times \text{WD}_s} \right)^2 \right), \end{aligned}$$

and

$$\log(\text{AGR}_{i,s,t-1} + 1) = \log(\widehat{\text{AGR}}_{i,s,t-1} + 1) + \varepsilon_i,$$

with

$$\varepsilon_i \sim \mathcal{N}(0, \theta_{13}).$$

where $p_{i,s,t}$ is the probability of dying of tree i of species s between time $t - 1$ and t ; $\widehat{\text{AGR}}_{i,s,t-1}$ is the predicted growth between time $t - 2$ and time $t - 1$; $\text{AGR}_{i,s,t-1}$ is the observed growth between time $t - 2$ and time $t - 1$; DBHmax_s , Hmax_s , WD_s , Tough_s and $\delta 13C_s$ are functional traits of species s to which tree i belongs (see Table 4.1); $\theta_1, \theta_2, \dots, \theta_{13}$ are parameters to be estimated, and ε_i is an individual error term following a normal distribution; γ_1 and γ_2 are the parameter vectors linking the climate predictors with the processes of mortality and growth respectively; clim_1 and clim_2 are the vectors of climate predictors included in the processes of mortality and growth, respectively.

3.3 Variable selection

To identify the different axes of variation of our climate data set and avoid including collinear variables in the model, we realized a principal component analysis (PCA) on the climate variables. We included all climate variables one by one in each process of the model and computed the partial likelihood

for each sub-model of growth or mortality we obtained. This provides a first result about the importance of each climate variable. Depending on these results and on their degree of collinearity from the PCA, we selected some climate variables and included them in the growth model and in the logit function of mortality.

3.4 Model inference

We implemented a MCMC algorithm to estimate the model parameters (Robert and Casella, 2004). A random walk was used as a proposal distribution to sample new values of parameters that were or were not selected, using the ratio of Metropolis-Hasting. Only standard deviation was sampled in an inverse-gamma posterior distribution with a Gibbs sampler. All the algorithms and statistical treatments were implemented with R software (core Team, 2014).

3.5 Functional trait and forest dynamic responses

Wood density and DBH of each individual tree are often expected to play roles in the tree water budget (see Table 4.3). Thus, we included in the model an interaction between wood density and the drought estimator A_{under} , an interaction between DBH and A_{under} , and an interaction between DBH and precipitation Pre .

The current tree diameter may also influence resistance drought events or other climatic perturbations (Nepstad *et al.*, 2007; Condit *et al.*, 2004). Two main hypotheses may be tested. First, small, young trees that are not well established and that do not have deep roots may be more sensitive and may suffer under stressful water conditions. Second, large, older trees may feel water stress because they must maintain their photosynthesis activities and carry sap to a higher altitude. We tested these two hypotheses using interaction effects (see Table 4.3).

Species vary over one order of magnitude in their wood density (WD), ranging from 0.08 to 1.39 g.cm³ (Iida *et al.*, 2012), and the encountered range of wood density is particularly large in species-rich tropical rainforests (Chave *et al.*, 2006, 2009). Wood density is a key functional trait because of its importance for mechanical stability, defence against herbivores, hydraulic conductivity, photosynthetic carbon gain and diameter growth rates of plants (Poorter *et al.*, 2008). High wood density implies thin and short xylem vessels with small pit-pores, which decrease the risk of embolism and cavitation. Trees with high wood density are then expected to be less sensi-

TABLE 4.3 – **Functional variability of responses to climate variables for growth (top) and mortality (bottom)**. The functional variability is included in the model with an interaction term, *i.e.*, multiplying a climatic variable with a given tree feature. Most hypotheses were not verified, but two significant effects are highlighted (*) : large trees reduce their growth more during dry years, and trees with high wood density reduce their growth less during dry years.

Climatic variable	Tree feature	Expected effect	Reference
Growth			
A_{under}	DBH	Big trees reduce their growth more during drought*	Condit <i>et al.</i> (2004)
A_{under}	DBH_{max} -DBH	Small trees reduce their growth more during drought	Hanson <i>et al.</i> (2001)
A_{under}	WD _{max} -WD	Trees with high wood density reduce their growth less during drought*	Markestijn (2010)
Mortality			
A_{under}	DBH	Big trees have a higher probability of dying during drought	Nepstad <i>et al.</i> (2007)
A_{under}	DBH_{max} -DBH	Small trees have higher probability of dying during drought	Hanson <i>et al.</i> (2001)
A_{under}	WD _{max} -WD	Trees with high wood density better resist drought	Phillips <i>et al.</i> (2009)
Pre	DBH	Big trees have higher probability of falling during high precipitation	Ferry <i>et al.</i> (2010)

tive to drought. The term A_{under} multiplied by $WD_{max} - WD$ accounts for the effect of drought on trees with low wood density. This term is added in growth and mortality to test this effect (see Table 4.3).

4 Results

4.1 Variable selection

The variable selection was realised using the literature, the PCA results, and the results of the univariate analysis.

4.1.1 PCA

The PCA underlines one principal axis, explaining 48% of the inertia and strongly negatively correlating with variables Tmp and Pet . The variables Wet and Cld are positively correlated with this axis, while Vap , A_{under} and Nb_{under} are negatively correlated with this axis (see Figure 4.1). The second axis is strongly negatively correlated with Pre and $Area_{over}$. The third axis is essentially negatively correlated with A_{under} .

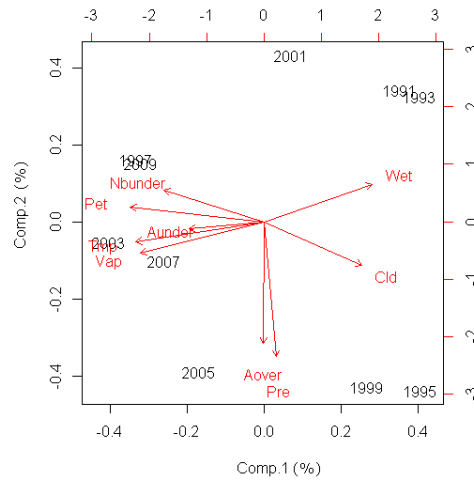


FIGURE 4.1 – **Results of the principal component analysis performed on climatic variables.** The first axis (46% of variance) is mainly driven by the variables Pet (potential evapo-transpiration) and tmp (temperature). The second axis (20% of variance) is mainly driven by A_{over} (area over REW and <0.4) and Pre (precipitation) and may be interpreted as an axis representing the excess of water. The third axis (not represented here, 13% of variance), is mainly driven by A_{under} (area under REW and >0.95), which is an indicator of water stress.

4.1.2 Univariate analyses

When the climate variables are included one by one in each model, all variables but precipitation (*Pre*) had an effect in the growth process, while only few had an effect in the mortality process (see Table 4.4). The climate variables associated with the mortality process are *Pre*, $N_{b_{under}}$ and A_{under} . In the growth model, A_{under} is the best predictor according to the likelihood. In the mortality process, the best value of likelihood is obtained when N_{under} is included.

TABLE 4.4 – **Results of the estimation process for each parameter associated with the climate variables.** The variables were added in the growth process or in the mortality process in an univariate way, *i.e.*, one by one, and all parameters were estimated using a Metropolis-Hastings algorithm. Only significant results are represented.

Variable	Growth		Mortality	
	Estimator	95% credibility interval	Estimator	95% credibility interval
<i>Cld</i>	0.027	[0.025 ; 0.029]	-	-
<i>Pet</i>	-0.033	[-0.035 ; -0.031]	-	-
<i>Pre</i>	-	-	0.00035	[0.00022 ; 0.00048]
<i>Tmp</i>	-0.17	[-0.25 ; -0.06]	-	-
<i>Vap</i>	-0.0048	[-0.0052 ; -0.0043]	-	-
<i>Wet</i>	0.0010	[0.0006 ; 0.0014]	-	-
$N_{b_{under}}$	-0.0017	[-0.0023 ; -0.0011]	-0.0026	[-0.0035 ; -0.0018]
A_{under}	-0.0060	[-0.0076 ; -0.0042]	-0.0075	[-0.0113 ; -0.0039]
A_{over}	-0.013	[-0.015 ; -0.011]	-	-

4.1.3 Variable selection

The *Pet* and temperature are indicators of the energy that the system receives and are expected to play a role in tree growth (Clark *et al.*, 2003; Dong *et al.*, 2012). These variables are strongly correlated together ($r=0.8$) and negatively correlated with the first axis of the PCA (*Pet*, $C=-0.45$ and *Tmp*, $C=-0.44$). This is not surprising, as *Pet* is computed using the temperature (Allen *et al.*, 1998). As these two variables are strongly correlated, we finally included the temperature, which had a better likelihood score than

Pet when it is included in the growth model. Neither *Pet* nor the temperature had an effect if included in the mortality process. The second axis of the PCA is related to water saturation and is correlated with *Pre* (C=-0.68) and *A_{over}* (C=-0.61); only *A_{over}* had an effect when included in the growth process, but the likelihood is the worst score obtained, which is why we did not include this variable in the final model. Concerning mortality, *Pre* had an effect and is thus included in both the final growth and mortality model. The third axis of the PCA is strongly correlated with the drought estimator *A_{under}*, which is the better climate driver of growth regarding the likelihood. *A_{under}* also had an effect on the mortality process, and is finally included in the two processes in the final model.

4.2 Full model inference

The growth trajectory was adjusted by a size-dependent diameter growth model. Parameters linking the maximal growth to the functional traits *WD*, *DBH_{max}*, *H_{max}* and $\delta^{13}C$ have similar values to (Hérault *et al.*, 2011) (see Table 4.5), *i.e.*, maximum growth rates increase with increasing *DBH_{max}*, and decreasing *WD*, *H_{max}* and $\delta^{13}C$. Diameter at maximum growth is attained for $0.794 * DBH_{max}$. The parameters linking the probability of mortality to *H_{max}*, *WD* and *Tough* converged around negative values, meaning that the probability of dying is lower when the tree is high, has a high wood density and/or high laminar toughness. The drought estimator (*A_{under}*) converged to negative values in the growth and mortality processes; thus growth and mortality computed at our biannual time-scale are lower when the drought estimator *A_{under}* is higher. The parameter linking mortality with precipitation (*Pre*) is positive. This finding implies that mortality rate is higher during two-year time-scale with high precipitation. The parameter linking temperature (*tmp*) and growth takes negative values; thus growth values are lower during the warmest periods.

4.3 Functional variability of responses

In the growth process, interaction between $WD_{max} - WD$ and drought is negative (Table 4.3), implying that trees with lower *WD* are more sensitive to drought and reduce their growth more. Moreover, interactions linking the current diameter and drought are also negative; thus larger trees are more sensitive to drought and reduce their growth more compared to smaller trees. None of the interaction terms included in the mortality process had an effect (Table 4.3).

TABLE 4.5 – **Result of the estimation process for the final model.** The Metropolis-Hastings algorithm ran with 2000 iterations, burning of 1000 iterations, thinning of 10 iterations.

Process	Variable	Parameter	Estimator	95% credibility interval
mortality	vigour	θ_1	-0.52	[-0.56 ; -0.49]
	DBH/ $DBHmax$	θ_2	-0.61	[-1.03 ; -0.30]
	$(DBH/DBHmax)^2$	θ_3	0.48	[0.30 ; 0.77]
	$Hmax$	θ_4	-0.40	[-0.44 ; -0.36]
	WD	θ_5	-2.8	[-3.0 ; -2.5]
	$Tough$	θ_6	-0.36	[-0.41 ; -0.30]
	Pre	γ_1	0.00032	[0.00021 ; 0.00044]
	A_{under}	γ_1	-0.0053	[-0.0087 ; -0.0023]
growth	$DBHmax$	θ_7	1.81	[1.78 ; 1.84]
	WD	θ_8	-0.40	[-0.44 ; -0.35]
	$Hmax$	θ_9	-0.063	[-0.070 ; -0.057]
	$\delta^{13}C$	θ_{10}	-0.21	[-0.22 ; -0.20]
	Dopt $DBHmax$	θ_{11}	0.80	[0.76 ; 0.84]
	K WD	θ_{12}	2.36	[2.27 ; 2.44]
	tmp	γ_2	-0.067	[-0.093 ; -0.045]
	A_{under}	γ_2	-0.0049	[-0.0054 ; -0.0044]
	ε	θ_{13}	0.579	[0.576 ; 0.583]

5 Discussion

We highlighted the climate drivers of forest dynamics in the Guianan tropical forest by using a community growth-mortality modeling framework. The Bayesian algorithms used to infer the model and select the best predictors allow us great flexibility. The vigour index is negatively related to mortality, *i.e.*, trees that grow more than expected have a lower probability of dying, and trees with lower-than-expected growth have a higher probability of dying. A limited number of interactions between climate variables and functional traits was tested because of our *a priori* selection of three climate predictors. One can argue that some climatic variables that were disregarded in the first step would increase the likelihood if included in interactions with a functional trait. This pathological case is very improbable (Wagner *et al.*, 2014) and will necessitate an impractical amount of computational time to be tested. One can also note that few climate variables had an effect

when included in the mortality process, while almost all had an effect in the growth process. However, the magnitude of the impact of climate variables is stronger in the mortality process (observed mortality rate varying between 1.6 and 2.5% of mortality/2 years, while observed growth rates vary between 1.9 and 2.5 mm/2 years, Figures 4.2 and 4.3).

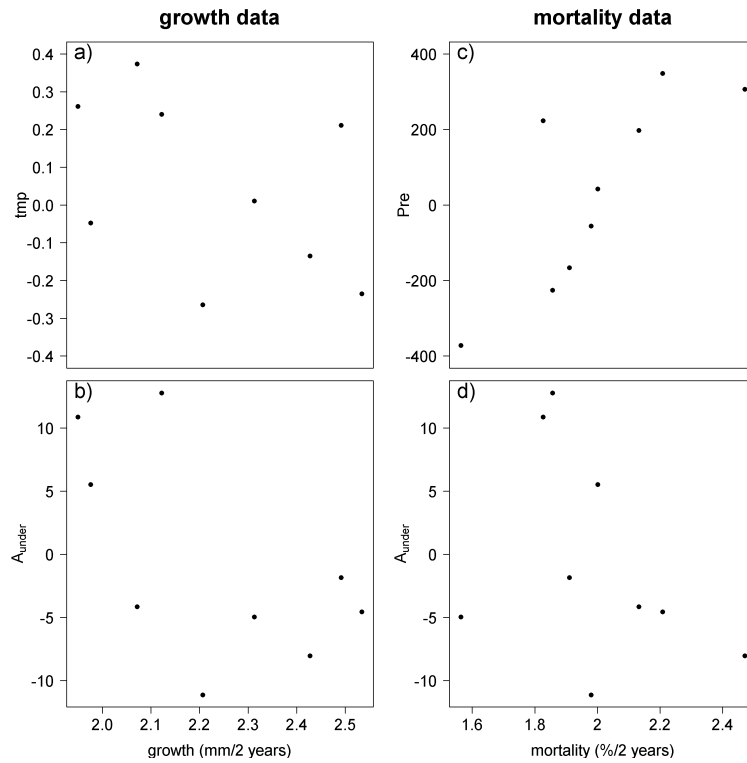


FIGURE 4.2 – **Climatic drivers of tree dynamics.** Observed mean growth (mm / 2 years) is plotted against temperature (a) and against the water stress (b). Observed mortality rate (proportion / 2 years) is plotted in abscissa against precipitation (c) and against the water stress (d).

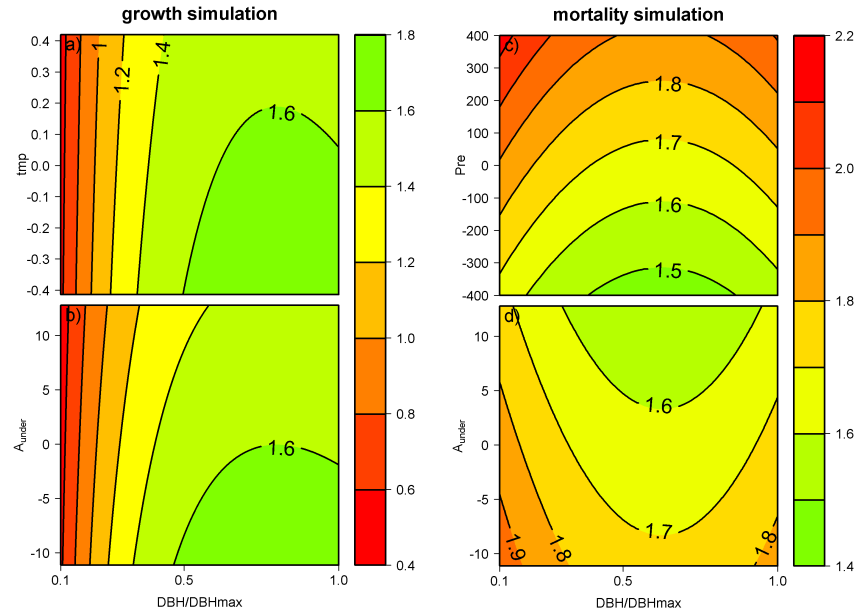


FIGURE 4.3 – **Climatic drivers of tree dynamics.** Simulations are made using median values for tree functional traits. Growth (in mm / 2 years) is computed with varying temperature (a) and with varying water stress (b) and is plotted against the ontogeny (DBH/DBHmax). Growth rises with reduced temperature and reduced water stress. This is more noticeable for large values of DBH/DBHmax, which means for large, old trees. Mortality (% per 2 years) is computed with varying precipitation (c) and with varying water stress (d) and is plotted against the ontogeny (DBH/DBHmax). Mortality rate rises with rising precipitation and reduced water stress. This illustration clearly shows the effects of climate variables and ontogeny on tree growth and mortality, but the median functional traits used do not represent a real ‘mean’ tree. To evaluate more precisely the dynamics for two different species, we plotted the same curves for *Oxandra asbeckii* and *Hevea guianensis* in appendix B.

5.1 Water stress

The water stress during the dry season, estimated with A_{under} , negatively impacts the growth and mortality processes. Trees will thus grow less quickly and have a lower probability of dying during two-year periods with the most intense dry seasons. The reduction of growth is expected, and has many ecophysiological causes. Indeed, water is essential for sap fluxes and for photosynthesis efficiency. The reduction of growth is furthermore linked with the current DBH and the species' wood density (Table 4.3). Big trees are more sensitive to water stress than small trees. This was expected in light of the results obtained after rainfall exclusion (da Costa *et al.*, 2010). Indeed, maintenance costs are higher for big trees, making these trees more vulnerable to the driest periods. Regarding the wood density, species with high values are more resistant to drought. This is consistent with our hypothesis that high wood density implies thin and short xylem vessels and thus decreases the risk of embolism and cavitation. As the ability of trees to recover from periods of sustained drought is strongly related to their embolism resistance (Choat *et al.*, 2012), a tree with high wood density will be more able to maintain growth during dry years. For similar reasons, we expected a positive impact of A_{under} on mortality, as long-time drought may increase mortality rates. Results showed the inverse pattern, but this may be explained by some field observations. After experimental trough-fall exclusions, high mortality rates were observed in Tapajos and Caxiuaña, and our results seemed to be contradictory. The real intensity of the drought during the driest seasons in our dataset is, by far, less stressful than the 50% rainfall exclusion performed during the experiment (Nepstad, 2002). Moreover, our time-scale of two years and our framework prevented us from seeing long-term effects induced by repeated drought events. When plotting tree mode of death against drought estimator (A_{under}), no evidence was observed for a potential trend (Figure 4.4), suggesting that standing death is not more frequent during the driest periods. To conclude, our results confirmed that the relationship between drought and mortality may be challenging to estimate and to link with their underlying causes at an inter-annual time scale.

5.2 Water saturation

Water saturation had a strong effect on mortality; mortality rate varied between 1.5 and 2% per 2-years with increasing total precipitation. This is consistent with the hypothesis that trees are more vulnerable when the soil is saturated. When looking at the cause of tree death, about half of tree

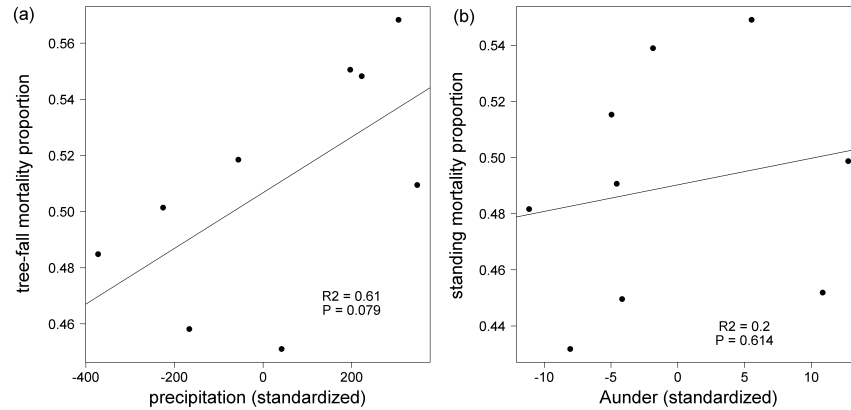


FIGURE 4.4 – **Proportion of dead trees caused by tree-fall plotted against the climate variable Pre (a) and proportion of dead trees caused by standing death plotted against the climate variable A_{under} (b).** About 50% of tree deaths are tree-fall; this proportion is higher during 2-yr periods with high precipitation. No significant correlation between the mode of death and the drought intensity A_{under} was noted.

deaths are due to standing death and half to tree-fall. This ratio is strongly correlated with precipitation, and when the precipitation increased, the mode of death is mostly tree-fall (Figure 4.4). This confirms the observation of Ferry *et al.* (2010) and the hypothesis that waterlogged soils in space or in time are risky for trees. Moreover, during the rainy season, strong rainfall events often come with strong winds that may accelerate this process (Toledo *et al.*, 2011). Studies observing a relationship between tree mortality and excess of water in the soil primarily focus on geographical variation (Ferry *et al.*, 2010; de Toledo *et al.*, 2012) and conclude that excess water in the soil restricts root establishment because productivity of fine roots and rooting depth are generally low in sandy soils and soils with high moisture content. Our results highlight that the time dimension is also very important and should be reassessed.

5.3 Temperature

Temperature is identified as predictor of trees' decreasing growth. As the temperature rises, the velocity of reacting molecules increases, leading to more rapid reaction rates but also to damage of the tertiary structures of the enzymes and reduced enzyme activity and reaction rates (Fitter and Hay,

2001; Lloyd and Farquhar, 2008). These two processes are responsible for a bell-shaped curve of growth response to temperature (Fitter and Hay, 2001). Temperature can affect photosynthesis through modulation of the rates of activity of photosynthetic enzymes and the electron transport chain, and in a more indirect manner, through leaf-temperatures defining the magnitude of the leaf-to-air vapour pressure difference, a key factor influencing stomatal conductances (Lloyd and Farquhar, 2008). In tropical forests, as temperatures are already high, rising temperatures may imply lower growth, consistent with results from Clark *et al.* (2003). This temperature effect may become the most problematic for forest dynamics, considering the rising temperatures that are predicted, with a great degree of certainty, by climate models for the next century (IPCC, 2013). As no consensus has been reached yet, additional studies using regular inventories are urgently needed (Reed *et al.*, 2012; Corlett, 2011) to explain the conflicting patterns found in the extant literature (Dong *et al.*, 2012).

6 Conclusions

Our study highlights the complex link between the various components of the climate and tropical forest dynamics. Our modelling framework allows us to study inter-annual variations of climatic variables and identify which of these climatic variables are the drivers of tree dynamics in the study site of Paracou, French Guiana. Drought, precipitation and temperature were highlighted as strong drivers of tree growth and/or mortality. Drought is expected to become longer and stronger in the future ; precipitation is expected to be drastically reduced, and the temperature will rise drastically during the next century. Thus, in light of our results, raising awareness of the potential impacts of climate changes on tropical forest dynamics is urgent.

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4.A Total likelihood of the growth-mortality model

Growth and mortality processes were linked through tree vigour and are parametrized simultaneously. If tree i stays alive, it grows at a growth rate $AGR_{i,s,t}$, and its diameter $D_{i,t-1}$ becomes $D_{i,t}$. The joint model likelihood is then

- $\prod_{t=1}^n f(D_{i,t}|D_{i,t-1}) * (1 - p_{i,s,t})$ if tree i stays alive during the length of the studied period,
- $p_{i,s,k} * \prod_{t=1}^{k-1} (f(D_{i,t}|D_{i,t-1}) * (1 - p_{i,s,t}))$ if tree i dies between time $k-1$ and time k ,

where

- $f(D_{i,t}|D_{i,t-1})$ is the probability density for a tree with diameter $D_{i,t-1}$ at time $t-1$ to have a diameter $D_{i,t}$ at time t ; this quantity is used to compute the vigour estimator.
- $p_{i,s,t}$ is the probability of dying between time $t-1$ and time t , which depends on the vigour estimator, added in the model by multiplying the vigour estimator by β_0 .

The model computes a mortality probability $p_{i,s,t}$ and a predicted growth rate $\widehat{AGR}_{i,s,t}$.

4.B Growth and mortality simulations for *Oxandra* and *Hevea*

Simulations presented in Figure 4.3 are realized using median values for tree functional traits. These median values do not have any ecological meaning, and the figure was realized only to show how climatic drivers impact the tree growth and mortality in reality (Figure 4.2) and in our model (Figure 4.3). To show more realistic simulations, the same patterns are plotted for two species that differ in their ecological strategies in Figure 4.5. The first column shows the simulated dynamics of *Oxandra asbeckii*, a relatively small tree. The second column shows the simulated dynamics of *Hevea guianensis*, which is a canopy tree reaching heights of 50 meters and which has a low wood density. These two strongly contrasting species show two different growth and mortality rates, although the effects of climatic drivers stay the same.

4.B. GROWTH AND MORTALITY SIMULATIONS FOR *OXANDRA* AN *HEVEA*

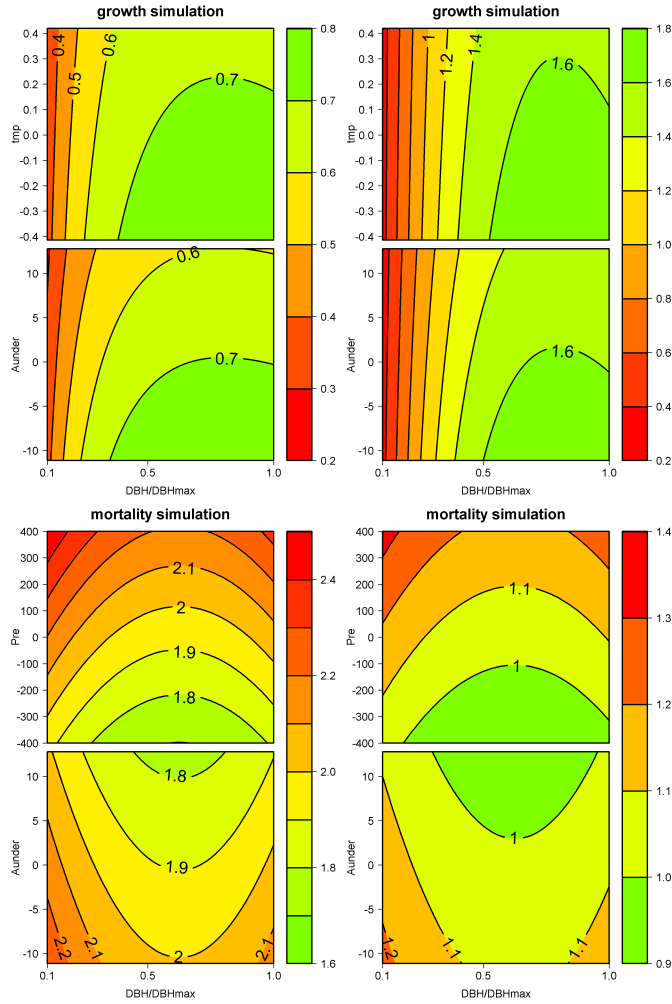


FIGURE 4.5 – Predictions of growth and mortality depending of climatic drivers for *Oxandra asbeckii* and *Hevea guianensis*. Simulations are made using the functional traits values of the species *Oxandra asbeckii* (left) and *Hevea guianensis* (right). Growth (in mm / 2 years) is computed with varying temperature (first line) and with varying water stress (second line), and is plotted against the ontogeny (DBH/DBHmax). Growth rises with reduced temperature and reduced water stress. This is more noticeable for large values of DBH/DBHmax, which means large, old trees. Mortality (% per 2 years) is computed with varying precipitation (third line) and with varying water stress (fourth line) and is plotted against the ontogeny (DBH/DBHmax). Mortality rate rises with rising precipitation and reduced water stress.

CHAPITRE 5

WILL TROPICAL FORESTS FACE SLOW DOWN WITH ONGOING CLIMATE CHANGES ?

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Un modèle de croissance et de mortalité climat-dépendant a été construit pour la forêt tropicale de Paracou, et les dernières prédictions climatiques du GIEC pour le siècle prochain sont disponibles. Il ne reste donc plus qu'un pas à faire pour simuler la dynamique de la forêt tropicale de Paracou soumise aux changements climatiques prévus. C'est ce que je propose de faire dans ce dernier chapitre grâce au simulateur SELVA. La communauté d'arbre est simulée et à chaque pas de temps, le recrutement, la croissance et la mortalité sont modélisés. En utilisant des scénarios climatiques basés sur les prédictions du dernier rapport du GIEC, nous observons une diminution de la croissance et de la mortalité, accompagnées par une diminution de la surface terrière, du diamètre quadratique et de la biomasse de notre communauté. Ces simulations, loin de prédire l'avenir, montrent comment la température peut impacter les processus, et donnent des pistes de réflexions pour mieux envisager la réponse des forêts tropicales aux changements climatiques.

1 Abstract

- Climate changes are expected to continue all over the world. Below the tropics, temperatures are expected to rise and dry periods to be stronger and longer. As some climate variables were identified as key drivers of tropical forest dynamics, the later will likely be deeply impacted.
- To provide some elements of response, we submitted a simulated tropical forest community to the climate changes expected over the next century. We used SELVA, an individual-based model calibrated with forest dynamic data from the Paracou study site in French Guiana to simulate the forest trajectory over the next 100 years. The model is climate dependent, such that temperature, precipitation and water stress are used as predictors of growth and/or mortality rates.
- We ran simulations for the next century using predictions of the IPCC 5AR, building three different scenarios corresponding to three relative concentration pathways. The basal area, above-ground fresh biomass, quadratic diameter, tree growth and mortality rates were then computed to characterize the resulting forest.
- All processes and resulting structure variables exhibited decreasing values as the scenario became pessimistic. A sensitivity analysis identified temperature as the stronger climate driver of this behaviour, highlighting a temperature-driven drop of 40% in average forest growth and a precipitation-driven drop of 30% in mortality rates for the RCP8.5 scenario.
- This conclusion is alarming, as temperature rises were predicted by all climate scenarios of the IPCC 5AR. Our study highlights the potential slow-down danger that tropical forests will face during the next century.

2 Introduction

In the context of climate changes, more and more efforts are being made to describe the climatic drivers of tropical forest dynamics. The identification of these drivers is essential to model and predict the implications for the forest dynamics. Water and temperature are currently the two principal drivers of interest.

Water comes in a variety of indexes, (i) water availability for trees most appropriate to estimate drought (Wagner *et al.*, 2011; Malhi *et al.*, 2009) or

(ii) total precipitation, *i.e.* the total amount of water annually entering the system (Condit *et al.*, 2004). The consensus among researchers is that the greatest effect of drought on tropical tree dynamics is a rise in tree mortality, especially among big trees (Phillips *et al.*, 2009; Choat *et al.*, 2012; Allen *et al.*, 2010). The experimental throughfall exclusion in Brazil (Nepstad *et al.*, 2007; Brando *et al.*, 2008; da Costa *et al.*, 2010), and the observed effects of the drought of 2005 and 2010 (Phillips *et al.*, 2009; Lewis *et al.*, 2011), were considerably useful to address this issue. The convergence on a risky hydraulic strategy exhibited by many species over the world can be understood as the result of a trade-off that balances growth with protection against risk of mortality (Choat *et al.*, 2012). Total precipitations are typically used to characterise wet and dry study sites. Wet sites are characterised by higher tree growth and higher mortality (Condit *et al.*, 2004).

There is no consensus about the effect of temperature on forest dynamics (Dong *et al.*, 2012). For instance, results arising from the Amazon-based RAINFOR network of plots suggested that increasing temperature may be an underlying cause of accelerating forest dynamics and increasing turnover (Baker *et al.*, 2004; Lewis *et al.*, 2004), while at La Selva, Costa Rica, a negative correlation between the annual diameter growth rate of trees and the annual mean of daily minimum temperature was found (Clark *et al.*, 2003). These apparently conflicting results may be explained by the independent effects of variability in solar radiation and daily minimum temperature on tree growth (Dong *et al.*, 2012).

Understanding the effects of temperature on tree dynamics is of particular interest regarding the predictions of the last intergovernmental panel on climate change (IPCC) report. Indeed, rising temperatures are consensually predicted by all models used for the fifth assessment report (5AR) and all over the world. For the business-as-usual scenarios (representative concentration pathway 8.5, RCP8.5), temperature is expected to gain between 2.6 and 4.8 °C on the earth during the next century (IPCC, 2013). On the contrary, drought evolutions, which have had a consensual effect on tree dynamics, are not as marked as temperature evolutions because there is little agreement on the evolution of the dry season. Fu *et al.* (2013) assumed that the variability of the dry season length and its controlling processes are underestimated in the models used by the IPCC 5AR. Nevertheless, an increase of two weeks for the dry season is highlighted by Joetzjer *et al.* (2013) for the RCP8.5; whereas the IPCC 5AR forecasts an increase in the strength of climate variability due to El Niño events. We clearly lack the scaling up tools needed to use the observed predicted changes on a finer scale and apply it to larger areas.

To gain better understanding of how climate changes may affect forest dynamics in the long-term, climate predictions must be combined with dynamics models, and then used as basic dynamic processes in forest simulators. Climate-driven processes observed at the tree scale are not directly transposable at the community level because of factors such as compensatory effects between demographic processes (growth, mortality) (Chao *et al.*, 2008) or non-linear response with ontogeny (Hérault *et al.*, 2011; Lasky *et al.*, 2013). We must therefore simulate forest dynamics under climate changes to go beyond the analytical studies of our current statistical models. As tropical forest communities are highly diverse, functional traits may be useful tools to take this diversity into account and to identify the underlying ecophysiological processes of tree dynamics (McMahon *et al.*, 2011).

In this study, we built climatic scenarios based on the predictions of the IPCC AR5 (IPCC, 2013). These scenarios were then used in a forest dynamics simulator to investigate the evolution of a tropical tree community over the next century. Some output variables were then calculated, and a sensitivity analysis was realized to identify the key climate drivers.

3 Materials and methods

3.1 Data

To initialize the tree population, we used the tree inventories of the experimental site of Paracou, French Guiana, censused in 2001. The experimental site of Paracou (5°18'N,52°55'W) is a lowland tropical forest near Sinnamary, French Guiana. The forest is a typical Guiana shield forest, with dominant tree families including *Fabaceae*, *Chrysobalanaceae*, *Lecythidaceae*, and *Sapotaceae*. There are more than 500 woody species attaining 10 cm diameter at breast height (DBH) at the site. Six unlogged plots of 6.25 hectares with 22,401 censused trees were used to constitute the initial population in the forest simulator.

Functional traits associated with these trees were needed to run the growth-mortality model. These five traits are summarized in Table 5.1 and were extracted from a large database (Baraloto2010ab).

3.2 Climate change scenarios

Building on the forest dynamic joint model of chapter 4, three climate variables were needed to run the growth-mortality model (Table 5.2) : a water stress estimator (A_{under}), the annual precipitation (Pre) and the daily mean

TABLE 5.1 – **The five functional traits used in the growth-mortality model.** Description, name used in this study and range observed in our data set.

Functional traits	Variable name	Range
Maximum diameter (m)	<i>DBHmax</i>	[0.13 ;1.11]
Maximum height (dm)	<i>Hmax</i>	[0.8 ;5.6]
Trunk xylem density (g.cm ⁻³)	<i>WD</i>	[0.28 ;0.91]
Laminar toughness (N)	<i>Tough</i>	[0.22 ;11.4]
Foliar $\delta^{13}C$ composition (‰)	<i>$\delta^{13}C$</i>	[-3.61 ; -2.62]

temperature (*tmp*). Four climate scenarios were investigated. The first scenario, named A, is equivalent to the RCP2.6, the second, named B, is an intermediary scenario, the third, named C, is equivalent to the RCP8.5, and the fourth scenario, named BASE, is a reference scenario built using the current values of the selected climatic variables.

The predicted temperatures and rain of the IPCC report (IPCC, 2013) for the next century were used to create the *Pre* and *tmp* trajectories. To compute the water stress estimator A_{under} , a linear regression was used to link A_{under} with the length of the dry season in days. Estimated change of the dry season length is plus two weeks for the RCP8.5 (Joetzjer *et al.*, 2013), corresponding to our precipitation scenario C, while no consensual change was observed for the RCP2.6. This 2-week increase is equivalent to an increase of 5.6 units of the water stress estimator A_{under} for the trajectory C, and no change for A (Table 5.2).

At each time step, climate variables were sampled in a normal distribution with standard deviation currently observed in the field, and the mean changing over time for each scenario. Reference values of the mean and variance for each climate variable were computed for climatic variable values between 1991 and 2011 using climatic data from the Climatic Research Unit (CRU) at the University of East Anglia (Mitchell and Jones, 2005).

$$clim_{\Delta t,s} \sim \mathcal{N}(clim_0 + \Delta t \times \delta_{clim,s}, \sigma_{clim}^2),$$

where $clim_{\Delta t,s}$ is the value of the climatic variable at time 2001 + Δt for the scenario s ; $clim_0$ is the reference mean value for climatic variable $clim$; $\delta_{clim,s}$ is the increment of climatic variable $clim$ for the scenario s computed

hypothesising a linear increase with time to reach the predicted values in 2101; and σ_{clim}^2 is the variance of climatic variable *clim*.

For instance, to compute the water stress estimator A_{under} in year 2100 and for scenario C, we used :

$$A_{under,2100,C} \sim \mathcal{N}(A_{under,0} + 100 \times \delta_{A_{under,C}}, \sigma_{A_{under}}^2)$$

TABLE 5.2 – **The climate variables included in the growth-mortality model.** The variables are : the area over the REW curve and under the threshold of 0.4 (A_{under}), the precipitation (Pre) and the daily mean temperature (Tmp). For this three variables, standard deviation (σ) observed in the actual (1991-2011) data set, actual mean value, predicted values for 2101 in the three scenarios (μ) and associated annual increment δ . REW is the relative extractable water index, computed with the model developed in (Wagner *et al.*, 2011).

Variable	σ	BASE	A		B		C	
			μ	δ	μ	δ	μ	δ
A_{under}	8.1	20.2	20.2	0	22.9	0.0275	25.6	0.050
Pre (mm/2 years)	261.4	5858.6	5565.6	-2.99	5272.7	-5.98	4979.8	-8.97
Tmp (°C)	0.26	26.5	27.8	0.013	29.4	0.029	31	0.046

3.3 Simulator

The simulator SELVA (Gourlet-Fleury, 1999) is an individual-based forest simulator set-up on the CAPSIS 4.0 Java platform (de Coligny *et al.*, 2003). In the simulator, individual growth, mortality and recruitment are described by sub-models on a two-year time step. Each tree i is described with the diameter at breast height (DBH_i), the species (s) and a set of functional traits associated with each species.

The model used in this study was developed in chapter 4 and consists in a joined growth-mortality model for the whole community. A vigour index was added to the mortality process, taking the past growth into account.

$$\begin{aligned}
 p_{i,s,t} = & \text{logit}^{-1} \left(\theta_1 \times A_{under,t} + \theta_2 \times Pre_t + \theta_3 \times Vigour_{i,s,t} \right. \\
 & + \theta_4 \times \frac{DBH_{i,s,t-1}}{DBHmax_s} + \theta_5 \times \left(\frac{DBH_{i,s,t-1}}{DBHmax_s} \right)^2 \\
 & \left. + \theta_6 \times Hmax_s + \theta_7 \times WD_s + \theta_8 \times Tough_s \right)
 \end{aligned}$$

and

$$\begin{aligned}
 \log(\widehat{AGR}_{i,s,t-1} + 1) = & (\theta_9 \times tmp_{t-1} + \theta_{10} \times A_{under,t-1} \\
 & + \theta_{11} \times A_{under,t-1} \times (WD_{max} - WD_s) \\
 & + \theta_{12} \times A_{under,t-1} \times DBH_{i,t-2} + \theta_{13} \times DBHmax_s \\
 & + \theta_{14} \times WD_s + \theta_{15} \times Hmax_s + \theta_{16} \times \delta 13C_s) \\
 & \times \exp \left(-\frac{1}{2} \left(\frac{\log \left(\frac{DBH_{i,t-2}}{\theta_{17} \times DBHmax_s} \right)}{\theta_{18} \times WD_s} \right)^2 \right),
 \end{aligned}$$

and

$$\log(AGR_{i,s,t-1} + 1) = \log(\widehat{AGR}_{i,s,t-1} + 1) + \varepsilon_i$$

with $\varepsilon_i = \alpha_i + \beta$,

and $\alpha_i \sim \mathcal{N}(0, \theta_{19})$, and $\beta \sim \mathcal{N}(0, \theta_{20})$,

where $p_{i,s,t}$ is the probability of the death of tree i of species s between time $t - 1$ and t ; $Vigour_{i,s,t}$ is the vigour estimator for tree i of species s between time $t - 1$ and t ; and $\widehat{AGR}_{i,s,t-1}$ is the predicted growth between time $t - 2$ and time $t - 1$. $AGR_{i,s,t-1}$ is the observed growth between time $t - 2$ and time $t - 1$; $DBHmax_s$, $Hmax_s$, $Ortho_s$, WD_s , $Tough_s$ and $\delta 13C_s$ are functional traits of species s to which tree i belongs (Table 5.1). $\theta_1, \theta_2, \dots, \theta_{18}$ are parameters sampled in normal distributions, with the mean and standard deviation computed using the MCMC method developed in chapter 4 and detailed in Appendix 5.A (see Table 5.4). $A_{under,t}$, tmp_t and Pre_t are the climatic variables computed between times $t - 2$ and $t - 1$ (see chapter 4). $A_{under,t-1} \times (WD_{max} - WD_s)$ is an interaction term to account for the sensitivity of a tree with low wood density to water stress; and $A_{under,t-1} \times DBH_{i,t-2}$ is an interaction term to account for the sensitivity of a big tree to water stress. α_i is an individual effect sampled in a normal law centred on 0, and β is a residual error sampled in a normal law centred on 0.

3.4 The vigour term

Two hypotheses can be made on the estimation of the vigour : $Vigour_{i,s,t}$. The first hypothesis assumes that the vigour estimator is not impacted by climatic variables that affect the growth, whereas the second hypothesis assumes that climatic variables that impact the community growth also affect the vigour and, consequently, the mortality. Two versions of the model corresponding to these two hypotheses were used in our study. In the model version 1, the vigour estimator is computed as the error of the growth model, $Vigour_{i,s,t} = \log\left(\frac{AGR + 1}{\widehat{AGR} + 1}\right) = \log(AGR + 1) - \log(\widehat{AGR} + 1)$. In the model version 2, an alternative definition of the vigour is used. The vigour estimator is computed as the error of a growth model that does not take climate predictors into account and therefore becomes : $AltVig_{i,s,t} = \log(AGR + 1) - \left(\log(\widehat{AGR} + 1) - (\theta_9 \times Pre_{t-1} + \theta_{10} \times A_{under,t-1} + \theta_{11} \times A_{under,t-1} \times (WD_{max} - WD_s) + \theta_{12} \times A_{under,t-1} \times DBH_{i,t-1})\right)$. If a tree's growth is negatively impacted by climate drivers, this will impact the vigour in the same way. This hypothesis implies that a climate predictor that reduces growth automatically increases mortality.

The vigour estimator $Vigour_{i,s,t}$ is of particular interest for simulations. Indeed, this vigour may be described as an individual effect of genetics or a microsite effect, for instance, but it may also be described as a temporal effect of more or less favourable years. On the other hand, vigour may be described as an additional error, independently sampled at each time step, and the result of multiple environmental causes, for instance. To take these two effects into account, the computed term of error ε_i was modelled by a mixed model with an individual effect, a time effect and a residual error. The total variance of the vigour estimator was mostly due to the individual effect (42%), whereas no time effect was observed (0.005% of variance). The residual error accounted for more than one half of the variance (57%). To apply these results in the simulator, when a tree was recruited, an individual error was sampled and did not change during the life of the tree (α_i). The additional error (β) was sampled at each time step and added to the individual error to compute the vigour estimator (parameters detailed in Appendix 5.B). The recruitment sub-model is neutral, based on the assumption that each dead tree is replaced by a new recruited tree with DBH 10 cm, respecting the proportion of each species in the total community.

3.5 Outputs

To study the evolution of the community in SELVA, we built outputs of interest at year 2101 (Table 5.3). Some of these outputs were used to characterise the community structure, which is the basal area per hectare, the quadratic diameter and the above-ground fresh biomass (AGFB). As only the DBH was available for each tree, AGFB was computed using an allometry model to first compute tree height, followed by an AGFB model, both detailed in Molto *et al.* (2013, 2014). Other computed outputs related to forest dynamics were the average growth and mortality rates.

3.6 Sensitivity analysis

A sensitivity analysis was conducted using a complete factorial design. Three scenarios were created with three climate variables; thus, the complete factorial design include 27 scenarios. After considering the evolution of the standard deviation evolution of each output during 100 iterations, we decided to run each scenarios 50 times because the standard deviations stabilized after about 40 repetitions. We ran the 27 scenarios 50 times and computed the first-order sensitivity index of Sobol (Sobol, 1990) :

$$S_i = \frac{V[E(Y_j|X_i)]}{V(Y_j)},$$

X_i is an input variable from the vector $X = (A_{under}, Pre, TMP)$, and Y_j is an output variable from the vector $Y = (BA, morta, growth, AGFB, DG)$.

4 Results

4.1 Climate change scenarios

Means and standard deviations of outputs for the reference scenario BASE, the optimist scenario A, the intermediary scenario B and the business-as-usual scenario C, realized with the model version 1, are presented in Table 5.3. The two forest dynamic processes decreased as the scenario became pessimistic (most pessimistic scenario is C), with the community mortality rate falling from 2 to 1.4%.2 years⁻¹ and a community growth rate going from 0.25 to 0.16 mm per 2 years for the C business-as-usual scenario.

Evolutions of growth and mortality during the simulations are plotted in Figure 4.1. The reduction in growth is almost the same for models 1 and 2, and is progressive between 2001 and 2100. The reduction in mortality is

much clearer for model 1 than for 2, with a minimum for scenario C observed at $1.4\% \cdot 2 \text{ years}^{-1}$ for model 1 (also in table 5.3) and a minimum of $1.7\% \cdot 2 \text{ years}^{-1}$ for model 2.

TABLE 5.3 – **Outputs of the simulator for model version 1.** Basal area, mortality rate, average growth rate, above ground fresh biomass and quadratic diameter : abbreviation used in the paper, units and values. Values are presented at the beginning of the simulation (2001) and mean values are presented at the end of the simulation (2101) for the four scenarios : BASE, A, B and C, with the standard deviations.

name	units	2001	BASE	A	B	C
<i>BA</i>	$\text{m}^2 \cdot \text{ha}^{-1}$	30.4	30.7 ± 0.27	30.6 ± 0.27	30.4 ± 0.25	30.1 ± 0.26
<i>morta</i>	$\% \cdot 2 \text{ years}^{-1}$	2.1	2 ± 0.04	1.8 ± 0.03	1.6 ± 0.04	1.4 ± 0.03
<i>growth</i>	$\text{mm} \cdot 2 \text{ years}^{-1}$	0.26	0.25 ± 0.002	0.22 ± 0.002	0.19 ± 0.002	0.16 ± 0.001
<i>AGFB</i>	$\text{t} \cdot \text{ha}^{-1}$	436	456 ± 6.3	455 ± 5.4	450 ± 4.7	444 ± 5.1
<i>DG</i>	cm	25.1	25.6 ± 0.1	25.5 ± 0.1	25.5 ± 0.1	25.3 ± 0.1

4.2 Sensitivity analysis

The results of models 1 and 2 are similar (see Figure 4.2). Growth varied mainly because of temperature, whereas mortality varied because of precipitation. Resulting processes DG, AGFB and basal area were mostly impacted by temperature (on average 67% of variance) and less by precipitation (between 29 and 31% of variance) (see Figure 4.2). Almost no effect of the drought estimator A_{under} was observed (0.7 % of variance, see Figure 4.2).

5 Discussion

Our methodology allowed us to run simulations of tropical forest dynamics for the next century and to highlight the strong impact of temperature warming on forest dynamics. Temperature was identified as a strong predictor of growth (chapter 4), and temperature is expected to increase in the next century ; therefore average community growth may consequently decrease. The greater the temperature rise, the slower the community grows, resulting in a 40% decrease for the business-as-usual scenario C. The two models differed in the ways that vigour was constructed. In model 1, the reduction of growth due to higher temperature did not influence the mortality rate,

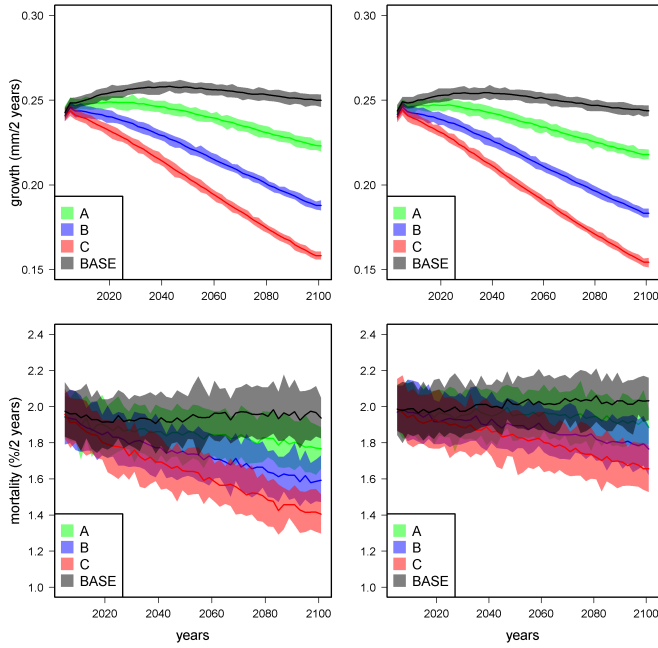


FIGURE 5.1 – **Growth and mortality evolution for four climate scenarios and the two forest dynamic models.** Growth rates (**a** and **c**) and mortality rates (**b** and **d**) for model 1 on the left (**a** and **b**) and model 2 on the right (**c** and **d**). In model 1, we assumed that the vigour estimator is not impacted by climatic variables that impact the growth, whereas in model 2, we assumed that climatic variables that impact the community growth also impact the vigour and, consequently, the mortality. If climate variables stay in a stable state, no major change is noted (BASE scenario : dark). The idealized A scenario, corresponding to the RCP2.6 of the CMIP5, showed reductions in growth and mortality (green), stronger effect for the intermediate scenario B (blue), and even stronger for the business-as-usual scenario C corresponding to RCP8.5 (red). Models 1 and 2 differed in mortality rates ; as growth reduction occurred, the mortality rate in model 2 (**d**) had a less pronounced decrease due to the lower vigour implied by low growth.

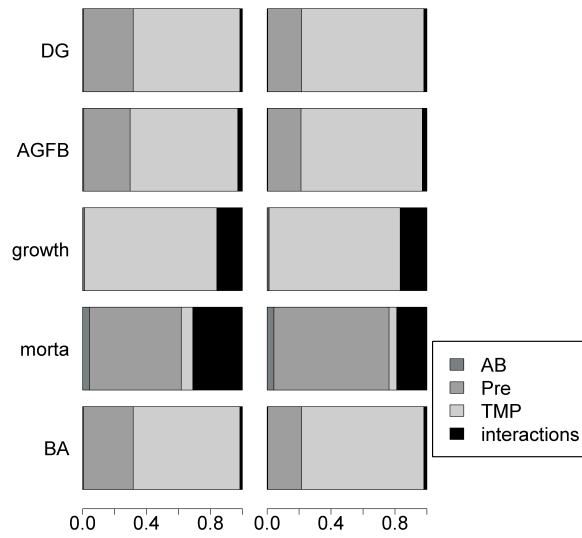


FIGURE 5.2 – **Results of the sensitivity analysis.** Mean of the 50 Sobol indexes computed for each input and output variable. Results of model 1 are on the left and model 2 on the right. Almost all outputs are primarily impacted by the temperature changes. Only the mortality is strongly impacted by the precipitation changes.

leading to decreasing mortality rates due to rain diminution. In model 2, the reduction of growth due to higher temperature induced a reduction of vigour and impacted mortality, leading to a less marked decrease in mortality rates than in model 1. These two hypothetical forest dynamic behaviours imply two divergent approaches to mortality and vigour. Model 1 is better adapted to simulate the actual dynamics observed in our study site in French Guiana, as no evident relation was found between factors such as temperature and mortality in chapter 4. Thus, the rise in temperature impacts the growth but not the mortality process. This implies a weak vigour-mediated relationship between growth and mortality. If all trees decrease their growth under climate pressures, mortality rates would not be impacted. On the contrary, model 2 assumed that climate variables that impact the growth process also impact the mortality process indirectly. Indeed, the vigour estimator will be lower due to a decrease in growth, the mortality will rise as a consequence. This implies that the mortality of the community will change drastically if growth does, and that over-mortality may be observed due to climate-induced loss of growth. Such a strong link between growth and mortality is already well documented (Chao *et al.*, 2008), and past growth is often used as a predictor of mortality (e.g. Rüger *et al.* (2011)). During experimental throughfall exclusion in Brazil, a decrease in growth was observed (Nepstad, 2002), followed by an increase in mortality rates (Nepstad *et al.*, 2007). These experimental results are more consistent with model 2 and underlined the probable links between growth and mortality after environmental stress. We ignore how forest dynamics will behave in the next century under the climate pressures that will be different from those observed, because the hypotheses we used to build our models will probably be wrong. The reality will probably fall between models 1 and 2, but these two models are useful to explore the possible futures and to measure the impacts of the different hypotheses we put forward to construct our simulations.

The sensitivity analysis points out two climate drivers. Temperature rise is by far the strongest driver of almost all output variability. Precipitation variability primarily influence the mortality rates. However, these results must be considered with caution because the range of variation of climatic variables depends on the IPCC 5AR predictions. The relative changes in temperature values in the three climate scenarios are higher than the relative changes for precipitation and water stress, which is one cause for the results observed in Figure 4.2. Even so, our results underlined the important role of temperature rises in community dynamics and structure. In our simulations, growth is the most impacted process, and this slowing-down dynamic implies a slight reduction in above-ground fresh biomass, quadratic diameter

and basal area. If, as highlighted by the results from model 2, a higher mortality follows the growth reduction, the population will change significantly with few large old trees and more small trees. This community change will impact the basal area (from $30.1\text{m}^2\cdot\text{ha}^{-1}$ for scenario C with model 1 to $26\text{m}^2\cdot\text{ha}^{-1}$ for scenario C with model 2) and the above-ground fresh biomass (from $444\text{t}\cdot\text{ha}^{-1}$ for scenario C with model 1 to $369\text{t}\cdot\text{ha}^{-1}$ for scenario C with model 2). Temperature is expected to rise of 4.5°C during the next century in French Guiana. Higher temperature can drastically affect photosynthesis by causing irreversible damage to leaves (Doughty, 2011) and, currently, no forests in the world exist in areas with mean temperatures of 31°C . Concerning precipitation, a noticeable reduction in mortality appeared in our simulations. This is due to the predicted reduction of precipitations. In the model developed in chapter 4, the stronger driver of mortality is precipitation, which positively impacts mortality rates. This is partly due to the increase in falling trees during the most rainy years (see chapter 4), because trees are more vulnerable when the soil is saturated (Ferry *et al.*, 2010). Consequently, the decrease of precipitation predicted for the next century implies consequently a decrease in mortality rates in the simulated communities. But the IPCC AR5 also forecasts an intensification of abundant rain events in the tropics (IPCC, 2013), that may play the inverse role, increasing the mortality. The problem is that such events are not currently well quantified, and relations between mortality and extreme events are complex to model. In addition to the variability observed between models 1 and 2, this makes mortality a crucial process that is difficult to model as properly as is growth.

There are no studies simulating the future of forest dynamics under climate changes with which to compare our results. This kind of combined approach may help us identify potential consensual risks for the tropical forests for the next century. If, as expected by Fu *et al.* (2013), the dry season length is underestimated in the models used by the IPCC, one more challenge for the future will be quantifying this underestimation, which could add uncertainty to the inputs of forest simulators. Global models that take uncertainties into account will be inestimable tools to identify gaps in our knowledges and to point out useful studies in the future.

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5.A Adaptation of the joined growth-mortality model to simulator SELVA

Each individual error ε_i is modelled by a mixed model with an individual effect α_i and a time effect γ_t :

$$\varepsilon_{i,t} \sim \mathcal{N}(\alpha_i + \gamma_t, \beta),$$

where $\alpha_i \sim \mathcal{N}(0, \theta_\alpha)$ and $\gamma_t \sim \mathcal{N}(0, \theta_\gamma)$

With this model, the parameter α_i accounts for 42% of the variance, the estimator γ for 0.005% and the residual effect accounts for the remaining 57%. This is why, in the final model, the growth model takes only the individual effect α_i into account.

What is more, trees with DBH higher than the maximum DBH observed for the species multiplied by 1.2 have a probability of dying equal to 1 to avoid trees reaching unrealistic DBH in the simulator.

5.B Parameters of the simulator SELVA

TABLE 5.4 – **Parameters used in the simulator.** Each parameter is sampled at each time step in a normal distribution with mean and standard deviation computed in chapter 4. θ_{19} and θ_{20} are the standard deviation used to compute the individual effect and the residual error of the growth model.

parameter	mean	standard deviation
θ_1	- 0.0062	0.002
θ_2	0.00032	0.000074
θ_3	- 0.53	0.024
θ_4	- 0.6	0.21
θ_5	0.48	0.13
θ_6	- 0.4	0.022
θ_7	- 2.8	0.15
θ_8	- 0.36	0.031
θ_9	- 0.076	0.011
θ_{10}	- 0.0056	0.002
θ_{11}	0.0066	0.0027
θ_{12}	- 0.00016	0.000021
θ_{13}	1.8	0.018
θ_{14}	- 0.37	0.033
θ_{15}	- 0.062	0.0039
θ_{16}	- 0.2	0.0078
θ_{17}	0.79	0.022
θ_{18}	2.35	0.052
θ_{19}	0.58	-
θ_{20}	0.5	-

DISCUSSION ET PERSPECTIVES : QUELLES ÉCHELLES POUR RÉPONDRE À QUELLES QUESTIONS ?

1 De la photosynthèse aux changements climatiques

1.1 Du minuscule au gigantesque

La photosynthèse s'effectue au niveau des feuilles de l'arbre, et implique des photons, des molécules, et des enzymes qui ne peuvent être observés à l'œil nu. C'est grâce à cette photosynthèse que l'arbre pourra se développer, grandir, se reproduire. C'est ce même arbre qui en interaction avec les autres arbres, les autres végétaux et les animaux, formera la forêt tropicale. En Amazonie, cette forêt recouvre 5,5 millions de km². On dénombre plus de 16 000 espèces d'arbres, avec une canopée atteignant parfois 60 mètres de hauteur. A chaque échelle, des processus sont à l'œuvre qui sont responsables du développement de cet écosystème exceptionnel.

A Paracou, sur 6 parcelles de 6.25 hectares, nous étudions grâce à plus de 20 000 individus recensés très régulièrement la dynamique d'une communauté que nous prenons pour représentative du plateau des Guyanes, mais notre échelle spatiale, centrée sur l'individu, reste située à mi-chemin entre la feuille et la forêt.

1.2 De la seconde au millénaire

L'étude de la dynamique forestière est une tâche d'autant plus ardue que l'espérance de vie d'un être humain ne dépasse pas le siècle, tandis que les

arbres qui peuplent la forêt tropicale Amazonienne atteignent des âges cano- niques de plusieurs centaines voire, exceptionnellement, un millier d'années (Chambers *et al.*, 1998). En s'intéressant à la croissance annuelle d'un arbre, on se positionne à une échelle de temps certes commode pour l'être humain, mais qui peut paraître dérisoire en comparaison de la longévité des arbres.

Les changements climatiques, quant-à-eux, sont des processus de grande ampleur, qui se réalisent à des échelles de temps et d'espace trop importantes pour que l'on puisse les percevoir de façon globale. Mais l'heure est aux chan- gements d'échelles, et à mesure que les changements climatiques s'accélèrent, on voit apparaître des phénomènes concrets à notre échelle, marques inquié- tantes de l'accélération de ces changements.

Lorsque l'on souhaite étudier les impacts des changements climatiques sur la forêt tropicale, on se heurte à la question fondamentale de l'échelle à laquelle on va se placer. Cette question est d'autant plus importante que les processus des différentes échelles ont tous leurs importances, et que l'étude de chaque échelle peut répondre à des questions bien précises. En étudiant la dynamique sur un pas de deux ans pendant 20 ans comme c'est le cas dans cette thèse, on se place à une échelle de temps intermédiaire, entre la variabilité intra-annuelle fine et rapide et les changements globaux plus lents.

2 Modéliser la diversité

Les modèles utilisés actuellement pour modéliser les changements clima- tiques et leurs potentiels impacts sur la végétation sont principalement des modèles de dynamique végétation globaux (Dynamic global vegetation model, DGVM), des modèles qui fonctionnent par couches, et qui prennent des comportements moyens en compte. Ces modèles se placent au-dessus des processus dynamiques, contrairement à ce qui est fait dans cette thèse, ils permettent de modéliser à un niveau supérieur, mais sans lien direct avec le fonctionnement individuel des arbres.

2.1 Peut-on tout modéliser ?

"Time to model all life on Earth" (Purves, 2013)

En utilisant de tels modèles, la forêt entière est modélisée, elle est re- présentée par une couche mise en relation avec la couche atmosphère et la couche sol. Ces modèles permettent donc d'étudier les processus à grande échelle et de répondre à des questions globales. Pour passer à ce niveau, l'arbre individuel disparaît au profit d'une feuille géante, la photosynthèse

devient le processus central, ces modèles se basent donc bien sur des hypothèses physiologiques. Mais l'échelle intermédiaire de l'arbre n'apparaît pas entre la feuille et la forêt.

Les modèles sont de plus en plus sophistiqués, et on peut raisonnablement se demander si les connaissances actuelles nous permettent de modéliser à des échelles encore plus grandes et en prenant la plus grande diversité possible en compte. C'est ce que propose Drew Purves en 2013 dans le journal *Nature* (Purves, 2013). Pour lui, nos connaissances sont suffisantes pour commencer à chercher à répondre à des questions globales, qui prennent tous les écosystèmes en compte. Or, je pense qu'il faut avoir les ambitions adaptées à l'échelle à laquelle on se place et je me demande s'il est judicieux de modéliser à un niveau élevé sans savoir modéliser à un niveau plus bas. Ainsi, pour beaucoup de modélisateurs en écologie, les processus de chaque niveau inférieur restent omniprésents, et il semble absurde de modéliser au niveau de la communauté lorsque l'on ne sait pas le faire au niveau de l'arbre ou de la feuille, on manque alors une étape qui nous permettrait de poser les hypothèses (physiologiques par exemple) qui permettent de construire le modèle de niveau haut. Toutefois, ces restrictions ne me semblent pas toujours justifiées lorsqu'il s'agit de modéliser car c'est bien par essence qu'un modèle caricature la réalité.

2.2 Doit-on tout modéliser ?

"Essentially, all models are wrong, but some are useful." George EP Box

"All models are right, most are useless." Thaddeus Tarpey

Bien que la perspective de tout modéliser soit scientifiquement alléchante, on peut douter de l'efficacité d'une telle approche. En effet, si l'on en croit les travaux de Dirk Helbing et de son équipe (Helbing *et al.*, 2012), une nouvelle aire sociale pourrait voir le jour si l'on réussissait à modéliser l'intégralité des processus sociaux en jeux. Cette vision des choses me paraît bien utopiste si l'on garde en tête que la modélisation peut nous apprendre des choses comme outil de prédiction, mais qu'elle n'impacte évidemment pas directement les processus. Comprendre un processus est une chose, savoir avec certitude comment il répondra à une contrainte en est une autre, et pouvoir créer ou éviter cette contrainte en est encore une autre.

2.3 Quelles hypothèses pour répondre à quelles questions ?

Dans le cadre de cette thèse, la modélisation est utilisée comme outil, pour apporter un élément de réponse aux questions qui taraudent la communauté scientifique à propos de l'impact des changements climatiques sur la dynamique de la forêt tropicale. Pour apporter cette pierre à l'édifice, on a vu qu'il nous a été nécessaire de poser un certain nombre d'hypothèses. Ces hypothèses sont lourdes de sens, mais ce sont elles qui permettent de construire un modèle.

Ainsi, un arbre est représenté par un DBH, des traits fonctionnels et un stade ontogénique. Son environnement, notamment le sol ou la compétition, ne sont pas pris en compte dans mes modèles. De plus, tous les arbres sont soumis au même modèle de croissance et de mortalité, ce qui lisse fortement le signal et empêche certains comportements exceptionnels potentiellement importants. On peut se demander quelles sont les conséquences de telles hypothèses sur notre habilité à répondre à des questions d'écologie. Dans notre cas, la communauté entière est représentée, avec les traits fonctionnels qui permettent de prendre en compte la diversité sans devoir créer de groupes artificiels. Mais les comportements extrêmes sont laissés pour compte, que ce soit par exemple le comportement des très gros arbres ou la croissance particulièrement rapide de certains individus.

3 Modéliser la complexité

Si notre approche permet de modéliser la diversité en forêt tropicale, elle gomme par endroit sa complexité. Les comportements extrêmes sont les moins bien représentés, bien que l'on sache qu'ils sont d'une grande importance. Les très gros arbres, les événements rares, les comportements marginaux sont autant de sources de potentiels changements brutaux de dynamique, ce que l'on appelle des black swan (Taleb, 2010). La croissance par exemple, est très faible dans la forêt étudiée à Paracou, ce qui nous conduit à prédire des taux de croissance très faibles. Pourtant on sait que certains individus, parfois indépendamment de leur espèce, peuvent croître de façon inattendue. La vigueur, introduite dans le troisième chapitre, permet de mieux prendre en compte cette variabilité résiduelle sur les processus. Toutefois, la façon dont la vigueur est prise en compte dans les modèles peut changer drastiquement les résultats comme le montre le chapitre 5, encore une fois ceci dépend des hypothèses qui ont été formulées.

3.1 Les propriétés émergentes

Les hypothèses que l'on fait ont un impact fort sur les résultats observés, et on peut voir apparaître des propriétés émergentes qui n'avaient pas été initialement prévues. C'est parfois le cas d'effet de seuil ou de rétroaction. Dans notre cas, nous ne voyons pas de tels effets se manifester. Toutefois, on peut prendre conscience de l'importance de nos hypothèses en constatant les différents résultats. Le calcul de la vigueur prend toute son importance lorsque l'on regarde son effet sur des simulations de 100 ans. S'il n'y a pas d'effet lors de l'inférence des paramètres, il y en a par contre un lors de la simulation de la communauté. Si l'effet de la sécheresse sur la croissance se répercute sur la mortalité, alors on observe une diminution plus faible de la mortalité. Toutefois, si la sécheresse devait avoir un effet sur la mortalité, on s'attend à ce que notre modèle l'ait pris en compte. La forêt telle qu'on l'observe n'est probablement ni tout l'un ni tout l'autre. En effet, si l'on cherche à comprendre ce que de telles hypothèses impliquent, écologiquement parlant, on voit alors deux types de caricatures possibles. La mortalité peut être vue comme un processus relativement stable, qui épure la forêt de ses arbres les moins bons. A chaque pas de temps, un certain nombre d'arbres va donc mourir et pour déterminer lesquels mourront, on peut regarder le stade ontogénique, l'environnement, ou d'autres facteurs. D'une autre façon, la mortalité peut être perçue comme un processus sans borne, qui va simplement supprimer les arbres les moins vaillants sous une contrainte donnée, quitte à voir disparaître la moitié de la forêt si la contrainte est forte. La réalité est bien sûr différente, puisque le processus de mortalité est complexe, et reste pour le moment relativement constant, autour de 1% par an sur le site de Paracou. Toutefois, ces deux visions extrêmes et caricaturales nous permettent de mieux nous interroger sur les scénarios possibles concernant la mortalité en forêt tropicale.

3.2 L'effet individuel

L'introduction de la vigueur pose la question d'un effet individuel. De tels effets sont amplement étudiés en écologie, grâce à l'essor des modèles mixtes et leur facilité d'utilisation. L'ajout d'effets aléatoires, que ce soit spécifiques, ou individuels, permet de prendre ce genre de variabilité en compte et de définir à quel niveau chaque effet intervient. Toutefois, si ces modèles sont très informatifs, on peut se demander quel est leur pouvoir de prédiction. Si la variabilité individuelle des réponses de dynamique aux changements climatiques apparaît importante, quelle doit être la conclusion pour prédire la

réponse de la forêt ? On peut décider de modéliser dans son ensemble, comme je l'ai fait, mais en se concentrant plus sur la structuration de la variance résiduelle par cet effet individuel. Compte tenu de la distribution non normale des DBH et des processus complexes qui interviennent au niveau individuel, une telle approche nous permettrait potentiellement d'observer l'émergence de propriétés non observées durant cette thèse. C'est ce qui est recherché lors de la construction de modèle individus-centrés. Les propriétés émergentes, qui sont parfois surprenantes, permettent de comprendre l'apparition de phénomènes à l'échelle globale qui n'était pourtant pas implémentés à l'échelle individuelle. C'est notamment ce qui permet de modéliser les mouvements des étourneaux sans avoir à implémenter les formes parfois complexes qui en résultent. Dans le cas de la dynamique des arbres en forêt tropicale, il est difficile de fixer le niveau auquel les processus doivent être modélisés pour répondre le mieux à notre question. Contrairement à un étourneau, un arbre restera toute sa vie au même endroit, il est donc crucial de s'intéresser à l'environnement proche. De même, de nombreuses interactions peuvent entrer en jeu, car la diversité animale et végétale en forêt tropicale est grande, ce qui a amené les nombreuses espèces à créer un grand nombre de mécanismes de coexistence. Ces processus, aux aussi, peuvent entrer en compte lors de changements climatiques. Il est donc justifié de vouloir s'intéresser à l'individu, et de modéliser à un niveau bas. Mais cette approche, gourmande en temps et en énergie se pose à l'encontre des modèles DVGM dont il a été question plus haut. En effet, une propriété émergente, par définition, doit être irréductible. C'est-à-dire qu'elle ne peut pas être déduite des niveaux plus bas à partir desquels elle émerge. Dans cette thèse, aucune propriété émergente n'a été observée. Si la descente d'échelle impliquée par la prise en compte d'un effet individuel fort n'entraîne pas l'apparition de propriétés émergentes, on peut raisonnablement se demander si elle a un intérêt.

3.3 Comment concilier complexité et diversité ?

Il existe donc deux approches, l'une à un niveau bas, centrée sur l'arbre individuel, et l'autre à un niveau haut, centrée sur les processus. De nombreux modèles se situent bien sûr entre ces deux extrêmes. Si l'on se rappelle la classification des modèles proposée par Porté and Bartelink (2002) décrite en introduction, on se souviendra que les deux grandes classes de modèles sont les stand models, basé sur des morceaux de forêt considérés comme homogènes, et les tree models basés sur des arbres modélisés individuellement. Cette structuration prend tout son sens lorsque l'on sait que ces deux niveaux correspondent à deux approches bien différentes, et servent à répondre à des

questions différentes. En effet, après avoir proposé une classification, Porté propose une étude comparative des modèles pour savoir quels modèles sont adaptés pour quelles questions. La première question qui nécessite de tels modèles concerne la sylviculture, et s'intéresse à la croissance et à la production. Un autre objectif est celui de comprendre la dynamique et la succession en tenant compte des perturbations et de la structure de la communauté. Les modèles utilisés pour une question ne le sont pas forcément pour l'autre, et Porté met en valeur la nécessité de s'intéresser à l'échelle la plus pertinente en fonction de la question que l'on se pose.

Zuidema *et al.* (2013) nous propose d'identifier les trous de connaissance aux différentes échelles auxquelles on peut considérer la forêt (Figure 5.3). Il met en évidence un manque au niveau du passage de la feuille à l'arbre. Il conseille aux scientifiques de s'intéresser à l'arbre au lieu de se placer à l'échelle de la feuille ou de la communauté, de s'intéresser aux effets sur le long terme (il entend par là, plutôt dizaine d'années voire siècle), et de comprendre les mécanismes, plutôt que de se baser sur des études empiriques. La plupart des lacunes soulevées concernent l'arbre et la population, ce qui nous pousse à penser que les échelles intermédiaires sont celles sur lesquelles on se doit de travailler pour combler ces lacunes.

4 Modéliser pour simuler

"Trying to predict the future is a mugs' game. But increasingly it's a game we all have to play because the world is changing so fast and we need to have some sort of idea of what the future's actually going to be like because we are going to have to live there, probably next week." (Adams, 2002)

Notre objectif dans cette thèse était de simuler une communauté d'arbres, en s'intéressant aux signaux communs, aux réponses aux variables climatiques, et en mettant des stratégies en évidence. Pour ce faire, nous avons donc posé des hypothèses, nous nous sommes placés au niveau de l'arbre individuel, mais tout en cherchant à retrouver le signal observé à l'échelle de la communauté. Des signaux communs ont été observés, entre les traits fonctionnels et la dynamique, puis entre les variables climatiques et la dynamique, en incluant les interactions potentielles entre les traits et les variables climatiques. Une telle approche nous a permis de simuler l'évolution d'une communauté pendant un siècle, et d'observer les évolutions qui apparaissent au sein de cette communauté. L'outil développé dans cette thèse nous apporte donc des éléments de réponses, et nous permet d'apporter notre pierre

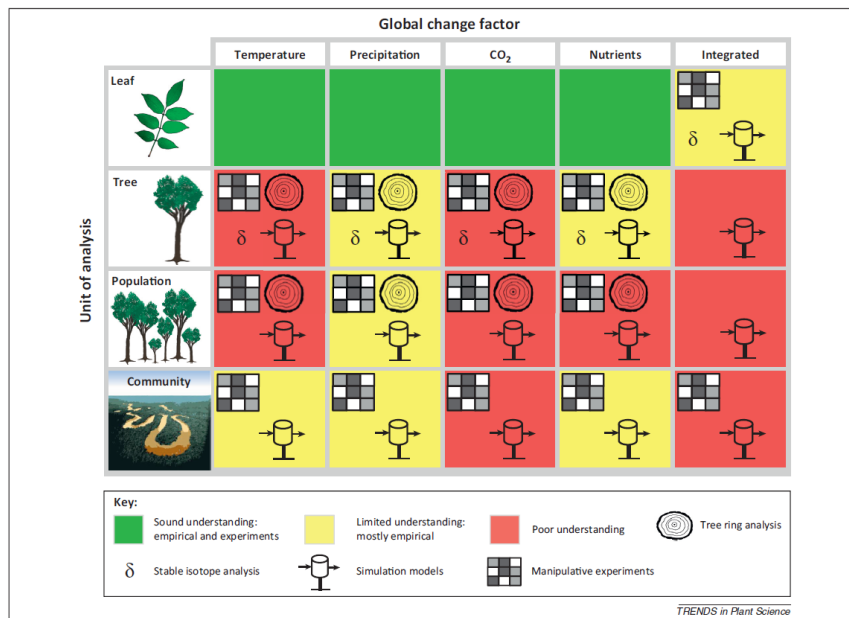


FIGURE 5.3 – Connaissances actuelles, et nouvelles approches dans le domaine des impacts des changements globaux sur les forêts tropicales, tiré de Zuidema *et al.* (2013). La couleur indique le niveau de compréhension de la réponse des feuilles, des arbres individuels, de la population, et de la communauté par rapport à quatre facteurs, et leurs effets intégrés. Les symboles indiquent les recherches proposées pour combler les lacunes.

à l'édifice.

Les échelles auxquelles on s'intéresse sont d'une grande importance, en plus de l'échelle spatiale qui permet de passer de la feuille à la forêt, l'échelle temporelle ne doit pas être perdue de vue. En effet, il est particulièrement difficile d'appréhender des processus qui se réalisent à des échelles de temps très supérieures à la nôtre. De fait, on ne sent pas la température évoluer au jour le jour en Guyane, et il n'est donc pas intuitif de s'y intéresser. Les changements climatiques et la dynamique forestière sont des processus lents, et notre propre perception du temps nous empêche parfois d'étudier convenablement de tels processus.

"Prediction is very difficult, especially if it's about the future." Niels Bohr

Si les changements climatiques suivent les prédictions les plus pessimistes de l'IPCC, alors la température à la surface du globe va conséquemment augmenter d'ici quelques décennies. Les hypothèses qui nous ont permis de construire nos modèles seront alors probablement fausses. Les processus que nous avons considérés linéaires sur nos intervalles peuvent ne pas l'être sur des intervalles plus grands. Les variables qui n'ont pas été sélectionnées dans le chapitre 4 car elles n'ont actuellement pas d'impact sur la dynamique peuvent devenir cruciales. Les effets de seuils ou des hystérésis peuvent apparaître. L'étude des systèmes complexes nous permet de mieux comprendre ces effets, et dans certains cas de les modéliser. Mais il ne faut pas perdre de vue qu'il est très difficile de trouver quelque chose quand on ne le cherche pas, et de s'imaginer le futur alors que celui-ci n'a pas encore eu lieu.

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