# Rôle de la lumière dans la coexistence des espèces d’arbres de forêt tropicale humide: analyse des variations inter- et intra-spécifiques des performances et des traits fonctionnels.

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# THÈSE
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**Présentée par Marilyne Laurans**

# Rôle de la lumière dans la coexistence des espèces d'arbres de forêt tropicale humide: analyse des variations inter- et intra-spécifiques des performances et des traits fonctionnels.

**Soutenue le 13 décembre 2013 devant le jury composé de :**

| | |
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| Frans BONGERS, Professeur, Université de Wageningen | Président du jury |
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Montpellier SupAgro

# Rôle de la lumière dans la coexistence des espèces d'arbres de forêt tropicale humide: analyse des variations inter et intra-spécifiques des performances et des traits fonctionnels.

# Rôle of light in tropical tree species coexistence: analyse of inter- and intraspecific variations of performance and functional traits.

Cette thèse a été réalisée au sein de l'UMR AMAP à Montpellier. Les missions de terrain en Guyane ont été financées par le projet européen DYGEPOP "DYnamique et GEstion des POPulations d'arbres en forêt guyanaise aménagée ».

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A Michaël Guéroult,

# Table des matières

# Introduction

Les forêts tropicales couvrent 8% des terres émergées et abritent 0,5 milliard d'êtres humains et plus de la moitié des espèces animales et végétales de la planète. A titre de comparaison, on compte autant d'espèces d'arbres (plus d'un millier) sur une parcelle d'un demi km$^2$ de Bornéo ou d'un quart de km$^2$ en Equateur que sur les 4 millions de km$^2$ de forêts d'Europe, d'Asie et d'Amérique du nord réunies (Wright 2002). La régression accélérée de la forêt tropicale sous l'effet de l'exploitation forestière et de la conversion agricole ainsi que sa réponse aux changements climatiques soulèvent de multiples enjeux et débats à l'échelle nationale et internationale : conservation de la biodiversité, gestion des ressources naturelles, régulation des cycles biogéochimiques[1]. La prédiction de la distribution et de la dynamique futures de la biodiversité tropicale exige de comprendre les processus contribuant à son maintien ainsi que la réponse des espèces et des communautés aux effets directs et indirects des changements anthropogéniques. Le travail de thèse présenté dans ce mémoire s'inscrit au cœur de ces recherches. Il explore plus précisément le rôle des perturbations de la canopée dans les processus d'assemblage local des espèces d'arbres de la forêt tropicale guyanaise dans la perspective de prédire l'impact d'un changement du régime de perturbation sous l'effet du climat ou de l'exploitation forestière, sur la structure et la composition des communautés végétales.

## I. Théories de la diversité à l'échelle locale

Comment plusieurs centaines d'espèces dépendantes d'un même petit nombre de ressources peuvent-elles coexister sur un seul hectare ? Cette réalité va à l'encontre du principe d'exclusion compétitive formulé par (Gause 1934) et stipulant que si plusieurs espèces sont en compétition pour une unique ressource, toutes sauf une doivent être éliminées sur le long terme. L'exclusion compétitive est prédite par de nombreux modèles théoriques et mathématiques mais les nombreuses conditions requises par cette théorie sont rarement observées dans les milieux naturels. Ainsi, plus de 100 mécanismes retardant ou empêchant l'exclusion compétitive ont été proposés et ont été regroupés autour de six conditions nécessaires à l'exclusion compétitive :

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[1] Les forêts tropicales stockent 25% du carbone terrestre et un tiers de la productivité primaire nette (Bonan 2008).

1) les espèces rares ne doivent pas être favorisées démographiquement,
2) les espèces doivent pouvoir entrer en compétition,
3) l'environnement est constant dans le temps et dans l'espace,
4) le temps doit être suffisamment long pour permettre l'exclusion,
5) la croissance est limitée par une seule ressource,
6) il n'y a pas d'immigration de nouvelles espèces.

C'est également autour de ces six conditions que (Wright 2002) fédère les principales hypothèses avancées pour expliquer la coexistence des plantes de forêt tropicale. Chacune des conditions requises pour l'exclusion compétitive est enfreinte par une ou plusieurs hypothèses. La détection et l'estimation de la force des mécanismes sous-jacents ont fait l'objet de nombreux travaux théoriques et empiriques et constituent de fait une question centrale de l'écologie des communautés.

Deux cadres théoriques de nature très différente ont été ainsi invoqués et débattus pour expliquer la coexistence d'un grand nombre d'espèces au sein d'une communauté végétale: la théorie de la niche et la théorie neutraliste. Ces théories proposent un mécanisme d'assemblage local des espèces permettant de prédire la distribution et l'abondance relative des espèces. Après avoir été longtemps opposés sur la base de leurs limites respectives, de nombreux travaux tentent aujourd'hui de les « réconcilier » en essayant de déterminer leur échelle et leur mode d'action respectifs ainsi que leur importance relative (Gravel et al. 2006).

## I.1 Principe de la théorie de la niche

L'hétérogénéité spatio-temporelle des ressources qui caractérise la majorité des habitats met en défaut le principe de Gause et sert de fondement à la théorie de la niche.

D'après la définition de (Hutchinson 1957), la niche est un « hyperspace » à n dimensions propre à chaque espèce dans lequel chaque dimension (ou axe de la niche) correspond à une ressource ou une condition environnementale. La niche représente donc la gamme des « conditions » environnementales qui permettent à une espèce de former une population viable en absence (niche fondamentale) ou en présence de compétiteurs (niche réalisée). La niche de régénération (Grubb 1977) est le sous-ensemble de la niche de l'espèce qui concerne les processus de régénération.

L'existence de compromis entre les différents traits de vie et fonctions biologiques empêche l'apparition d'une super-espèce qui serait la plus compétitive sur tous les axes de la niche. Deux espèces ayant des niches similaires auront tendance à s'exclure compétitivement (principe de Gause) ou à modifier leur niche par un processus de déplacement de caractère (différentiation et divergence d'un caractère phénotypique héritable impliqué dans le processus de compétition) - (Pfennig et al. 2006). Ce déplacement de caractère peut être fixé ou facultatif (plasticité phénotypique). La proportion et la coexistence d'espèces généralistes et spécialistes dépend du motif d'hétérogénéité spatio-temporelle à savoir sa fréquence, son échelle, sa prédictibilité mais également d'un compromis entre le degré de compétitivité et le taux de colonisation ou la capacité à coloniser une large gamme d'habitats (Weiner and Xiao 2012, Nagelkerke and Menken 2013).

Ce processus d'évitement de la compétition produit une différentiation des espèces en termes de niche et de traits, qui rend possible la coexistence. Le degré de chevauchement des niches ne doit pas dépasser un seuil critique pour que les espèces coexistent (Macarthur and Levins 1967). La compétition interspécifique est ainsi un facteur d'évolution d'espèces en interaction.

Ainsi dans cette vision de la communauté, la coexistence est stable[2] et résulte de la différentiation de niche des espèces en réponse à la compétition interspécifique et à l'hétérogénéité de l'environnement. Ce processus de spécialisation se traduit par une réponse différentielle des espèces à l'hétérogénéité de l'environnement et implique que la compétition intra-spécifique devienne plus forte que la compétition interspécifique: les individus d'espèces différentes ne sont plus en situation de compétition mais les individus d'une même espèce le sont. Cet effet stabilisateur (Chesson 2000) limite l'extension d'une espèce et favorise les espèces rares. En termes de structuration des communautés, la théorie de la niche décrit l'assemblage local des espèces comme un échantillon du pool régional d'espèce délimité par un ensemble de filtres. Le filtre abiotique, correspondant à la niche fondamentale, détermine si une espèce a les traits requis pour s'établir et persister dans un habitat donné tandis que le filtre biotique, correspondant à la niche réalisée, est imposé par les interactions avec les autres espèces. Le premier filtre tend à produire une similarité des espèces. Ce filtrage environnemental peut être relativement important le long de gradients topographiques ou le long de forts gradients édaphiques ou climatiques (John et al. 2007, Kraft et al. 2008, Cornwell and Ackerly 2009, Baraloto et al. 2012a). Le second filtre tend à produire au contraire une sur- dispersion des espèces. L'analyse de la distribution des traits des espèces est ainsi une façon de détecter ces filtrages, en prenant comme référence ou modèle nul la distribution aléatoire des traits prédite par la théorie neutraliste (Kraft et al. 2008, Baraloto et al. 2012a) et en supposant que l'espace des traits est corrélé à l'espace de la niche.

## I.2 Principe de la théorie neutraliste

La théorie neutraliste a été formulée dans les années 80 (Hubbell 1979) pour expliquer la coexistence des arbres de forêts tropicales. Cette théorie explique l'assemblage local des espèces et la distribution de leur importance relative par le jeu de facteurs historiques et stochastiques : selon ses auteurs, des espèces identiques peuvent coexister indéfiniment si leur apparition et leur disparition se

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[2] La coexistence est dite stable si la densité des espèces ne montre pas de tendance à long terme. Si les densités fluctuent, elles finissent par revenir à leur état initial (moyenne et variance sont constantes). La coexistence est dite instable s'il n'y a pas d'effet de retour à l'état initial et que les espèces ne sont pas maintenues dans le système à long terme (Chesson 2000).

produisent de façon aléatoire. L’hypothèse d’équivalence signifie que les différences entre espèces sont déconnectées des traits qui influencent leur fitness ou leur démographie et donc leurs interactions avec leur environnement biotique et abiotique (Leibold and McPeek 2006). Le postulat de base de la théorie neutre est donc l’équivalence fonctionnelle des espèces, donc des individus. La communauté étant un assemblage éphémère d’espèces, la coexistence est transitoire. La théorie neutre s’est avérée performante pour prédire les patrons aire-espèce[3] et les patrons de distribution de l’abondance relative des espèces (Hubbell 2001). Les tenants de cette théorie ont interprété ces résultats comme une validation de l’hypothèse de stochasticité démographique et de limitation de la dispersion. Cependant, des travaux récents ont mis en évidence la difficulté d’inférer les processus sous-jacents à ces patrons de distribution. Les empreintes laissées par les processus stochastiques ou déterministes sur les patrons d’abondance et de distribution des espèces peuvent être indiscernables (Du et al. 2011).

Les faibles densités de population conjuguées à la longue durée des temps de génération sont un obstacle majeur à l’évaluation expérimentale des mécanismes de coexistence.

## I.3 Déclinaison de la théorie de la niche aux forêts tropicales humides

Selon l’hypothèse de la niche, la coexistence exige que les espèces diffèrent dans des caractères déterminant leur réponse à l’hétérogénéité de l’environnement. L’hétérogénéité spatiale et temporelle de la ressource lumineuse est importante en forêt tropicale humide et a été identifiée comme un moteur potentiel de la coexistence des espèces d’arbres tropicaux. Selon l’hypothèse de perturbation intermédiaire, le régime de perturbation peut également avoir une forte influence sur la diversité et la composition des communautés d’arbres (Molino and Sabatier 2001). La réponse différentielle des espèces à l’hétérogénéité de la lumière est structurée par un compromis démographique entre la croissance à la lumière et la survie à l’ombre (Grubb 1977). Un frein à l’étude à large échelle de la théorie de la niche a longtemps résidé dans la difficulté de discriminer plus d’une poignée de stratégies écologiques. Jusqu’il y a peu en effet, les espèces d’arbres tropicaux étaient classées empiriquement en groupes successionnels (espèces pionnières vs. espèces tolérantes à l’ombre). Dans ce contexte, il s’avérait difficile d’expliquer la coexistence d’un nombre d’espèces supérieur au nombre de groupes décrits et donc d’expliquer la coexistence des espèces au sein des groupes successionnels. Les avancées récentes dans le domaine de l’écologie fonctionnelle ont permis une quantification plus précise et continue des stratégies écologiques le long de quelques axes de variation liés aux stratégies d’acquisition des ressources, à la niche de régénération ou aux traits de vie (Kraft et al. 2008). Ainsi, il semble qu’un continuum de stratégies se soient différenciées en réponse à la variabilité spatiale de l’éclairement (Poorter and Bongers 2006).

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[3] Une courbe aire-espèce décrit l’augmentation du nombre d’espèces observées en fonction de la surface échantillonnée.

Cette présentation succincte des mécanismes de maintien de la diversité montre clairement que le degré de différentiation des espèces est une clé de compréhension majeure de leur coexistence à l'échelle locale et que l'enjeu dans ce domaine de recherche est plus quantitatif que qualitatif. Quelle fraction de la communauté coexiste par des mécanismes de différentiation de niche ?

# II. Différentiation des espèces en terme de tolérance à l'ombre

## II.1 Hétérogénéité spatio-temporelle de la lumière en forêt tropicale humide

L'hétérogénéité environnementale des forêts tropicales humides s'exprime à différentes échelles. A l'échelle locale qui nous intéresse, une description multivariée de la structure spatiale des microhabitats réalisée en Guyane française a montré que la variabilité de l'environnement était aussi importante entre deux points distants de 30 cm qu'entre deux points distants de 20 m (Baraloto and Couteron 2010). Le grain de l'hétérogénéité des ressources et des conditions environnementales est donc très fin.

En ce qui concerne la ressource lumineuse, les arbres de forêt tropicale sont soumis à une hétérogénéité tridimensionnelle. L'organisation spatiale d'un couvert forestier tropical crée un fort gradient vertical d'éclairement : le niveau d'énergie auquel un arbre a accès est donc conditionné par sa hauteur : seulement 1 à 5% du rayonnement solaire (Poorter 1999) parvient au niveau du sol. La croissance en hauteur va donc exposer les plantes à ce gradient vertical.

La dynamique produite par l'ouverture de la canopée consécutive à la chute d'arbres (chablis) ou de branches (volis) se traduit par :

- un gradient spatial horizontal : l'éclairement est de l'ordre de 10% du rayonnement incident dans un petit chablis et de 40% dans un grand chablis. Ce gradient horizontal décroît avec la hauteur. (Lieberman and Lieberman 1989) ont bien mis en évidence l'existence d'un continuum dans le niveau d'éclairement entre le sous-bois et le centre d'une trouée ;
- des variations temporelles d'éclairement : la fermeture du couvert est un événement progressif et prédictible, signalé par une variation de la quantité et de la qualité de l'éclairement à laquelle échappent les espèces les plus compétitives. L'ouverture du couvert par volis ou chablis est au contraire aléatoire et imprévisible : en Guyane, sur la piste de St Elie, on estime qu'en moyenne chaque année, les chablis affectent environ 1% de la surface forestière (Riéra and Alexandre 1988), ce qui correspond en moyenne à 0,75 chablis/ha/an.

L'éclairement peut également fluctuer à une échelle temporelle et spatiale beaucoup plus fine du fait des tâches de soleil. Le grain de l'hétérogénéité de la lumière est donc très variable : il va de quelques cm$^2$ à plusieurs dizaines ou centaines de m$^2$ au niveau spatial et de quelques secondes à plusieurs années au niveau temporel.

## II.2 Compromis entre croissance à la lumière et survie à l'ombre : de la niche aux traits fonctionnels

La dynamique de la structure de la canopée permet la différentiation des espèces le long d'un axe de niche correspondant au gradient d'éclairement. La position des espèces sur cet axe de niche est souvent exprimée en termes de tempérament, de degré de tolérance à l'ombre ou de degré d'héliophilie. Le tempérament peut être quantifié de manière continue par des données de distribution relative des espèces le long du gradient lumineux (Poorter and Arets 2003, Vincent et al. 2011b) ou plus indirectement par des traits démographiques (Gourlet-Fleury et al. 2005). En effet la différentiation de niche se traduit par une réponse différentielle des espèces à l'éclairement et un compromis entre la croissance à la lumière et la survie à l'ombre. Ce compromis a fait l'objet de nombreux travaux empiriques et théoriques et constitue sans doute l'axe de variation de traits de vie le mieux établi en forêt tropicale (Grubb 1977, Davies 2001, Baraloto et al. 2005, Poorter et al. 2008, Wright et al. 2010). A une extrémité du trade-off se trouvent les espèces pionnières qui se régénèrent dans des trouées de taille suffisante, montrent une croissance rapide et sensible au degré d'éclairement, et meurent si elles sont ombragées. A l'autre extrémité, les espèces sciaphiles se caractérisent par des vitesses de croissance faibles, peu sensibles aux variations d'éclairement et une bonne survie à l'ombre. Entre les deux se trouvent un continuum de stratégies et d'espèces plus ou moins capables de se maintenir le long du gradient lumineux. Les espèces non-pionnières, c'est-à-dire les espèces intermédiaires et les espèces sciaphiles ont longtemps été regroupées sous le nom d'espèces tolérantes à l'ombre conduisant ainsi à une classification dichotomique des espèces d'arbres. Comme cela a été mentionné plus haut, le compromis croissance-mortalité n'a pas été validé pour des espèces intermédiaires en termes de tempérament. L'analyse de (Bloor and Grubb 2003) conduite sur les plantules de 15 espèces non-pionnières a conclu à l'absence de compromis.

Plus récemment, les performances relatives des espèces le long du gradient lumineux ont été significativement corrélées à des traits biologiques (Walters and Reich 1999, Poorter and Bongers 2006, Sterck et al. 2006a). Ces traits, mesurables à l'échelle individuelle, sont nommés « traits de performance » s'ils influencent directement le fitness des individus et « traits fonctionnels » s'ils l'influencent indirectement via les traits de performance (Violle et al. 2007). L'analyse de la diversité des traits fonctionnels et de leurs covariations a permis des avancées significatives dans la caractérisation des axes de différentiation interspécifique le long des gradients environnementaux, prolongeant et généralisant les travaux de Grime (stratégies CSR (Grime 2001)).

Les espèces tolérantes à l'ombre se caractérisent par une capacité photosynthétique plus faible, un bois plus dense et des feuilles de surface massique (LMA) plus grande et de durée de vie (LLS) plus longue que les espèces pionnières (Reich et al. 2003). Dans un cadre d'analyse coût-bénéfice, le faible turnover des feuilles est interprété comme un retour sur l'investissement que représente la construction et la maintenance des feuilles dans un contexte de contrainte lumineuse où le bénéfice, à savoir le gain en carbone, se cumule lentement (Williams et al. 1989). Il peut également correspondre à une utilisation parcimonieuse des nutriments. La variation des traits associés au compromis croissance-survie correspond de façon plus générale à un compromis entre une acquisition rapide des ressources (forte teneur en azote massique et capacité photosynthétique, faible LMA, longue durée de vie des feuilles) et une conservation des nutriments (longue durée de vie des feuilles, fort LMA, faible teneur en azote massique et capacité photosynthétique). Ce compromis s'inscrit ainsi dans un schéma universel de gestion des ressources établi sur plus de 2500 espèces réparties dans différents biomes (Wright et al. 2004). Les co-variations LMA-durée de vie des feuilles constituent un axe majeur de diversité fonctionnelle des espèces (Westoby et al. 2002). Un fort LMA ne paraît pas avantageux pour les espèces de sous-bois dans la mesure où il augmente le coût de construction des feuilles. En revanche, il semble requis pour augmenter la résistance mécanique des feuilles. Une feuille est constituée d'une composante symplastique (contenu cellulaire) et d'une composante structurale (parois cellulaires) dont dépendent les propriétés mécaniques. Des études récentes (Lusk et al. 2010, Westbrook et al. 2011) ont montré que la fraction de parois cellulaire dans les feuilles et la force nécessaire à la perforation étaient plus corrélés au degré de tolérance à l'ombre et aux propriétés mécaniques foliaires que le LMA.

Ces travaux permettent d'explorer la capacité des traits fonctionnels à prédire les performances des espèces (Herault et al. 2011, Aubry-Kientz et al. 2013) et leur sensibilité à l'ouverture de la canopée (Herault et al. 2010, Rüger et al. 2012), moteur potentiel de leur coexistence sous une hypothèse déterministe. La mise en relation des traits fonctionnels avec le tempérament des espèces permet de s'approcher des processus de coexistence (Sterck et al. 2011). Ainsi un nombre croissant de travaux s'intéresse à la capacité des traits fonctionnels à prédire la niche des espèces (Violle and Jiang 2009, Kearney et al. 2010). Cette relation a un double intérêt :

- si les traits fonctionnels s'avèrent être des proxy fiables de la niche des espèces vis-à-vis de la ressource lumineuse, cela facilitera la caractérisation de la niche d'un grand nombre d'espèces;
- cette relation traits-niche est requise pour inférer les processus de coexistence à partir de la distribution des traits fonctionnels au sein d'une communauté (Kraft et al. 2008, Hammond and Niklas 2009, Baraloto et al. 2012a, Adler et al. 2013, Swenson 2013).

## II.3 Limites et enjeux

Bien que la pertinence d'une approche intégrative soit largement reconnue aujourd'hui (Wildova et al. 2007), la diversité fonctionnelle a principalement été caractérisée à l'échelle foliaire, sans doute parce qu'elle a intéressé davantage les écophysiologistes que les morphologistes des plantes. Dans la base de données mondiale TRY, les traits relatifs au houppier représentent 1.5% du nombre total de traits (39% pour les traits foliaires), 0.2% des données (32% pour les traits foliaires) et concernent 60 espèces en moyenne (de 1 à 239 espèces) alors que les traits foliaires concernent 663 espèces en moyenne (de 1 à 16542 espèces). Les traits morphologiques relatifs aux branches ou au houppier sont souvent négligés au profit des traits foliaires alors qu'ils jouent un rôle déterminant dans le fonctionnement des arbres et en particulier dans l'acquisition de la ressource lumineuse. Par ailleurs la coordination des traits morphologiques avec les syndromes de traits foliaires a été rarement explorée jusqu'ici. Une telle analyse a été conduite récemment sur les traits du bois de 668 espèces d'arbres tropicaux et a montré qu'ils représentent un axe de différentation orthogonal à celui des traits foliaires (Baraloto et al. 2010). La contribution des traits foliaires au compromis croissance à la lumière-survie à l'ombre, s'élève à environ 50% de la variation des traits de performance ou traits de vie (Sterck et al. 2006a). L'intégration de traits définis à l'échelle des branches, du houppier et de la plante entière pourrait permettre de mieux comprendre les déterminants des performances relatives le long du gradient lumineux ou les relations complexes entre traits, performances et niche (Wright et al. 2010).

Le compromis démographique entre la croissance à la lumière et la survie à l'ombre et les covariations traits-niche ont été décrits dans de nombreux travaux empiriques (Wright et al. 2003, Baraloto et al. 2005, Poorter et al. 2008). Néanmoins, ces études basées pour la plupart sur des corrélations intègrent systématiquement les espèces situées aux deux extrémités du gradient successionnel et ne permettent donc pas de tester la validité de ce compromis pour les espèces intermédiaires ni la capacité des traits fonctionnels à prédire des variations fines de tempérament. Ces espèces intermédiaires constituant la majorité des espèces (Welden et al. 1991, Wright et al. 2003), le principal argument des détracteurs de la théorie de la niche est que celle-ci ne permet pas de comprendre comment coexistent la majorité des espèces d'arbres de forêt tropicale (Hubbell 2005). Selon eux ces mécanismes déterministes sont trop faibles pour maintenir les niveaux d'alpha-diversité observés (Welden et al. 1991, Hubbell et al. 1999, Brokaw and Busing 2000).

Les mécanismes proposés pour expliquer la coexistence des espèces se situent à l'échelle de l'espèce et s'appuient ou non sur l'existence de différences entre espèces. Un nombre croissant de travaux empiriques ou théoriques montre l'importance de considérer l'échelle individuelle. C'est en effet à l'échelle de l'individu que se jouent, entre autres, les processus de compétition pour les ressources et de sélection naturelle. Bien que des travaux aient montré que dans les bases de données à large échelle le degré de variation intraspécifique des traits fonctionnels était négligeable en regard de leur variation interspécifique (Wright et al. 2004), il n'est pas évident que cette variabilité intraspécifique soit négligeable lorsqu'on examine les espèces à une échelle géographique plus restreinte à laquelle la gamme de variation interspécifique est plus faible (Hulshof and Swenson 2009, Messier et al. 2010). Ainsi certains travaux suggèrent que la variabilité intraspécifique est un déterminant essentiel de la structure des communautés végétales (Pachepsky et al. 2007, Clark 2010). Les variations intraspécifiques de traits et de performances sont susceptibles de favoriser la coexistence des espèces en créant un recouvrement dans la distribution des performances individuelles des espèces (Clark et al. 2003a).(Clark 2010) défend l'idée que les variations interindividuelles de traits et de performances permettent aux espèces de se différencier en terme de réponse à l'environnement en dépit du fait qu'elles ne diffèrent pas en moyenne. Selon cet auteur, ignorer les variations intraspécifiques de traits peut conduire à surestimer l'amplitude des variations interspécifiques, ce qui revient à dire que les variations intraspécifiques tendent à brouiller ou « neutraliser » les différences entre espèces. L'étude de (Jung et al. 2010) montre que la variabilité intraspécifique des traits fonctionnels influence la coexistence des espèces en leur permettant de passer le filtre des facteurs biotiques et abiotiques. (Paine et al. 2010) montrent que les analyses ignorant la variabilité intraspécifique des traits sous-estiment l'effet de ces filtres comparativement à une analyse qui les prend en considération. La prise en compte de la variation intraspécifique apparaît ainsi nécessaire dans la quantification des processus de filtrage environnemental et différentiation de niche qui s'appuient sur la distribution des valeurs moyennes de traits fonctionnels par espèce (Kraft et al. 2008). Le degré de variabilité intraspécifique varie selon le trait considéré, le signal environnemental, le stade ou l'âge des arbres, le génotype et donc l'espèce (Bloor and Grubb 2004, Albert et al. 2010).

Dans ce contexte, une première étape dans la prise en compte de la variabilité intraspécifique repose sur la recherche de cohérences dans ses différentes sources de variation (Schmitz et al. 2003, Nicotra et al. 2010).

## III. Variations intra-spécifiques des traits fonctionnels: existe-t-il des cohérences écologiques dans leurs variations ?

"We hope to convince the reader that the way organisms respond to their environment through adaptive (and non-adaptive) changes in traits, particularly in response to other species with which they interact, can have major effects on the dynamics and structure of a community. Finding the unifying patterns and principles that organize this additional complexity is likely to be a necessary step in advancing our capacity to understand communities and predict their responses to perturbation. » Schmitz 2003, Ecology

Un nombre croissant d'études utilisent les bases de données de traits pour expliquer les patrons de communautés. Les valeurs de traits utilisées correspondent à des valeurs moyennes établies selon un protocole de mesure et d'échantillonnage standardisé (Cornelissen et al. 2003) : ainsi par exemple, afin de minimiser la variabilité des traits foliaires liée à l'ontogénie, la topologie ou l'environnement local, seules les feuilles matures et éclairées sont prélevées. Malgré cet effort de normalisation, la valeur moyenne d'une espèce mesurée dans ces conditions ne représente pas nécessairement la valeur moyenne de toutes les populations ou individus de cette espèce.

La variabilité intraspécifique est produite par deux mécanismes constituant deux types de réponses complémentaires à l'hétérogénéité de l'environnement : la variabilité génétique et la plasticité phénotypique. La plasticité phénotypique définit la capacité d'un génotype donné d'exprimer différents phénotypes en réponse à des variations de conditions environnementales (Bradshaw 1965). Elle est déterminée génétiquement. Toutes les réponses plastiques à l'environnement n'ont pas une valeur adaptative. Beaucoup d'entre elles sont la conséquence de réductions passives de la croissance due à une limitation des ressources. Contrairement aux réponses passives, les réponses « actives » exigent un système de perception et de transduction du signal environnemental. De plus, la plasticité phénotypique peut évoluer à cause de corrélations génétiques avec des traits sous sélection ou à cause de la dérive génétique. La valeur adaptative d'une réponse plastique est difficile à établir formellement in situ puisqu'elle requiert de mettre en relation le degré de plasticité d'un génotype donné avec son fitness. Les nombreux travaux théoriques et expérimentaux relatifs à cette question ont donc porté sur des clones ou des familles de génotypes/lignées. Une façon indirecte d'étayer la dimension adaptative de la plasticité est de mettre en relation le degré de plasticité d'une population avec l'hétérogénéité environnementale à laquelle elle est exposée (Donohue et al. 2000, Weinig 2000) ou de s'appuyer sur les connaissances acquises en écophysiologie pour interpréter fonctionnellement la réponse observée. Ainsi la valeur adaptative de la plasticité observée chez les plantes a été établie formellement pour un petit nombre de traits. L'élongation de la longueur des entre-nœuds en réponse à l'ombrage et plus spécifiquement à une variation de la qualité de la lumière (rapport rouge sombre-rouge clair) en constitue un exemple (Ballaré 2009). Il faut noter toutefois que réponse passive et réponse active peuvent se produire en réponse à un même signal et s'additionner ou se compenser selon leur amplitude et direction respectives. Pour reprendre l'exemple ci-dessus, en réponse à la compétition, une plante peut développer une réponse active d'allongement de ses entre-nœuds pour positionner ses feuilles dans des conditions d'éclairement plus favorables et en même temps réduire la longueur des entre-nœuds à cause de la limitation des ressources.

En conséquence de la difficulté d'étudier la plasticité phénotypique in situ et alors que l'expression de la plasticité phénotypique est largement illustrée et documentée dans la littérature, sa dimension écologique reste peu explorée et donc peu connue (Sultan 2003). Les travaux théoriques et expérimentaux menés dans le champ de l'écologie évolutive ont permis d'identifier les conditions environnementales favorisant l'émergence de la plasticité phénotypique et de postuler l'existence d'une relation entre plasticité phénotypique et amplitude de niche. Cette relation a été surtout étudiée chez des plantes annuelles (Sultan 2001) : ces études montrent une plus grande plasticité chez les espèces généralistes que chez les espèces spécialistes. Chez les arbres tropicaux le patron de plasticité en fonction de l'amplitude de niche a été peu étudié alors qu'il existe une forte hétérogénéité des ressources. A notre connaissance, l'étude de (Popma et al. 1992) est la seule à ce jour à s'être intéressée à cette question. Ces auteurs examinent 68 espèces mexicaines d'arbres et montrent que le degré de plasticité des traits foliaires en réponse à une contrainte lumineuse est moins important chez les espèces spécialisées. On peut également attendre une plus forte plasticité chez les espèces de grande taille exposées à une plus grande variabilité des conditions lumineuses au cours de leur vie. Les observations de (Cai et al. 2005, Rozendaal et al. 2006) confirment cette hypothèse relativement à la plasticité foliaire de 38 espèces d'arbres tropicaux. La relation plasticité-niche a ainsi un fondement déterministe qui précise et assoit l'hypothèse d'une relation entre variabilité intraspécifique des traits fonctionnels de réponse et amplitude de niche proposée par (Violle and Jiang 2009).

En fait, les études analysant les variations interspécifiques du degré de plasticité des arbres tropicaux ont surtout cherché à mettre celui-ci en relation avec la position des espèces sur le gradient successionnel, en s'appuyant sur l'hypothèse que l'hétérogénéité de la lumière serait plus importante à l'extrémité du gradient correspondant aux milieux ouverts. Ainsi les espèces pionnières sont supposées être plus plastiques que les espèces tolérantes à l'ombre (Nicotra et al. 1997). La littérature montre sur cette question des résultats divergents et qui dépendent du type de trait considéré. Certains travaux mettent en évidence une plus forte plasticité morphologique et une plus faible plasticité physiologique chez les espèces de fin de succession (Strauss-Debenedetti and Bazzaz 1991, Valladares et al. 2000, Rozendaal et al. 2006), tandis que d'autres montrent le contraire (Gilbert et al. 2001, Takahashi et al. 2001, Muth and Bazzaz 2003, Bloor and Grubb 2004). L'importance relative de la plasticité morphologique et de la plasticité physiologique est interprétée dans un cadre d'analyse coût-bénéfice. Les espèces pionnières ou héliophiles auraient la capacité de supporter, grâce à la disponibilité en lumière, non seulement le coût signalétique de la plasticité mais aussi le supplément de coût de construction (en carbone) associé à une réponse morphologique. Selon Grime (1986), cette réponse plastique correspond à une stratégie de « resource foraging » cohérente avec la forte compétitivité des espèces spécialisées vers des environnements productifs ou riches en ressources. Le degré élevé de plasticité physiologique observé dans certains travaux pour les espèces de fin de succession correspondrait à une stratégie de réponse moins coûteuse en carbone, réversible et leur permettant de capter des pulses éphémères et imprévisibles de ressources (Grime et al. 1986). Dans le scénario opposé, la forte plasticité physiologique des espèces pionnières est expliquée par la forte sensibilité du taux de croissance (efficience de conversion de l'énergie lumineuse) nécessaire pour la colonisation rapide des trouées tandis que la plasticité morphologique des espèces de fin de succession permettrait d'optimiser la capture du rayonnement lumineux (Bazzaz and Carlson 1982, Walters and Reich 1999, Portsmuth and Niinemets 2007). La disparité de ces résultats peut être expliquée par la relative faiblesse du nombre de travaux comparatifs sur la plasticité morphologique et la forte hétérogénéité de celle-ci. Les divergences observées pourraient ainsi résulter de la variabilité des traits mesurés et des méthodes de quantification de la plasticité, de l'absence de normalisation des résultats vis-à-vis de la taille, de l'âge et du stade de développement ou enfin d'une confusion entre l'effet de la phylogénie et celui du groupe successionnel (dans le cas de la comparaison d'un nombre réduit d'espèces). Enfin et surtout, les critères de définition des groupes écologiques peuvent différer d'une étude à l'autre et réunir des espèces très variables au regard de traits potentiellement liés à des différences significatives de plasticité (Poorter et al. 2005), comme l'amplitude de niche et la hauteur maximale des espèces. Ces divergences traduiraient ainsi l'absence de relation significative entre le degré de plasticité et le tempérament des espèces.

# IV. Questions et démarche

## IV.1 Questions de recherche

L'ambition de ce projet doctoral est de contribuer à la compréhension des mécanismes d'assemblage des communautés végétales tropicales et de leur réponse aux perturbations procédant directement ou indirectement de l'activité humaine. Nous nous plaçons dans une perspective déterministe de l'assemblage local des arbres tropicaux en prenant comme axe de niche le gradient spatial d'éclairement.

Plus spécifiquement, les enjeux de cette thèse sont i) d'évaluer la validité des hypothèses et corollaires de la théorie de la niche pour des espèces intermédiaires en terme de tempérament au stade juvénile, ii) d'analyser l'importance et la valeur fonctionnelle et écologique de la variabilité intraspécifique des traits fonctionnels exprimée en réponse à une contrainte lumineuse.

Compte tenu du lien potentiel entre plasticité et niche, la recherche de cohérence dans les sources de variabilité intraspécifique sera abordée en s'intéressant à la composante environnementale de cette variabilité intraspécifque, c'est-à-dire ici à la plasticité phénotypique exprimée en réponse à une contrainte lumineuse[4].

Les questions traitées sont les suivantes :

1) Les compromis et les syndromes de traits décrits entre espèces pionnières et espèces sciaphiles sont-ils valides pour les espèces d'arbres situées à une position intermédiaire sur le gradient successionnel ?
2) Le degré de plasticité des traits fonctionnels en réponse à une contrainte lumineuse est-il corrélé à la position et/ou à l'amplitude de niche des espèces vis-à-vis de la ressource lumineuse ?
3) La considération des traits morphologiques et de la plasticité phénotypique permet-elle de mieux comprendre les relations entre traits foliaires, performance et niche ainsi que le mécanisme de tolérance à l'ombre ?
4) Quelle est l'importance relative des variations intraspécifiques de la croissance produites par la compétition pour la lumière ?

## IV.2 Démarche

Nous avons mis en œuvre dans cette thèse une approche expérimentale comparative des traits fonctionnels et des performances pour 14 espèces d'arbres de Guyane française au stade juvénile ainsi qu'une approche de modélisation de la croissance des arbres adultes étendue à l'ensemble de la communauté.

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[4] En conséquence, dans la suite du document et sauf mention contraire, le terme de variation intraspécfique aura un sens équivalent à celui de plasticité.

Un dispositif expérimental a ainsi été mis en place de juin 2007 à novembre 2009 sur la station expérimentale de Paracou en Guyane française pour étudier la plasticité des traits et des performances exprimée en réponse à une contrainte lumineuse : il concerne quatorze espèces d'arbres présentant des modes de croissance et des tempéraments relativement contrastés. Une description de ces espèces est donnée dans le chapitre 3.

Le suivi annuel de croissance in situ a été réalisé sur 900 individus de 1 à 3 m de haut, au stade juvénile. Le niveau d'éclairement a été estimé par un indice (LI pour Light index) détaillé dans le chapitre 1. Le protocole (détaillé en annexe) comprend des mesures d'accroissement en diamètre (axe principal), en hauteur et en nombre de feuilles (axe principal + 3 branches), des mesures du houppier (largeur et profondeur relative) et des mesures de traits foliaires (masse surfacique des feuilles, teneur en azote massique et surfacique, durée de vie des feuilles). Les analyses biochimiques ont été confiées à un laboratoire commercial.

Dans la majorité des travaux d'écologie fonctionnelle, les traits de performance sont représentés par la biomasse totale, le nombre de graines et le taux de mortalité (Violle et al. 2007). Dans notre étude, compte tenu de la difficulté de réaliser des mesures destructives dans des parcelles permanentes, nous avons utilisé une acception plus large des performances et utilisé l'accroissement diamétrique de l'axe principal comme trait de performance de la plante entière (Poorter and Bongers 2006). Le dispositif en place ne nous permettant pas d'estimer le taux de mortalité le long du gradient lumineux, nous avons appréhendé le compromis croissance à la lumière-survie à l'ombre à travers les traits fonctionnels auxquels il a été associé jusqu'ici, à savoir la surface massique et la durée de vie des feuilles.

Les premiers résultats ayant suggéré que les caractéristiques plus fines de la stratégie de croissance des différentes espèces en réponse à des variations de ressource lumineuse ne seraient pas bien décrites avec le protocole utilisé, un deuxième dispositif a été mis en œuvre en avril 2009 dans le cadre du stage de césure d'Olivier Martin afin de préciser et confirmer les tendances observées pour un sous-ensemble d'espèces : des variables indicatrices de la plasticité morphologique propres à chaque espèce ont été mesurées en 2009 dans des conditions d'éclairement variées.

La plasticité comporte des propriétés spécifiques. La plus importante est qu'elle est le plus souvent et notamment dans le cas d'une variabilité spatiale de l'environnement qui nous intéresse ici, non exprimée et non mesurable sur un même individu. Pour une espèce donnée et un trait donné, la plasticité est mise en évidence par la mesure de ce trait sur des individus exposés à différents niveaux d'éclairement. Le nombre de répétitions (environ 20 individus par niveau d'éclairement) et l'analyse de variance nous permettent de discerner l'effet de l'environnement (plasticité) d'un effet du génotype des individus sur la valeur du trait ou d'une interaction génotype-environnement. Le terme de plasticité est donc employé lorsque l'effet de l'éclairement (LI) est significatif. Bien que d'autres indices existent (Valladares et al. 2006), la plasticité est mesurée comme la différence de valeurs médianes du trait entre individus dans deux environnements.

Les paramètres (position et amplitude) de l'axe de la niche représentant le niveau d'éclairement ont été estimés à partir du travail de (Vincent et al. 2011b) mené sur le site de Paracou et sont présentés au chapitre 2 (Table 3). Nous utiliserons dans la suite de ce document le terme de « niche de régénération » pour qualifier l'axe de la niche correspondant à la disponibilité de la ressource lumineuse. Ce jeu de données sur les arbres juvéniles a été analysé au moyen de modèles linéaires simples et d'analyses multivariées.

Le deuxième aspect de ce travail concerne la quantification de l'importance relative des variations intraspécifiques d'accroissement diamétrique produites par le gradient lumineux à l'échelle de la communauté et au stade adulte (diamètre à hauteur de poitrine $\geq$ 10 cm). Nous nous sommes appuyés sur les données de diamètre à hauteur de poitrine (DBH, diameter at breast height) relevées tous les ans ou tous les 2 ans (selon les périodes) dans le cadre du dispositif permanent de Paracou (Gourlet-Fleury et al. 2004). L'indice de Dawkins (Dawkins 1958) a été utilisé comme indicateur du niveau d'éclairement reçu. Sa pertinence est justifiée dans le chapitre 1 par une comparaison avec d'autres indices basés sur le diamètre ou la hauteur des arbres voisins.

## IV.3 Structure du mémoire

La présente thèse est rédigée « sur articles » : les chapitres 2 à 4 sont rédigés sous forme d'article publié, soumis ou en voie de l'être. Le chapitre 1 présente les méthodes de quantification de la lumière utilisées dans les chapitres suivants. Le chapitre 2 traitant les questions 1 et 2, est axé sur les variations des traits foliaires au stade juvénile et sur la signification écologique de leur plasticité. Le chapitre 3 apporte une contribution aux questions 3 et 4 et s'intéresse à la valeur fonctionnelle des traits morphologiques et de leur plasticité en relation avec les traits foliaires et la niche de régénération. Le chapitre 4 propose une quantification de l'importance relative de la intraspécifique de la croissance produite par la compétition pour la lumière au stade adulte et pour l'ensemble de la communauté. Le dernier chapitre fait la synthèse des résultats obtenus en revenant sur les questions formulées dans l'introduction et propose quelques pistes de recherche.

# 1$^{\text{ère}}$ Partie :

## Quantification of light conditions

We conducted two independent comparative studies of light measurement methods. The first one was performed on saplings and compared canopy closure index (LI) with a direct measure and an indirect measure of solar radiation. The second was performed on trees with a DBH>10 cm and compared crown position index (CP) with diameter- and height-based competition indices.

The scarcity of studies quantifying light as a growth driver is probably a consequence of the difficulty to estimate light availability for large trees over large areas in spite of the considerable research effort devoted to the measurement of light (Jennings et al. 1999, Engelbrecht and Herz 2001). Direct measurements of the solar irradiance within a forest canopy can be very accurate but such measurements are time-consuming and therefore unsuitable for large-scale studies (Engelbrecht and Herz 2001). Moreover by providing an instantaneous estimate of the irradiance at one point, these methods are susceptible to the large and rapid temporal variations of irradiance occurring on several scales (within a day, day-to-day and seasonal). Because of the technical difficulty and the financial cost associated with keeping numerous sensors over long time period within a forest canopy, these methods have failed to provide a robust estimation of the light regime experienced by large trees. Consequently, indirect estimates based on canopy structure are widely applied for ecological and forestry purposes and particularly for predicting tree growth. A large body of literature has shown the strong relationship between forest canopy structure and understory light transmittance (Nicotra et al. 1999, Lhotka and Loewenstein 2006, Takashima et al. 2006). In addition to basic metrics of forest structure such as stem density and basal area, hemispherical photography, canopy cover and canopy closure have been used to indirectly assess competition for light. In temperate one-species or even-aged forests where most studies on competition indices have been conducted, competition indices based on basal area showed good performances (Biging and Dobbertin 1995). In structurally complex forests, light interception might depend more strongly on individual tree position inside the canopy and on the surrounding canopy structure than on the basal area of neighboring trees. A reference study on a mixed conifer stands (Biging and Dobbertin 1992) reported that crown-based competition indices outperformed all the conventional competition indices. A few studies carried out in tropical heterogeneous forests (Gourlet-Fleury 1998, Moravie et al. 1999) found that competition indices based on tree crown position within the canopy were more accurate predictors of diameter increment than competition indices based on basal area.

## I. Estimation of light conditions experienced by juvenile trees

Tree light environment was evaluated at each census using a light index (LI) as the mean of two observers' scores (see also (Clark and Clark 1992). This index is a visual estimate of light regime based on the vegetation structure above and around the focal sapling: 1= no direct light, dense understorey; 2= light understorey (some lateral light due to close by gap, or thin upper canopy layer); 3= significant direct illumination associated to position either on the border of a large gap or well inside a small gap; 4=abundant vertical illumination (large gap center, track side).

The reliability of this index was assessed by a comparison with two others methods of characterization of light environment:

1) A direct measure of solar radiation with a quantum sensor. Photosynthetically active radiation transmission (%PAR) was estimated by the ratio of radiation measured on the top of the sapling to incident radiation in an open adjacent site supposed to depict incoming radiation on the top of the canopy. Subcanopy measures were performed with a LI-190 quantum PAR censor and referenced to an identical censor located less than 3 km apart in the open recording data continuously to a data logger (CR10X, Campbell scientific Inc.). Measures were made under overcast sky in April to August 2009 with no direct sunlight. This avoided most of the temporal and spatial variability associated to sunflecks.
2) An indirect method by hemispherical photography (Jennings et al. 1999). Digital hemispherical photographs were taken above selected saplings (180° fisheye lens, Nikkor 8mm f/2.8) before sunrise. The resulting image was analyzed using gap light analyzer software (GLA, (Frazer et al. 1999) to calculate Global Site Factor which is the fraction of total radiation received relative to that received above the canopy integrated over a year time.

We compared the ability of the various light indices (LI score, diffuse PAR transmission, GSF) to predict diameter increment ($GR_{DIA}$) and leaf mass per area (LMA) using the following linear model:

$$\text{Response Variable} = \text{Species} + \text{LI} + \text{Species} \times \text{LI}$$

As few saplings were characterized by the three estimates, we compared them by pairs. LI was the best predictor of diameter increment (highest $r^2$, Table 1). Whereas the best predictor of LMA was %PAR, yet LI was a better predictor than GSF.

The poor performance of hemispherical photography in our test is probably due to its low resolution under closed canopies, consequence of the difficulty to find a consistent threshold value to discriminate canopy from sky and the high sensitivity of GSF to this calibration. The problem is particularly acute under dense canopies (Ishida et al. 2003). Quantum sensor appears a more suitable method for very shady environment but it is subject to the large and rapid temporal variations of irradiance, reliable measure can only be taken under uniform overcast sky to avoid effect of highly localized sunflecks or possible interaction between gap direction and time of measurement in case of direct sunlight. This is a strong practical limitation. In any case the overall excellent performance of LI scores and its implementation easiness which allowed repeated assessment was favored. Later we report the mean of index values over the different censuses. Correspondence between LI score and %PAR are given in Table 1.

Table 1. a) Predictive value of two response variables (diameter growth rate GRDIA and leaf mass per area LMA) by three light estimates : percentage of photosynthetically active radiation (%PAR), global site factor (GSF) and light index (LI). R-squared (r2), root-mean squared error (RMSE) and sample size (N) are given. b) Correspondence between light index (LI) classes and percentage of photosynthetically active radiation (%PAR).

a)

| | | $GR_{DIA}$ | | | LMA | | |
|---|---|---|---|---|---|---|---|
| Sample n° | Light estimate | $r^2$ | RMSE | N | $r^2$ | RMSE | N |
| 1 | % PAR | 0.47 | 0.64 | 117 | 0.87 | 7.38 | 116 |
| | LI | 0.48 | 0.64 | 117 | 0.84 | 8.17 | 116 |
| 2 | % PAR | 0.8 | 0.45 | 26 | 0.95 | 6.47 | 25 |
| | GSF | 0.75 | 0.50 | 26 | 0.97 | 5.21 | 25 |
| | LI | 0.82 | 0.39 | 26 | 0.94 | 6.60 | 25 |
| 3 | GSF | 0.44 | 0.64 | 60 | 0.81 | 7.20 | 60 |
| | LI | 0.63 | 0.52 | 60 | 0.91 | 4.98 | 60 |

b)

| LI | | %PAR | | |
|---|---|---|---|---|
| | N | mean | standard deviation | min-max |
| 1 | 59 | 1.3 | 0.7 | 0.5-4 |
| 2 | 34 | 2.8 | 1.5 | 1.2-6.5 |
| 3 | 26 | 4.7 | 1.9 | 1.9-8.6 |
| 4 | 1 | 11 | _ | _ |

## II. Estimation of light conditions experienced by adult trees

Height-based competition indices have seldom been evaluated although they might capture the main effect of the vertical organization of canopy structure. As crown characterization or individual tree height measurement requires significant additional monitoring effort, it is of obvious interest to ascertain the information added by crown-based competition or height-based competition indices to simpler diameter- based competition indices. To do so we compared local competition indices derived from stem diameter or stem height with a crown exposure score rated in the field.

## II.1 Competition indices

### II.1.1 Crown-based competition index

Crown position scores are defined as follows Figure 1 (Synnot 1979):

1) lower understorey trees, entirely shaded vertically and laterally by others crowns
2) upper understorey trees entirely shaded vertically but with some direct side light
3) lower canopy trees, partly exposed and partly shaded vertically by others crowns
4) upper canopy trees, exposed in entire vertical plan but with other crowns laterally
5) emergent, entirely exposed, free from competition for light, at least within the 90 inverted cone in which the crown lies.
6) The crown-based competition index was the crown position (CP) of each individual tree of the six plots and was measured in 2007 at the Paracou experimental site (22917 trees). Crown position indices allow standardized visual assessment of the relative position of individual tree crowns within the forest canopy.

### II.1.2 Diameter-based competition indices

We computed two diameter-based competition indices: 1) local basal area (LBA) was calculated as the sum of the basal area of the neighboring trees in a circular plot (15m-radius), 2) social status index (SSD) was an asymmetric index calculated as the difference between the dbh of the focal tree and the quadratic mean of the dbh of the neighboring trees. These indices are distance independent i.e. they do not take into account the distance between the focal tree and its competitors within the prescribed plot area.

### II.1.3 Height-based competition index

The height-based competition index (LIEB) is derived from (Lieberman and Lieberman 1989) and is based on distance and height of neighboring trees :

$\mathrm{LIEB} = \sum_{i=1}^{n} \Delta h/d$ (Eq.1)

n is the number of trees taller than the subject tree situated within a circular plot (radius=15m), $\Delta h$ is the difference between the height of subject tree and the height of neighbor i, d is the distance between the top of subject tree and the top of neighbor i.

Individual tree height was predicted by a Weibull non-linear model (Temesgen and Gadow 2004) adjusted on tree height and dbh data recorded in 2012 on 670 individual trees in the Paracou experimental. A single equation was used for all species.

CP is negatively correlated to tree competition pressure whereas LBA and LIEB increase with the level of competition. All species were treated as equivalent regarding the competition pressure (species identity was not considered).

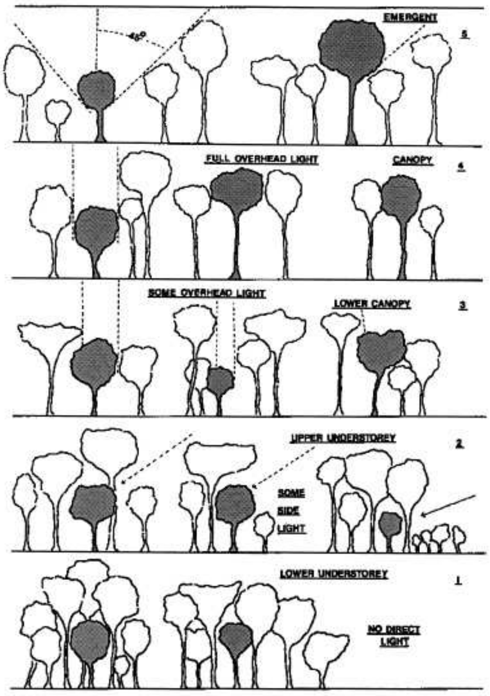

Figure 1. The five classes of canopy position in accordance with the Dawkins index (from Synnott 1979).

Table 2. a) Correlation matrix among competition indices: LBA (local basal area), SSD (social status index) and LIEB (Lieberman index). b) Error rate and Cohen's kappa coefficient relatives to the prediction of CP by competition indices.

a)

| | LBA | | SSD | | LIEB | |
|---|---|---|---|---|---|---|
| | r | p_value | r | p_value | r | p_value |
| LBA | 1 | | 0.36 | *** | -0.2 | *** |
| SSD | 0.36 | *** | 1 | | -0.83 | *** |
| LIEB | -0.2 | *** | -0.83 | *** | 1 | |

b)

| | Error rate | Cohen's kappa coefficient κ |
|---|---|---|
| LBA | 0.60 | 0.05 |
| SSD | 0.46 | 0.3 |
| LIEB | 0.46 | 0.3 |

## II.2 Prediction of CP by diameter- and height-based competition indices

### II.2.1 Method

To evaluate how much redundancy occurred between the various indices based on local basal area (and possibly height derived from an allometric model) on the one hand and the independently assessed CP indices on the other hand we used ordinal regression (*ordinal* R- package (R Development Core Team 2011)). Predictive ability of LBA, SSD and LIEB over all the trees of plots (16217 trees) was evaluated by the error rate between predicted and observed values of CP. For each variable, we also calculated the Cohen's kappa coefficient κ, which accounts for the agreement occurring by chance. κ ranges between 0 (no agreement) and 1 (complete agreement).

### II.2.2 Results

Relationships between competition indices are shown in Table 2 SSD and LIEB were strongly correlated ($r=0.77$, $p<0.001$).

Error rate in the prediction of CP varied from 0.59 to 0.46 (Table 2). Asymmetric competition indices (LIEB and SSD) outperformed symmetric and diameter-based competition indices (LBA) (Table 2). There was no difference in predictive power between diameter- and height-based asymmetric competition indices (SSD and LIEB). Cohen's kappa coefficient showed the same rank of indices but increased the gap between asymmetric and symmetric competition indices.

The ordinal regression showed that CP was neither reducible to diameter-based nor to height-based competition indices. Accounting for size-asymmetry improved CP prediction by 14% in term of error rate. Accounting for neighbor tree height in addition did not improve more CP prediction. It might partially result from the use of a single height-dbh allometry for all trees. We further performed the ordinal regression on a subplot (636 trees) where height was available for all the trees. In this context, considering height decreased further the error rate in CP prediction by 6% in comparison to the diameter-based and asymmetric competition index (SSD). The error rate in CP prediction was still equal to 40% probably as a result of the high variability of crown size and shape for a given height. These results underscore the size-asymmetric nature of competition for light and the limitations of applying diameter-based indices in tropical forest stands. Nevertheless DBH is still the standard and unique tree dimension recorded extensively on permanent sample plots in tropical forests because of the difficulty to measure tree height. Improving the accuracy of characterization of canopy structure would require an extensive effort of measurement difficult to carry out at the community scale. To overcome this problem, remote sensing technology appears as a promising technique for direct 3D measurement of plant structure (Todd et al. 2003, Falkowski et al. 2006, Coops et al. 2007, Pedersen et al. 2012).

# 2$^{ème}$ Partie :

# Functional traits and their plasticity predict regeneration niche even among tropical tree species with intermediate light requirements

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## Abstract

Niche differentiation is a key issue in the current debate on community assembly mechanisms. In hyper-diverse moist tropical forests, tree species sensitivity to canopy openness is thought to be a major axis in niche differentiation. In the past, the syndrome of traits driving the demographic trade-off involved in the niche-based theory of coexistence has always been established among species situated at the two extremities of the shade-tolerance gradient, even though most tropical tree species have intermediate light requirements. In addition, trait plasticity has seldom been linked to tropical tree species distribution along environmental gradients.

This paper examines covariations between leaf traits, whole-plant traits and niche parameters among 14 tree species with intermediate light requirements in French Guiana and across a range of canopy openness. Each functional trait measured under field conditions was characterized by a median value and a degree of plasticity expressed under contrasting light regimes. Niche differentiation was characterized in terms of spatial light gradient. We first examined covariations between functional traits then explored to what degree the median value and plasticity in functional traits could predict light niche characteristics at the sapling stage and the ontogenetic change in light availability estimated by adult stature.

Leaf mass per area (LMA) was positively correlated with leaf lifespan (LLS); species with higher LMA and higher LLS displayed lower diameter growth rates and lower responsiveness to canopy gap at both whole-plant and population levels. This proved that the relationships previously established over a broader range of species held true within the narrow range of the light requirements covered. Height growth rate plasticity accounted for 49% of the variation in light niche optimum. LMA plasticity, unlike LLS plasticity, was significantly correlated with light niche breadth and adult stature.

This study demonstrates the relevance of considering the phenotypic plasticity in functional traits in community ecology, particularly for quantifying breadth of species distribution over environmental gradients. Our findings did not support Hubbell's hypothesis of functional equivalence and suggest that even a rather subtle variation in forest canopy disturbance promotes the coexistence of tropical tree species.

**Key-words**: canopy disturbance, determinants of plant community diversity and structure, growth rate, irradiance, leaf lifespan, leaf mass per area, niche differentiation, phenotypic plasticity, shade-tolerance, tropical moist forest.

# I. Introduction

Niche differentiation is a key issue in the current debate on community assembly mechanisms (Leibold and McPeek 2006). Based on field experience on the island of Barro Colorado, Hubbell (2006) argued that most tree species are not niche differentiated and developed the “core hypothesis” of functional equivalence that contrasts with the deterministic niche-based view of community assemblage (Silvertown 2004, Kraft et al. 2008). The niche theory assumes that species respond differently to ecological heterogeneities and these differences are usually the result of trade-offs in the abilities of species to interact with various features of their environment (Kneitel and Chase 2004, Leibold and McPeek 2006). In moist tropical forests, the response of tree species to canopy openness is thought to be a major source of niche differentiation (Poorter and Arets 2003, Vincent et al. 2011b). Canopy disturbance regimes can therefore have a marked impact on community diversity and composition (Molino and Sabatier 2001). A demographic trade-off between high-light growth rate versus low-light survival rate has been identified in many studies (Davies 2001, Wright et al. 2003, Baraloto et al. 2005, Poorter et al. 2008) as a potential driver of tropical trees’ coexistence and has been associated with a syndrome of functional traits (Poorter and Bongers 2006, Sterck et al. 2011). This is challenged by the following argument: demographic trade-off occurs among species situated at the two extremities of the differentiation axis (Hubbell 2005), namely pioneer species and truly shade-tolerant species. But such species are scarce in tropical trees community (Clark and Clark 1992, Wright et al. 2003). Consequently, the niche theory has so far failed to explain how most tropical tree species coexist. In support of this and to the best of our knowledge, all studies investigating trade-offs among tropical tree species have included pioneer and truly shade-tolerant species. One exception is the study conducted by (Bloor and Grubb 2003) which corroborated the previous argument in that the authors found no relationship between survival in low light conditions and relative growth rate in high-light conditions. However, as this study considered 15 shade-tolerant tree species at the seedling stage and grown under controlled conditions, doubt persists as to whether niche theory assumptions hold for the majority of tropical tree species. The first objective of the study described herein was to address this question by testing the validity of the trait covariations observed between pioneer and truly shade-tolerant species in a subset of tropical tree species from which all pioneer and truly shade-tolerant species had been excluded. This group of species will hereinafter be referred to as ‘species with intermediate light requirements. The significant contribution of leaf traits to plant performance has previously been assessed by a modelling approach which showed that specific leaf area, photosynthetic capacity and leaf survival rate may jointly explain 50% of the growth-survival trade-off (Sterck et al. 2006a). Shade-tolerant species tend to have lower photosynthetic capacities, higher wood densities, higher leaf mass per area and longer leaf lifespans than pioneer species (Reich et al. 2003). Leaf mass per area and leaf lifespan are believed to have a direct effect on plant carbon budget and drive interspecific variations in growth rates and plant survival by controlling leaf investment returns (Westoby et al. 2002, Vincent 2006). Thus, functional traits have been widely used to predict species performance and demographic characteristics (Poorter et al. 2008, Wright et al. 2010, Herault et al. 2011). To date, functional traits have only seldom been linked to tropical tree species distributions along environmental gradients (Poorter and Bongers 2006, Sterck et al. 2011), though some recent studies advocate their usefulness for quantifying a species' niche (Mc Gill et al. 2006, Violle and Jiang 2009). In the study described herein, we tested whether the slow-fast syndrome of traits described above occurs among species with intermediate light requirements only and whether it is linked to species distribution along a light gradient resulting from canopy openness.

Intraspecific trait variability and phenotypic plasticity (Bradshaw 1965) have seldom been used to analyse functional traits, though an increasing number of studies report that they are, in many cases, quantitatively not negligible when compared to interspecific variability (Albert et al. 2010, Messier et al. 2010, Violle et al. In Press) and that they affect key ecological processes (Grime et al. 1986, Lecerf and Chauvet 2008, Violle and Jiang 2009, Berg and Ellers 2010, Jung et al. 2010)). Phenotypic plasticity is an important means by which individual plants can cope with environmental heterogeneity. Several studies have evaluated the relationship between phenotypic plasticity and niche breadth in annual species (Sultan et al. 1998, Sultan 2001)) and have provided evidence that generalist species show higher levels of phenotypic plasticity than specialist species. Very little is known about the role of phenotypic plasticity in environmental responsiveness among tropical tree species. We hypothesize that phenotypic plasticity in response to light plays an important role in shaping the niche of tropical trees. This is supported by the fact that most species have to cope with highly variable light conditions across (i) the understorey-gap horizontal gradient at the juvenile stage and (ii) the understorey-canopy vertical gradient along ontogenetic stages. To the best of our knowledge, only one study (Popma et al. 1992) has investigated the link between plasticity and light niche breadth in tropical trees: the authors showed among 68 Mexican tropical tree species that leaf traits variations in sun vs. shade environments were less significant for gap-specialist and understorey-specialist species than for gap-dependent species that occur over a wider range of light environments. Similarly, very few studies (Cai et al. 2005, Martinez-Garza and Howe 2005, Rozendaal et al. 2006) have examined the relationship between phenotypic plasticity and the range of light environments experienced along ontogenetic stages that are usually estimated through adult stature. Cai *et al.* (2005) and to a lesser extent Rozendaal *et al.* (2006), reported that leaf traits plasticity was greater in tall species that experience major, predictable changes in irradiance throughout their development than in smaller species that always remain in understorey or gap light conditions. By contrast, Martinez-Garza (2005) failed to find any such relationship among eight non-pioneer species.

The study described herein aimed to determine how leaf traits, whole-plant traits and niche parameters varied among 14 tropical tree species of intermediate light requirements across a range of canopy openness values. We focused on the sapling stage of development as differences in shade tolerance early in tree ontogeny are known to be a strong determinant of forest dynamics. Leaf mass per area and leaf lifespan were chosen as key descriptors of the species resource investment pattern. Whole-plant functional traits were derived from diameter and height growth rates under contrasting light environments. Each functional trait was characterized by a median value and a degree of plasticity in response to light level. Firstly, we aimed to test whether covariations between leaf mass per area and leaf lifespan and between leaf traits and whole-plant traits, held true for species known to have intermediate light requirements. Secondly, we investigated the relationship between functional traits and niche differentiation characterized in terms of spatial light gradient. We addressed the following questions: (i) to what degree can leaf or whole-plant traits (median value and degree of plasticity) predict population response to canopy disturbance (light niche optimum)? (ii) is leaf or whole-plant trait plasticity related to light niche breadth and/or adult stature?

# II. Materials and methods

This study made use of two independent data sets collected at the same experimental site in French Guiana. Values for functional traits were measured over the 2007─2009 period and niche parameters were derived from data previously published (Vincent et al. 2011b) and reanalysed in the present study.

## II.1 Study site and field measurements

The study was conducted in a lowland tropical rain forest at the Paracou experimental site (5o 18' N, 52o 55 'W) in French Guiana. Rainfall averaged 2,875 mm year$^{-1}$ over the 1986─2005 period with a 3-month dry season (less than 100mm month$^{-1}$) from mid-August to mid-November. The 14 non pioneer co-occurring species studied are common forest species in French Guiana (Table 3) and account for 27% of the total tree population (> 10cm diameter at breast height) at the Paracou experimental site.

In order to evaluate species-specific responses to different light regimes, an extensive search throughout the Paracou experimental station was conducted to identify suitable saplings (0.5─3m tall) in all light regime classes. These saplings were to be located outside seasonally flooded areas and any obviously resprouted stems were excluded (

Table 4). In all, 41─76 saplings per species (total 844) were selected, tagged and mapped. All saplings and their light environments were measured annually from 2007 to 2009 (or from the date of first encounter, after 2007).

## II.2 Light measurement

The light environment of each sapling was evaluated during each census by two observers using a light regime visual estimate based on the structure of the vegetation above and around the sapling. We used a scoring system similar to (Clark and Clark 1992) adapted to suit the forest structure at Paracou where 1= no direct light, dense understorey; 2= light understorey (some lateral light due to close by gap, or thin upper canopy layer); 3= significant direct illumination associated with position either on the edge of a large gap or well inside a small gap; 4=abundant vertical illumination (large gap center, track side). The mean of the two observers' scores was recorded for each census and the average light environment for each sapling was described by calculating the mean light index value for all the different censuses.

The reliability of this index was assessed for a subset of individual plants by comparing values with two other methods. Although these methods are potentially more accurate, they were unsuitable for use with large data sets over rugged terrain.

The first method consisted in a direct measurement of incoming solar radiation at the top of the sapling using a LI-190 quantum PAR sensor. An identical censor located less than three km away at an open site recorded data continuously to a data logger (CR10X, Campbell scientific Inc.) and thus provided a measurement of incoming radiation at the top of the canopy. Photosynthetically active radiation (% PAR) received by the sapling was estimated by calculating the ratio between incoming radiation measured at the top of the sapling and the incident radiation measured simultaneously in the open adjacent site. Measurements were made under an overcast sky (no direct sunlight) from April to August 2009 to avoid the temporal and spatial variability associated with sunflecks.

For the second comparison we used hemispherical photography (Jennings et al. 1999). Here, digital hemispherical photographs were taken above selected saplings (180° fisheye lens, Nikkor 8mm f/2.8) before sunrise. The resulting image was analyzed by gap light analyser software (GLA) (Frazer et al. 1999) to calculate the Global Site Factor (GSF), i.e. the fraction of total radiation received relative to that received above the canopy integrated over a year.

Light Index (LI) was seen to be closely correlated with both %PAR (Pearson correlation coefficient = 0.78, d.f. = 115, $P$ <0.001) and with GSF (Pearson correlation coefficient = 0.87, d.f. = 20, $P < 0.001$).

Table 3. List of study species with family name (following the Angiosperm Phylogeny Group classification (Angiosperm Phylogeny Group 2009)) abbreviations used (genus initial followed by species initial) in the figures, number (N) of saplings per species and by light index (LI) class and diameter range (min-max). Light niche parameters are indicated: POP-RESP is a measurement of the correlation between abundance and degree of canopy openness and reflects the niche optimum; degree of specialisation reflects species sensitivity to canopy openness and indicates species niche breadth; Hmax indicates adult stature.

| Family | Species | Abbreviation | N |  |  |  |  | Diameter range (mm) | POP-RESP | Degree of specialisation | Hmax |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | LI= 1 | LI= 2 | LI= 3 | LI= 4 | total |  |  |  |  |
| Fabaceae | Bocoa prouacensis | BP | 27 | 14 | 3 | 0 | 44 | 5.6-20 | -0,03 | 1,9 | 34 |
| Fabaceae | Dicorynia guianensis | DG | 24 | 21 | 16 | 2 | 63 | 6-20.2 | 0,00 | 1,2 | 52 |
| Fabaceae | Eperua falcata | EF | 24 | 25 | 20 | 4 | 73 | 5-18.5 | 0,03 | 1,7 | 44 |
| Fabaceae | Eperua grandiflora | EG | 33 | 24 | 18 | 1 | 76 | 5.2-17.2 | -0,06 | 2,1 | 42 |
| Lecythidaceae | Gustavia hexapetala | GH | 20 | 17 | 4 | 0 | 41 | 8.3-18.3 | 0,04 | 1,8 | 20 |
| Chrysobalanaceae | Licania alba | LA | 31 | 21 | 22 | 0 | 74 | 5-17.2 | 0,00 | 1,2 | 31 |
| Lecythidaceae | Lecythis persistens | LP | 20 | 21 | 12 | 1 | 54 | 8.7-19.3 | -0,02 | 1,3 | 37 |
| Annonaceae | Oxandra asbeckii | OA | 20 | 24 | 21 | 0 | 65 | 5.9-17 | -0,08 | 2,2 | 18 |
| Sapotaceae | Pradosia cochlearia | PC | 20 | 10 | 5 | 1 | 36 | 5.6-17.2 | -0,05 | 1,6 | 49 |
| Vochysiaceae | Qualea rosea | QR | 21 | 20 | 14 | 0 | 55 | 5.5-17.9 | 0,03 | 1,6 | 46 |
| Lauraceae | Sextonia rubra | SR | 21 | 25 | 4 | 0 | 50 | 4.8-20.2 | 0,00 | 1,4 | 44 |
| Clusiaceae | Symphonia sp. 1 | SS | 22 | 25 | 25 | 1 | 73 | 6-16.6 | 0,00 | 2,6 | 26 |
| Fabaceae | Tachigali melinonii | TM | 17 | 25 | 19 | 3 | 64 | 5.4-16 | 0,08 | 3,5 | 35 |
| Myristicaceae | Virola michelii | VM | 23 | 30 | 21 | 2 | 76 | 3.1-23.2 | 0,07 | 2,8 | 41 |

Table 4. Median values at low light (LI = 1) and plasticity index for leaf mass per area (g.m$^{-2}$), leaf lifespan (months), diameter growth rate (mm year$^{-1}$) and height growth rate (cm year$^{-1}$). Monotonic increases and decreases in functional trait median values with light level are indicated by sign”+” and”-“, respectively. Plasticity index standard deviations (SD, calculated by bootstrapping) are given. The Kruskall-Wallis test was applied to functional trait values across the two light classes corresponding to maximum and minimum median values. Levels of significance in this test are shown with *P* < 0.1, **P* < 0.05, ** *P* < 0.01, ****P* < 0.001.

| **Species name** | **Leaf mass per area (g.m$^{-2}$)** |  |  |  | **Leaf lifespan (months)** |  |  |  | **Diameter growth rate (mm.year$^{-1}$)** |  |  |  | **Height growth rate (cm.year$^{-1}$)** |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | Median at low-light | Plasticity index | SD | P | Median at low-light | Plasticity index | SD | P | Median at low-light | Plasticity index | SD | P | Median at low-light | Plasticity index | SD | P |
| *Bocoa prouacensis* | 69 | 7 | 3.7 | . | 102 | 54 | 34 |  | 0.2 | + 0.9 | 0.7 | ** | 4.2 | 9.3 | 4.6 |  |
| *Dicorynia guianensis* | 41 | + 17 | 2.1 | *** | 29 | 8 | 5 | * | 0.6 | + 1.3 | 0.3 | *** | 6.1 | + 25.5 | 4.6 | *** |
| *Eperua falcata* | 52 | + 12 | 2.1 | *** | 86 | - 55 | 30 | ** | 0.4 | + 1.1 | 0.1 | *** | 4.1 | + 8.7 | 3.0 | *** |
| *Eperua grandiflora* | 74 | + 12 | 2.8 | *** | 121 | - 52 | 38 | ** | 0.2 | + 0.8 | 0.2 | *** | 4.6 | + 10.2 | 3.2 | ** |
| *Gustavia hexapetala* | 47 | + 8 | 3.5 | * | 59 | 15 | 15 |  | 0.5 | + 1.0 | 0.3 | ** | 3.1 | + 10.0 | 3.1 | ** |
| *Licania alba* | 74 | + 17 | 2.5 | *** | 85 | 50 | 36 | . | 0.3 | + 1.1 | 0.2 | *** | 0.5 | + 26.6 | 6.6 | *** |
| *Lecythis persistens* | 87 | + 15 | 3.4 | *** | 110 | 51 | 67 |  | 0.3 | + 0.7 | 0.2 | *** | 9.5 | + 0.6 | 4.3 | * |
| *Oxandra asbeckii* | 64 | + 11 | 2.8 | *** | 71 | - 34 | 44 | * | 0.3 | + 0.8 | 0.1 | *** | 2.0 | + 6.7 | 4.4 | * |
| *Pradosia cochlearia* | 59 | + 24 | 6.5 | ** | 51 | - 28 | 14 | * | 0.4 | + 0.1 | 0.3 |  | 1.6 | + 7.3 | 1.5 | ** |
| *Qualea rosea* | 51 | + 15 | 1.9 | *** | 37 | - 15 | 4 | ** | 1.0 | + 2.4 | 0.7 | *** | 7.8 | + 26.2 | 10.1 | *** |
| *Sextonia rubra* | 51 | + 18 | 3.7 | * | 43 | 14 | 5 | ** | 0.3 | + 1.1 | 0.4 | * | 2.0 | + 19.8 | 5.7 | ** |
| *Symphonia sp. 1* | 64 | + 11 | 3.7 | *** | 56 | - 25 | 6 | *** | 0.9 | + 0.9 | 0.2 | *** | 7.9 | 20.0 | 4.0 | *** |
| *Tachigali melinonii* | 50 | + 9 | 1.8 | *** | 45 | - 17 | 6 | *** | 0.4 | + 1.1 | 0.4 | *** | 3.7 | + 33.1 | 10.6 | *** |
| *Virola michelii* | 45 | + 14 | 3.6 | *** | 32 | 5 | 8 |  | 0.7 | + 2.2 | 0.6 | *** | 2.6 | + 40.3 | 9.1 | *** |

## II.3 Whole-plant functional traits

*Diameter and height growth rates ($GR_{DIA}$ and $GR_{HT}$)* - Stem diameter was measured using Vernier callipers (precise to within one tenth of a millimeter) at a marked position on the stem 20 cm from the ground and in 2 orthogonal directions. The height of the main stem was determined using a measuring tape. Annual growth rate (GR) was assumed to be linear over the study period and was calculated as:

$$\mathrm{GR} = \frac{\mathrm{dG}}{\mathrm{dt}} = [(\mathrm{G2} - \mathrm{G1})/(\mathrm{t2} - \mathrm{t1})] \times 365$$

where G1 and G2 are diameter (mm) or height (m) at t1 (date of first census) and t2 (date of last census).

Annual growth rates were further tested for sapling size effect and, when appropriate, corrected as follows. A linear model using LI (categorical variable) and initial diameter (or height) as predictors was fitted for each species. If the size effect was significant ($P < 0.05$), the model was applied to the original dataset replacing observed diameter (or height) by species median diameter (or height) for all individuals. LI was left unchanged. The residuals associated with the original dataset were then added to model predictions. Adjusted growth rates were used instead of the original observed growth rates. The size effect was found to be significant in two species for diameter growth rate and in two species for height growth rates. This size effect was in all cases weak and the correction procedures only marginally affected the raw data values.

*Plasticity in growth rates* - Median $GR_{DIA}$ and $GR_{HT}$ values were computed for three light environments (low-light LI = 1, medium-light LI = 2, high-light LI = 3) after rounding each individual Light Index score. As the 14 species were not evenly represented in LI–4 (

Table 4), this light class was excluded from the analysis. Plasticity was quantified by the following index:

$$\text{Plasticity index} = \text{maximum median} - \text{minimum median}$$

In most cases, maximum median growth rate was observed under high-light conditions and minimum median under low-light conditions. The sign of the trait variation following an increase in light levels is given in Table 5. The significance of the plasticity index was tested by Kruskall-Wallis test on whole-plant trait values observed in the two light classes corresponding to maximum and minimum median values. Standard deviations were computed for the plasticity index estimate using bootstrap resampling (*Boot* package in R software (R Development Core Team 2011)).

## II.4 Leaf functional traits

*Leaf lifespan (LLS)* - Leaf censuses were conducted on the main axis of each sapling. In *Oxandra asbeckii,* which has no leaves on the main axis, we selected actively growing branches (i.e. avoiding lower most branches) that were sufficiently old to show some leaf abscission (most apical branches were therefore excluded). A leaf sequence was defined from the youngest leaf (fully expanded at the first census) to the oldest leaf found at the base of the axis. In the first census (conducted in June 2007, November 2007 or February 2008), a record was made of the number of leaves on each monitored axis and the position of the youngest leaf in the sequence was marked using colored adhesive tape. The number of leaves remaining in each sequence was further recorded (in July 2008 then in July or November 2009), yielding a sampling period of 5— 30 months depending on axis lifetime.

LLS (days) was estimated for each individual plant as the ratio of leaf number (N) to leaf death rate (T): $\mathrm{LLS} = \mathrm{N}/\mathrm{T}$

This approach has been successfully applied to leaf lifespan estimations in previous studies (Southwood et al. 1986, Ackerly 1996, Wright et al. 2002, Navas et al. 2003). The model (Little 1961), assumes a steady-state system, meaning that the axis must be in a process of active leaf production and loss. Because of the discrete leafing (flushes) of some species, leaf loss rate (T) was used instead of leaf arrival rate in this model. A final leaf population of 8625 leaves was used in the analysis, with an average of 616 leaves per species.

*Leaf mass per area (LMA)* - Five punches were taken between the main veins of leaves with a core (diameter = 16 mm) of standardized area in July 2008. Leaf mass per area ($\mathrm{g.m^{-2}}$) was calculated from leaf punch dry mass (oven-dried for 96h at 65°C) and punch area.

*Plasticity in leaf traits* - We used the same method as described for whole-plant traits.

## II.5 Functional trait analysis

Species median values under low, medium and high light conditions and the species plasticity index of functional traits formed the basis of the analysis of cross-species trait relationships. We computed Spearman's correlation coefficient (noted $r_s$) to evaluate ranking consistency among all the traits. The strength of the correlation between the various functional traits was dependent on light conditions, with correlations always being stronger for trait values measured under low or high light conditions (LI = 1 and LI = 3). One possible reason might be that the middle light index class (LI = 2) was less homogeneous, notably by including most cases of unstable LI over the monitoring period. As most of the saplings were located under closed canopy and because the species under high-light conditions showed an unbalanced distribution, only the correlation results obtained for saplings growing under low-light conditions (LI = 1) are presented and discussed herein. Nevertheless, plastic variations in functional traits across light environments were taken into account by considering the plasticity index.

## II.6 Maximum adult stature (Hmax)

This parameter was taken from (Favrichon 1995) for *Tachigali melonii* and from (Herault et al. 2010) for the 13 other species. Adult stature was used in the current study as a surrogate of the ontogenetic change in light availability experienced by a given species. Species Hmax ranged from 20 m to 52 m (Table 3).

## II.7 Light niche characterization

Light niche parameters at the sapling stage of the 14 species examined in the study were derived from the dataset and from results of a previous study conducted at the Paracou field station (Vincent et al. 2011b). These authors investigated the relative roles of habitat specialisation and dispersal limitation in shaping the spatial distribution of species. They provided a ranking of 49 tropical tree species based on how previous canopy disturbance affected the likelihood of saplings of each species being present. They quantified this sensitivity to canopy disturbance as the minus log of the odds ratios associated with a unit increase in log-distance to the nearest canopy disturbance. This index is termed POP-RESP (population response to canopy disturbance) in the current study. POP-RESP ranged from -0.23 to 0.56 for the 49 species found to be sensitive to disturbance and ranged from -0.08 to 0.08 for the subset of species considered in the present study (Figure 2). Of the 14 species studied here, 5 had a value greater than 0, indicating that species abundance decreased with distance from disturbed areas, 5 had values below 0, indicating an opposite trend and four had values not significantly different from 0, suggesting that disturbance had no – monotonic - effect on sapling abundance. POP-RESP was used as a proxy of the light niche optimum.

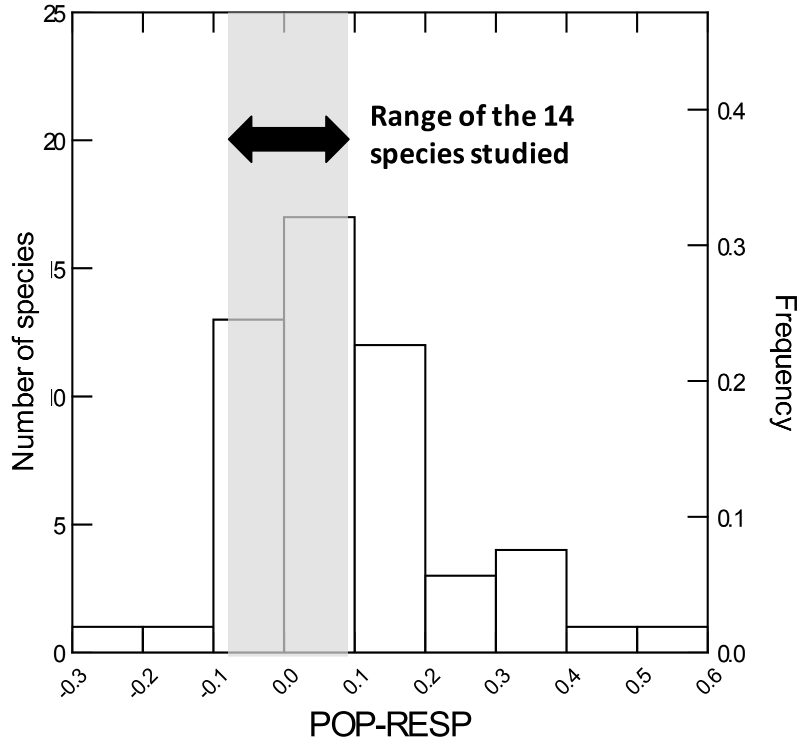


Figure 2. Distribution of 49 French Guianan tree species according to POP-RESP value (minus log of OddDist from Vincent *et al.* 2011). The position and the range of the 14 study species is indicated by a black arrow.

Niche breadth was assessed by determining the degree of specialisation to canopy disturbance regime. Hereafter, we use the expression "light niche breadth" to refer to this variable degree of specificity in light requirement. We re-analyzed the sapling inventory data collected by Vincent *et al.* (2011) to produce estimates of relative sapling abundance per class of disturbance. The original model was rerun after converting log transformed distance to nearest canopy disturbance into a categorical variable (four-level factor corresponding to 1 < 2.2 m, 2 < 7.2 m, 3 < 40 m and 4 > 40 m from canopy disturbance area). The predicted relative frequency of quadrats containing the target species per disturbance class was used to compute the degree of specialisation as the ratio of maximum to minimum relative frequencies. Lower degree of specialisation values were indicative of a broader niche (Thompson et al. 1998).

In order to analyse the multivariate association of leaf, growth trait and niche parameters, we conducted a principal component analysis based on a correlation matrix of median values obtained for low-light traits and trait plasticity in all the species. The median value of $GR_{HT}$ was excluded from the correlation matrix as it did not show a species effect (tested by a one-way ANOVA). Niche parameters (POP-RESP and degree of specialisation) and Hmax were later correlated with the PCA axes. Statistical analyses were performed by R software (R Development Core Team 2011) on untransformed values of LMA, LLS, $GR_{DIA}$ and $GR_{HT}$.

# III. Results

## III.1 Light niche characterization

Canopy disturbance had a non-significant effect on four species. Two of these (*Symphonia sp1.* and *Licania alba*) showed a clear hump-shaped response (Distance class effect $P$ value $< 0.05$) whereas the two others (*Dicorynia guianensis* and *Sextonia rubra*) did not (Figure 3). None of the 14 species studied showed the monotonic and systematically decreased abundance with distance to canopy disturbance typical of pioneer species. Pattern variability in each response group (Figure 3) indicated a great diversity of habitat specialisation, with some species preferring intermediate light conditions (*Symphonia sp1.* and *Licania alba*). The different species also exhibited a variety of light niche breadths, with degree of specialisation ranging from 1.2 to 3.5 (Table 3).

## III.2 Across-species correlation between leaf lifespan and leaf mass per area

Median LMA values ranged from 41 $g.m^{-2}$ to 87 $g.m^{-2}$ in low-light conditions and median LLS values ranged from 29 mo. to 121 mo. (Table 2). Leaf mass per area was seen to be closely correlated with leaf lifespan (LI = 1, $r_s = 0.83$, d.f. = 12, $P < 0.001$, Table 5).

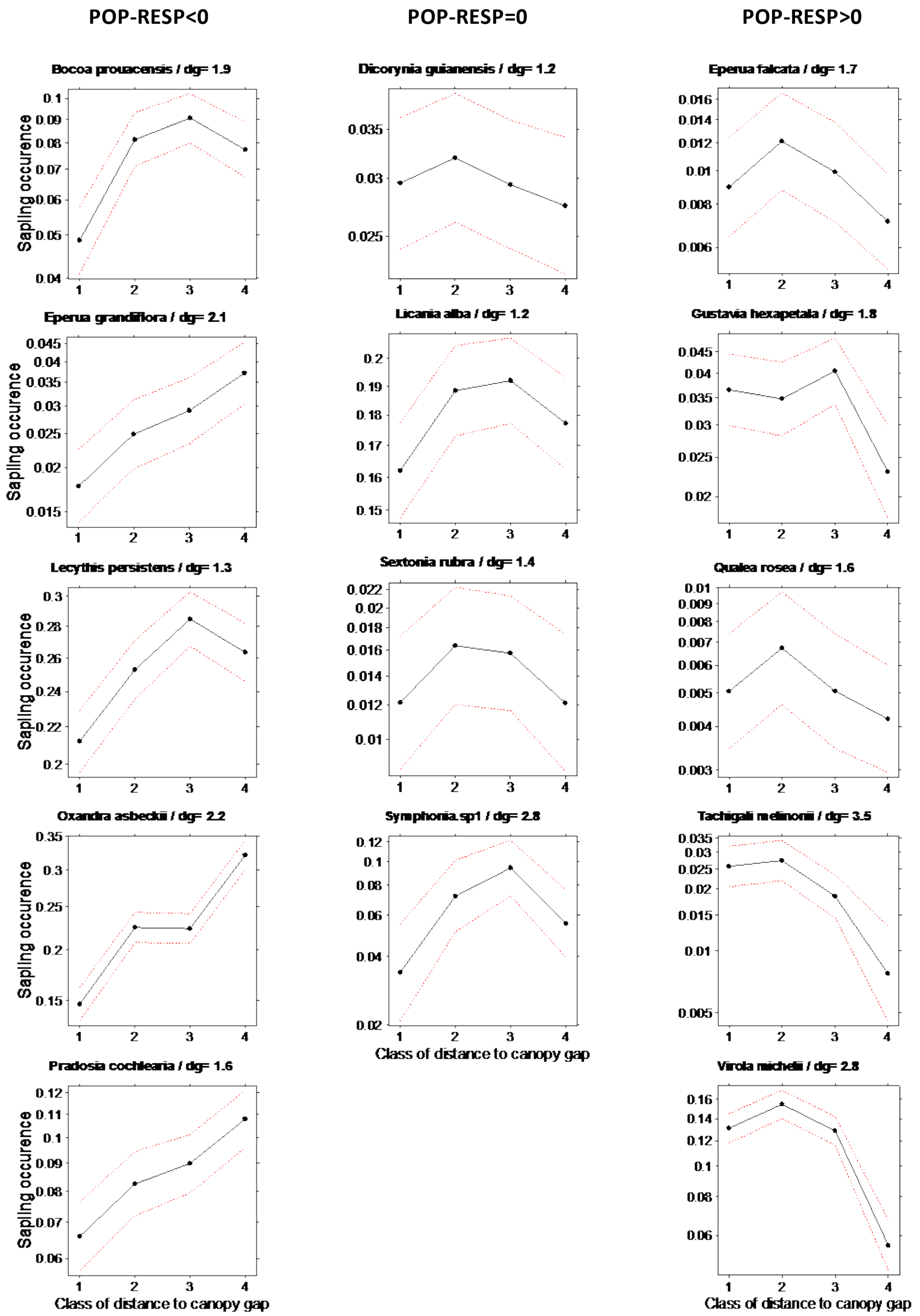
## III.3 Across-species correlations between leaf traits and whole-plant traits

Median growth rates under low-light conditions varied more than five-fold across species for $GR_{DIA}$ (0.2-1 mm $year^{-1}$) and 20-fold for $GR_{HT}$ (0.5-9.5 cm $year^{-1}$) (

Table 4). Canopy openness increased diameter growth rate (as indicated by a “+” before plasticity values in Table 2): the effect of LI on diameter growth rate ($GR_{DIA}$) was significant for all species except *Pradosia cochlearia* but the strength of the growth response (quantified by a growth rate plasticity index) differed among species. Growth rate plasticity was positively correlated with high-light diameter growth rate ($r_s = 0.85$, d.f. = 12, $P < 0.001$). Canopy openness also increased height growth rate for all species except *Bocoa prouacensis* (

Table 4). Additionally, $GR_{HT}$ plasticity varied markedly (0.6 to 40.3 cm year-$^{1}$) and was higher for saplings growing faster under high-light conditions (Spearman correlation coefficient of 0.93 between $GR_{HT}$ plasticity and high-light $GR_{HT}$).

LMA was negatively related to diameter growth rate and to diameter growth rate plasticity (Table 3). Species with a faster and more responsive diameter growth rate had lower leaf mass per area. No significant relationship was detected between LMA and height growth strategy. LLS was significantly and negatively correlated with diameter growth rate and with diameter and height growth rate plasticity indices (Table 5).



POP-RESP<0

POP-RESP=0

POP-RESP>0

Bocoa prouacensis / dg= 1.9

Dicorynia guianensis / dg= 1.2

Eperua falcata / dg= 1.7

Eperua grandiflora / dg= 2.1

Licania alba / dg= 1.2

Gustavia hexapetala / dg= 1.8

Lecythis persistens / dg= 1.3

Sextonia rubra / dg= 1.4

Qualea rosea / dg= 1.6

Oxandra asbeckii / dg= 2.2

Symphonia sp1 / dg= 2.8

Tachigali melinonii / dg= 3.5

Pradosia cochlearia / dg= 1.6

Virola michelii / dg= 2.8

Figure 3. Plot of relative sapling occurrence according to distance to canopy gap (as a categorical variable with 4 levels corresponding to 1 < 2.2 m, 2 < 7.2 m, 3 < 40 m and 4 > 40 m from canopy disturbance area) for 14 tropical tree species. Species name and degree of specialisation (dg) are indicated above each plot. Note that the vertical axis log scale differs among species. Dotted red lines indicate 95% confidence interval. Species-specific plots are grouped in three columns according to the sign of the population response to canopy disturbance (POP-RESP).

## III.4 Across-species correlations between functional traits, light niche parameters and adult stature

POP-RESP quantified the combined effects of differential growth, recruitment and survival for a period of a decade after a disturbance in alternate light environments and was used as a proxy of light niche optimum. POP-RESP and LMA were significantly correlated (see table 3 for Spearman's coefficient correlation, Pearson's correlation coefficient = -0.59, d.f. = 12, $P < 0.05$) though no significant relationship was found between POP-RESP and LLS (Table 5). Diameter growth rate plasticity showed the strongest rank correlation with POP-RESP ($r_s = 0.75$, d.f. = 12, $P < 0.01$) and explained 38% of POP-RESP variation (Pearson's correlation coefficient = 0.62, d.f. = 12, $P < 0.05$, Figure 4). The rank correlation between POP-RESP and height growth rate plasticity was less close than with diameter growth rate plasticity ($r_s = 0.66$, d.f. = 12, $P < 0.05$), but the predictive value of $GR_{HT}$ plasticity was higher (Pearson's correlation coefficient = 0.69, d.f. = 12, $P < 0.01$). The species studied showed differences in LMA and LLS plasticity (

Table 4). LMA increased monotonically with LI for all species while LLS decreased monotonically for seven of the 14 species (

Table 4).

LMA plasticity was significantly correlated with degree of specialisation ($r_s = -0.68$, d.f. = 12, $P < 0.01$) and with adult stature ($r_s = 0.64$, d.f. = 12, $P < 0.05$). It accounted for 25% of interspecific variations in degree of specialisation (Pearson's correlation coefficient = -0.5, d.f. = 12, $P < 0.01$) and for 38% of interspecific variations in adult stature (Pearson's correlation coefficient = 0.61, d.f. = 12, $P < 0.05$). By contrast, leaf lifespan, height growth rate and diameter growth rate plasticity did not show any significant relationship with degree of specialisation or adult stature (Table 5). Associations among the traits were analyzed by principal component analysis (Figure 5). The first PCA axis explained 59% of the variation and the second axis 17% of overall trait variation (Figure 5). The first axis reflects components of the species' successional status: negative coordinates were indicative of the most shade-tolerant species showing lower growth rates, higher LMA and LLS and a negative response to canopy disturbance; positive coordinates were indicative of species taking advantage of canopy disturbance with the highest and most responsive growth rates and the lowest LMA and LLS values. The second axis (dominated by LMA plasticity) is less readily interpretable but seems to mirror light niche breadth (expressed in terms of degree of specialisation) and to a lesser extent adult stature, with generalist and large-statured species at the bottom experiencing a wide range of irradiance regimes at the juvenile stage or along their lifecycle and displaying high LMA plasticity.

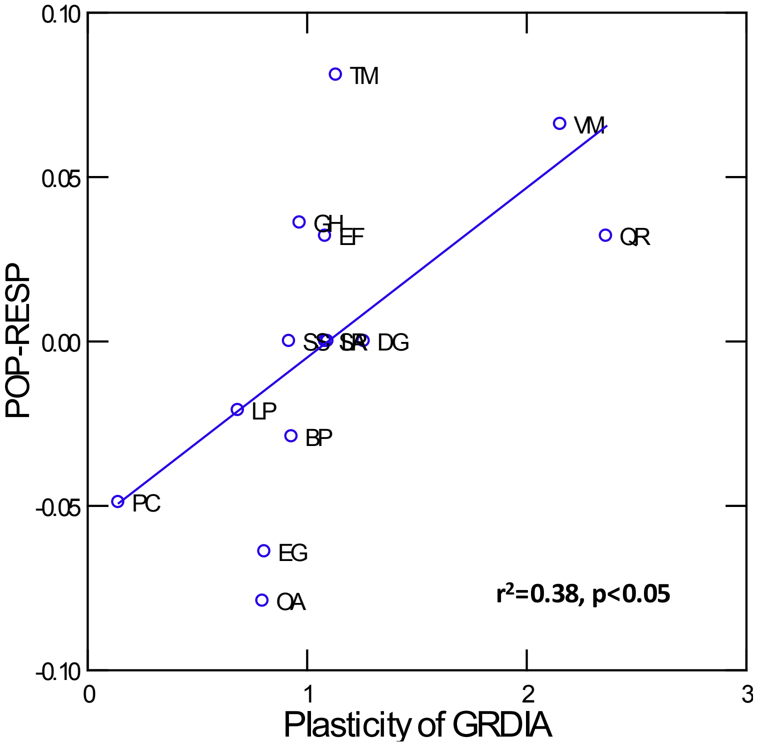


Figure 4. Across-species correlations between canopy disturbance response (POP-RESP) and diameter growth rate ($GR_{DIA}$) plasticity. Species are abbreviated as in Table 1. Regression line, coefficient of determination and significance level are shown.

Table 5. Spearman's correlation coefficients between POP-RESP, degree of specialisation, Hmax, median values by light index class and plasticity index for leaf mass per area (LMA), leaf lifespan (LLS), diameter growth rate ($GR_{DIA}$) and height growth rate ($GR_{HT}$). Levels of significance are shown with *$P < 0.05$, ** $P < 0.01$, ***$P < 0.001$.

| | | Leaf traits | | | | Whole-plant traits | | | | Light niche parameters | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $LMA_{LI1}$ | LMA plasticity | $LLS_{LI1}$ | LLS plasticity | $GR_{DIALI1}$ | $GR_{DIA}$ plasticity | $GR_{HT\ LI1}$ | $GR_{HT}$ plasticity | POP-RESP | Degree of specialisation | Hmax |
| Leaf traits | $LMA_{LI1}$ | | 0.03 | 0.83 *** | 0.76 * | -0.64 * | -0.64 * | 0.10 | -0.59 | -0.67 ** | -0.13 | -0.33 |
| | LMA plasticity | 0.03 | | -0.30 | -0.24 | 0.03 | 0.04 | -0.30 | 0.01 | -0.20 | -0.68 ** | 0.64 * |
| | $LLS_{LI1}$ | 0.83 *** | -0.30 | | 0.95 *** | -0.75 ** | -0.66 ** | 0.14 | -0.71 * | -0.51 | 0.03 | -0.41 |
| | LLS plasticity | 0.76 * | -0.24 | 0.95 *** | | -0.26 | -0.71 * | 0.05 | -0.76 * | -0.46 | 0.01 | -0.24 |
| Whole-plant traits | $GR_{DIALI1}$ | -0.64 * | 0.03 | -0.75 ** | -0.26 | | 0.48 | 0.14 | 0.53 | 0.55 * | 0.13 | 0.18 |
| | $GR_{DIA}$ plasticity | -0.64 * | 0.04 | -0.66 ** | -0.71 * | 0.48 | | -0.01 | 0.84 ** | 0.75 ** | -0.07 | 0.27 |
| | $GR_{HTLI1}$ | 0.10 | -0.30 | 0.14 | 0.05 | 0.14 | -0.01 | | 0.41 | 0.02 | 0.00 | 0.11 |
| | $GR_{HT}$plasticity | -0.59 | 0.01 | -0.71 * | -0.76 * | 0.53 | 0.84 ** | 0.41 | | 0.66 * | 0.17 | 0.10 |
| Light niche parameters | POP-RESP | -0.67 ** | -0.20 | -0.51 | -0.46 | 0.55 * | 0.75 ** | 0.02 | 0.66 * | | 0.19 | 0.04 |
| | Degree of specialisation | -0.13 | -0.68 ** | 0.03 | 0.01 | 0.13 | -0.07 | 0.00 | 0.17 | 0.19 | | -0.46 |
| | Hmax | -0.33 | 0.64 * | -0.41 | -0.24 | 0.18 | 0.27 | 0.11 | 0.10 | 0.04 | -0.46 | |

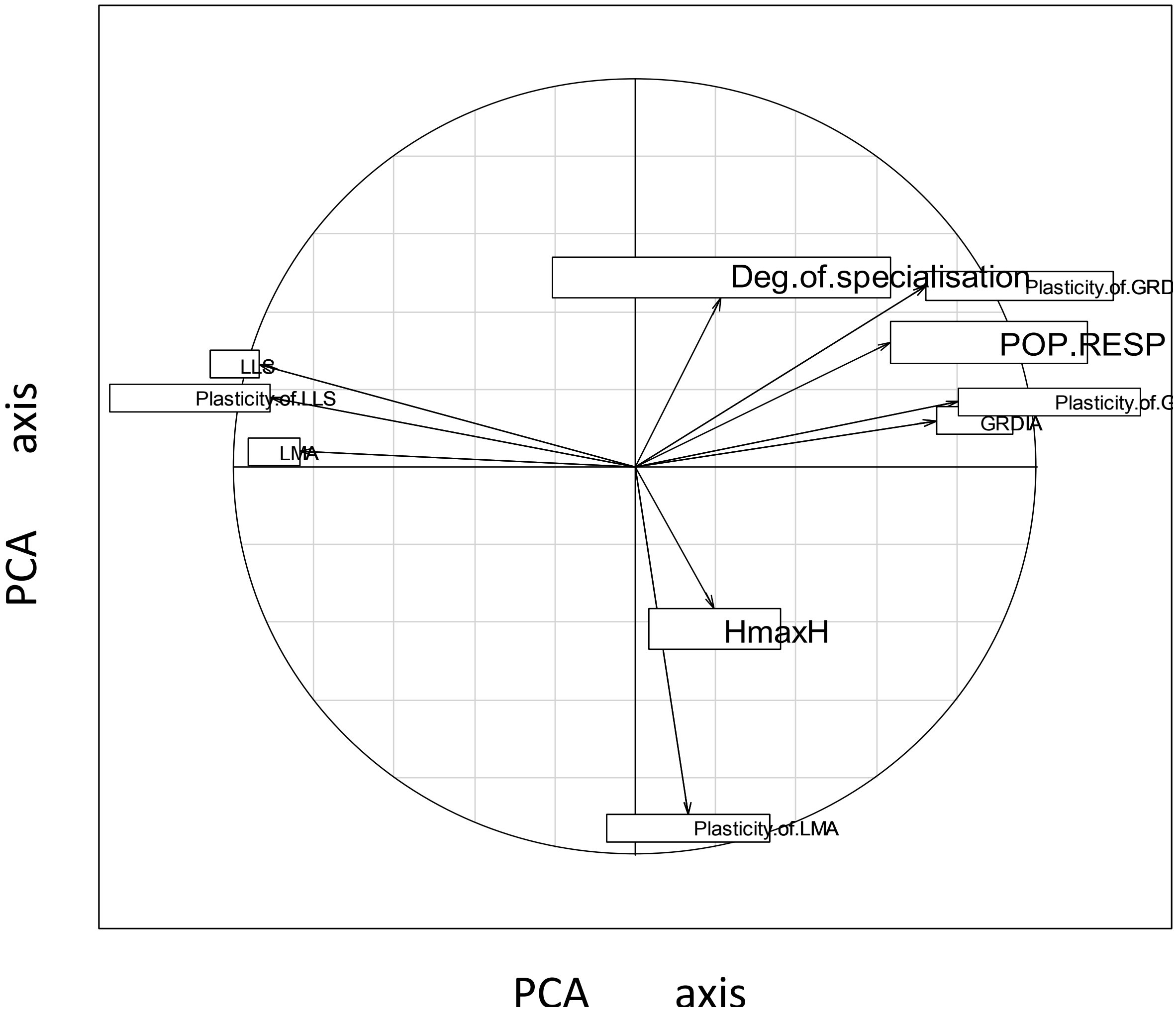


Figure 5. Plot of principal-component analysis ordination diagram showing traits (arrows). The first two axes jointly capture 76% of total variation in trait data. Population response to canopy disturbance (POP-RESP), degree of specialisation (Deg.of.specialisation) and Hmax were not included in the PCA analysis but were subsequently correlated with the PCA axis.

# IV. Discussion

This study aimed to test whether the pattern of trait covariation observed previously at the entire community level of tropical moist forests held true among the subset of species with intermediate light requirements and whether median values and plasticity in functional traits were related to niche parameters. Study results show first that leaf lifespan was closely correlated with leaf mass per area, even within this limited range of species light requirements. Second, whole-plant traits (and to a lesser extent leaf traits) correlated with the light niche optimum. Third, leaf mass per area plasticity in response to light was predictive of light niche breadth and adult stature.

## IV.1 General trends in trait covariations among species with intermediate light requirements

In spite of subtle differences regarding population responsiveness (POP-RESP), all 14 species studied showed differences at leaf and whole-plant levels that could be meaningfully linked with environmental factors. The interspecific variability noted in the leaf traits (twofold for LMA, four-fold for LLS) clearly demonstrates a marked functional diversity within the group of species studied. In comparison, (Sterck et al. 2006a) reported that leaf mass per area varied by a factor of ~4 and leaf lifespan by a factor of ~10 among saplings of 50 sympatric tree species in a Bolivian rain forest spanning the whole shade-tolerance gradient. We found that the LMA-LLS axis, which is a major dimension in plant ecological strategy (Westoby et al. 2002), emerged in 14 tropical tree species with intermediate light requirements. The evolutionary coordination of leaf lifespan and leaf mass per area is believed to have led to a higher leaf mass per area in the most shade-tolerant species (Lusk et al. 2008) despite the carbon-balance advantages of a low leaf mass per area in shaded conditions (lower construction costs per area and lower maintenance costs). However, we also observed that the relatively long leaf lifespan of two species (*Eperua falcata* and *Gustavia hexapetala*, see Figure 6) was associated with low to medium leaf mass per area. This may be explained by the differential contribution of leaf mass per area components to leaf lifespan. LMA can be described as the product of lamina depth and tissue density. Long leaf lifespan may therefore be achieved by a medium LMA through low leaf depth and relatively high tissue density or a large proportion of structural components that provide protection against herbivores and physical stress. (Lusk et al. 2010) reported that leaf cell wall fraction and punch strength were more robust correlates of juvenile light requirement than LMA. And additionally to mechanical resistance, long leaf lifespan can result from a great diversity of defense strategies: to date, no consistent syndrome of defensive investment in terms of chemical compounds, leaf toughness (component of LMA) or leaf nitrogen content has been found (Fine et al. 2006).

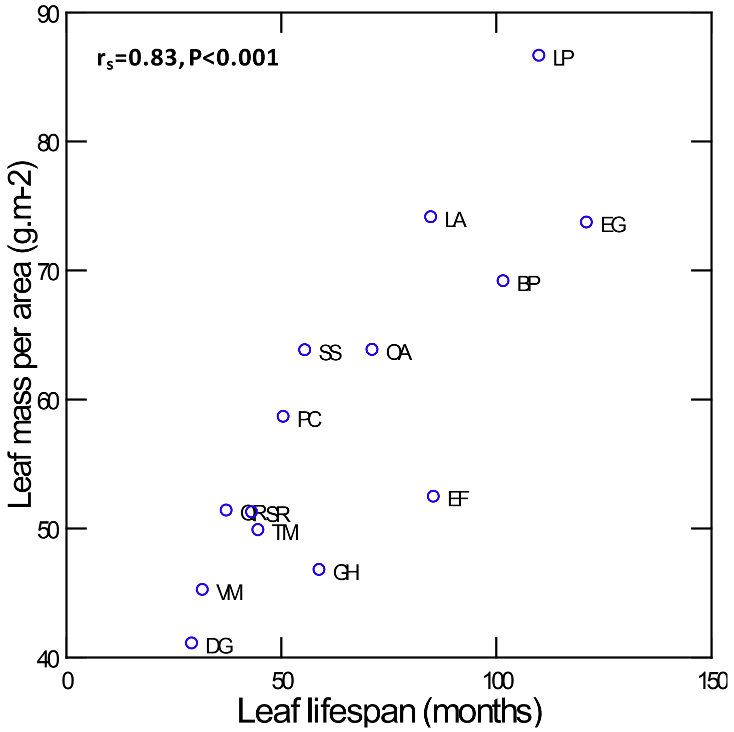


Figure 6. Across-species correlations between leaf trait values in low-light conditions (LI=1): leaf mass per area (g. $m^{-2}$) and leaf lifespan (months). Species are abbreviated as in Table 1. Spearman's rank correlation ($r_s$) and significance level are given.

Leaf traits and whole-plant traits provide a coarse yet consistent ranking of species in terms of degree of shade tolerance. To date, close correlations among functional traits have been established in most cases across different ecosystems (Reich et al. 1992). Regarding tropical moist forests, such trait-based approaches have been applied at the community level among species spanning the whole shade-tolerance gradient (Poorter and Bongers 2006) though (Wright et al. 2003) showed in a Panamanian tropical forest that few species are located at the extremities of the gradient and that most species have intermediate light requirements. We demonstrated here in this study that the syndrome of traits driving the demographic trade-off involved in the niche-based theory of coexistence held indeed among a set of 14 species from which all pioneer and truly shade-tolerant species had been excluded. As expected, we found that species with higher LMA and longer-lived leaves displayed lower diameter growth rate and lower responsiveness to canopy gap at both the whole-plant and population levels (Figure 5), thus suggesting an overall adaptation to an understorey hab*it*at. For example, long leaf lifespans are required under low light conditions to pay back the investment made in leaves. This is apparently achieved by a high LMA that should limit growth rate and responsiveness to gap opening. Conversely, species with lower LMA and short-lived leaves have a faster diameter growth rate and higher responsiveness to canopy openness. Low LMA and fast turnover of plant parts permit an efficient light capture and a more flexible response to light availability. Our study detected few significant correlations between leaf traits and height growth rate across species. This result is not entirely consistent with the study by (Poorter and Bongers 2006) involving 53 pioneer and shade-tolerant rain forest tree species at the sapling stage, which reported a significant linear trend between height growth rate and LMA ($r^2 = 0.19$, $P < 0.01$) and LLS ($r^2 = 0.19$, $P < 0.001$). Height growth rate might be less relevant in the present study because of the absence of pioneer species for which height growth is crucial to outcompete neighbors and survive.

## IV.2 Prediction of light niche parameters and ecological significance of plasticity

Whole-plant traits correlated more closely with light niche optimum than did leaf traits (Table 5). Height growth rate plasticity accounted for 49% of light niche optimum (POP-RESP). Contrary to the hypothesis put forward by (Violle and Jiang 2009), we observed that whole-plant traits plasticity was related to niche optimum, not to niche breadth. This result is consistent with previous findings among non pioneer species (Poorter and Arets 2003) and among pioneer and shade-tolerant rain forest tree species (Valladares et al. 2000). One possible explanation might be that species adapted to low-resource habitats may be less plastic in traits directly related to fitness, e.g. growth rate, and this as a by-product of specialisation to this environment (Lortie and Aarssen 1996). Shade-tolerant species, which are unable to make full use of abundant light and have a low average growth rate, are expected to show smaller differences in growth rate between high and low light environments. Therefore, restricting performance traits to vegetative biomass, reproductive output and plant survival, as proposed by (Violle et al. 2007) and as applied in our study, clearly showed its limits: it might be more relevant to consider diameter and height growth rates as performance traits rather than functional traits.

Median LMA accounted for 35% of the interspecific variation in light niche optimum (POP-RESP). In a study over 53 tree species spanning the whole range of shade-tolerance gradients, Poorter and Bongers (2006) found specific leaf area (1/LMA) ($r^2 = 0.50$) to be more predictive than we did. This difference in LMA predictive capacity might result from the wider range of LMA and niche optimum values investigated in the Poorter and Bongers study (2006). Again, in contrast with this study, we found LLS and light niche optimum to be only marginally correlated ($r_s = -0.51$, $P < 0.06$), perhaps for the same reason, i.e. that the variance in niche optima in our study was limited, thus reducing the power of the analysis. Predictions of plant or population performance along an environmental gradient might be further improved by considering traits related to stem economic spectrum (Chave et al. 2009) and shown to vary independently of leaf economic spectrum (Baraloto et al. 2010). (Poorter et al. 2010) demonstrated that wood density was also linked with growth and survival in large rainforest trees and that wood spectra were related to regeneration light requirement. Wood density is likely to shape plant functioning through its impact on carbon gain, biomechanical and hydraulic safety and defense. In support of this, (Herault et al. 2011) found that wood density was a significant predictor of ontogenetic variation in diameter growth rate among 50 rainforest tree species in French Guiana.

As expected, the study described herein provided evidence of a negative relationship between LMA plasticity and degree of specialisation along the light gradient ($r_s = -0.68$, $P < 0.01$), despite the exclusion of gap and understorey specialists from our subset of species. Species with a low degree of specialisation (occurring with an even frequency over the light gradient) exhibited greater LMA plasticity than species more specialised at one end of the light gradient. This underlines the adaptive value of LMA response to light level. One hypothesis underlying this adaptive response is that interception is optimized in low-light through a greater leaf area per unit leaf biomass; under high-light conditions, photosynthesis rates are increased by greater leaf biomass for a given unit of leaf area. This has been corroborated by comparisons between sun and shade leaves (Onoda et al. 2008); the results showed sun leaves to contain larger amounts of palisade mesophyll associated with a higher photosynthetic capacity (Niinemets 1997). Overall, this finding suggests that leaf mass per area plasticity might enable species to enlarge their light niche breadth. In the past, the literature on LMA and other leaf trait plasticity in tropical trees mainly focused on the correlation with light niche optimum. These studies (Valladares et al. 2000, Rozendaal et al. 2006, Lusk et al. 2010) did not result in a clear consensus but postulated that plasticity is greater in pioneer species as these experience more pronounced and more predictable light variations. This lack of consistency might stem from differences between studies in terms of ontogenetic stage (plasticity is likely to depend on ontogenetic stage, see (Thomas and Winner 2002), observational conditions (field versus controlled environment) and methods of plasticity quantification. These conflicting results may also suggest that there is no significant relationship between LMA plasticity and light niche optimum. Our findings point toward phenotypic plasticity in functional traits that warrants further investigation in relation to niche breadth. The present study also supported the working hypothesis that leaf plasticity in response to light level is higher for species subjected to a major ontogenetic change in light availability, reflected by high adult stature (Table 5). This result suggests that LMA plasticity expressed at the sapling stage may reflect adaptation to the spatial heterogeneity of light conditions encountered both at the sapling stage and along several ontogenetic stages.

## V. Conclusion

This study provides insights into the spectrum of trait values found under natural conditions in a set of 14 co-occurring rain forest tree species from which all pioneer and truly shade-tolerant species had been excluded. The leaf mass per area─leaf lifespan differentiation axis captured important features of adaptation along the gap-understorey continuum and provided an accurate prediction of whole-plant traits. We confirmed that in spite of the variety of trait combinations, tropical tree species with intermediate light requirements can be ranked along a continuum of leaf traits that scale with response to canopy disturbance (Wright et al. 2003). Also, in line with the assumptions made by (Violle and Jiang 2009) and with recent papers promoting the ecological significance of intraspecific variability and functional trait plasticity (Berg and Ellers 2010, Albert et al. 2011, Violle et al. In Press), this study clearly demonstrated the usefulness of taking functional trait plasticity into account when quantifying the niche parameters of tropical tree species over environmental gradients.

The functional equivalence hypothesis is the keystone of neutral theory (Hubbell 2005): it states that species differences are independent of traits influencing their fitness or their demography and their interactions with the biotic and abiotic environment (Leibold and McPeek 2006). Our findings did not support this hypothesis, at least for tropical tree species, as we found that leaf traits, growth rates, growth response to light and spatial distribution correlated significantly with respect to light across species with intermediate light requirements. Hence, differences among species, reflecting the majority of tropical tree species, in terms of light requirement, were related to differential responses to environmental heterogeneities that are expected to promote coexistence by stabilizing mechanisms (Chesson 2000). Our results constitute a significant step toward validation of the assumptions made in the niche-based theory of coexistence in the whole community of tropical forests and underline the important role played by canopy disturbance in promoting the coexistence of tropical tree species, as reported by (Molino and Sabatier 2001). By characterizing species distribution along an environmental gradient from functional traits, this approach provides a basis for predicting the effects of human- or climatic-induced changes of canopy disturbance regimes on species assemblages and thus potentially contributes to "rebuilding community ecology from functional traits" (Mc Gill et al. 2006).

# Références

Ackerly, D.D. (1996). Canopy structure and dynamics: integration of growth proceeses in tropical pioneer trees. In *Tropical forest plant ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 619-658. Chapman and Hall, New York.

Albert, C.c.H., Grassein, F., Schurr, F.M., Vieilledent, G., & Violle, C. (2011) When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 217-225.

Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S., & Lavorel, S. (2010) A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology*, **24**, 1192-1201.

Angiosperm Phylogeny Group (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linnean Soc.*, **161**, 105-121.

Baraloto, C., Goldberg, D.E., & Bonal, D. (2005) Performance trade-offs among tropical tree seedlings in constrasting microhabitats. *Ecology*, **86**, 2461-2472.

Baraloto, C., Timothy Paine, C.E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., Hérault, B., Patiño, S., Roggy, J.-C., & Chave, J. (2010) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**, 1338-1347.

Berg, M. & Ellers, J. (2010) Trait plasticity in species interactions: a driving force of community dynamics. *Evolutionary Ecology*, **24**, 617-629.

Bloor, J.M. & Grubb, P.J. (2003) Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. *Journal of ecology*, **91**, 77-85.

Bradshaw, A.D. (1965) Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, **13**, 115-155.

Cai, Z.Q., Rijkers, T., & Bongers, F. (2005) Photosynthetic acclimation to light changes in tropical monsoon forest woody species differing in adult stature. *Tree Physiol*, **25**, 1023-1031.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351-366.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual review of ecology and systematics*, **31**, 343-366.

Clark, D.A. & Clark, D.B. (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs*, **62**, 315-344.

Davies, S.J. (2001) Tree mortality and growth in 11 sympatric Macaranga species in Borneo. *Ecology*, **82**, 920-932.

Favrichon, V. (1995) Modèle matriciel déterministe en temps direct. Application à l'étude de la dynamique d'un peuplement forestier tropical humide (Guyane française). Claude Bernard, Lyon

1, Lyon.

Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Sääksjärvi, I., Schultz, J.C., & Coley, P.D. (2006) The growth defence trade-off anf habitat specialization by plants in Amazonian forests. *Ecology*, **87**, 150-162.

Frazer, G.W., Canham, C.D., & Lertzman, K.P. (1999) Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs *Copyright 1999: Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, New York; (http://www.rem.sfu.ca/forestry/index.htm or http://www.ecostudies.org).*

Grime, J.P., Crick, J.C., & Rincon, J.E. (1986). The ecological significance of plasticity. In *Plasticity in plants* (eds D.H. Jennings & A.J. Trewavas), pp. 5-29, Pindar, Scarborough, UK.

Herault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C.E.T., Wagner, F., & Baraloto, C. (2011) Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of ecology*, **99**, 1431-1440.

Herault, B., Ouallet, J., Blanc, L., Wagner, F., & Baraloto, C. (2010) Growth responses of neotropical trees to logging gaps. *Journal of applied ecology*, **47**, 821-831.

Hubbell, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, **19**, 166-172.

Jennings, S.B., Brown, N.D., & Sheil, D. (1999) Assessing forest canopies and understorey illumination : canopy closure, canopy clover and other measures. *Forestry*, **72**.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. (2010) Intraspecific variability and trait-based community assembly. *Journal of ecology*, **98**, 1134-1140.

Kneitel, J.M. & Chase, J.M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, **7**, 69-80.

Kraft, N.J.B., Valencia, R., & Ackerly, D.D. (2008) Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. *Science*, **322**, 580-582.

Lecerf, A. & Chauvet, E. (2008) Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology*, **9**, 598-605.

Leibold, M.A. & McPeek, M.A. (2006) Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, **87**, 1399-1410.

Little, J.D.C. (1961) A Proof of the Queueing Formula $L = \lambda W$. *Operations Research*, **9**, 383-387.

Lortie, C.J. & Aarssen, L.W. (1996) The specialization hypothesis for phenotypic plasticity in plants. *International Journal of Plant Science*, **157**, 484-487.

Lusk, C.H., Onoda, Y., Kooyman, R., & Gutiérrez-Girón, A. (2010) Reconciling species-level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. *New Phytologist*, **186**, 429-438.

Lusk, C.H., Reich, P.B., Montgomery, R.A., Ackerly, D.D., & Cavender-Bares, J. (2008) Why are evergreen leaves so contrary about shade? *Trends in Ecology & Evolution*, **23**, 299-303.

Martinez-Garza, C. & Howe, H.A.F. (2005) Developmental strategy or immediate responses in leaf traits of tropical tree species? *International Journal of Plant Sciences*, **166**, 41-48.

Mc Gill, B.J., Enquist, B.J., Weiher, E., & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178-185.

Messier, J., McGill, B.J., & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838-848.

Molino, J.-F. & Sabatier, D. (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science*, **294**, 1702-1704.

Navas, M.-L., Ducout, B., Roumet, C., Richarte, J., Garnier, J., & Garnier, E. (2003) Leaf life span, dynamics and construction cost of species from Mediterranean old-fields differing in successional status. *New Phytologist*, **159**, 213-228.

Niinemets, Ü. (1997) Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. *Functional Ecology*, **11**, 518-531.

Onoda, Y., Schieving, F., & Anten, N.P.R. (2008) Effects of light and nutrient availability on leaf mechanical properties of *Plantago major*: a conceptual approach. *Annals of Botany*, **101**, 727-736.

Poorter, L. & Arets, E. (2003) Light environment and tree strategies in a Bolivian tropical moist forest: an evaluation of the light partitioning hypothesis. *Plant Ecology*, **166**, 295-306.

Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, **87**, 1733-1743.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J.-C., Peña-Claros, M., Sterck, F., Villegas, Z., & Sass-Klaassen, U. (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*, **185**, 481-492.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manriquez, G., Harms, K.E., Licona, J.C., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Pena-Claros, M., Webb, C.O., & Wright, I.J. (2008) Are functional traits good predictors of demographic rates ? Evidence from five neotropical forests. *Ecology*, **89**, 1908-1920.

Popma, J., Bongers, F., & Werger, M.J.A. (1992) Gap-dependence and leaf characteristics of trees in a tropical lowland rain forest in Mexico. *Oikos*, **63**, 207-214.

R Development Core Team (2011) R : A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Reich, P., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., & Walters, M.B. (2003) The evolution of plant functional variation : traits, spectra, and strategies. *International Journal of Plant Science*, **164**, 143-164.

Reich, P.B., Walters, M.B., & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365-392.

Rozendaal, D.M.A., Hurtado, V.H., & Poorter, L. (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology*, **20**, 207-216.

Silvertown, J. (2004) Plant coexistence and the niche. *Trends in Ecology & Evolution*, **19**, 605-611.

Southwood, T.R.E., Brown, V.K., & Reader, P.M. (1986) Leaf palatability, life expectancy and herbivore damage. *Oecologia*, **70**, 544-548.

Sterck, F., Markesteijn, L., Schieving, F., & Poorter, L. (2011) Functional traits determine trade-offs and niches in a tropical forest community. *Proceedings of the National Academy of Sciences*.

Sterck, F., Poorter, L., & Schieving, F. (2006) Leaf traits determine the growth-survival trade-off across rain forest tree species. *The American Naturalist*, **167**, 758-765.

Sultan, S.E. (2001) Phenotypic plasticity for fitness components in polygonum species of contrasting ecological breadth. *Ecology*, **82**, 328-343.

Sultan, S.E., Wilczek, A.M., Hann, S.D., & Brosi, B.J. (1998) Contrasting ecological breadth of co-occurring annual Polygonum species. *Journal of ecology*, **86**, 363-383.

Thomas, S.C. & Winner, W.E. (2002) Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree physiology*, **22**, 117-127.

Thompson, K., Hodgson, J.G., & Gaston, K.J. (1998) Abundance–range size relationships in the herbaceous flora of central England. *Journal of ecology*, **86**, 439-448.

Valladares, F., Wright, S.J., Lasso, E., Kitajima, K., & Pearcy, R.W. (2000) Plastic response to light of 16 congeneric shrubs from a panamanian rainforest. *Ecology*, **81**, 1925-1936.

Vincent, G. (2006) Leaf life span plasticity in tropical seedlings grown under contrasting light regimes. *Annals of Botany*, **97**, 245-255.

Vincent, G., Molino, J.-F., Marescot, L., Barkaoui, K., Sabatier, D., Freycon, V., & Roelens, J.B. (2011) The relative importance of dispersal limitation and habitat preference in shaping distribution of saplings in a tropical moist forest : a case study along a combination of hydromorphic and canopy disturbance gradients. *Annals of forest science*, **68**, 357-370.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.c.H., Hulshof, C., Jung, V., & Messier, J. (In Press) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution*.

Violle, C. & Jiang, L. (2009) Towards a trait-based quantification of species niche. *J Plant Ecol*, **2**, 87-93.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882-892.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., & Wright, I.J. (2002) Plant ecological strategies:

some leading dimensions of variation between species. *Annual review of ecology and systematics*, **33**, 125-159.

Wright, I.J., Westoby, M., & Reich, P.B. (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of ecology*, **90**, 534-543.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Diaz, S., Engelbrecht, B.M.J., Harms, K.E., Hubbell, S.P., Marks, C.O., Ruiz-Jaen, M.C., Salvador, C.M., & Zanne, A.E. (2010) Functional traits and the growth mortality trade-off in tropical trees. *Ecology*, **91**, 3664-3674.

Wright, S.J., Muller-Landau, H.C., Condit, R., & Hubbell, S.P. (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology,* **84**, 3174-3185.

# 3ème Partie:

# Plastic and evolutionary variations of tropical trees crown depth are not related to light harvesting strategy

En préparation

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## Abstract

The ecological importance of morphogenetic adaptation is not broadly recognized compared to physiological adaptation even though morphological variation in light-foraging strategies potentially play important roles in efficient light utilization and carbon assimilation in spatially and temporally heterogeneous environments. We conducted a field comparative study in French Guiana among tree saplings of 14 co-occurring species differing in light-niche optimum and breadth to examine functional value of morphological diversity and plasticity in response to canopy openness. We addressed the following questions: i) Are among species differences in crown depth related to leaf lifespan? ii) Does morphological plasticity contribute to optimize light capture and reduce self-shading under low light as suggested by the carbon gain hypothesis?

We did not found parallel patterns between shade-tolerant and heliophilic species and between shade and sun plants. Across species, multiple regression analysis showed that relative crown depth was significantly correlated with leaf-life span (LLS) (rs=-0.62, $P<0.05$) and not correlated with crown length extension. Within species displaying a reduction of crown depth in the shade, we found a significant positive correlation between crown vertical extension and relative crown depth. This result suggests that plastic adjustment of relative crown depth does not reflect a strategy of reduction of self-shading. In contrast, our study provides examples of morphological plastic responses which extend the maintenance of efficient foliage and enable to optimize light capture in shaded conditions. Integrating and scaling-up leaf-level dynamics to shoot- and crown-level helps to interpret in functional and adaptive terms inter- and intraspecific pattern of crown traits and to better understand mechanism of shade-tolerance.

Keywords: French Guiana, phenotypic plasticity, leaf lifespan, crown shape, shade-tolerance, self-shading.

# I. Introduction

Physiological adaptation of photosynthesis to light regime has long been recognized as a key process in determining plant acclimation and plant successional status. The ecological importance of morphogenetic adaptation is not so broadly recognized even though variation in light-foraging strategies and associated variation in tree morphology potentially play important roles in efficient light utilization and carbon assimilation in spatially and temporally heterogeneous environments. Selection for performance in the strongly limiting light conditions of forest understorey is likely to maximize light capture (Givnish 1988). Hence the carbon gain hypothesis of shade-tolerance (Sterck and Schieving 2007, Valladares and Niinemets 2008) states that maximization of net carbon gain drives evolutionary and plastic responses to light gradients. For reducing self-shading, shade-tolerant species are expected to have mono-layered crown and shallower crown forms than pioneer species. This hypothesis was verified across temperate deciduous tree species ((Horn 1971, Kikuzawa 2003, Valladares and Niinemets 2008, Niinemets 2010) but see (Lorimer 1983)) whereas studies conducted across tropical evergreen tree species (Poorter and Werger 1999, Sterck et al. 2001) but see (Kohyama and Hotta 1990) found the opposite pattern. Regarding leaf and performance traits, shade-tolerance has rather been related to the ability to survive in low-light conditions at the expense of high-light growth. Long leaf life span and high LMA drive this conservative resource/ stress-tolerance strategy (Westoby et al. 2002, Reich et al. 2003, Sterck et al. 2006a, Sterck et al. 2011) whereas rapid leaf turnover observed in pioneer species maximize carbon gain by keeping leaf area in high-light environments: through nitrogen resorption and recycling, it maximizes the efficiency of deployment of nitrogen resources (Hikosaka 2005). Plant crowns perform multiple functions including supply of water, biomechanical support of leaves and reproductive organs, and therefore have multiple constraints on their form and function (Pearcy et al. 2004). The differentiation of crown form of tropical trees might be explained by the role of leaf longevity as a component and a potential constraint on crown architecture (Pearcy and Valladares 1999). Crown depth is determined by the balance between crown apical extension and crown rise due to branch shedding (or leaf shedding in unbranched saplings). Hence, in species with erect orthotropic main shoot and lateral branches, crown rise is driven by organ (leaf or branch) lifespan (Seiwa et al. 2006). The influence of leaf life span on crown depth was theoretically verified with a functional-structural plant growth model (Sterck et al. 2005) but it has not yet, to our knowledge, been validated in a field comparative study.

At the intraspecific level, maximization of net carbon gain is also expected to determine how trees respond to light gradient. (Givnish 1988) postulated that evolutionary response may parallel plastic responses to shade. At the leaf level, this assumption has been challenged by a divergence of plastic and evolutionary responses of LMA to shade (Lusk et al. 2010). Three processes are likely to drive crown depth along the light gradient : 1) a reduction of leaf life span in the shade because of a negative carbon gain (higher dark respiration rate and compensation point) or because of a strategy of carbon and nutrients recycling (Hikosaka 2005): so far to our knowledge reduced lifespan of shaded leaves was only observed among temperate and deciduous light-demanding tree species (Seiwa et al.

2006),or in perennial herb (Hirose et al. 1988), 2) an increase of leaf lifespan in shaded conditions presumably resulting of a slower photosynthetic metabolism which delays leaf senescence (Vincent 2006). LLS was found to be negatively correlated within species to photosynthetic capacity in several studies ranging from herbaceous desert perennial to tropical tree species 3) a reduction of relative crown length in the shade resulting from a slower extension of the main stem (combination of reduction in leaf emission rate and unchanged leaf lifespan).

We conducted a field comparative study in French Guiana among tree saplings of 14 co-occurring species differing in light-niche optimum and breadth to examine inter-and intraspecific pattern of crown shape. The first objective was to test the hypothesis that among species difference in crown depth adjustment in the shade could be related to leaf lifespan. To determine which process may be shaping the response of the 14 species studied we examined relationships between leaf lifespan, crown depth and crown apical extension across species and light regimes.

The variety of shoot and crown morphologies capable of efficiently capturing light in tropical understorey is great and extends over species with very different phyllotactic patterns, crown architectures, leaf sizes and morphologies (Valladares et al. 2002, Valladares and Niinemets 2008). Hence, the second objective of the present study was to investigate plasticity in crown depth and crown slenderness in relation to plasticity in branching pattern and foliage display. We expected i) that low-light saplings would have more sparsely foliated crown and invest proportionally more in horizontal crown growth than in vertical crown growth (Sterck 1999), and ii) that these plastic adjustments would be more clearly expressed in less specialized species given that phenotypic plasticity is a potential adaptation to environmental heterogeneity (Alpert and Simms 2002).

In summary, the present study addressed the following questions:

- Does difference in leaf longevity explain the differences between interspecific and intraspecific crown adjustments to shade?
- Does morphological plasticity contribute to optimize light capture and reduce self-shading under low light as suggested by the carbon gain hypothesis?
- Is morphological plasticity higher in species with a large light regeneration niche than in species specialized in high- or low- light environment?

# II. Materials and methods

## II.1 Study site and field measurements

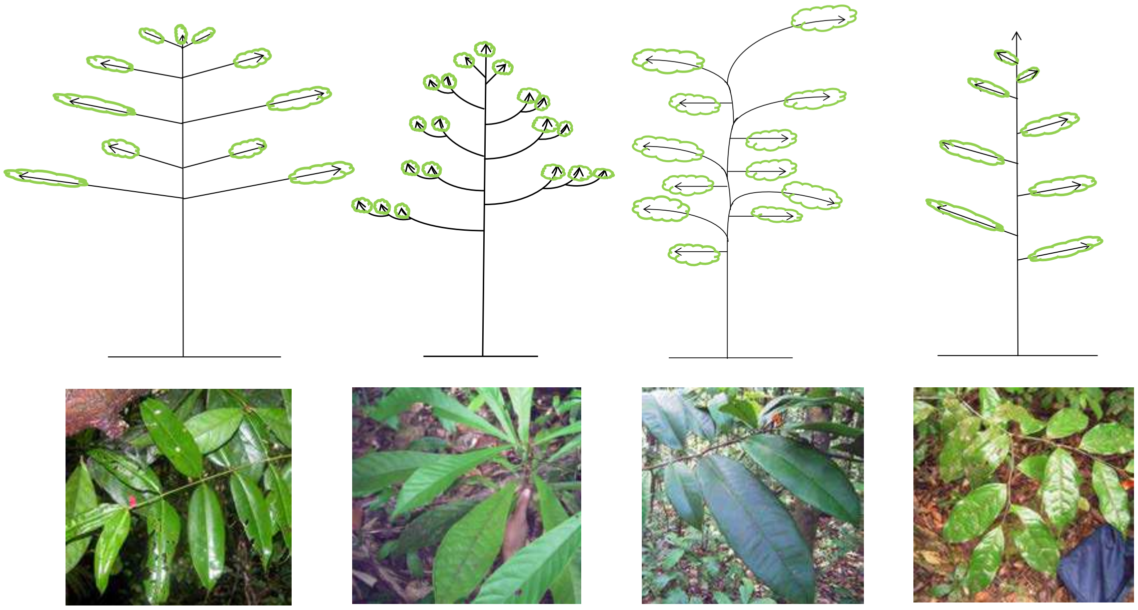
The study was conducted in a lowland tropical rain forest at the Paracou experimental site (5o 18' N, 52o 55 'W) in French Guiana. Rainfall averaged 2,875 mm year$^{-1}$ over the 1986-2005 period with a 3-month dry season (less than 100mm. month$^{-1}$) from mid-August to mid-November. The 14 non pioneer co-occurring species studied are common forest species in French Guiana () and account for 27% of the total tree population (> 10cm diameter at breast height) at the Paracou experimental site.

In order to evaluate species-specific responses to different light regimes, an extensive search throughout the Paracou experimental station was conducted to identify suitable saplings (0.5-3m tall) in all light regime classes. These saplings were selected outside seasonally flooded areas and any obviously resprouted stem was excluded. Overall, 41—76 saplings per species (total 844) were selected, tagged and mapped. All saplings and their light environments were measured annually from 2007 to 2009 (or from the date of first encounter, after 2007).

## II.2 Species description

Tropical trees have been classified into 23 different growth models by Hallé (1978) based on differences in axis orientation, growth rhythmicity and terminal or lateral position of flowers. The fourteen species exhibited contrasted architectures and inherited developmental patterns (Table 6 and Figure 7) and can be divided into four categories. Three species (*Symphonia*, *Virola* and *Qualea*) with a monopodial main stem differentiate plagiotropic and monopodial lateral branches from the orthotropic leader stem. These species are assigned to Massart's model in Hallé classification. The development of *Oxandra* corresponds to Roux' model with a monopodial orthotropic stem growing continuously like its plagiotropic branches whereas the development of *Tachigali* corresponds to Rauh' model with differentiation of monopodial stem growing rhythmically. Six species (*Bocoa, Dicorynia, Eperua f., Eperua g., Licania, Lecythis*) have a main stem formed sympodially from plagiotropic shoots and correspond to Troll's model. Among them, two species (*Eperua f., Bocoa*) displayed saplings with all axes more or less plagiotropic. For these species, leader stem and branches cannot be distinguished from one another within the developing crown. Thus the highest shoot was defined as the top of the main stem and other axes branching from this main stem were treated as lateral branches. At a later stage, a stem becomes visible as the axis that is most upright and that is thicker than the other axes which are eventually shed or develop more horizontally. In conformity with Aubreville's model (Fisher and Hibbs 1982), saplings of three species (*Gustavia, Pradosia and Sextonia*) develop sympodial, plagiotropic branches. *Pradosia* was the only species which modified its entire physiognomy along the light gradient. In the shaded understorey, it exhibits a plagiotropic and polyarchic development whereas in gap conditions, it exhibits an orthotropic and hierarchical development.

The sampled species can be divided into two groups of leaf type: those with large compound leaves (*Dicorynia, Eperua f., Eperua g.* and *Tachigali*) and those with smaller simple leaves (*Bocoa, Gustavia, Licania, Lecythis, Oxandra, Pradosia, Qualea, Sextonia, Symphonia, Virola*).We defined as 'leader stem' the axis responsible for the height growth and as 'branch' any other axis within the crown.

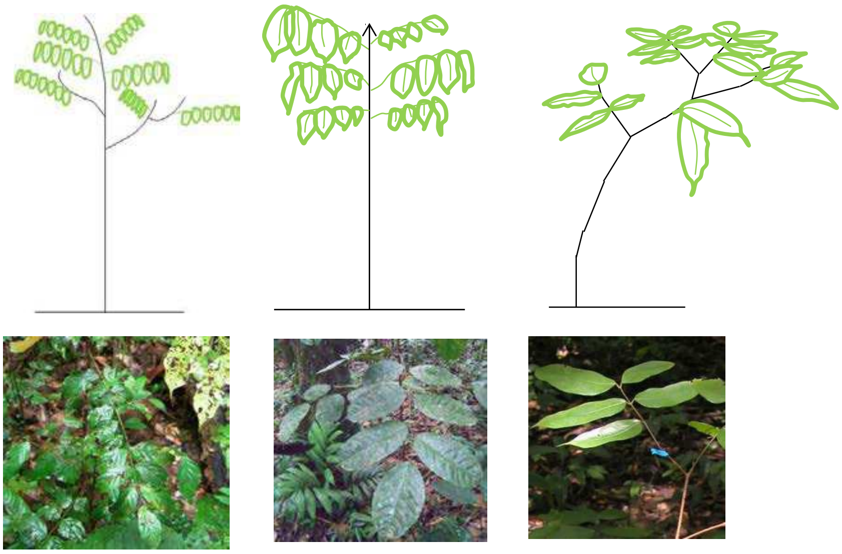


**Qualea r.,** Symphonia sp1, Virola m.

Gustavia h**., Sextonia r.**

**Lecythis p.,**Licania a.

**Oxandra a.**



Tachigali m.

Dicorynia g.

**Eperua f.,**Eperua g., Bocoa p.

Pradosia c.

Figure 7. Architectural pattern of the 14 studied species. Each green foliage symbol represents a leaflet of compound leaves or a pack of simple leaves. Photography represents the foliage of the species name printed in bold character.

Table 6. List of study species with abbreviations used (initial of genus followed by initial of species) in the figures, diameter range (min-max), architectural model as defined by Hallé et al. (1978), leaf type (C=compound,S=simple). Light-related niche traits are indicated: POP-RESP is a measure of the correlation between abundance and degree of canopy openness which reflects the niche optimum, degree of specialization reflects the species sensitivity to canopy openness and indicates species niche breadth, Hmax indicates the adult stature.

| Family | Species | Abbreviation | Diameter range (mm) | Architectural model | Leaf type | Phyllotaxy | POP-RESP | Degree of specialisation | Hmax |
|---|---|---|---|---|---|---|---|---|---|
| Fabaceae | Bocoa prouacensis | BP | 5.6-20 | Troll ? | S | Altern | -0,03 | 1,9 | 34 |
| Fabaceae | Dicorynia guianensis | DG | 6-20.2 | ? | C | Altern | 0,00 | 1,2 | 52 |
| Fabaceae | Eperua falcata | EF | 5-18.5 | Troll | C | Altern | 0,03 | 1,7 | 44 |
| Fabaceae | Eperua grandiflora | EG | 5.2-17.2 | Troll | C | Altern | -0,06 | 2,1 | 42 |
| Lecythidaceae | Gustavia hexapetala | GH | 8.3-18.3 | Aubréville | S | Altern | 0,04 | 1,8 | 20 |
| Chrysobalanaceae | Licania alba | LA | 5-17.2 | Troll | S | Altern | 0,00 | 1,2 | 31 |
| Lecythidaceae | Lecythis persistens | LP | 8.7-19.3 | Troll | S | Altern | -0,02 | 1,3 | 37 |
| Annonaceae | Oxandra asbeckii | OA | 5.9-17 | Roux | S | Altern | -0,08 | 2,2 | 18 |
| Sapotaceae | Pradosia cochlearia | PC | 5.6-17.2 | Aubréville | S | Opposite | -0,05 | 1,6 | 49 |
| Vochysiaceae | Qualea rosea | QR | 5.5-17.9 | Massart | S | Opposite | 0,03 | 1,6 | 46 |
| Lauraceae | Sextonia rubra | SR | 4.8-20.2 | Aubréville | S | Altern | 0,00 | 1,4 | 44 |
| Clusiaceae | Symphonia sp. 1 | SS | 6-16.6 | Massart | S | Opposite | 0,00 | 2,6 | 26 |
| Fabaceae | Tachigali melinonii | TM | 5.4-16 | Rauh | C | Altern | 0,08 | 3,5 | 35 |
| Myristicaceae | Virola michelii | VM | 3.1-23.2 | Massart | S | Opposite | 0,07 | 2,8 | 41 |

## II.3 Light measurement

The light environment of each sapling was evaluated during each census by two observers using a light regime visual estimate based on the structure of the vegetation above and around the sapling. We used a scoring system similar to (Clark and Clark 1992) adapted to suit the forest structure at Paracou where 1= no direct light, dense understorey; 2= light understorey (some lateral light due to close by gap, or thin upper canopy layer); 3= significant direct illumination associated with position either on the edge of a large gap or well inside a small gap; 4=abundant vertical illumination (large gap center, track side). The mean of the two observers' scores was recorded for each census and the average light environment for each sapling was described by calculating the mean light index value for all the different censuses. The reliability of this index was assessed for a subset of individual plants by comparing values with two other methods detailed in (Laurans et al. 2012) and found acceptable. Although these other methods were potentially more accurate, they were unsuitable for use with large data sets over rugged terrain.

We evaluated a series of plant traits at three different levels of organization: whole-plant, crown and leaf (listed in Table 7). We report the median value per light environment and per species and the plasticity across light environments of those traits.

## II.4 Whole-plant functional traits

*Diameter and height growth rates ($GR_{DIA}$ and $GR_{HT}$)* - Stem diameter was measured at a marked position on the stem ~20 cm from the ground and in two orthogonal directions. Verniers calipers were precise to within one tenth of a millimeter.

Table 7. Functional traits used to describe the leaf display, crown shape and growth of saplings.

| Level | Traits (units) | Abbreviations |
|---|---|---|
| Leaf | Unit leaf area ($cm^2$) | ULA |
| | Leaf mass per area ($g.m^{-2}$) | LMA |
| | Leaf lifespan (days/mo) | LLS |
| Axis | Leaf loss rate ($leaves.y^{-1}$) | LR |
| | Leaf production rate ($leaves.y^{-1}$) | GR |
| | Branch lifepan (mo) | BLS |
| | Internode length (cm) | IL |
| | Leaf cohort length (leaves) | leaf cohort/LC |
| | Branch extension ($cm.y^{-1}$) | LG |
| | Stem slenderness | hd |
| Crown | Branch spacing (cm) | brspacing |
| | Depth (cm) | CD |
| | Relative depth (%) | RCD |
| | Total leaf area ($cm^2$) | TLA |
| | Crown slenderness | CSHAPE |
| | Vertical extension ($cm.y^{-1}$) | vertical ext |
| | Branch number | nb |
| Plant | Diameter growth rate ($mm.y^{-1}$) | GRDIA |

The height of the main stem was determined using a measuring tape. For species displaying a bending main stem (*Eperua f., Eperua g.* and *Gustavia*), plant height reflects the height of the highest shoot.

Annual growth rate (GR) was assumed to be linear over the study period and was calculated as:

$$\mathrm{GR} = \frac{\mathrm{dG}}{\mathrm{dt}} = [(\mathrm{G2} - \mathrm{G1})/(\mathrm{t2} - \mathrm{t1})] \times 365$$

where G1 and G2 are diameter (mm) or height (m) at t1 (date of first census) and t2 (date of last census).

## II.5 Leaf traits

*Leaf life span (LLS, months), leaf loss rate (LR, $leaves.y^{-1}$), leaf production rate (GR, $leaves.y^{-1}$)* - Leaf censuses were conducted on the main axis and on three first-order branches of each sapling. A leaf cohort was defined from the youngest leaf (fully expanded at the first census) to the oldest leaf found at the base of the axis. In the first census (conducted either in June 2007, November 2007 or

February 2008), a record was made of the number of leaves on each monitored axis and the position of the youngest leaf in the cohort was marked using colored adhesive tape. The number of leaves remaining in each sequence was further recorded (in July 2008 then in July or November 2009), yielding a sampling period of 5— 30 months depending on axis lifetime. Leaf death rate (T) and leaf production rate (P) were estimated for each axis respectively as the ratio of the number of new or dead leaves with the sampling period.

The model applied is a biological application of a widely-used law in queuing theory called Little's law (Little 1961) which states that the time average number of arrivals in a queuing system, l, is equal to arrival rate λ times the average sojourn time w. Numerous studies have applied this approach to leaf lifespan estimations (Southwood et al. 1986, Ackerly 1996, Wright et al. 2002, Navas et al. 2003). This model assumes a steady-state system, meaning that the axis must be in a process of active leaf production and loss. This hypothesis was not verified for most branches, so they were excluded from the LLS sample, except for *Oxandra* which has no leaf on the leader shoot (orthotropic shoot). For that species, only plagiotropic branches bear the photosynthetic leaves. So only actively growing branches (i.e. avoiding lower most branches) and old enough branches (i.e. excluding apical branches showing no leaf abscission at first monitoring date) were used. Because of the discrete leafing (flushes) of some species (*Eperua f., Eperua g.*), leaf loss rate (LR) was used instead of leaf arrival rate. LLS (months) was estimated per individual plant as the ratio of leaf number (N) to leaf death rate (T) on the main axis of each sapling.

$$\mathrm{LLS} = \mathrm{N}/\mathrm{LR}$$

Final size of leaf population used in the analysis was 8625 leaves, with an average of 616 leaves per species.

*LMA* – We collected five punches between the main veins of leaves with a core of standardized area (diameter = 16 mm) in July 2008. LMA (g $m^{-2}$) was calculated from leaf punch dry mass (oven-dried for 96h at 65°C) and punch area.

*Unit leaf area (ULA, $cm^2$)* - A sample of leaves (1-4) was collected in a sub-sample of saplings per species. After leaf scanning, leaf area was quantified with the software Image J (http://rsb.info.nih.gov/ij/index.html). Unit leaf area of a given sapling was calculated as the mean of leaf area.

## II.6 Axis and crown traits

The number of leaves and of branches was counted annually. The height of the lowest leaf or branch, the maximum crown width and the crown width perpendicular to it were also measured annually.

*Total leaf area* (TLA, $cm^2$) - was the product of the mean leaf area and the total number of leaves.

*Crown depth* (CD, cm) - was defined as the difference between plant height and the height of the lowest leaf or branch. Most saplings of *Dicorynia, Sextonia* and *Eperua g.* (more than half of saplings) were unbranched, consequently for these species, crown represents most often leaf number and arrangement whereas for the others species, crown represents branch number and arrangement.

*Relative crown depth* - (RCD) was calculated as: crown depth/plant height.

*Crown slenderness* - (CRshape) was defined as the ratio between crown depth and maximum crown width.

*Stem slenderness* - (HD) was defined as the ratio between stem height and stem diameter.

*Mean branch spacing* - (BRspacing, cm) was calculated as the ratio between crown length and the number of tiers for *Virola* and the number of branches for the others species. It is considered a proxy of vertical self-shading within the crown.

*Internode length* - (IL, cm) was estimated for the shoot of the leader stem developed during the census period. IL was calculated as the ratio between the length and the number of nodes of this shoot portion.

*Differential growth between main stem and first-order branches* - The length of the main (vertical) axis and of plagiotropic branches was measured at the beginning and the end of the experiment. We then calculated and compared the extension rate of these axis over the sampling period ("vertical_ext" for the main axis and "lateral_ext" for the maximum value of branches extension rate in cm.y$^{-1}$) to evaluate the strength of apical control in contrasted light environments. Apical control regulates the amount of elongation and diameter growth of branches ; there is a wide range of levels of apical control under different conditions both between and within individual plants (Wilson 2000). A preferential investment in horizontal growth is likely to reduce self-shading.

*Crown rise* (CRrise in cm.y$^{-1}$)*:* from the repeated measures of the height of the lowest (hl) branch or leaf, we computed a rate of branch shedding (or leaf shedding in case of main stem was unbranched) over the sampling period as follow:

$$\mathrm{CRrise} = \left[(\mathrm{hl2} - \mathrm{hl1})/(\mathrm{t2} - \mathrm{t1})\right] \times 365$$

*Branch lifespan* (BLS, mo): leaf lifespan is likely to not correlate with branch lifespan and hence crown depth especially if branches display an indeterminate growth.

As we did not measure the rate of branch death or branch production, we estimated it from crrise and branch density (1/brspacing). Then we applied the model of Little to compute BLS:

$$\mathrm{BLS} = \text{number of branches} \,/ \left[\mathrm{CRrise} \times \left(\frac{1}{\mathrm{BRspacing}}\right)\right]$$

We excluded from this analysis three species (BP, EF, EG) which displayed a bending main stem and for which, consequently, branch shedding is not necessarily correlated with crown rise.

*Crown structure of Pradosia* - As preliminary observations showed that *Pradosia* exhibited a significant architectural variation along the light gradient we recorded for this species a specific categorical trait with two modalities: saplings displaying a plagiotropic and polyarchic crown structure were noted “P” whereas saplings displaying a hierarchic crown structure and an orthotropic leader stem were noted “O” (Figure 7).

## II.7 Sapling size effect

In spite of the small range of sapling size investigated, we tested the occurrence of a size effect on the whole set of measured traits (Table 11 en annexe). For most species, we observed a significant effect of stem diameter on crown dimensions, vertical extension, stem diameter increment, unit leaf area, number of leaves and number of branches. The significance of the size effect on the others traits depended on species .Size effect was controlled for by fitting a species-specific linear relationship between trait values, LI and stem diameter. If the size effect was significant ($P<0.05$), we applied the model to the original dataset by replacing, for all individuals, observed diameter values by species median diameter value and by leaving LI unchanged. Trait values were then recomputed by adding residuals of the original dataset to the model predictions. We used these values instead of the original observed trait values.

## II.8 Plasticity in functional traits

Median values of functional traits were computed for three light environments (low-light LI = 1, medium-light LI = 2, high-light LI = 3) after rounding each individual Light Index score. As the 14 species were not represented in LI=4 (Table 3), this light class was excluded from the analysis. Plasticity was quantified by the following index:

$$\text{Plasticity index} = \text{maximum median} - \text{minimum median}$$

The significance of the plasticity index was tested by a Kruskall-Wallis test on functional trait values observed in the three light classes. Standard deviations were computed for the plasticity index estimate using bootstrap resampling (*Boot* package in R software (R Development Core Team 2011)).

## II.9 Light niche characterization

Quantitative measures of light-niche parameters, namely niche optimum (POP-RESP) and niche breadth (degree of specialization), were estimated independently from dataset and results of (Vincent et al. 2011b). Data and methods are described in (Laurans et al. 2012).

## II.10 Interspecific and intraspecific variation analysis

We conducted a multiple regression analysis in order to estimate the respective influence of leaf life span and crown length extension on relative crown depth (RCD~LLS+vertical _ext).

The morphogenetic plasticity of *Pradosia cochlearia* was assessed by analyzing the distribution of species habit per light level (and its significance evaluated by a two-way chi-2 test). The general pattern of inter and intraspecific variation of crown shape was evaluated by principal components analysis of species median values of crown traits measured in low-, medium- and high-light conditions. For evaluating the correlation between species light requirement and the degree of morphological plasticity, we conducted a second principal components analysis based on species plasticity trait values and light-niche parameters.

We conducted a more in-depth analysis of plasticity strategy for five species (*Qualea*, *Virola*, *Symphonia*, *Pradosia*, *Oxandra*) displaying a varying degree of shade-tolerance and of specialization. We ran PCA successively for these five species on data at the individual level.

Statistical analyses were performed with the R software (R Development Core Team 2011) on untransformed values of traits (apart for the size effect correction as explained in the previous paragraph).

# III. Results

## III.1 General trend of inter- and intraspecific variation of crown shape

The PCA performed with species- and LI-specific median values of leaf, crown and whole-plant showed orthogonality between species and LI effects (Figure 8). The first axis of PCA explained 37% of traits variations and reflected the light spatial gradient whereas the second axis explained 26% of trait variation and reflected the shade-tolerance gradient with positive values corresponding to the most shade-tolerant species. Counter gradient variation of traits produce the following patterns: the most shade-tolerant species displayed the highest LMA, the longest LLS, the deepest and the most slender crown. Shade trees displayed longer LLS, but lower branch number, lower LMA, shallower and less slender crown than sun trees.

## III.2 Determinants of inter- and intra-specific variations of relative crown depth

Relative crown depth (RCD) in low-light was significantly correlated with POP.RESP ($r_s$=-0.54, P<0.05) indicating that more shade tolerant species tended to have deeper crowns. Across species, Spearman correlation analysis showed that relative crown depth was significantly correlated with leaf-life span (LLS) ($r_s$=0.61, P<0.05) and not correlated with crown length extension ($r_s$=-0.015, ns) (Figure 9). Spearman correlation analysis was only significant across species traits values measured in low-light conditions. We verified that LLS correlated positively with branch lifespan among the set of eleven species which exhibited a clear hierarchical branching pattern (r=0.83, P<0.01).

Within species, multiple regression analysis showed the significant positive effect of crown vertical extension on RCD for species displaying a reduction of crown depth in the shade and no significant correlation between LLS and RCD except for *Qualea* (Table 8).

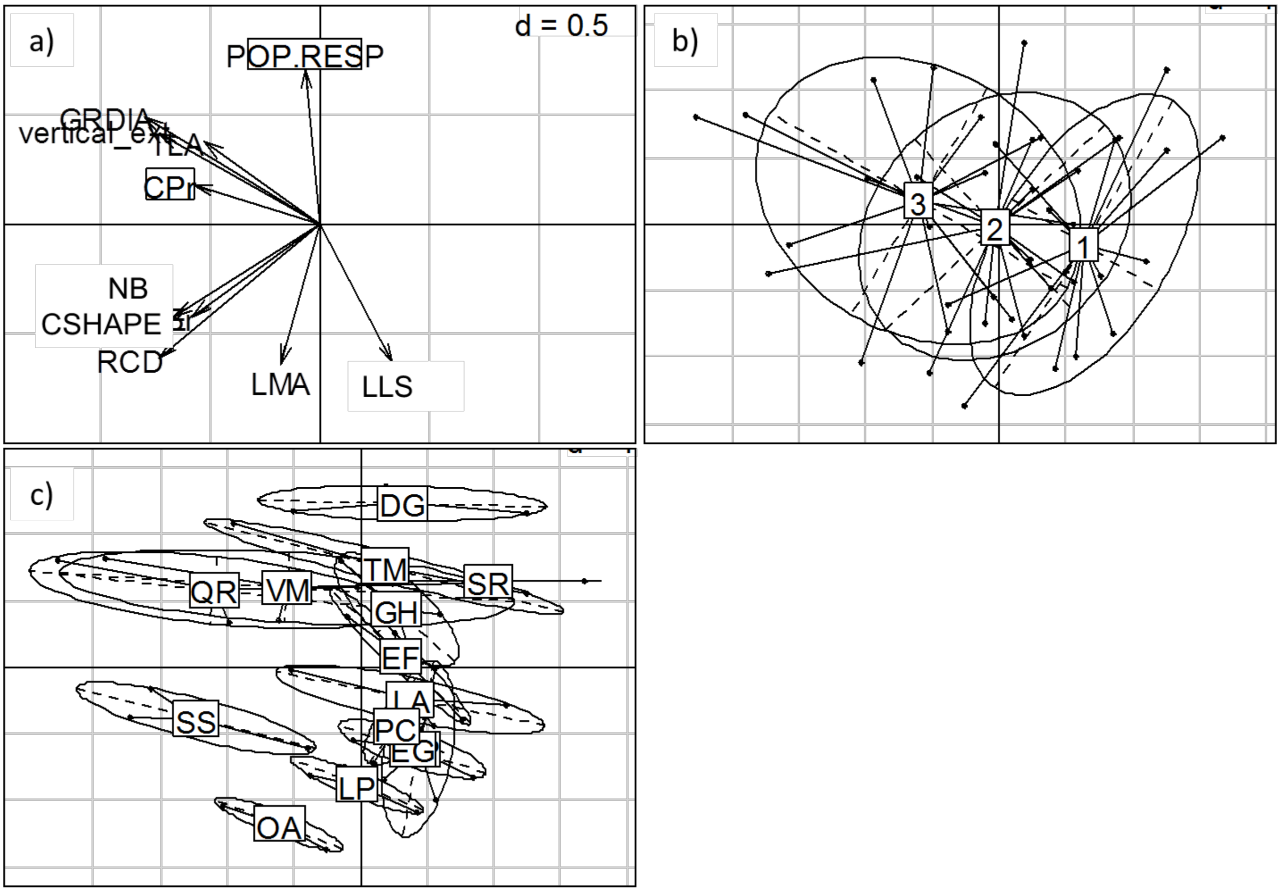


Figure 8. Plot of principal-component analysis ordination diagram showing traits (arrows in fig. a). Species and traits abbrevisations are detailed in Table 6. Fig. b and c represent dispersion of species and population in the trait space: b) trait syndromes averaged at the LI class level are spread around the trait syndrome averaged at the species level, c) trait syndromes averaged at the species level are spread around the trait syndrome averaged at the LI class level.

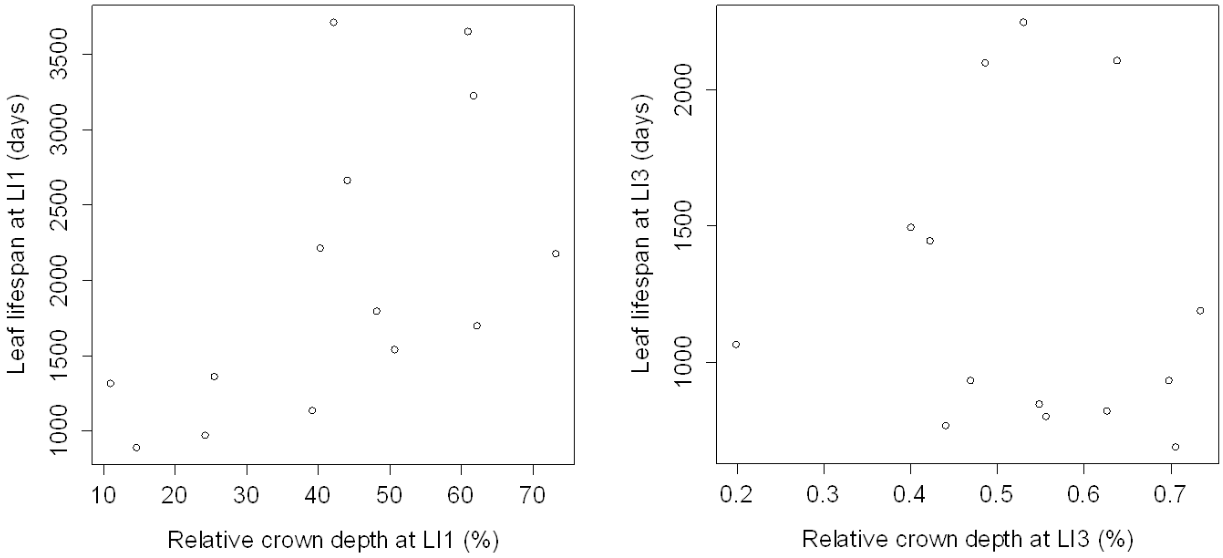


Figure 9. Scatterplot of relative crown depth (RCD) with leaf life span (LLS) in low-light (LI1) and high-light (LI3) conditions.

## III.3 Is morphological plasticity lower for the more specialized species?

The first axis of the PCA conducted on species plasticity trait values and light-niche parameters explained 33.5% of variation and the second axis 21.5% (Figure 10). The first axis predominantly reflects components of the species' successional status: negative coordinates were indicative of species taking advantage of canopy disturbance with the highest plasticity in growth rate, crown shape, total leaf area, relative crown depth and the lowest plasticity in LLS. The second axis related to the degree of specialization with negative coordinates indicating generalist species with highest plasticity in LMA. Plasticity in internode length only marginally contributes to the second axis.

Table 8. Multiple regression between relative crown depth and crown vertical extension. F value are given and Significance levels are shown with . P<0.1, *P <0.05, ** P<0.01, ***P<0.001. Underscored species names indicate a significant effect of LI on species RCD.

| | LLS vs.RCD | | | Crown extension vs. RCD | | |
|---|---|---|---|---|---|---|
| Esp | F | coef | P | F | coef | P |
| BP | 0,62 | 0,00001 | | 0,33 | -0,001 | |
| DG | 0,13 | 0,00001 | | 23,11 | 0,006 | *** |
| EF | 1,04 | 0,00002 | | 0,86 | -0,002 | |
| EG | 0,59 | 0,00001 | | 4,28 | 0,007 | * |
| GH | 4,84 | 0,00005 | * | 0,74 | -0,004 | |
| LA | 0,14 | -0,00001 | | 1,85 | 0,004 | |
| LP | 0,72 | 0,00001 | | 0,47 | -0,001 | |
| OA | 0,00 | 0,00000 | | 0,08 | 0,000 | |
| PC | 0,00 | 0,00000 | | 0,09 | 0,002 | |
| QR | 9,55 | -0,00008 | ** | 19,48 | 0,005 | *** |
| SR | 1,00 | -0,00003 | | 1,50 | 0,004 | |
| SS | 0,02 | 0,00001 | | 7,30 | 0,002 | ** |
| TM | 3,33 | -0,00005 | . | 6,72 | 0,004 | * |
| VM | 0,79 | -0,00004 | | 12,50 | 0,004 | *** |

Table 9.Plasticity index of crown, axis and leaf traits. Monotonic increase or decrease of median values with light level are indicated respectively by the sign "+" and the sign"-". Standard deviation (sd, calculated by bootstrapping) of plasticity index is given. Significance levels of this test are shown with . P<0.1, *P <0.05, ** P<0.01, ***P<0.001.

| Species | Oxandra asbeckii | Pradosia cochlearia | Qualea rosea | Symphonia sp1. | Virola michelii |
|---|---|---|---|---|---|
| | + | + | + | + | + |
| Plasticity of CSHAPE | 0,24 | 0,32 | 0,51 | 0,46 | 0,80 |
| sd | 0,12 | 0,31 | 0,10 | 0,12 | 0,17 |
| P | | | *** | . | *** |
| | + | + | + | + | + |
| Plasticity of RCD | 0,0751 | 0,1385 | 0,3371 | 0,1225 | 0,3746 |
| sd | 0,04 | 0,09 | 0,07 | 0,04 | 0,06 |
| P | | | *** | | *** |
| | + | - | + | + | + |
| Plasticity of TLA | 717 | 1622 | 2524 | 1480 | 1456 |
| sd | 281 | 827 | 1359 | 481 | 523 |
| P | | | | . | * |
| | - | - | + | + | + |
| Plasticity of BRspacing | 1,73 | 3,07 | 3,33 | 2,15 | 15,75 |
| sd | 0,888 | 2,173 | 0,781 | 1,362 | 2,740 |
| P | | | *** | | *** |
| | + | + | - | + | - |
| Plasticity of HD | 1,75 | 3,97 | 1,41 | 1,86 | 1,36 |
| sd | 0,953 | 2,175 | 0,734 | 0,822 | 0,722 |

| Species | Oxandra asbeckii | Pradosia cochlearia | Qualea rosea | Symphonia sp1. | Virola michelii |
|---|---|---|---|---|---|
| P | | | | . | |
| | + | + | + | + | + |
| Plasticity of vertical extension | 8,1 | 7,1 | 26,2 | 23,1 | 35,3 |
| sd | 4,4 | 1,5 | 10,1 | 4 | 9,1 |
| P | | * | *** | *** | *** |
| | - | - | + | + | + |
| Plasticity of CRrise | 0,49 | 7,93 | 10,38 | 5,08 | 14,21 |
| sd | 0,73 | 7,28 | 6,15 | 2,70 | 6,76 |
| P | | | ** | | |
| | + | + | + | + | + |
| Plasticity of GR BRHIGH | 0,0042 | 0,0092 | 0,0130 | 0,0052 | 0,0096 |
| sd | 0,001995664 | 0,003386988 | 0,005459487 | 0,002735906 | 0,002698059 |
| P | * | ** | ** | | * |
| | + | + | + | - | NA |
| Plasticity of GR BRLOW | 0,0025 | 0,0076 | 0,0076 | 0,0036 | 0,0000 |
| sd | 0,001199746 | 0,002748823 | 0,0048235 | 0,001755102 | 0,002034222 |
| P | | . | * | | |
| | + | + | + | + | + |
| Plasticity of GR BRMED | 0,0040 | 0,0075 | 0,0083 | 0,0044 | 0,0081 |
| sd | 0,0015 | 0,0036 | 0,0051 | 0,0026 | 0,0033 |
| P | . | ** | | . | |
| | + | + | + | + | + |
| Plasticity of GRA0 | 0,0027 | 0,0088 | 0,0217 | 0,0219 | 0,0147 |
| sd | 0,0012 | 0,0037 | 0,0073 | 0,0054 | 0,0046 |
| P | | * | *** | *** | *** |
| | + | + | + | + | + |
| Plasticity of ILA0 | 3,75 | 1,07 | 1,565 | 1,56 | 3,12 |
| sd | 1,944365885 | 0,567893737 | 0,367311838 | 0,440301211 | 0,686028713 |
| P | . | | *** | *** | ** |
| | + | + | + | - | + |
| Plasticity of IL BRLOW | 0,45 | 0,47 | 1,31 | 0,38 | 0,68 |
| sd | 0,317635005 | 0,265511809 | 0,350182367 | 0,254195572 | 0,317318293 |
| P | | | * | | . |
| | + | + | + | + | + |
| Plasticity of IL BR MED | 0,5 | 0,53 | 0,86 | 0,29 | 0,365 |
| sd | 0,312967655 | NA | 0,478501109 | 0,194533572 | 0,256040848 |
| P | | | | . | |
| | + | + | + | + | + |
| Plasticity of IL BR HIGH | 0,8 | 0,8 | 0,5 | 0,9 | 0,5 |
| sd | 0,5 | 0,7 | 0,2 | 0,2 | 0,3 |
| P | | . | * | *** | . |
| | + | + | + | + | + |

| Species | Oxandra asbeckii | Pradosia cochlearia | Qualea rosea | Symphonia sp1. | Virola michelii |
|---|---|---|---|---|---|
| Plasticity of LG BRHIGH | 3,6 | 6,3 | 15,5 | 7,4 | 4,1 |
| sd | 1,3 | 3,9 | 3,9 | 2,4 | 1,8 |
| P | * | ** | ** | ** | * |
|  | + | + | + | + | + |
| Plasticity of LG BRLOW | 1,5 | 2,4 | 6,0 | 1,7 | 2,3 |
| sd | 0,8 | 1,6 | 4,1 | 0,8 | 1,0 |
| P | * | * | ** |  | . |
|  | - | - | - | + | - |
| Plasticity of ULA | 4,2 | 5,8 | 3,2 | 3,7 | 1,2 |
| sd | 1,1 | 3,5 | 2,8 | 0,8 | 0,4 |
| P | *** |  |  | ** | ** |
|  | + | - | - | + | + |
| Plasticity of leaf cohort BRHIGH | 2 | 3 | 8,5 | 5 | 4,5 |
| sd | 0,8 | 1,4 | 2,4 | 2,3 | 1,1 |
| P |  |  | ** | . |  |
|  | + | + | - | + | + |
| Plasticity of leaf cohort BRMED | 4 | 3 | 6 | 3 | 3,5 |
| sd | 1,4 | 1,6 | 3,1 | 1,6 | 2,1 |
| P | * |  |  |  | * |
|  | NA | - | - | + | + |
| Plasticity of leaf cohort BRLOW | 2 | 3 | 3,5 | 3 | 4 |
| sd | 1,1 | 2,3 | 2,1 | 1,5 | 1,6 |
| P |  |  |  |  | * |
|  | + | + | + | + | + |
| Plasticity of LMA | 11 | 21 | 14 | 10 | 15 |
| sd | 2,8 | 6,5 | 1,9 | 3,7 | 3,6 |
| P | *** | ** | *** | *** | *** |
|  | - | - | - | - | - |
| Plasticity of LLS | 34 | 30 | 15 | 24 | 8 |
| sd | 44 | 14 | 4 | 6 | 8 |
| P | * | *** | ** | *** |  |

## III.4 Does plastic response to shade enhance light interception?

Crown slenderness (ratio of crown depth with crown width) significantly changed across light conditions for *Qualea* and *Virola* (Figure 11). Relative crown depth of these two species declined in shaded conditions from 0.7 to 0.4 for *Qualea* and from 0.6 to 0.2 for *Virola*. Branch spacing and internode length were also significantly reduced in low-light (Table 9). These species displayed contrasted variation in others traits. Total leaf area of *Qualea* was constant along the light gradient. Extension rates were the same between main stem and upper branches in high-light conditions while conditions extension rate was higher in upper branches in low-light (Table 10). Length of leaf cohorts was higher in low-light conditions for upper and medium branches. Leaf life span of *Qualea* was significantly higher in low-light conditions.

Table 10. Significance of ANOVA comparing the extension of the main stem (vertical_ext) versus the extension of an upper-branch (lateral_ext). Significance levels of this test are shown with . P<0.1, *P <0.05, ** P<0.01, ***P<0.001.

| | CP1 | | | CP3 | | |
|---|---|---|---|---|---|---|
| Esp | Ratio vertical_ext/lateral_ext | Response | P | Ratio vertical_ext/lateral_ext | Response | P |
| BP | 1,21 | vert=lateral | | 0,21 | vert=lateral | |
| EF | 1,01 | vert=lateral | | 2,03 | vert>lateral | . |
| EG | 2,17 | vert>lateral | * | 1,66 | vert=lateral | |
| GH | 0,79 | vert=lateral | | 2,04 | vert=lateral | |
| LA | 3,26 | vert>lateral | * | 2,20 | vert>lateral | * |
| LP | 3,60 | vert>lateral | * | 1,28 | vert=lateral | |
| OA | 1,51 | vert=lateral | | 2,46 | vert>lateral | * |
| PC | 1,33 | vert=lateral | | 0,99 | vert=lateral | |
| QR | 0,55 | vert<lateral | ** | 1,28 | vert=lateral | |
| SR | 1,09 | vert=lateral | | 7,32 | vert=lateral | |
| SS | 1,23 | vert=lateral | | 2,74 | vert>lateral | *** |
| TM | 1,41 | vert=lateral | | 2,26 | vert>lateral | * |
| VM | 1,28 | vert=lateral | | 6,21 | vert>lateral | ** |

Total leaf area of *Virola* was significantly reduced in low-light conditions (Table 9). Extension rates were the same between main stem and upper branches in low-light whereas extension rate was higher on main stem in high-light conditions (Table 10). The number of branches and tiers for a given plant size and the length of leaf cohorts (number of leaves emitted per terminal meristem per flush) were reduced in low-light (Figure 11). Leaf life span varied independently of the light gradient. Unit leaf area of *Virola* decreased in high-light conditions.

*Symphonia* displayed a variation in crown slenderness across light conditions but no variation in crown depth (Figure 11). This change in crown form could result from the change in extension ratio: like *Virola*, extension rates were the same in upper branches and main stem in low-light conditions whereas the latter dominated in high-light conditions (Table 10). Unit leaf area, total leaf area, branch spacing and internode length significantly decreased in low-light conditions (Table 9).

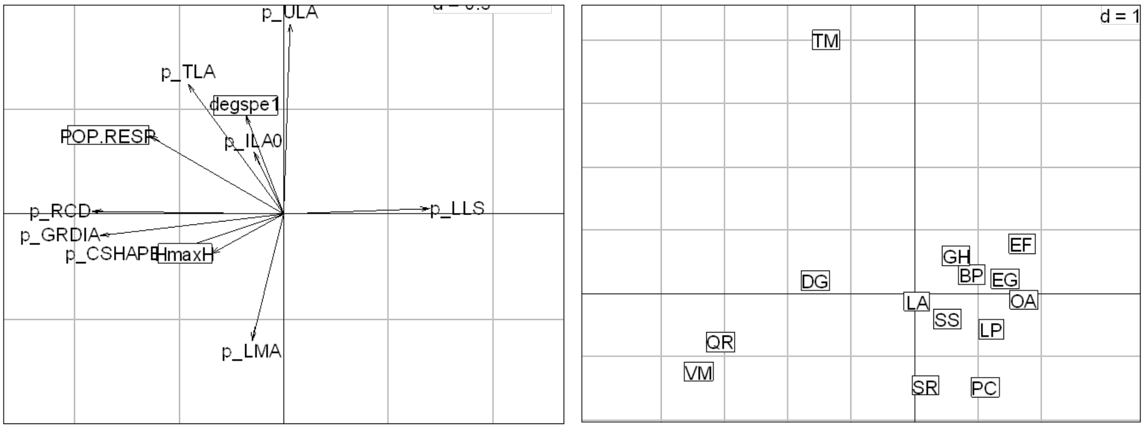


Figure 10. Plot of principal-component analysis ordination diagram showing traits (arrows). The first two axes jointly capture 55% of total variation in trait data.

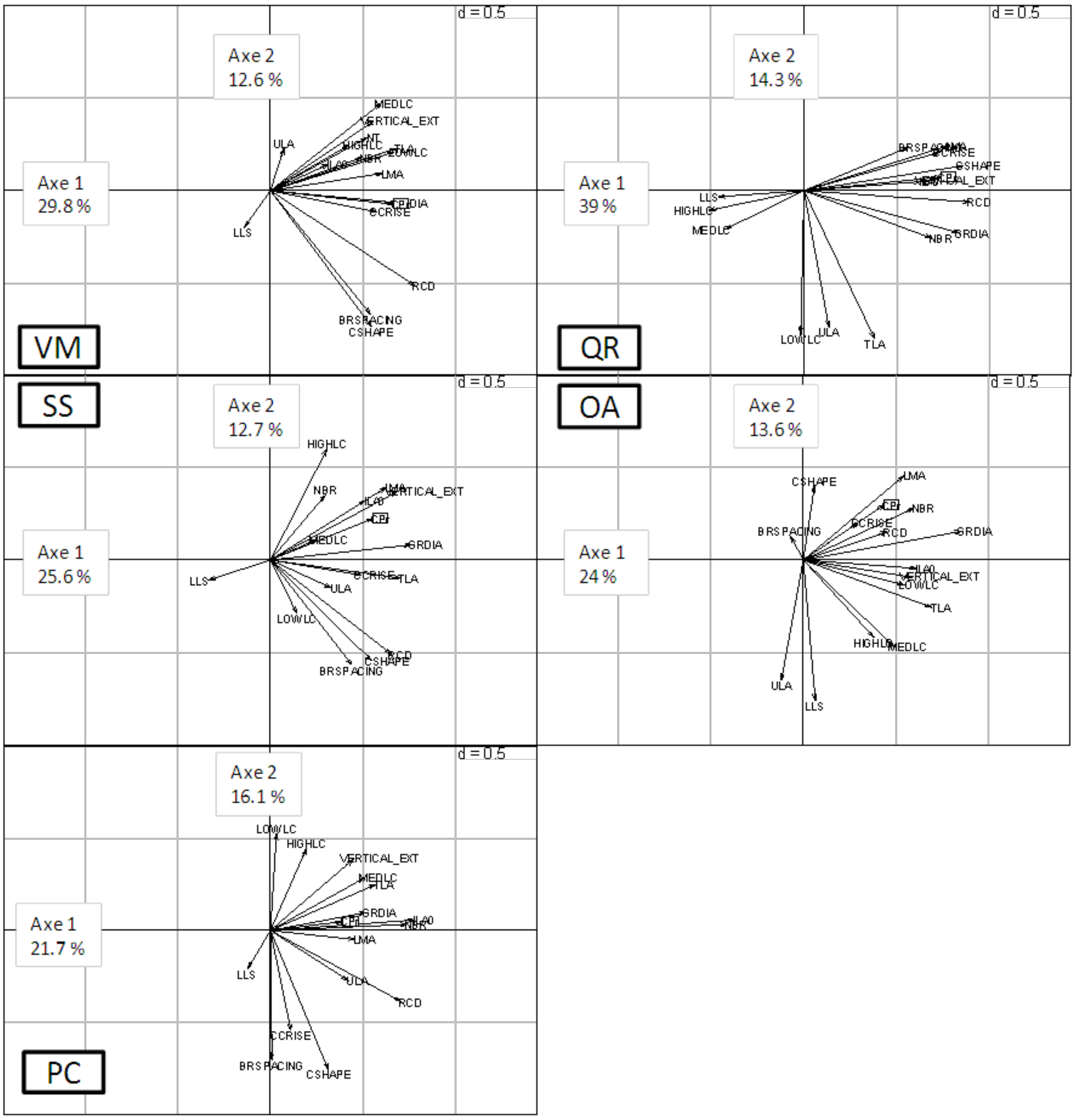


Figure 11. Plot of principal-component analysis based on individual trait values for five species (abbreviations are given in Table 3). LOWLC, MEDLC, HIGHLC refers to leaf cohort length of respectively, lower, medium, and higher branch. Abbreviations of the others traits are given in Table 7.

*Oxandra* displayed no significant variation in crown slenderness or crown depth across light conditions (Figure 11). Branch spacing and total leaf area were the same in low- and high-light conditions. Extension rate of the main stem was higher than branches in high-light conditions but equivalent in low-light conditions. Leaf life span and unit leaf area increased in low-light.

The proportion of saplings of *Pradosia* displaying a plagiotropic or polyarchic crown structure was significantly higher in low-light compared to high-light conditions (X-squared = 22.4, df = 4, p-value < 0.001). Inversely there were significantly more saplings with an orthotropic and hierarchic crown structure in high-light than in low-light conditions.

# IV. Discussion

## IV.1 Can leaf life span and vertical crown extension explain inter- and intra-specific patterns of crown depth?

As expected, we did not found parallel patterns between shade-tolerant and heliophilic species and between shade and sun plants. Plastic and evolutionary responses to shade were not congruent. Shade-tolerant species did not exhibit shallow and flat crown but shade trees did. This countergradient variation of crown traits is consistent with previous studies conducted in tropical forests (Sterck et al. 2001). As hypothesized we found that that across species variations of crown depth results from a leaf-level constraint. The significant correlation between leaf lifespan and branch lifespan explains why in spite of a faster crown length extension, the number of branches and the relative crown depth of heliophilic species is lower than the ones of the most shade-tolerant species. Hence high- light species tended to have sparser/shorter crowns. Correlation between leaf lifespan and branch lifespan has been previously reported in deciduous temperate trees (Seiwa et al. 2006, Shirakawa and Kikuzawa 2009). Seiwa (2006) provided also evidence of a close relationship between shoot lifespan and successional status. The deep crown of shade-tolerant species follows from a high longevity of resource-acquiring tissues which compensates for limited carbon fixation rate. At the whole-plant level, long leaf lifespan enable accumulation of a large foliage area which directly enhance carbon gain in low-light (King 1994, Lusk 2002). According to (Lusk 2002), this feature did not result from high allocation to leaf but rather from the very low leaf loss rates. Furthermore, reduction of tissue loss reduces carbon demand for growth (Walters and Reich 1999) and allows a greater allocation to other processes that directly contribute to stress resistance. In contrast a much shorter leaf lifetime is consistent with a strategy optimizing resource acquisition because rapid tissue turnover keeps the leaf area in favorable light conditions, where resource gain can be maximized and because it maximizes the efficiency of resource deployment, as a result of nutrients recycling (Seiwa et al. 2006). However as most of the carbon and more than half of the nutrients in individual leaves and shoots are lost at senescence (Seiwa et al. 2006), this strategy is only beneficial in high light conditions or in the case of a steep vertical light gradient between the base and the top of crown and probably in relatively fertile conditions.

Thus variation of crown depth across species showed the opposite trends to those predicted by carbon gain hypothesis stating that shade-tolerant species would increase light capture by reducing self-shading. However our results suggest that leaf traits of shade-tolerant species may enhance energy capture, carbon gain and indirectly survival in low-light through the accumulation of high leaf area. Moreover crown depth is a crude surrogate of self-shading and a deep crown is not necessarily incompatible with a low level of self-shading. Considering the other architectural determinants of self-shading might show that the two selective pressures outlined above (prolongation of leaf lifespan and reduction of self-shading) are not as strongly opposed as one can imagine. Trees can avoid self-shading by others morphological traits such as phyllotaxy, leaf shape, leaf and/or shoot angles (Posada et al. 2012). Changes in petiole, leaf or shoot angles might be an energetically cheap and efficient plastic response to reduce self-shading and enhance light interception. An alternative explanation would be that the consequences of selection for long lifespan outweigh those of selection for an optimal light capture at the crown scale.

Concerning within species variations along light gradient, we observed that relative crown depth was shorter in low-light than in high-light conditions. This pattern is consistent with previous studies conducted in tropical studies (Poorter and Werger 1999, Sterck et al. 2001). We found that plastic variations in relative crown depth reflected variations in crown extension rather than adjustment of leaf or branch longevity: shallow crown of low-light trees predominantly result from low crown apical extension. We did not found evidence of a reduction of leaf lifespan or an increase of branch shedding under deep shade which would be the sign of self-shading or of an adaptive strategy of nutrients recycling. In contrast we observed stable or longer leaf lifespan in the shade. Correlation between crown vertical extension and relative crown depth suggests that relative crown depth could be used as a surrogate of height growth rates of shade-intolerant species. (King and Clark 2004) previously showed among three tropical tree species the strong correlation between leaved stem growth and height growth rate. The emerging within species pattern was consistent with carbon gain hypothesis (shallower crowns expected under lower light) but the underlying mechanisms, namely reduction of crown extension, does not support the interpretation in terms of self-shading reduction. Nevertheless it doesn't exclude other adaptive responses to shade.

## IV.2 Is morphological plasticity lower for the less specialized species?

The degree of plasticity of several traits was found to be related to the degree of shade-tolerance whereas others were more related to the degree of specialization (Figure 10). The former (RCD, TLA, CSHAPE) were also positively correlated to growth performances. This syndrome of trait plasticity was described in the previous paragraph and observed for the less shade-tolerant species which were also the most responsive to light in terms of height growth. This result suggests that the variation in the interplay of leaf lifespan and crown vertical extension may explain the decline of total leaf area in the shade for shade-intolerant species which would not produce enough leaves or branches to compensate for their short leaf and branch lifespan. Thus the ability of a given species to survive in shaded conditions may be directly determined by its ability to maintain an extensive leaf area. These findings suggest that plastic adjustment of crown depth would not be an adaptive response to shade. This hypothesis is corroborated by the findings of (King 1994) in unbranched saplings of ten tropical tree species. According to this author, saplings of shade-intolerant species are excluded from typical understory sites not because of higher compensation points but because their short leaf lifespan necessitate higher production rates to maintain their canopies. Shade-intolerant species have higher compensation point defined as the amount of biomass production rate required to just maintain current leaf area including replacement of senescent leaves (King 1994). Our findings are in agreement with those of (Sterck et al. 2006a) who found that leaf lifespan was a good predictor of survival in low-light conditions.

The second axis of the PCA conducted on species median values of crown traits measured in low-, medium- and high-light conditions reflects an axis of degree of specialization along the light gradient. We expected that species experiencing the widest range of light conditions would display some morphological adaptive response to the variation of light conditions. We found that these species had a higher plasticity degree in LMA and a lower plasticity in unit leaf area. LMA decrease in low-light conditions is a key response enhancing both the harvesting of low light and photosynthetic capacity at high-light conditions. Indeed, lower LMA in low-light conditions allows saplings to construct larger foliar area for a given biomass investment in leaves and thus to maximize light interception while in high-light conditions, higher LMA allows saplings to maximize photosynthetic capacity by a larger amount of symplastic components (cell contents) per area (Lusk et al. 2008). Thus the higher degree of plasticity in LMA of generalist species is consistent with our work hypothesis.

Leaf size showed contrasting patterns of plasticity across species. Decrease in leaf size observed in eight species in high-light may be a way to prevent overheating of the leaf by increasing convective heat loss (Rozendaal et al. 2006, Poorter and Rozendaal 2008) whereas increase of leaf size observed in six species might be a vigor effect. The former may increase tolerance to gap microclimate and thereby broaden the light-niche while one expects the latter to be higher in shade-intolerant species showing a stronger growth response to shade and so to be more linked to the degree of shade-tolerance than to the degree of specialization.

## IV.3 Are crowns of shade trees more efficiently organized for light capture?

Whole-plant energy capture critically depends on the integration of foliage into an efficient canopy (Valladares and Niinemets 2008), thus the consideration of tree morphology variation among and within species might be essential for understanding light assimilation and growth strategies. We characterized morphological plasticity of five species differing in light-niche position and breadth and analyzed to what extent their saplings optimize light capture and carbon gain through a combination of crown structure and foliar characteristics.

### IV.3.1 Variations in crown structure

Plasticity in crown slenderness was significant for *Qualea* and *Virola* and to a lesser extent to *Symphonia*. This response results from the reduction of crown vertical elongation discussed above and from adjustments in allocation of growth between vertical and lateral directions (Table 10). *Qualea* was the only species to grow more in horizontal direction than in vertical direction in the shade. Horizontal crown expansion is assumed to optimize light capture of new leaves and to minimize self-shading in the light-limited understorey (Kohyama and Hotta 1990, Valladares et al. 2002).

Distribution of *Pradosia* is negatively affected by canopy disturbance but *Pradosia* is not highly specialized to shade conditions (Table 3). *Pradosia* was the only species to exhibit a qualitative change in crown architecture along the light gradient. Gap saplings displayed an orthotropic vertical stem and a hierarchical structure whereas shaded saplings displayed plagiotropic axis and polyarchic structure. This response may result from vertical stem reorientation and development of plagiotropic reiterations (sensu (Barthélémy and Caraglio 2007). Vertical stem reorientation may result from a change in apex growth direction or from an up-righting movement of the stem itself. The relative importance of these processes could be estimated by measuring geometrical and architectural features of trees before and after a canopy disturbance. The study of (Collet et al. 2011) conducted on two temperate shade-tolerant species showed that uprighting stem movement was the primary determinant of stem reorientation for both species but that development of reiteration and change in growth direction also contributed to stem reorientation for one of two species. Increase of stem inclination is likely to optimize light capture by reducing self-shading of recently expanded leaves. It could also be part of a strategy of space exploration to exploit fine-scale spatial and temporal heterogeneity of light conditions in understorey. Similarly, vertical stem reorientation allows high-light saplings of *Pradosia* to increase efficiency of light capture.

### IV.3.2 Variations in leaf display

We observed decreasing branch spacing with decreasing light for *Qualea*, *Virola* and to a lesser extent for *Symphonia*. This pattern can result from a reduction in branching frequency and/or in reduction of internode length. Our observations (Table 9) suggest that reduction of internode length was systematic in line with the findings of (King et al. 1997) within saplings of 14 tropical tree species in Panama. These authors verified that reduction of branch spacing observed in shaded conditions did not result from a reduction of branching frequency. Shorter branch spacing is likely to impact negatively light interception by increasing self-shading but at the same time it could reduce structural costs of foliage support. (King et al. 1997) suggest that the close branch spacing of shaded saplings may be an expression of low allocation to stem growth in energetically constrained plants. It is noteworthy that no species, even among the most light-demanding, displayed an increase in internode length in shade, a shade-avoidance syndrome largely described in the literature (Gilbert et al. 2001) within herbaceous species but also within tropical tree species through plasticity of stem slenderness (Harja et al. 2012). In the present study, results relative to stem slenderness variation confirmed absence of such a syndrome.

Total leaf area can be viewed as the product of first-order branch number by mean leaf number per branch by mean unit leaf area. *Virola* was the only species out of five to display a significant reduction of TLA (around 30%) in shaded conditions. The number of first-order branches was reduced in shade because of the concomitant reduction of leader stem growth rate and steady LLS. In addition the number of leaves per branch was also reduced because of the reduction of branch growth rate and concomitant steady LLS. Indeed we observed a reduction of leaf cohort length on low and medium-branches in low-light conditions but not on upper branches. This reduction of leaf number on the lower branches is likely to counter the reduction of stem and branches internode length and tier spacing under shade. Absence of significant plasticity in LLS for *Virola* is surprising and could result from the interplay in shaded conditions of the reduction of metabolic activity which enhances LLS and the occurrence of a negative carbon gain at the leaf scale which by accelerating leaf senescence may decrease LLS.

The absence of significant reduction of TLA is noteworthy in the case of *Qualea* as this species in the shade showed a significant reduction in crown depth and in leaf and branch production rate. This pattern can be explained by the strong increase of leaf lifespan (from 23 to 37 months) in the shade which may counter the reduction of leaf production rate. Our observations at the branch level confirmed this interpretation as the length of leaf cohorts was constant along the light gradient for low and medium- branches and even higher for upper branches in low-light conditions. The excess of leaf number supported by upper branches compared to lower branches may result from their higher leaf production rate associated with the release of apical control. Concerning the leader stem, the reduction of first-order branch number under shade indicates that increase of LLS did not outweigh the strong reduction of stem growth rate and can explain the constancy of TLA of *Qualea* along the light gradient. Thus, preferential growth investment in upper plagiotropic branches enables to optimize light capture and extends, in combination with the plasticity of LLS, the maintenance of efficient foliage in shaded conditions. This morphological response might contribute to a potential better survival of *Qualea* than *Virola* in low-light conditions and explain the lower degree of specialization of Qualea (Table 3). This hypothesis is consistent with the larger niche breadth of *Qualea* compared to *Virola* (Table 3). The case of *Symphonia* is interesting as this species closely resembled the most shade-tolerant species in some traits such as mean values of LMA, LLS and a low morphological plasticity while showing affinities with the less shade-tolerant species in some others traits such as mean growth rate. The only morphological response that we detected for this species was a release of apical control in the shade which could cause the observed shift in crown slenderness. Total leaf area of *Symphonia* was also constant along the light gradient consistently with the maintenance of its crown length but in contrast with the strong decrease of stem growth rate. Here again, variation in leaf longevity (from 31 to 56 months) is likely to counter variation in first-order branch production rate. At the branch level, we did not observe any significant variation in leaf production rate along the light gradient whatever the branch position on the stem. In this context one could expect an increase of total leaf area in shade. The decrease of unit leaf area in the shade might be one possible explanation to this constancy of TLA.

# V. Conclusion

This study aimed to examine morphological diversity and plasticity in response to canopy openness of 14 tree species of French Guiana differing in light-niche optimum and breadth. Our findings help disentangle adaptive response or strategies and constraint effects regarding crown shape of tropical trees. Branching patterns are strongly controlled by physiological, biomechanical and environmental factors, as well as by genetic factors under phylogenetic constraints so their evolution is the result of reconciling these different design requirements (Seiwa et al. 2006). Integrating and scaling-up leaf-level dynamics to shoot- and crown-level helps to interpret in adaptive terms inter- and intraspecific pattern of crown traits and to better understand species growth strategies. Even though inter and intraspecific variation of crown depth showed opposite patterns, the analysis of their determinants suggests that neither is an adaptive response to shade aimed at reducing self-shading. This study suggests that carbon gain and stress-tolerance hypothesis of shade-tolerance are not mutually exclusive: long leaf lifespan enables maintenance of an extensive leaf area which increases low-light carbon gain while at the same time high leaf mass per area increases tolerance to biotic stresses. Our findings provide evidence of a close linkage between leaf lifespan, relative crown depth and degree of shade-tolerance. Consequently, relative crown depth might be a surrogate of low-light survival ability, easier to measure than leaf life span. Such a marker of shade-tolerance has been already applied in temperate sylviculture (Lorimer 1983). At the intraspecific level, foresters need also simple surrogates of vigor for selecting trees with good future growth and survival prospects (Sterck et al. 2003). Relative crown depth may be useful in making qualitative assessments of growth and assessing the vigour of individual trees.

# Références

Ackerly, D. D. 1996. Canopy structure and dynamics: integration of growth proceeses in tropical pioneer trees. Pages 619-658 in S. S. Mulkey, R. L. Chazdon, and A. P. Smith, editors. Tropical forest plant ecophysiology. Chapman and Hall, New York.

Alpert, P. and E. L. Simms. 2002. The relative advantages of plasticity and fixity in different environments : when is it good for a plant to adjust ? Evolutionary Ecology **16**:285-297.

Barthélémy, D. and Y. Caraglio. 2007. Plant architecture : a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Annals of Botany:1-33.

Clark, D. A. and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs **62**:315-344.

Collet, C., M. Fournier, F. Ningre, A. P.-I. Hounzandji, and T. Constant. 2011. Growth and posture control strategies in Fagus sylvatica and Acer pseudoplatanus saplings in response to canopy disturbance. Annals of Botany **107**:1345-1353.

Fisher, J. B. and D. E. Hibbs. 1982. Plasticity of tree architecture: specific and ecological variations found in Aubreville's model. American Journal of Botany **69**:690-702.

Gilbert, I. R., P. G. Jarvis, and H. Smith. 2001. Proximity signal and shade avoidance differences between early and late successional trees. Nature **411**:792-795.

Givnish, T. J. 1988. Adaptation to sun and shade: A whole-plant perspective. Australian Journal of Plant Physiology **15**:63-92.

Harja, D., G. Vincent, R. Mulia, and M. van Noordwijk. 2012. Tree shape plasticity in relation to crown exposure. Trees - Structure and Function **26**:1275-1285.

Hikosaka, K. 2005. Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. Ann Bot **95**:521-533.

Hirose, T., M. J. A. Werger, T. L. Pons, and J. W. A. Rheenen. 1988. Canopy structure and leaf nitrogen distribution in a stand of Lysimachia vulgaris L. as influenced by stand density. Oecologia **77**:145-150.

Horn, H. 1971. The adaptive geometry of trees. Princeton University Press, NJ, USA.

Kikuzawa, K. 2003. Phenological and morphological adaptations to the light environment in two woody and two herbaceous plant species. Functional Ecology **17**:29-38.

King, D. A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. American Journal of Botany **81**:948-957.

King, D. A. and D. B. Clark. 2004. Inferring growth rates from leaf display in tropical forest saplings. Journal of tropical Ecology **20**:351-354.

King, D. A., E. G. Leigh, R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Relationships between branch spacing, growth rate and light in tropical forest saplings. Functional Ecology **11**:627-635.

Kohyama, T. and M. Hotta. 1990. Significance of allometry in tropical saplings. Functional Ecology **4**:515-521.

Laurans, M., O. Martin, E. Nicolini, and G. Vincent. 2012. Functional traits and their plasticity predict tropical trees regeneration niche even among species with intermediate light requirements. Journal of ecology **100**:1440-1452.

Little, J. D. C. 1961. A Proof of the Queueing Formula L = λ W. Operations Research **9**:383-387.

Lorimer, C. G. 1983. A test of the accuracy of shade-tolerance classifications based on physiognomic and reproductive traits. Canadian Journal of Botany **61**:1595-1598.

Lusk, C. H. 2002. Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. Oecologia **132**:188-196.

Lusk, C. H., Y. Onoda, R. Kooyman, and A. Gutiérrez-Girón. 2010. Reconciling species-level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. New Phytologist **186**:429-438.

Lusk, C. H., P. B. Reich, R. A. Montgomery, D. D. Ackerly, and J. Cavender-Bares. 2008. Why are evergreen leaves so contrary about shade? Trends in Ecology & Evolution **23**:299-303.

Navas, M.-L., B. Ducout, C. Roumet, J. Richarte, J. Garnier, and E. Garnier. 2003. Leaf life span, dynamics and construction cost of species from Mediterranean old-fields differing in successional status. New Phytologist **159**:213-228.

Niinemets, Ü. 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecological Research **25**:693-714.

Pearcy, R. W. and F. Valladares. 1999. Resource acquisition by plants : the role of crown architecture.*in* M. C. Press, J. D. Scholes, and M. G. Barjer, editors. Physiological plant ecology. Blackwell science.

Pearcy, R. W., F. Valladares, S. J. Wright, and E. L. De Paulis. 2004. A functional analysis of the crown architecture of tropical forest *Psychotria* species : do species cary in light capture efficiency and consequently in carbon gain and growth ? Oecologia **139**:163-177.

Poorter, L. and D. Rozendaal. 2008. Leaf size and leaf display of thirty-eight tropical tree species. Oecologia **158**:35-46.

Poorter, L. and M. J. A. Werger. 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. American Journal of Botany **86**:1464-1473.

Posada, J. M., R. SievÃ¤nen, C. Messier, J. Perttunen, E. Nikinmaa, and M. J. Lechowicz. 2012. Contributions of leaf photosynthetic capacity, leaf angle and self-shading to the maximization of net photosynthesis in Acer saccharum: a modelling assessment. Annals of Botany **110**:731-741.

R Development Core Team. 2011. R : A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Reich, P., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation : traits, spectra, and strategies. International Journal of Plant Science **164**:143-164.

Rozendaal, D. M. A., V. H. Hurtado, and L. Poorter. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Functional Ecology **20**:207-216.

Seiwa, K., K. Kikuzawa, T. Kadowaki, S. Akasaka, and N. Ueno. 2006. Shoot life span in relation to successional status in deciduous broad-leaved tree species in a temperate forest. New Phytologist **169**:537-548.

Shirakawa, H. and K. Kikuzawa. 2009. Crown hollowing as a consequence of early shedding of leaves and shoots. Ecological Research **24**:839-845.

Southwood, T. R. E., V. K. Brown, and P. M. Reader. 1986. Leaf palatability, life expectancy and herbivore damage. Oecologia **70**:544-548.

Sterck, F. 1999. Crown development in tropical rain forest trees in gaps and understorey. Plant Ecology **143**:89-98.

Sterck, F., F. Bongers, and D. M. Newbery. 2001. Tree architecture in a Bornean lowland rain forest : intraspecific and interspecific patterns. Plant Ecology **153**:279-292.

Sterck, F., L. Markesteijn, F. Schieving, and L. Poorter. 2011. Functional traits determine trade-offs and niches in a tropical forest community. Proceedings of the National Academy of Sciences **108**:20627-20632.

Sterck, F., M. Martinez-Ramos, G. Dyer-Leal, J. Rodrigez-Velasquez, and L. Poorter. 2003. The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest. Functional Ecology **17**:194-200.

Sterck, F., L. Poorter, and F. Schieving. 2006. Leaf traits determine the growth-survival trade-off across rain forest tree species. The American Naturalist **167**:758-765.

Sterck, F., F. Schieving, A. Lemmens, and T. L. Pons. 2005. Performance of trees in forest canopies : explorations with a bottom-up functional-structural plant growth model. New Phytologist **166**:827-843.

Sterck, F. J. and F. Schieving. 2007. 3-D growth patterns of trees : effect of carbon economy, meristem activity, and selection. Ecological Monographs **77**:405-420.

Valladares, F. and U. Niinemets. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. Annual Review of Ecology, Evolution, and Systematics **39**:237-257.

Valladares, F., J. B. Skillman, and R. W. Pearcy. 2002. Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures : a case of morphological compensation. American Journal of Botany **89**:1275-1284.

Vincent, G. 2006. Leaf life span plasticity in tropical seedlings grown under contrasting light regimes. Annals of Botany **97**:245-255.

Vincent, G., J.-F. Molino, L. Marescot, K. Barkaoui, D. Sabatier, V. Freycon, and J. B. Roelens. 2011b. The relative importance of dispersal limitation and habitat preference in shaping distribution of saplings in a tropical moist forest : a case study along a combination of hydromorphic and canopy disturbance gradients. Annals of forest science **68**:357-370.

Walters, M. B. and P. B. Reich. 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants : do winter deciduous and broad-leaved evergreen species differ ? New Phytologist **143**:143-154.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual review of ecology and systematics **33**:125-159.

Wilson, B. F. 2000. Apical control of branch growth and angle in woody plants. American Journal of Botany **87**:601-607.

Wright, I. J., M. Westoby, and P. B. Reich. 2002. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. Journal of ecology **90**:534-543.

# 4ème Partie :

## Vertical stratification reduces competition for light in dense tropical forests

En cours de soumission

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## Abstract

Differential response to light level is widely accepted as a potential mechanism for maintaining species richness in tropical forests. Paradoxically, the quantification of this mechanism and its importance relative to the other determinants of individual tree growth have been poorly documented at the adult stage. Herein we describe how we use a hierarchical Bayesian model to quantify the overall importance of light and belowground competition as tropical tree growth limiting factors. Light competitive status is assessed by a crown exposure score and below ground competition is estimated from local basal area. We examine species sensitivity to both types of competition and explore their interspecific variations in relation to adult stature.

Our dataset includes annual diameter increments in more than 13510 stems from 282 species monitored over 10 years. Results showed that mean annual growth rate was 0.11 cm.yr$^{-1}$ with species effect explaining 35% of the variation in growth rate. Light and belowground competition explained 3.5% and 2.4% of the variation in growth rate, respectively. Predicted changes in growth rate as light or belowground competition indices changed from lower to upper interquartile levels corresponded to 0.03 cm.y$^{-1}$ and 0.02 cm.y$^{-1}$, respectively. This “absolute importance” of light and belowground competition positively correlated i) with predicted growth rate at high-light standardized conditions and ii) with adult stature.

This vertical niche partitioning is invoked to explain the limited contribution made by level of competition for light when predicting individual tropical tree growth as the community-level response is dominated by the abundance of small-statured species with low sensitivity to light level.

Light appears to drive the stem growth rate of tropical trees through species differentiation more than through individual tree growth limitation. This vertical stratification complements the previously reported regeneration niche and together these provide evidence for light niche partitioning in the three-dimensional space of tropical forests.

**Keywords**: adult stature; belowground competition; hierarchical Bayesian model; niche partitioning

# I. Introduction

Growth and survival response to changing light levels is a fundamental component of the life-history strategy of juvenile trees in tropical forests (Poorter and Arets 2003) and has been proposed as a potential mechanism for the maintenance of species richness (Brokaw and Busing 2000). Differential light requirements are a key characteristic of species successional status after forest disturbance (Oldeman and van Dijk 1991), to such an extent that most forest modelers rely on light-explicit growth models to simulate in silico forest dynamics (Pacala et al. 1996). Paradoxically, although the effect of light on tree growth is widely acknowledged, its quantification relative to other determinants of individual tree growth has been poorly documented, particularly at the adult stage. (Rüger et al. 2011) found that size and light explained on average 12% of growth rate variations in a tropical forest community in Panama, and that size was slightly less determinant than light. This contrasted with a large body of literature assuming that light availability shapes tree growth (Valladares 2003). Competition for water and nutrients, estimated by diameter-based competition indices (e.g. local density), has been considered in a few studies (Gourlet-Fleury 1998, Moravie et al. 1999, Uriarte et al. 2004) but, to the best of our knowledge, its importance has seldom been examined in combination with competition for light. Very recently, (van Breugel et al. 2012) found that, despite low soil fertilities, competition for light was more important than belowground competition for nutrients in limiting the growth of two pioneer species during early succession. Competition for belowground resources is often seen as size-symmetric, based on the assumption that nutrient uptake is proportional to plant size (Cahill and Casper 2000). In contrast, competition for light is assumed to be size-asymmetric as taller individuals pre-empt resources by casting shade on their shorter neighbors and depriving them of light disproportionately to their size (Schwinning and Weiner 1998, Freckleton and Watkinson 2001). The inherent asymmetry of light-competition and symmetry of below-ground competition suggests that it may be possible to disentangle their effects (by accounting for all neighboring trees or only those taller than the focal tree in competition indices) and compare their importance in shaping forest dynamics. Size-asymmetric competition will hereinafter be referred to as ‘aboveground competition’ or ‘competition for light’, and size-symmetric competition will hereinafter be referred to as ‘belowground competition’.

The study described herein aimed to use a hierarchical Bayesian model to quantify the overall importance of asymmetric and symmetric competition in determining tropical tree growth, and examine species growth sensitivity to both types of competition. Adult tree height is indicative of the position of the species in the hierarchy of the canopy and is considered an important indicator of light capture strategy, even if the small-large paradigm for adults has received considerably less attention than the gap-shade paradigm for juveniles. Here in this study we specifically addressed the following questions: i) Is competition for light more important than competition for belowground resources? ii) What proportion of growth variation is due to competition for light? iii) Are small-statured species less sensitive to competition than high-statured species that experience major changes in light availability throughout their development (Thomas and Bazzaz 1999) ?

# II. Material and methods

## II.1 Inventory data

The study was carried out at the lowland tropical forest Paracou experimental site in French Guiana (Gourlet-Fleury et al. 2004). Mean annual rainfall was 2.875 ± 510 mm over the 1986-2005 period with a 3-month dry season from mid-August to mid-November (Wagner et al. 2011). The study site is characterized by a patchwork of hills (100–300 m in diameter and 20–50 m high) separated by streams. Its tree community shows the high species diversity typical of tropical rainforest and a very high proportion of rare species: in our dataset 75% of species account for 10% of the total tree population (>10cm diameter at breast height, DBH).

Each tree >10cm DBH in six 6.25 ha plots of unlogged forest was mapped, identified and its circumference measured every one or two years from 2003 to 2011. In order to reduce the effects of year-to-year measurement inaccuracy and errors, annual diameter growth rate (cm.y$^{-1}$) in 2007 was calculated as a weighted mean (weights were inter-annual census periods in days) of growth rates over the 2003-2011 census period. Mean annual growth rate was log-transformed to homogenize the variance of the residuals. As a few trees had negative growth rates over the period, a constant value of +0.2 cm.y$^{-1}$ (corresponding to the minimum negative growth rate value of -0.19 cm.y$^{-1}$) was added to the observed growth rates to obtain strictly positive values prior to log-transformation. To avoid edge effects when calculating competition indices, all individuals within 15m of plot boundaries (4198 trees) were excluded from the growth modeling (but were included in computations of competition indices).

## II.2 Competition indices

Local basal area (LBA) was calculated as the sum of the basal area of the neighboring trees in a circular plot. Preliminary tests were conducted on a subset of fairly abundant species (N>30, 74 species) to determine the optimal neighborhood for the evaluation of local crowding (LBA). We applied successively the following linear model with LBA indices based on a neighborhood radius of 10, 15 and 20 m:

$$\begin{aligned}\log(\mathrm{G}+0{,}2) \sim\ & \mathrm{DBH} \\ & + \log(\mathrm{DBH}) + \log(\mathrm{CP}) \\ & + \log(\mathrm{LBA}) + \mathrm{species} \times [\mathrm{DBH} + \log(\mathrm{DBH}) + \log(\mathrm{CP}) + \log(\mathrm{LBA})]\end{aligned}$$

The model minimizing AIC involved LBA indices based on a neighborhood radius equal to 15m.

This is a distance-independent index in that it does not take into account the distance between the focal tree and its competitors within the prescribed plot area.

The scarcity of studies quantifying light as a growth driver is partly a consequence of the difficulties encountered when attempting to estimate individual light availability over large sampling areas. The crown-based competition index used here corresponded to the crown position (CP) of each individual tree in the six plots and was measured at the Paracou experimental site in 2007 (22917 trees). Crown position indices are used to standardize visual assessments of the relative position of individual tree crowns in the forest canopy. Crown position scores are defined as follows (Synnot 1979):

1) lower understorey trees, entirely shaded vertically and laterally by others crowns
2) upper understorey trees entirely shaded vertically but with some direct side light
3) lower canopy trees, partly exposed and partly shaded vertically by others crowns
4) upper canopy trees, exposed in entire vertical plan but with other crowns laterally
5) emergent, entirely exposed, free from competition for light, at least within the 90 inverted cone in which the crown lies.

As CP values of 5 were rare (< 2%) we decided to pool these with CP values of 4 in our growth models. This decision was motivated by the fact that preliminary tests with models using CP as a categorical predictor suggested that the response was linear up to CPscore = 4 but tended to saturate beyond. CP was considered as a quantitative variable (measurement variable sensu (Sokal and Rohlf 2010)) in the subsequent analysis. CP is negatively correlated with tree competition pressure whereas LBA increases with level of competition. All species were treated as equivalent for competition pressure (species identity was not considered).

## II.3 Growth model

Palm species (*Arecaceae*) that have no secondary growth were excluded from the analysis (388 trees). Similarly, trees whose taxonomic resolution was not achieved to species level and trees for which height of DBH measurement had been changed over the census period were also excluded from the growth analysis (3870 trees). In all, 13510 individuals representing 282 species were included in the growth analysis.

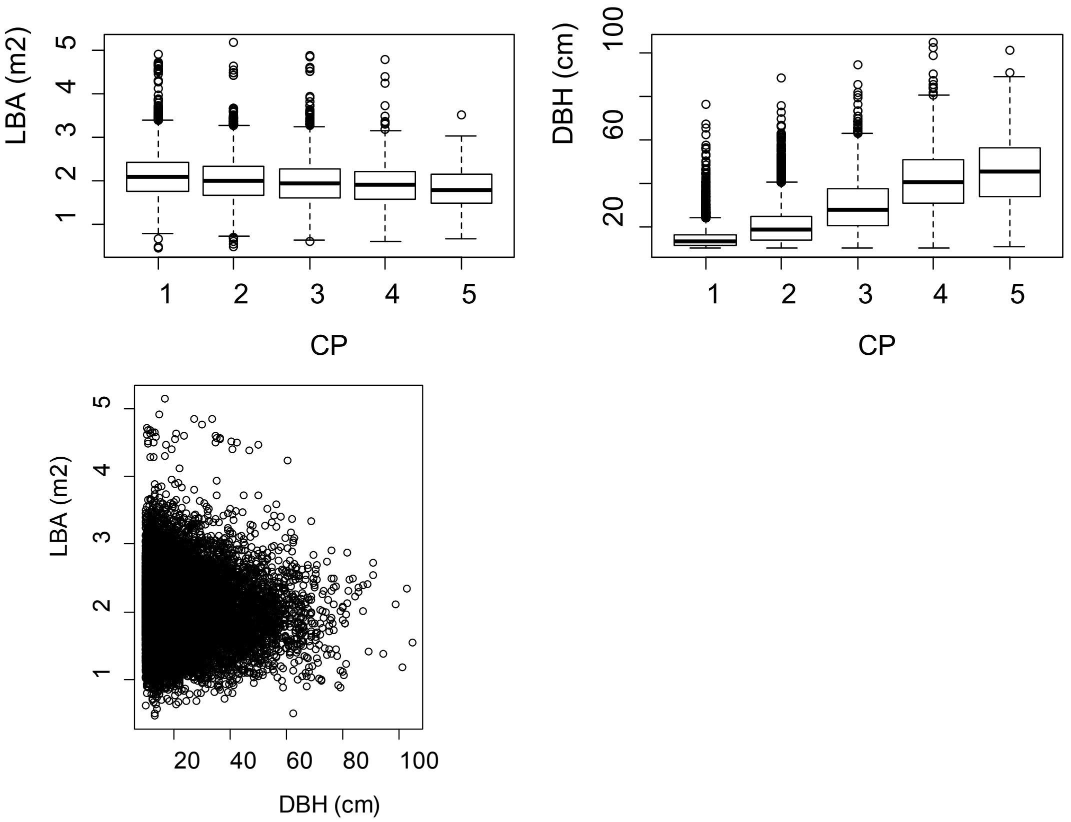

Figure 12. Relationships among model predictors: CP, LBA (m$^2$) and DBH (cm).

## II.4 Model specification

We used a hierarchical Bayesian model, which included a species random effect, to quantify growth response to DBH, CP and LBA. This approach was selected as it can include rare species and provide robust estimates despite their low abundance (Dietze et al. 2008, Rüger et al. 2011). Relationships among predictors are shown in Figure 12. To evaluate how much redundancy occurred between LBA, DBH and CP indices we used linear discriminant analysis to predict CP from either LBA or DBH. We then computed Cohen's kappa coefficient $\kappa$, which accounts for the agreement occurring by chance. $\kappa$ ranges between 0 (no agreement) and 1 (complete agreement). $\kappa$ was equal to 0.05 when LBA was used as predictor of CP and 0.29 when DBH was used. Therefore, we included LBA, CP and DBH as predictors. We compared different models consisting of i) a logarithmic transformation of CP and LBA, and ii) a log-transformed DBH term (allowing a humped-shape response form) in addition to DBH. We used the deviance information criterion (DIC) to select the best model.

The selected model minimizing DIC took the following form:

$$\log(G_{ik} + 0.2) = \beta_0 + b_{0,k} + (\beta_1 + b_{1,k})\log(DBH_i) + (\beta_2 + b_{2,k})\log(CP_i) + (\beta_3 + b_{3,k})DBH_i + (\beta_4 + b_{4,k})\log(LBA_i) + \varepsilon_i$$

with $n_k$ observations for each species k. $G_{ik}$ represents the DBH increment (cm.y$^{-1}$) of tree i of species k, 0.2 is the constant required by the occurrence of negative increments.

The process error $\varepsilon_i$ was modeled as a normal distribution:

$$\varepsilon_i \sim N(0, \sigma^2)$$

The model used a multivariate normal prior for the fixed $\beta_0$, $\beta_1$, $\beta_2$, $\beta_3$ and the random $b_0$, $b_1$, $b_2$, $b_3$ effects parameters:

$$[\beta_0, \beta_1, \beta_2, \beta_3] \sim N_4(\mu_\beta, V_\beta)$$

For $[b_{0k}, b_{1k}, b_{2k}, b_{3k}] \sim N_4(0, V_b)$

The variance matrix $V_b$ followed an Inverse-Wishart prior distribution:

$$V_b \sim \text{Inverse} - \text{Wishart}\ (r, R)$$

The residual error variance $\sigma^2$ followed an Inverse-gamma prior distribution:

$$\sigma^2 \sim \text{Inverse} - \text{Gamma}\ (u, 1/\delta)$$

A Bayesian inference of model parameters was performed using Algorithm 2 of (Chib and Carlin 1999). Bayesian analyses were carried out with the R software coda and twoe package (http://twoe.org/) (R Development Core Team 2011). To test if a species grew in a significantly different manner compared to mean species behavior, we computed the 95% credibility intervals of the species random effects from the posterior marginal distributions. The inclusion of zero in the interval was taken as an indication that the random species effect was not significantly different from zero and that the species did not grow in a significantly different manner from the average species.

## II.5 Absolute importance of above and belowground competition

The terminology used to quantify the effects of competition has been examined by (Welden and Slauson 1986) and has been the subject of long-running debate (Brooker et al. 2005, Freckleton et al. 2009, Damgaard and Fayolle 2010, Kikvidze et al. 2011, Rees et al. 2012). We followed (Craine 2009) and used *absolute* importance of competition to refer to the variation in DBH increment caused by competition (or one of its components), and *relative* importance to refer to the variation in DBH increment caused by competition (or one of its components) relative to all other factors driving DBH increment. We quantified the absolute importance of asymmetric ($CP\_imp_{abs}$) and symmetric competition ($LBA\_imp_{abs}$) for each species as the difference between the maximum and minimum predicted growth rate value for the whole-community interquartile range of CP (we applied a linear interpolation within each class of CP) and LBA. The fixed values of DBH, CP or LBA required for these predictions were computed as the median values across the community. Predicted DBH increment ($\text{pred}_{\log}$) of tree i of species k was back-transformed to the arithmetic scale ($\text{pred}_{\text{ari}}$) as follows:

$$\text{pred}_{\text{i,ari}} = e(\text{pred}_{\text{i,log}} + \frac{\sigma^2}{2})$$

We used the median of $\text{CP\_imp}_{\text{abs}}$ and $\text{LBA\_imp}_{\text{abs}}$ across species to compare the absolute importance of CP and LBA in unit growth rate. Absolute importance of competition was computed for a standardized and non-specific range of crown exposure index (CP) or local basal area (LBA) and thus reflected species growth responsiveness to competition.

## II.6 Relative importance of symmetric and asymmetric competition

Explained variance ($r^2$) of DBH increment (G) was calculated for the whole community as follows:

$$r^2 = 1 - \text{var}(\varepsilon)/\text{var}(G)$$

We evaluated the relative importance of each predictor as the difference between the $r^2$ value of the full model and the $r^2$ value of the model excluding the given predictor. The predictive ability of species identity was the $r^2$ of a linear model that included species as the single predictor.

As no suitable dataset was available, the model did not include the error on CP that is composed of i) an error resulting from the discretization of CP in four classes (even though light conditions vary continuously) and ii) an estimation error. The CP measurement repeatability test performed by (Vincent et al. 2002) showed an error rate of 26% between two independent estimates, confirming previous results from (Clark and Clark 1992). We investigated by numerical simulations the impact of the rounding error coupled with an error rate of 26% and estimated that the CP estimation error might account for about 2% of the total unexplained variance in DBH increment.

We used Pearson's correlation analysis to test for relationships between species-specific absolute importance of resource competition, median predicted growth rate under standardized conditions or CP score = 3, and adult stature. Adult stature was estimated by the 95th percentile of maximum DBH in trees with DBH>0.1*maximum DBH ($D95_{0.1}$ sensu (King et al. 2006)) hereinafter referred to as D95). We also tested the effect of rare species on the strength of these relationships by applying an abundance filter (from 5 to 500 individuals per species) to the dataset.

# III. Results

## III.1 Structure of the competitive environment

Coefficients of variation for CP and LBA were 0.48 and 0.25, respectively, indicating that light access was more variable than local crowding.

In all, 70% of the 13510 individuals were located in shaded conditions (CP=1 or CP=2) (Figure 13a) and had a DBH<25cm. At the species level, 75% of the 282 species had a median CP value of 2 or less, and a median DBH of 22 cm or less (Figure 13b). D95 varied from 11 to 92 cm, but 75% of the species did not exceed 41 cm (Figure 13b). CP median and standard deviation values across species correlated with D95 (Figure 14). Median individual DBH increment was 0.08 cm.y$^{-1}$. A simple regression between CP and species showed that species identity explained 17% of CP variation but only 5% of LBA variation. A Kruskall-Wallis test confirmed that species identity had a highly significant effect on CP (P<0.0001).

## III.2 Community pattern of growth sensitivity to resource competition and DBH

All but one species (*Pradosia cochlearia* (Lecomte) T.D.Penn.) grew faster at high light levels and 98% grew faster at low local density (see sign of alpha2g and alpha4g model parameters on Table 13 en annexe).

The most abundant species were moderately responsive to resource competition, and the rare species showed the entire range of growth responsiveness to resource competition. For 12 of the 282 species (4.2%) and 4138 of the 13510 trees (30.6%), the CP model parameter was significantly (significance level=5%) different (4 more, 8 less) from the species mean (Table 13 en annexe). For 16 of the 282 species (5.6%) and 4254 of the 13510 trees (31.5%), the LBA model parameter was significantly (significance level=5%) different (7 more, 9 less) from the species mean (Table 13 en annexe).

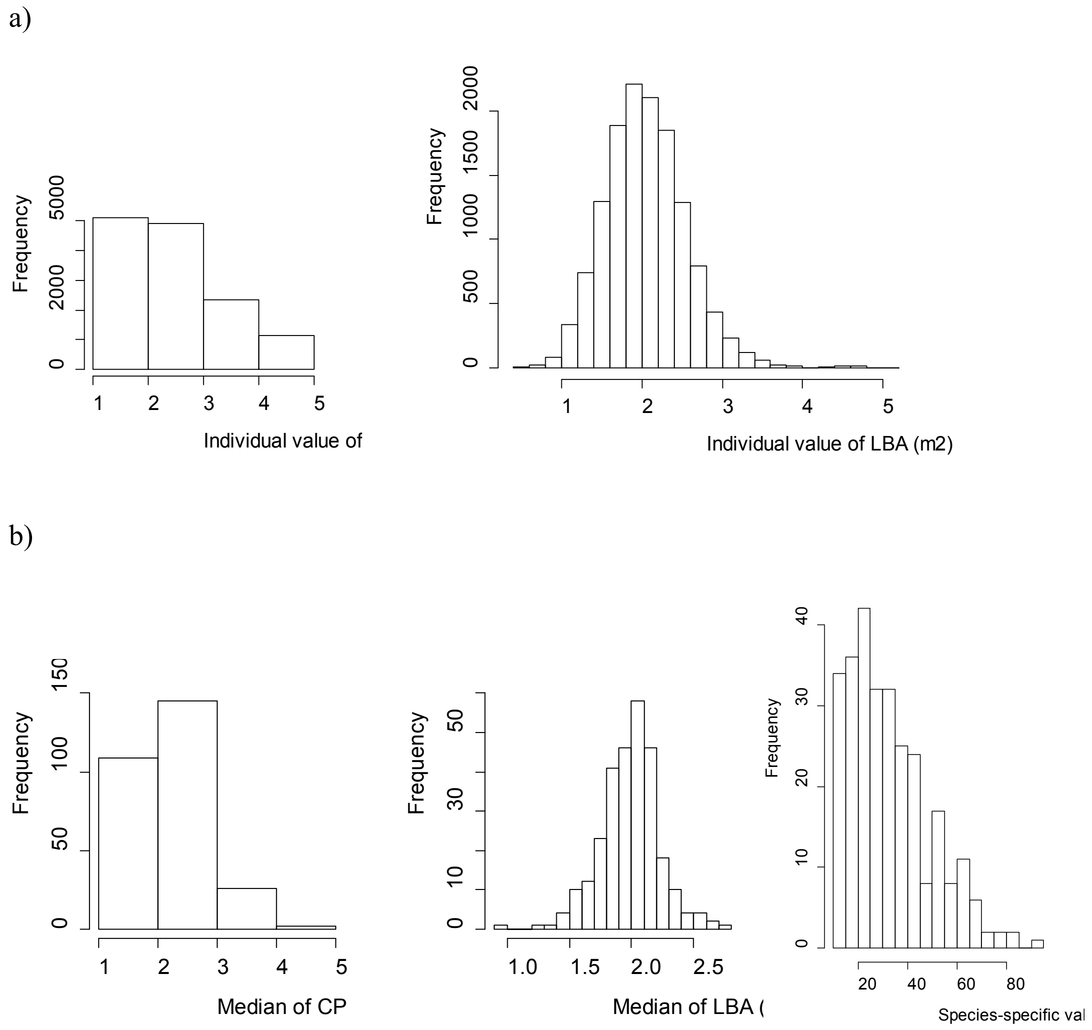

Figure 13. Distribution of a) individual values and b) median values for specific CP, LBA ($m^2$) and D95 (cm) at the Paracou experimental site.

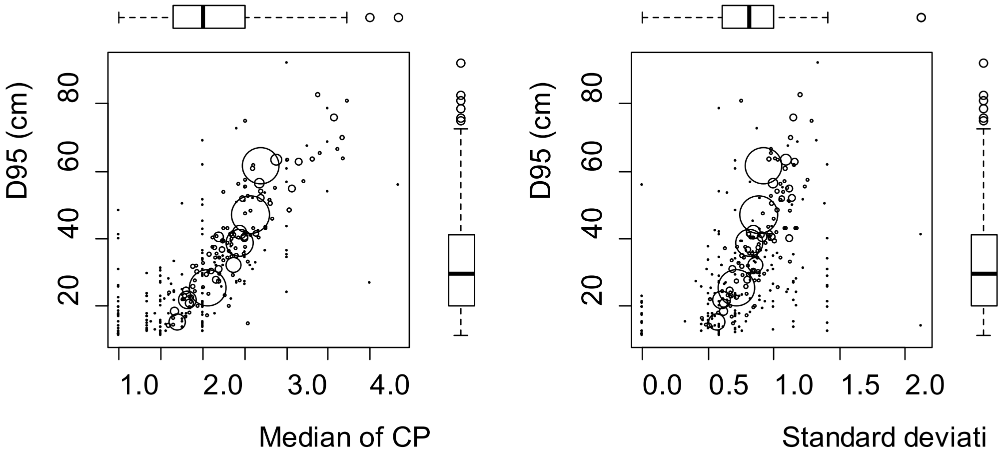

Figure 14. Relationship between species median and standard deviation values for CP and species D95 (cm) at the Paracou experimental site. Symbol size is proportional to species abundance. For 28 of the 282 species (10%) and 5409 of the 13510 trees (40%), the DBH or log DBH model parameter was significantly (significance level=5%) different from the species mean species (Table 13 en annexe).

Uncertainty over model parameters was exponentially and negatively related to species abundance. Consequently, the analysis of absolute and relative importance of CP and LBA, as described in the next section, was restricted to species represented by more than 20 individuals (101 of the 282 species).

## III.3 Absolute importance of CP and LBA

Species-specific CP and LBA absolute importance values ($CP\_imp_{abs}$ and $LBA\_imp_{abs}$) were evaluated under standardized conditions (DBH=18cm, CP=2.3, LBA=2 $m^2$) and a standardized range of variation (from 1.7 to 3 for CP and from 1.7 $m^2$ to 2.3 $m^2$ for LBA). CP absolute importance varied from 0.002 $cm.y^{-1}$ to 0.17 $cm.y^{-1}$ and LBA absolute importance from 0 $cm.y^{-1}$ to 0.11 $cm.y^{-1}$ across species (Figure 13 and Table S1). Median values for $CP\_imp_{abs}$ and $LBA\_imp_{abs}$ corresponded to 0.03 $cm.y^{-1}$ and 0.02 $cm.y^{-1}$, respectively. The median value for species-specific predicted growth rate under standardized conditions was found to be 0.15 $cm.y^{-1}$. CP absolute importance was higher than LBA absolute importance. The absolute importance of competition decreased as the threshold of species abundance increased (Table 14 en annexe): this trend suggests that abundant species are only moderately sensitive to resource competition.

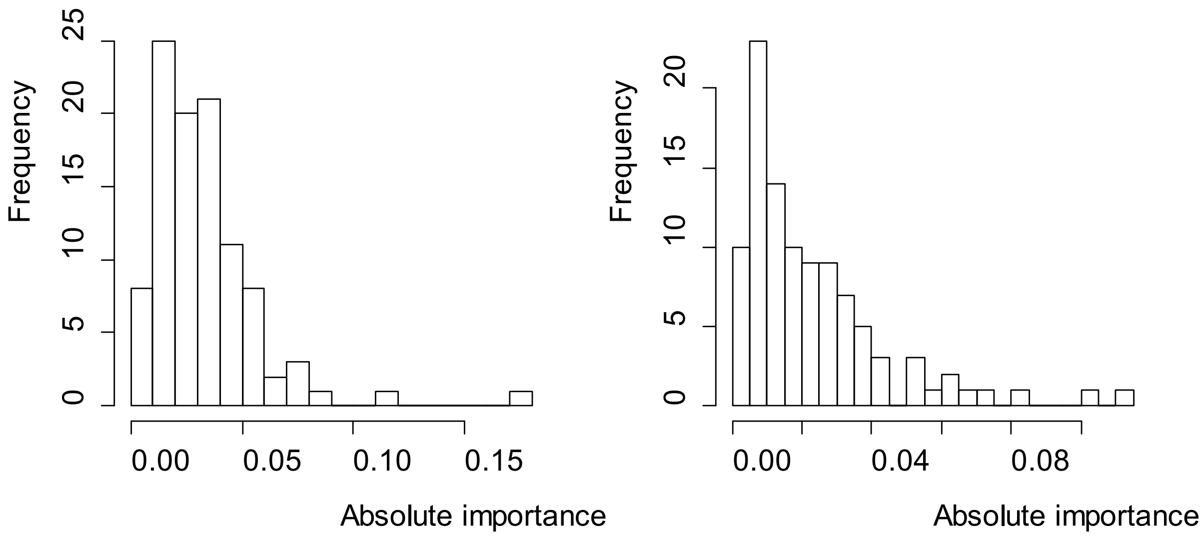

Figure 15. Distribution of species-specific absolute importance of asymmetric competition and symmetric competition for 101 species (N>20) at the Paracou experimental site.

## III.4 Interspecific variations in absolute importance of resource competition

Absolute importance of CP (CP_imp$_{abs}$) was significantly correlated with absolute importance of LBA (LBA_imp$_{abs}$) across species (Table 14 en annexe and Figure 16). The strength of the correlation between CP_imp$_{abs}$ or LBA_imp$_{abs}$ with adult stature (D95) depended on the presence of rare species (Table 15 en annexe). Also, CP_imp$_{abs}$ and LBA_imp$_{abs}$ were positively and significantly correlated with predicted growth rate under high-light standardized conditions (CP=3, DBH=19cm, LBA=1.9 m$^{-2}$) (Table 15 en annexe and Figure 17). Small-statured species showed slower growth rates than tall-statured species (Table 14 en annexe and Figure 18).

## III.5 Relative importance of CP and LBA

At the community level, about 54% of the variation in growth rate was accounted for by the hierarchical growth model. Species effect explained 35% of the variation in growth rate. CP competition index and LBA competition index explained 3.5% and 2.4% of the variation in growth rate, respectively. Tree size explained 6.3% of the variation in growth rate. The sum of each predictor contribution does not sum up to r$^2$ because we do not conduct a variance decomposition but rather estimate type III sum of square for LBA, CP and tree size (see Material and methods section).

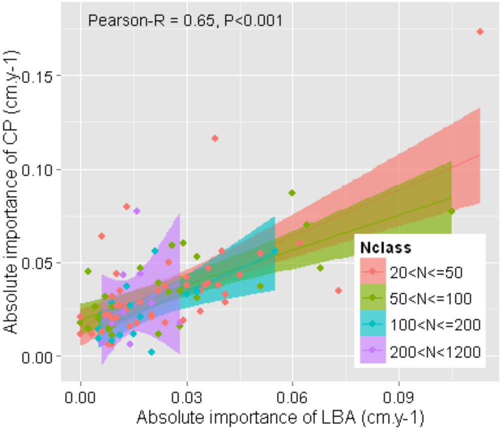

Figure 16. Relationship between CP and LBA absolute importance. Pearson's correlation coefficient was calculated for the 101 species with N>20 individuals but the 95% confidence interval was plotted for each class of species abundance.

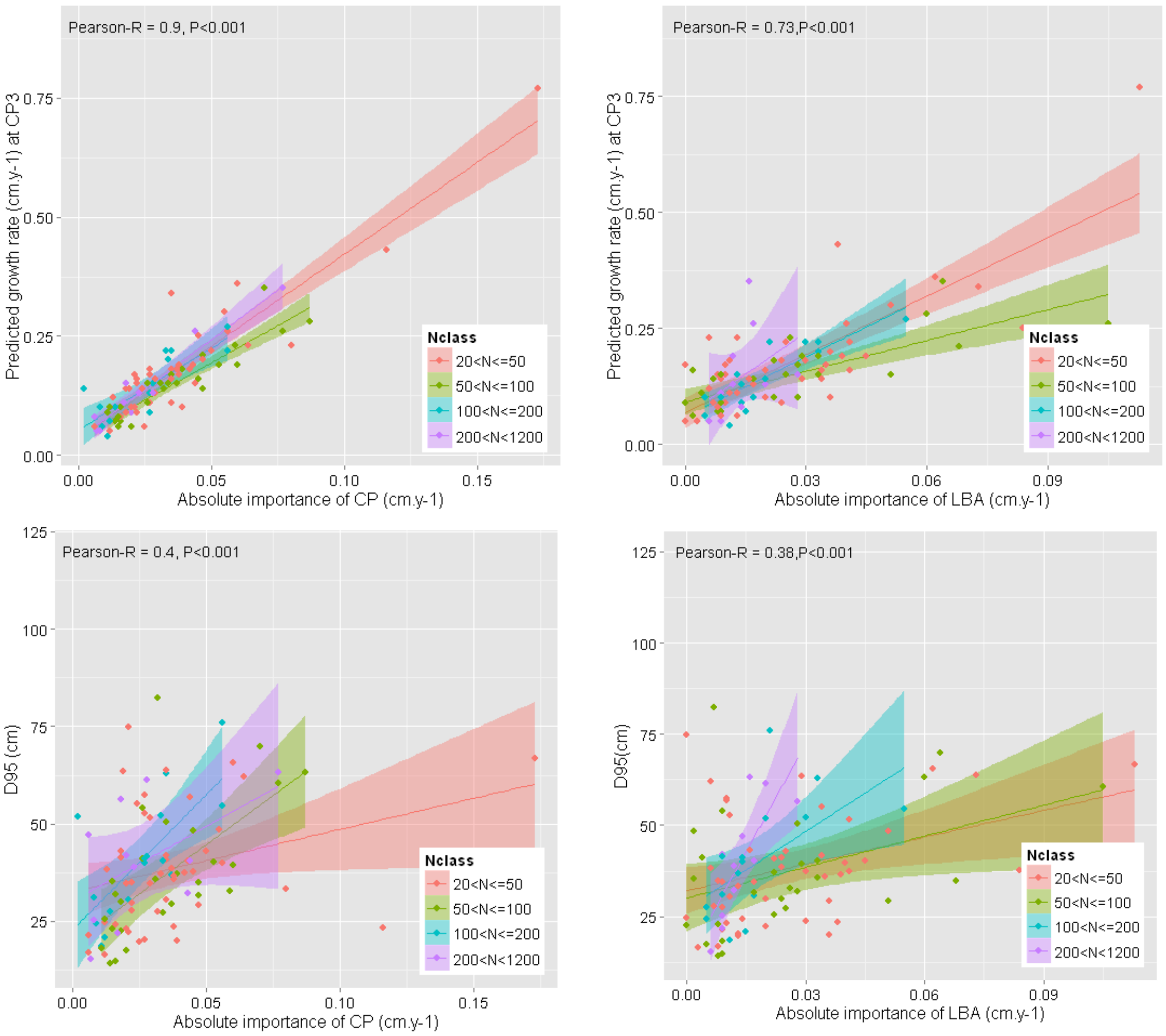

Figure 17.Relationship between CP (a, c) or LBA (b,d) absolute importance (cm.y$^{-1}$) with predicted growth rate under high-light conditions (CP=3, DBH=18cm and LBA=2 m$^2$) and maximum observed DBH (D95 in cm) by class of species abundance (Nclass). Pearson's correlation coefficient and the P-value given were calculated for the 101 species with N>20 individuals but the 95% confidence interval was plotted for each class of species abundance.

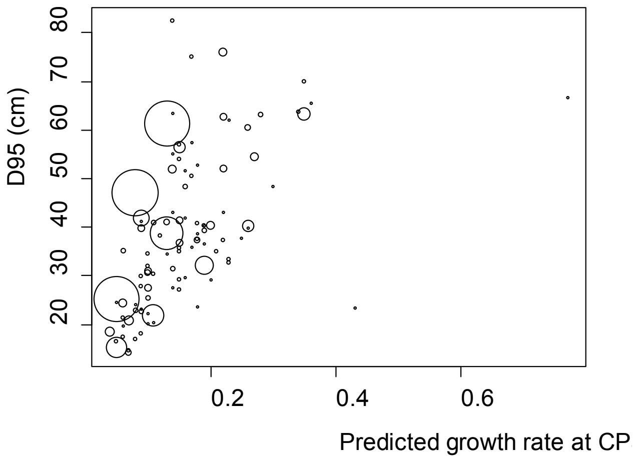

Figure 18. Relationship between predicted growth rate at CP3 (cm.y-$^1$) and species D95 (cm) at the Paracou experimental site. Symbol size is proportional to species abundance.

# IV. Discussion

## IV.1 Is aboveground competition more important than belowground competition in tropical forest?

Our results suggest that competition for light is more important both in relative and absolute terms than belowground competition in Paracou tropical forest. CP explained 3.5% and LBA 2.4% of the variation in DBH increment. The absolute importance of CP and LBA, quantified in growth rate units, was 0.03 cm.y$^{-1}$ and 0.02 cm.y$^{-1}$, respectively. Overall, our findings that competition for light is more important than belowground competition confirm and extend the results of (King et al. 2005) and (van Breugel et al. 2012) who focused on early succession stages.

## IV.2 Relationship between species sensitivity to light and to aboveground competition

In line with the hypothesis put forward by Grime (Grime 2001), and with studies conducted in temperate grasslands and reviewed by (Coomes and Grubb 2000), we found that fast-growing species had a greater capacity than slow-growing species to benefit both from increases in light and belowground resources (Figure 16 and Figure 17). This result appears to be consistent with the findings of previous studies in tropical moist forest (Uriarte et al. 2004, Rüger et al. 2012) and may reflect three distinct phenomena. First, this correlation might be an adaptive outcome of natural selection, representing a convergence of stress-tolerance traits syndrome. High LMA (Leaf Mass per Area), low photosynthetic capacity, and slow turnover of organs, simultaneously confer tolerance to shade and a shortage of nutrients (Veneklaas and Poorter 1998, Poorter and Werger 1999, Westoby et al. 2002) by increasing nutrients residence time. These traits generate slow growth rates and prevent a flexible response to the spatial patchiness of light and soil resources (Chapin et al. 1993, Westoby et al. 2002). Second, this correlation may indicate that the suite of traits that confers shade-tolerance and limits high-light growth rate also restricts the tree's ability to take advantage of a nutrients release in low density patches. Third, and conversely, as hypothesized by (Grime 2001), the suite of traits associated with slow growth rate and low responsiveness to light and nutrients shortage might be a response to competition for nutrients, not for light. Grime's reasoning was that canopy plants require large quantities of nutrients to sustain their high productivity, leaving little for the understorey (Craine 2005). The relevance of this reasoning in tropical trees is based on low nutrients availability for understorey plants and remains to be investigated.

## IV.3 Why is the predictive power of light competition so limited?

In the study described herein, most of the trees were located in shaded conditions, and all but one species responded positively to an increase in CP. These observations confirm the importance of competition for light, and its negative impact on tree growth in tropical forests. We found that the effect of competition for light on DBH increment was biologically significant since the median change in growth rate (0.03 $cm.y^{-1}$) associated with the CP interquartile range ($CP\_imp_{abs}$) should be compared to the medians of predicted mean DBH increment (0.14 $cm.y^{-1}$). This result is consistent with the widely recognized importance of light as a key limiting factor of growth in tropical forest. In contrast, competition for light explained only 3.5% of the total growth rate variation. Thus, light significantly limits DBH increment but is only one of the many factors determining this increment. Regarding the prediction of individual growth rate for the entire community, light availability was strikingly less predictive than species. The strength of the species effect has previously been reported (Gourlet-Fleury 1998) and is implicit in at least one other study conducted at the same site (Herault et al. 2011). However, this result may not have been clearly recognized or sufficiently highlighted. Below, we review the likely reasons why CP has such a limited predictive power for DBH increment. First, Dawkins index is based on a coarse, empirical and indirect quantification of the light resource. CP error is likely responsible for only c. 2% point of unexplained variance which, given the predictive power of CP (3.5%), is far from negligible. We consider that the noise affecting CP scores downplayed the relative importance of asymmetric competition but cannot explain much more than 2% of the unexplained variance.

Second, the highly skewed distribution of species median CP reflects the distribution of adult stature (Figure 14) which illustrates the species-specificity of stratum occupation. As a consequence, many species experience a limited range of light conditions and this limits the predictive power of CP. The segregation of species along the vertical light gradient is associated with the high abundance of small-statured species (D95<45cm for 80% of species). Small-statured species were shown to be slow-growing (Figure 18) and less sensitive to competition than high-statured species that experience a major ontogenetic change in light availability (Figure 17). Previous studies have shown that slow growth rate and low sensitivity of growth to light were associated with high survivorship in deep shade and formed part of a general strategy of resource conservation (Falster and Westoby 2005, Poorter et al. 2008). Thus, most species show a specialization to low-light understorey. It is likely - in these species - that full sunlight does not correspond to the most favorable growth conditions: the cost of thermal stress and evapotranspiration in high-light conditions might outweigh the benefits of increased light availability for photosynthesis (Givnish 1988, Vincent 2001, Semchenko et al. 2012). Thus, species differentiation, and indirectly the strength of the species effect in our model, may reflect adaptation to competition for light. We therefore consider that the minor importance of competition for light in determining individual tree growth results from the abundance of small-statured species which are specialized in low-light conditions. This interpretation is corroborated by the results of a recent study by (Rüger et al. 2012) who showed that adult stature was a significant predictor of species growth characteristics in a Panamanian tropical forest community. In summary, light vertical gradient probably does strongly influence tropical trees growth rate at the community scale, but more so through its effect on species vertical niche differentiation than through the limited access to light of individual trees.

## IV.4 Sources of unexplained inter-individual variation in growth rate

The 54% growth rate variation explained by our model is in line with a number of previous studies conducted in tropical tree communities (Gourlet-Fleury 1998, Rüger et al. 2011) that failed to explain much more than 50% of the growth variability observed. Three interdependent factors: size, species and light, typically explain about half of the average annual diameter growth variation in tropical forest. DBH measurement errors most likely contributed little to the growth rate residual variance since they were largely averaged out by considering DBH increment over a period of eight years. Higher predictive ability values for tropical tree species were reported in at least two studies, but these focused on selected trees at the juvenile stage (size class 8-20 cm dbh) (King et al. 2005) or on a single, highly-responsive fast growing species (Moravie et al. 1999). Stepping beyond the methodological limitations inherent to light exposure estimates and model specification, ecological considerations might also explain a large part of the unexplained intraspecific variance. First, growth allocation between diameter and height is likely to shift during tree life in response to changing environmental conditions (Collinet 1997, Henry and Aarssen 1999) and between the stem and other tree parts (Poorter and Nagel 2000).

Second, tree growth depends on individual genetics, age, stage of development (Clark et al. 2003b, Barthélémy and Caraglio 2007) and historical factors (e.g. herbivore or past physical damage, local physiological constraints) that determine tree vigour. In their study in Malaysia (Pasoh and Lambir LTP), (King et al. 2005) evaluated that 16% of all trees measured (865 trees, 21 species), had suffered severe crown damage. (Rutishauser et al. 2011) performed a crown assessment in French Guiana at the same study site (3752 individual trees > 40cm DBH) and also provided evidence of marked crown structure variability within species. These authors showed that crown fragmentation explained 14% to 31% of growth rate variation in six out of eight abundant species. (Vincent et al. 2002) came to a similar conclusion in Dipterocarp agroforests in Sumatra (Indonesia), using the crown form index proposed by at the time he proposed the CP index (Dawkins 1958): accounting for crown form (CF) to the growth model increased the variance explained by 7.8 to 25.6 % points depending on the experimental plot. A similar result was found in rubber agroforest (Vincent et al. 2011a). Remarkably, CF was a better predictor of growth than CP in both studies. Thus, major alterations in crown shape are likely to concern a significant part of the tree community and thus constitute an important driver of individual tree growth. Unfortunately, DBH is still the standard and only tree dimension recorded extensively in permanent sample plots of tropical forests because of the difficulties inherent to measuring canopy structure variables. To overcome this problem, LiDAR (Light Detection And Ranging) technology is potentially able to provide a detailed description of canopy geometry (Todd et al. 2003, Falkowski et al. 2006, Coops et al. 2007, Pedersen et al. 2012, Vincent et al. 2012), and is thus a means of estimating crown exposure and shape.

Third, the spatial heterogeneity of soil resources is a potential driver of tree growth (Davies 2001, Baker et al. 2003). But, when studying the effect of soil drainage quality on the structure and dynamics of the forest at our site, (Morneau 2007) found that soil type (drainage and topography) had hardly any measurable effect on individual tree growth in the few species spanning a large range of soil conditions, and this occurred in spite of a marked species segregation along drainage gradients. Therefore, the edaphic constraint mostly affected tree growth through environmental filtering.

# V. Conclusion

The study described herein sheds new light on the determinants of tropical tree growth and species differentiation in terms of sensitivity to light competition with respect to their adult stature. Our results crucially point to competition for light making an unexpectedly low contribution to individual tree growth variations, contrasting with a major effect of species identity. We showed that this pattern of variation is likely to result from a vertical niche partitioning of species and an abundance of small-statured species that are moderately responsive to light competition stemming from their adaptation to understorey conditions. Our findings suggest that light predominantly drives the stem growth rate of tropical trees through species differentiation rather than through individual tree growth limitation. This vertical stratification complements the previously reported regeneration niche and together provide evidence for light niche partitioning in the three-dimensional space of tropical forests. It is noteworthy that spatial segregation in relation to the local drainage regime, like vertical segregation into preferred canopy stratum, indirectly contributes to community forest dynamics by environmental filtering or niche differentiation (Sabatier et al. 1997, John 2007, Kraft et al. 2008, Vincent et al. 2011b).

Modeling of forest dynamics plays an important role in predicting carbon storage and the effect of natural (under the influence of global change factors) or anthropic-induced disturbances on the structure and functioning of tropical forests (Chave et al. 2008, Baraloto et al. 2012b). By explicitly considering resource competition, tree size and species, our model left about 45% of DBH increment variation unexplained. Part of this unexplained variance stems from errors in variable measurements and in model specification, and the rest from a number of additional effects - not considered here - that are either difficult to measure (genetics variability), difficult to predict (crown shape) or of low intensity with extremely local relevance (fertility pulse following past disturbance). Even though choosing appropriate growth predictors is contingent on the precise aims of a given modeling project, our findings suggest that competition for light may in first approximation be omitted from the growth models for most moist tropical tree species, though not for the highly-sensitive, tall-statured species that drive whole community structure and dynamics.

# Références

Baker, T. R., M. D. Swaine, and D. F. R. P. Burslem. 2003. Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. Perspectives in Plant Ecology, Evolution and Systematics **6**:21-36.

Baraloto, C., B. Hérault, C. E. T. Paine, H. Massot, L. Blanc, D. Bonal, J.-F. Molino, E. A. Nicolini, and D. Sabatier. 2012. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. Journal of applied ecology **49**:861-870.

Barthélémy, D. and Y. Caraglio. 2007. Plant architecture : a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Annals of Botany:1-33.

Brokaw, N. and R. T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. Trends in Ecology & Evolution **15**:183-188.

Brooker, R., Z. Kikvidze, F. I. Pugnaire, R. M. Callaway, P. Choler, C. J. Lortie, and R. Michalet. 2005. The importance of importance. Oikos **109**:63-70.

Cahill, J. J. F. and B. B. Casper. 2000. Investigating the relationship between neighbor root biomass and belowground competition: field evidence for symmetric competition belowground. Oikos **90**:311-320.

Chapin, F. S., K. Autumn, and F. Pugnaire. 1993. Evolution of suites of traits in response to environmental stresses. The American Naturalist **142**:78-92.

Chave, J., R. Condit, H. C. Muller-Landau, S. C. Thomas, P. S. Ashton, S. Bunyavejchewin, L. L. Co, H. S. Dattaraja, S. J. Davies, S. Esufali, C. E. N. Ewango, K. J. Feeley, R. B. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, T. B. Hart, C. HernÃ¡ndez, S. P. Hubbell, A. Itoh, S. Kiratiprayoon, J. V. LaFrankie, S. Loo de Lao, J.-R. m. Makana, M. N. S. Noor, A. R. Kassim, C. n. Samper, R. Sukumar, H. S. Suresh, S. Tan, J. Thompson, M. D. C. Tongco, R. Valencia, M. Vallejo, G. Villa, T. Yamakura, J. K. Zimmerman, and E. C. Losos. 2008. Assessing Evidence for a Pervasive Alteration in Tropical Tree Communities. PLoS Biol **6**:e45.

Chib, S. and B. P. Carlin. 1999. On MCMC Sampling in Hierarchical Longitudinal Models. Statistics and Computing **9**:17-26.

Clark, D. A. and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs **62**:315-344.

Clark, J. S., J. Mohan, M. Dietze, and I. Ibanez. 2003. Coexistence: How to identify trophic trade-offs. Ecology **84**:17-31.

Collinet, F. 1997. Essai de regroupements des principales espèces structurantes d'une forêt dense humide d'après l'analyse de leur structuration spatiale (Forêt de Paracou-Guyane). Université Claude Bernard Lyon.

Coomes, D. A. and P. J. Grubb. 2000. Impacts of Root Competition in Forests and Woodlands: A Theoretical Framework and Review of Experiments. Ecological Monographs **70**:171-207.

Coops, N., T. Hilker, M. Wulder, B. t. St-Onge, G. Newnham, A. Siggins, and J. Trofymow. 2007. Estimating canopy structure of Douglas-fir forest stands from discrete-return LiDAR. Trees - Structure and Function **21**:295-310.

Craine, J. 2009. Resource Strategies of Wild Plants. Princeton University Press

Craine, J. M. 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of ecology **93**:1041-1052.

Damgaard, C. and A. Fayolle. 2010. Measuring the importance of competition: a new formulation of the problem. Journal of ecology **98**:1-6.

Davies, S. J. 2001. Tree mortality and growth in 11 sympatric Macaranga species in Borneo. Ecology **82**:920-932.

Dawkins, H. C. 1958. The management of natural tropical highforests with special reference to Uganda. Imperial Forestry Institute, University of Oxford Institute **Paper 34**:p.155.

Dietze, M. C., M. S. Wolosin, and J. S. Clark. 2008. Capturing diversity and interspecific variability in allometries: A hierarchical approach. Forest Ecology and Management **256**:1939-1948.

Falkowski, M. J., A. M. S. Smith, A. T. Hudak, P. E. Gessler, L. A. Vierling, and N. L. Crookston. 2006. Automated estimation of individual conifer tree height and crown diameter via Two-dimensional spatial wavelet analysis of lidar data. Canadian Journal of Remote Sensing **32**:153-161.

Falster, D. S. and M. Westoby. 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. Journal of ecology **93**:521-535.

Freckleton, R. P. and A. R. Watkinson. 2001. Asymmetric competition between plant species. Functional Ecology **15**:615-623.

Freckleton, R. P., A. R. Watkinson, and M. Rees. 2009. Measuring the importance of competition in plant communities: Forum. Journal of ecology **97**:379-384.

Givnish, T. J. 1988. Adaptation to sun and shade: A whole-plant perspective. Australian Journal of Plant Physiology **15**:63-92.

Gourlet-Fleury, S. 1998. Indices de compétition en forêt dense tropicale humide : étude de cas sur le dispositif sylvicole expérimental de Paracou. Annals of forest science **55**:623-654.

Gourlet-Fleury, S., J.-M. Guehl, and O. Laroussinie, editors. 2004. Ecology and management of a neotropical rainforest. Lessons drawn from Paracou, a long-term experimental research site in French Guiana. Elsevier.

Grime, J. P. 2001. Plant strategies, Vegetation processes and Ecosystem Properties. 2nd edition, Chichester.

Henry, H. A. L. and L. W. Aarssen. 1999. Interpretation of stem diameter-height allometry in trees: biomechanical constraints, neighbour effects or biased regressions? . Ecology Letters **3**:89-97.

Herault, B., B. Bachelot, L. Poorter, V. Rossi, F. Bongers, J. Chave, C. E. T. Paine, F. Wagner, and C.

Baraloto. 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species. Journal of ecology **99**:1431-1440.

John, R. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proc. Natl Acad. Sci. USA **104**:864-869.

Kikvidze, Z., M. Suzuki, and R. Brooker. 2011. Conceptualizing importance: response to Freckleton and Rees. Trends in Ecology & Evolution **26**:499-500.

King, D. A., S. J. Davies, and N. S. M. Noor. 2006. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. Forest Ecology and Management **223**:152-158.

King, D. A., S. J. Davies, M. N. N. Supardi, and S. Tan. 2005. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. Functional Ecology **19**:445-453.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. Science **322**:580-582.

Moravie, M.-A., M. Durand, and F. Houllier. 1999. Ecological meaning and predictive ability of social status, vigour and competition indices in a tropical rain forest (India). Forest Ecology and Management **17**:221-240.

Morneau, F. 2007. Effets d'un gradient d'engorgement sur la structure et la dynamique d'une forêt tropicale humide. Ecole du Génie Rural, des Eaux et des Forêts.

Oldeman, R. A. A. and J. van Dijk. 1991. Diagnosis of the temperament of tropical trees. Pages 21-63 *in* A. Gomez-Pompa, T. C. Whitmore, and M. Hadley, editors. Rain Forest Regeneration and Management. UNESCO, Paris.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest Models Defined by Field Measurements: Estimation, Error Analysis and Dynamics. Ecological Monographs **66**:1-43.

Pedersen, R. Ã. s., O. M. BollandsÃ¥s, T. Gobakken, and E. NÃ¦sset. 2012. Deriving individual tree competition indices from airborne laser scanning. Forest Ecology and Management **280**:150-165.

Poorter, H. and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water : a quantitative review. Australian Journal of Plant Physiology **27**:595-607.

Poorter, L. and E. Arets. 2003. Light environment and tree strategies in a Bolivian tropical moist forest: an evaluation of the light partitioning hypothesis. Plant Ecology **166**:295-306.

Poorter, L. and M. J. A. Werger. 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. American Journal of Botany **86**:1464-1473.

Poorter, L., S. J. Wright, H. Paz, D. D. Ackerly, R. Condit, G. Ibarra-Manriquez, K. E. Harms, J. C. Licona, M. Martinez-Ramos, S. J. Mazer, H. C. Muller-Landau, M. Pena-Claros, C. O. Webb, and I. J. Wright. 2008. Are functional traits good predictors of demographic rates ? Evidence from five neotropical forests. Ecology **89**:1908-1920.

R Development Core Team. 2011. R : A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rees, M., D. Z. Childs, and R. P. Freckleton. 2012. Assessing the role of competition and stress: a critique of importance indices and the development of a new approach. Journal of ecology **100**:577-585.

Rüger, N., U. Berger, S. P. Hubbell, G. Vieilledent, and R. Condit. 2011. Growth strategies of tropical tree species: disentangling light and size effects. PloS One **6**:e25330.

Rüger, N., C. Wirth, S. J. Wright, and R. Condit. 2012. Functional traits explain light and size response of growth rates in tropical tree species. Ecology **93**:2626-2636.

Rutishauser, E., D. Barthélémy, L. Blanc, and N. Eric-André. 2011. Crown fragmentation assessment in tropical trees: Method, insights and perspectives. Forest Ecology and Management **261**:400-407.

Sabatier, D., M. Grimaldi, M.-F. Prévost, J. Guillaume, M. Gordon, M. Dosso, and P. Curmi. 1997. The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. Plant Ecology **131**.

Schwinning, S. and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia **113**:447-455.

Semchenko, M., M. Lepik, L. Götzenberger, and K. Zobel. 2012. Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? Journal of ecology **100**:459-466.

Sokal, R. R. and F. J. Rohlf. 2010. Biometry: the principles and practice of statistics in biological research. Freeman, New York.

Synnot, T. J. 1979. A manual of permanent plot procedure for tropical rainforests. Commonwealth Forestry Institute, University of Oxford.

Thomas, S. C. and F. A. Bazzaz. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology **80**:1607-1622.

Todd, K., F. Csillag, and P. M. Atkinson. 2003. Three-dimensional mapping of light transmittance and foliage distribution using lidar. Canadian Journal of Remote Sensing **29**:544-555.

Uriarte, M., C. D. Canham, J. Thompson, and J. K. Zimmerman. 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. Ecological Monographs **74**:591-614.

Valladares, F. 2003. Light heterogeneity and plants : from ecophysiology to species coexistence and biodiversity. Pages 439-471 *in* K. Esser, V. Lüttge, W. Beyschlag, and F. Hellwig, editors. Progress in Botany. Springer, Berlin.

van Breugel, M., P. van Breugel, P. Jansen, M. Martínez-Ramos, and F. Bongers. 2012. The relative importance of above- versus belowground competition for tree growth during early succession of a tropical moist forest. Plant Ecology **213**:25-34.

Veneklaas, E. J. and H. Poorter. 1998. Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. Pages 337-361 *in* H. Lambers, H. Poorter, and M. M. I. Van Nuren, editors. Inherent growth variation in plant growth.Physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden.

Vincent, G. 2001. Leaf photosynthetic capacity and nitrogen content adjustment to canopy openness in tropical forest tree seedlings. Journal of tropical Ecology **17**:495-509.

Vincent, G., F. Azhima, L. Joshi, and J. R. Healey. 2011a. Are permanent rubber agroforests an alternative to rotational rubber cultivation? An agro-ecological perspective. Forests, Trees and Livelihoods **20**:85-109.

Vincent, G., H. De Foresta, and R. Mulia. 2002. Predictors of tree growth in a Dipterocarp-based agroforest : a critical assessment. Forest Ecology and Management **161**:39-52.

Vincent, G., J.-F. Molino, L. Marescot, K. Barkaoui, D. Sabatier, V. Freycon, and J. B. Roelens. 2011b. The relative importance of dispersal limitation and habitat preference in shaping distribution of saplings in a tropical moist forest : a case study along a combination of hydromorphic and canopy disturbance gradients. Annals of forest science **68**:357-370.

Vincent, G., D. Sabatier, L. Blanc, J. Chave, E. Weissenbacher, R. Pélissier, E. Fonty, J. F. Molino, and P. Couteron. 2012. Accuracy of small footprint airborne LiDAR in its predictions of tropical moist forest stand structure. Remote Sensing of Environment **125**:23-33.

Wagner, F., B. Hérault, C. Stahl, D. Bonal, and V. Rossi. 2011. Modeling water availability for trees in tropical forests. Agricultural and Forest Meteorology **151**:1202-1213.

Welden, C. W. and W. L. Slauson. 1986. The Intensity of Competition Versus its Importance: An Overlooked Distinction and Some Implications. The quarterly review of biology **61**:23-44.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual review of ecology and systematics **33**:125-159.

# Synthèse et perspectives

L'ambition de ce projet doctoral était de contribuer à la compréhension des mécanismes d'assemblage local des communautés végétales tropicales et de leur réponse aux changements globaux. La théorie de la niche est soutenue par des travaux empiriques associant les espèces pionnières et les espèces sciaphiles mais ces espèces étant rares, elle serait mise en défaut sur sa capacité à expliquer la coexistence de la majorité des espèces d'arbres qui sont situées entre les deux extrémités du gradient successionnel (Hubbell 2005). Le cœur de ce travail de thèse résidait dans l'analyse de l'importance et de la signification écologique de la plasticité phénotypique des traits fonctionnels qui détermine la réponse des espèces à des variations de l'environnement et est susceptible d'influencer les processus de coexistence.

Les objectifs de cette thèse étaient plus précisément les suivants : i) examiner la pertinence des traits morphologiques et de la plasticité phénotypique de l'ensemble des traits fonctionnels pour mieux comprendre les relations entre les traits foliaires et la niche de régénération, ii) évaluer la capacité des traits fonctionnels à prédire les paramètres de la niche de régénération, iii) tester la validité des hypothèses et corollaires de la théorie de la niche pour des espèces d'arbres tropicaux intermédiaires en terme de tempérament, iv) quantifier l'importance relative de la variation intraspécifique de l'accroissement diamétrique produite par la compétition pour la lumière.

## I. Synthèse

### I.1 Les traits morphologiques et leur plasticité permettent-ils de mieux comprendre les relations traits-performances-niche et le mécanisme de tolérance à l'ombre ?

L'analyse comparative de la valeur moyenne et de la plasticité des traits et des performances le long du gradient lumineux s'inscrit dans une approche mécaniste de compréhension de la niche écologique des espèces dont le niveau d'éclairement constitue un axe majeur en forêt tropicale. Nos travaux se distinguent par la prise en compte d'une combinaison de traits morphologiques définis au niveau des branches et du houppier, de traits foliaires et de leur plasticité phénotypique. La mise en relation de ces traits fonctionnels avec les performances et les paramètres de niche nous permet d'interpréter leur valeur fonctionnelle et adaptative et de mieux comprendre et mieux prédire les relations entre traits fonctionnels et niche.

Le compromis croissance à la lumière et survie à l'ombre qui structure la différentiation de la niche de régénération a été associé à un syndrome de traits fonctionnels mesurés et interprétés majoritairement à l'échelle foliaire (biochimie, anatomie, morphologie). La variation interspécifique de la durée de vie des feuilles est ainsi classiquement analysée dans un cadre d'analyse coût-bénéfice comme un moyen d'ajuster la durée de retour sur investissement en carbone (Williams et al. 1989). La durée de vie des feuilles a été reliée à de nombreux autres traits à l'échelle foliaire (Reich et al. 1991, Shiodera et al. 2008) et à quelques traits à l'échelle de la plante entière tels que la croissance et l'allocation de biomasse foliaire (Reich et al. 1992). Nos résultats (Chapitre 2) permettent d'élargir le syndrome de traits foliaires établi à de nouveaux traits et montrent que la longue durée de vie des feuilles des espèces tolérantes à l'ombre, a priori favorable au bilan de carbone à l'échelle foliaire, pourrait aussi et surtout déterminer le bilan de carbone à l'échelle de la plante entière et la survie, par son impact sur la surface foliaire totale. De plus, relativement à cette fonction de maintien de la surface foliaire, la durée de vie des feuilles doit être considérée en interaction avec la vitesse d'émission foliaire : c'est l'équilibre entre la durée de vie des feuilles et la vitesse d'émission foliaire qui semble conditionner la capacité de survie le long du gradient lumineux. Nos observations montrent également que l'interprétation fonctionnelle et adaptative de la forme du houppier sans considérer les traits sous-jacents est délicate. Les variations de la profondeur du houppier observées ne correspondent pas à une maximisation de la capture de l'éclairement par une réduction de l'auto-ombrage comme le suppose l'hypothèse du gain de carbone maximum. Au niveau intraspécifique, nous avons montré que la réduction de la profondeur du houppier résultait d'une réduction de la vitesse d'extension du houppier et non d'une augmentation du taux de mortalité des feuilles ou des branches. Au niveau interspécifique, la profondeur du houppier des espèces tolérantes à l'ombre résulte de l'accumulation de branches produite par l'équilibre entre leur durée de vie de feuilles et leur vitesse d'émission foliaire.

En résumé, le compromis croissance à la lumière et survie à l'ombre peut être caractérisé par une combinaison de traits définis à l'échelle des feuilles, des axes et du houppier. Outre leur longue durée de vie de feuilles et leur forte surface massique, les espèces tolérantes à l'ombre se caractérisent par un houppier profond et élancé, une surface foliaire importante, une vitesse d'émission foliaire lente, et surtout une moindre plasticité de la forme du houppier, de la surface foliaire et de l'accroissement diamétrique. Les covariations de traits observées dans ce travail pourraient être formalisées par des analyses de piste qui s'appuient sur des hypothèses de causalité entre traits à la différence des analyses en composante principale (Vile et al. 2006). La faible disponibilité de traits morphologiques dans les bases de données tient peut-être à la diversité des modes de croissance et des modèles architecturaux qui complique les approches comparatives et a abouti à restreindre les traits morphologiques à des variables très intégratrices comme des allométries (Lida et al. 2012) ou des allocations de biomasse. De plus la structure d'une plante intégrant l'effet des conditions environnementales passées, la mise en relation de la structure et des conditions environnementales à un instant donné peut s'avérer délicate.

## I.2 Peut-on prédire l'amplitude de niche à partir de la plasticité des traits fonctionnels ?

Un nombre croissant de travaux récents montre que la variation intraspécifique des traits et des performances impacte les processus de coexistence (Berg and Ellers 2010). La considération de cet axe supplémentaire de variation reste cependant rare en écologie du fait de son absence dans les bases de données actuelles et de la lourdeur des mesures de terrain qu'elle implique. Nous nous sommes intéressés dans cette thèse à une composante environnementale de la variabilité intraspécifique, la plasticité phénotypique exprimée en réponse à une contrainte lumineuse. Le focus sur cette composante de la variabilité intraspécifique se justifie par la valeur potentiellement adaptative de la plasticité phénotypique et son implication écologique : la plasticité phénotypique permettrait une amplitude de niche plus large.

Nous avons mis en évidence (Chapitre 2) une corrélation significative entre la plasticité de la surface massique (LMA) et l'amplitude de la niche et la stature adulte. Distinguer conceptuellement les réponses phénotypiques qui relèvent d'une adaptation fonctionnelle de celles qui sont inhérentes aux processus biochimiques n'est pas aisé. Néanmoins les connaissances acquises en écophysiologie suggèrent que la variation plastique de la surface massique observée est adaptative et contribue à réduire la variance des performances le long du gradient lumineux et donc à étendre la niche de régénération. Pour la majorité des autres traits, le degré de plasticité est corrélé à la position sur la niche de régénération et dans certains cas à la valeur moyenne du trait dans un environnement donné. Par exemple, la plasticité de la surface foliaire totale est corrélée significativement à la valeur médiane de la surface foliaire totale dans des conditions d'éclairement fort, à la plasticité de l'accroissement diamétrique et à la position des espèces sur le gradient successionnel (Table 12 en annexe). La corrélation observée entre la plasticité de ce trait et la plasticité de l'accroissement diamétrique suggère que cette variation correspond à une réponse passive produite par la disponibilité de la ressource lumineuse. De plus, l'analyse des covariations de traits développée dans le Chapitre 3 montre que cette réduction de surface foliaire à l'ombre résulte d'une modification du rapport entre durée de vie des feuilles et rythme d'émission foliaire. Le degré de plasticité de la surface foliaire totale est donc étroitement lié à la durée de vie des feuilles et donc à la capacité de survivre dans des conditions de faible éclairement. Ainsi, bien que la plasticité de la surface foliaire totale ne présente pas une valeur adaptative, son amplitude reflète l'adaptation des espèces au gradient lumineux. L'absence de consensus sur la relation plasticité des traits et paramètres de niche dans la littérature pourrait donc résulter de la complexité des interactions entre traits et de la variabilité de la valeur adaptative des traits. Bien que la plasticité phénotypique ne constitue qu'une composante de la variabilité intraspécifique des traits fonctionnels, ce travail montre que l'usage de cette variabilité intraspécifique globale pour prédire l'amplitude de niche (Violle and Jiang 2009) est délicate et nécessite une analyse préliminaire de la valeur fonctionnelle des traits concernés.

Une approche mécaniste des variations intraspécifiques des traits apparaît ainsi pertinente dans une perspective de prédiction des paramètres de niche. L'analyse comparative de la plasticité des traits nous a ainsi permis de mieux comprendre la variation interspécifique des performances le long du gradient lumineux et donc la différentiation écologique des espèces.

## I.3 Peut-on étendre la validité de la théorie de la niche aux espèces intermédiaires en terme de tempérament ?

Dans une étude empirique sur l'île de Barro Colarado, (Hubbell 2005) met en évidence un compromis croissance à la lumière–survie à l'ombre entre les espèces situées aux deux extrémités de l'axe de différentiation. Ce résultat ne suffit pas selon cet auteur à créditer la théorie de la niche dans la mesure où, à une des extrémités de cet axe, se trouve un agrégat d'espèces indiscernables en terme de tolérance à l'ombre. La théorie de la niche ne concerne donc t'elle que le petit nombre d'espèces strictement pionnières et strictement tolérantes à l'ombre ? Nous avons examiné cette question à partir de la caractérisation fonctionnelle de 14 espèces intermédiaires en terme de tempérament (c'est-à-dire non-pionnières et non strictement tolérantes à l'ombre-Figure 2) et de la manière suivante : i) en vérifiant la validité du syndrome de traits déterminant le compromis croissance-survie qui structure la réponse des espèces à l'hétérogénéité de l'environnement et donc leur ségrégation, ii) en testant la significativité de la relation entre ces traits, la croissance et les paramètres de la niche. Cette relation est une hypothèse centrale des travaux recherchant l'empreinte des processus de filtrage environnemental ou différentiation de niche dans la distribution des traits fonctionnels à l'échelle de la communauté.

Les 14 espèces étudiées sont abondantes et représentent 27% de la population des arbres adultes (>10 cm de dbh) du site de Paracou. Nous avons montré qu'au stade juvénile, les syndromes de traits foliaires décrits entre les espèces situées aux deux extrémités du gradient lumineux étaient valides pour ces 14 espèces intermédiaires. L'axe surface massique-durée de vie des feuilles qui constitue un axe de différentiation majeur des espèces (Westoby et al. 2002) permet de discriminer ces espèces peu contrastées en terme de tempérament et rend compte d'environ 55% de la variance de l'accroissement diamétrique. Nous avons également mis en évidence une relation significative entre la position des espèces sur le gradient successionnel et la valeur moyenne de différents traits fonctionnels (Chapitres 2 et 3). Le meilleur prédicteur de la position de niche est la plasticité de l'accroissement en hauteur ($r^2 = 0,49$). La masse surfacique et la profondeur relative du houppier à l'ombre expliquent respectivement 34 et 30 % de la variation de position de niche. Les corrélations établies entre traits fonctionnels, performances et niche signifient que les espèces intermédiaires sont discernables et différenciées sur l'axe de niche correspondant à la disponibilité de la ressource lumineuse. Cette relation est fondamentale pour explorer les processus de coexistence à partir de la distribution des traits fonctionnels. Ces résultats mettent en défaut l'hypothèse d'équivalence fonctionnelle formulée par (Hubbell 2005) pour cette fraction de la communauté et constituent une première généralisation de la théorie de la niche écologique à l'ensemble de la communauté des arbres tropicaux. Ils confirment par ailleurs le rôle de l'ouverture de la canopée dans le processus de coexistence des espèces. De plus, l'analyse de la structuration spatiale de la communauté au stade adulte (Figure 13, distribution de la stature des espèces et Figure 14, relation stature adulte-CP moyen) montre une ségrégation des espèces le long du gradient lumineux vertical. Les covariations observées entre la stature adulte et les performances absolues et relatives le long du gradient lumineux ainsi que le faible rôle de la lumière dans la détermination de la croissance sont cohérents avec la théorie de la niche et le rôle central joué par la compétition pour la lumière dans la différentiation écologique des espèces.

## I.4 Quelle est l’importance relative des variations intraspécifiques de la croissance produites par la compétition pour la lumière ?

La compétition pour les ressources est une source de variation intraspécifique des performances des arbres de forêt tropicale humide. Ainsi, la compétition pour la lumière est généralement perçue comme un déterminant majeur de la croissance des arbres alors que les données d’éclairement sont rares et qu’on dispose de peu d’études quantifiant l’effet de la lumière sur la croissance relativement aux autres déterminants que sont l’espèce et la compétition pour les ressources souterraines. La hiérarchisation des déterminants de la croissance est un préalable à la prédiction de la croissance et de la biomasse produite dans un contexte de modélisation et apporte un élément de compréhension du rôle relatif des variations intra- et interspécifique des performances dans les processus d’assemblage local des espèces. Les données de position de houppier (CP) collectées en 2007 sur les parcelles non perturbées du dispositif permanent de Paracou couplées aux données d’accroissement diamétrique nous ont permis d’apporter un éclairage sur cette question.

Contrairement à l’idée reçue, nous avons mis en évidence (Chapitre 4) une faible importance de la compétition pour la lumière dans la détermination de la croissance des arbres à l’échelle de la communauté. L’analyse de la structuration spatiale de la communauté permet de comprendre cette faible réponse à la compétition. La distribution de la stature adulte des espèces (Figure 13) montre une forte abondance d’espèces d’une part peu sensibles et d’autre part exposées à un faible gradient d’éclairement du fait de leur stature moyenne. La corrélation significative observée entre la sensibilité à la compétition et la stature adulte accrédite l’hypothèse d’une adaptation des espèces aux conditions d’éclairement corroborée par l’importance de l’effet espèce observé (34 % de la variance de l’accroissement diamétrique). Ainsi le faible effet de la compétition pour la lumière sur la croissance à l’échelle de la communauté pourrait être expliqué par son rôle passé dans la différentiation des espèces, conformément à la théorie de la niche. Ces résultats confirment l’existence d’un axe de niche représenté par le gradient vertical du niveau d’éclairement complémentaire au gradient horizontal. Ils renforcent l’importance de caractériser les variations interspécifiques de la croissance ainsi que de hiérarchiser les autres sources de variabilité intraspécifique.

# II. Perspectives

## II.1 Prise en compte des contraintes biomécaniques

Après un long focus sur les traits foliaires, les traits structuraux émergent petit à petit dans le champ de l'écologie fonctionnelle en raison de leur importance dans la stabilité, l'acquisition de l'énergie lumineuse, la défense ou le fonctionnement hydraulique des plantes (Figure 19) (Chave et al. 2009, Poorter et al. 2010, Markesteijn et al. 2011, Patino et al. 2012).

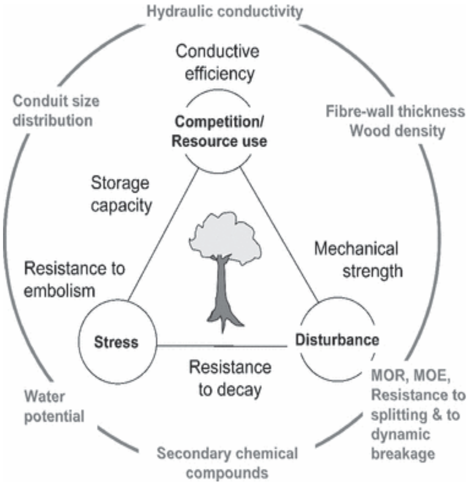

Figure 19. Le rôle du bois dans les principales fonctions écologiques (compétitivité, résistance aux stress et perturbation). Les propriétés du bois sont mentionnées autour du triangle: transport et stockage de l'eau, propriétés mécaniques, propriétés de défense (résistance à la décomposition et à l'embolisme). Le cercle extérieur relie les traits du bois à ces propriétés (Chave et al. 2009).

Nos résultats montrent que l'évolution de la forme et de la plasticité de la forme des jeunes arbres, comme celle d'autres traits, répond à de multiples fonctions et contraintes et soulignent les limites d'interpréter la forme des houppiers et les traits architecturaux vis-à-vis de la seule fonction que représente l'interception de l'énergie lumineuse. La compréhension des stratégies de croissance et de plasticité morphologique pourrait ainsi être significativement améliorée par la considération des contraintes biomécaniques. L'étude de (Sterck et al. 2006b) sur 30 espèces d'arbres tropicaux au stade juvénile a montré que la masse d'1 m de branche était corrélée négativement à celle d'1 m de tige, à la largeur du houppier et au degré de tolérance à l'ombre et non corrélée à la stature adulte. Les espèces tolérantes à l'ombre se caractérisaient par des branches résistantes (en terme de module de rupture), de petit diamètre et denses, peu coûteuses en carbone (biomasse sèche), un houppier large et une tige coûteuse en carbone. Les espèces pionnières produisaient au contraire une tige peu coûteuse en carbone et des branches courtes et coûteuses. La densité du bois a également été corrélée à la forme du houppier chez 145 espèces d'arbres de Malaisie (Lida et al. 2012). Les différences de coût de construction des branches semblent corrélées à la forme du houppier et au degré de tolérance à l'ombre et pourraient donc contribuer à la spécialisation des espèces le long du gradient lumineux.

Pourtant, les relations observées entre traits structuraux et tolérance à l'ombre ne font pas consensus. Alors que les résultats de (Poorter et al. 2010) obtenus sur 42 espèces d'arbres tropicaux au stade adulte confirment la corrélation entre tolérance à l'ombre et densité du bois, les observations de (Baraloto et al. 2010) réalisées sur 668 espèces d'arbres de Guyane française au stade adulte, ont mis en évidence l'orthogonalité de l'axe de traits foliaires gouvernant le compromis croissance à la lumière-survie à l'ombre avec l'axe des traits de la tige (densité du xylème et épaisseur de l'écorce pour le tronc et les branches). L'hétérogénéité des relations entre traits foliaires, traits du bois et tolérance à l'ombre pourraient résulter de leur interaction avec les traits associés au fonctionnement hydraulique (Poorter et al. 2010). Ces divergences illustrent une fois encore la complexité des relations entre traits fonctionnels et la nécessité d'élargir la gamme des traits mesurés à tous les niveaux d'organisation.

## II.2 Exploration du rôle des variations intraspécifiques dans la structuration des communautés végétales

Le Chapitre 4 de cette thèse a révélé la faible importance relative des variations intraspécifiques de la croissance produites par le gradient lumineux. Ce résultat remet en question la pertinence de représenter explicitement la compétition pour la lumière dans une démarche de modélisation de la dynamique ou de la diversité des forêts tropicales et donc de recueillir des données d'éclairement à l'échelle individuelle. L'examen de cette question constitue une perspective intéressante de ce travail de thèse et permettrait d'évaluer l'impact de cette composante de la variation intraspécifique de la croissance sur la dynamique, la composition et la structure de la communauté. Plus précisément, comparer dans un modèle individu centré, l'impact d'un patron de variabilité intraspécifique faible et aléatoire avec un patron de variabilité intraspécifique faible mais structurée spatialement (les individus recevant plus de lumière poussent plus vite) et écologiquement (la majorité des espèces et les espèces de petite taille sont peu sensibles à la compétition) apporterait des éléments de réponse et de décision. Cette approche revient à créer et comparer des communautés virtuelles différenciées par le niveau et la distribution des variations intraspécifiques de la croissance. Elle pourrait être élargie à l'étude de la variabilité intraspécifique globale et de la plasticité des relations allométriques entre la hauteur et le diamètre du tronc ou entre les dimensions de la tige et celles du houppier, qui montrent un degré de variabilité intraspécifique significatif chez les espèces tropicales (Antin et al. 2013). La relation allométrique hauteur-diamètre apparaît dans cette dernière étude particulièrement sensible aux conditions d'éclairement et pourrait faire l'objet d'une telle analyse, compte tenu des perspectives prometteuses offertes par la technologie Lidar pour acquérir des données de hauteur à grande échelle. Les travaux conduits par (Vieilledent et al. 2010) sur deux espèces d'arbres résineuses des Alpes françaises ont montré que la prise en compte de la variabilité intraspécifique des relations allométriques impactaient la distribution spatiale de l'éclairement et le processus de compétition entre les deux espèces. La prise en compte de la plasticité dans une démarche de modélisation individu centrée permettrait également d'évaluer l'influence de la plasticité des relations allométriques sur les performances individuelles et donc d'explorer les conditions dans lesquelles ces ajustements plastiques présentent une valeur adaptative.

# Références

Ackerly, D. D. 1996. Canopy structure and dynamics: integration of growth proceeses in tropical pioneer trees. Pages 619-658 *in* S. S. Mulkey, R. L. Chazdon, and A. P. Smith, editors. Tropical forest plant ecophysiology. Chapman and Hall, New York.

Adler, P. B., A. Fajardo, A. R. Kleinhesselink, and N. J. B. Kraft. 2013. Trait-based tests of coexistence mechanisms. Ecology Letters **16**:1294-1306.

Albert, C. c. H., F. Grassein, F. M. Schurr, G. Vieilledent, and C. Violle. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? Perspectives in Plant Ecology, Evolution and Systematics **13**:217-225.

Albert, C. H., W. Thuiller, N. G. Yoccoz, R. Douzet, S. Aubert, and S. Lavorel. 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. Functional Ecology **24**:1192-1201.

Alpert, P. and E. L. Simms. 2002. The relative advantages of plasticity and fixity in different environments : when is it good for a plant to adjust ? Evolutionary Ecology **16**:285-297.

Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linnean Soc. **161**:105-121.

Antin, C., R. Pélissier, G. g. Vincent, and P. Couteron. 2013. Crown allometries are less responsive than stem allometry to tree size and habitat variations in an Indian monsoon forest. Trees **27**:1485-1495.

Aubry-Kientz, M., B. Hérault, C. Ayotte-Trépanier, C. Baraloto, and V. Rossi. 2013. Toward Trait-Based Mortality Models for Tropical Forests. PloS One **8**:e63678.

Baker, T. R., M. D. Swaine, and D. F. R. P. Burslem. 2003. Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. Perspectives in Plant Ecology, Evolution and Systematics **6**:21-36.

Ballaré, C. L. 2009. Illuminated behaviour: phytochrome as a key regulator of light foraging and plant anti-herbivore defence. Plant, Cell & Environment **32**:713-725.

Baraloto, C. and P. Couteron. 2010. Fine-scale Microhabitat Heterogeneity in a French Guianan Forest. Biotropica **42**:420-428.

Baraloto, C., D. E. Goldberg, and D. Bonal. 2005. Performance trade-offs among tropical tree seedlings in constrasting microhabitats. Ecology **86**:2461-2472.

Baraloto, C., O. J. Hardy, C. E. T. Paine, K. G. Dexter, C. Cruaud, L. T. Dunning, M.-A. Gonzalez, J.-F. Molino, D. Sabatier, V. Savolainen, and J. Chave. 2012a. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. Journal of ecology **100**:690-701.

Baraloto, C., B. Hérault, C. E. T. Paine, H. Massot, L. Blanc, D. Bonal, J.-F. Molino, E. A. Nicolini, and D. Sabatier. 2012b. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. Journal of applied ecology **49**:861-870.

Baraloto, C., C. E. Timothy Paine, L. Poorter, J. Beauchene, D. Bonal, A.-M. Domenach, B. Hérault, S. Patiño, J.-C. Roggy, and J. Chave. 2010. Decoupled leaf and stem economics in rain forest trees. Ecology Letters **13**:1338-1347.

Barthélémy, D. and Y. Caraglio. 2007. Plant architecture : a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Annals of Botany:1-33.

Bazzaz, F. A. and R. W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late succesionnal plants. Oecologia **54**:313-316.

Berg, M. and J. Ellers. 2010. Trait plasticity in species interactions: a driving force of community dynamics. Evolutionary Ecology **24**:617-629.

Biging, G. S. and M. Dobbertin. 1992. A Comparison of Distance-Dependent Competition Measures for Height and Basal Area Growth of Individual Conifer Trees. Forest Science **38**:695-720.

Biging, G. S. and M. Dobbertin. 1995. Evaluation of Competition Indices in Individual Tree Growth Models. Forest Science **41**:360-377.

Bloor, J. M. and P. J. Grubb. 2003. Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. Journal of ecology **91**:77-85.

Bloor, J. M. G. and P. J. Grubb. 2004. Morphological plasticity of shade-tolerant tropical rainforest tree seedlings exposed to light changes. Functional Ecology **18**:337-348.

Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science **320**:1444-1449.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics **13**:115-155.

Brokaw, N. and R. T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. Trends in Ecology & Evolution **15**:183-188.

Brooker, R., Z. Kikvidze, F. I. Pugnaire, R. M. Callaway, P. Choler, C. J. Lortie, and R. Michalet. 2005. The importance of importance. Oikos **109**:63-70.

Cahill, J. J. F. and B. B. Casper. 2000. Investigating the relationship between neighbor root biomass and belowground competition: field evidence for symmetric competition belowground. Oikos **90**:311-320.

Cai, Z. Q., T. Rijkers, and F. Bongers. 2005. Photosynthetic acclimation to light changes in tropical monsoon forest woody species differing in adult stature. Tree Physiol **25**:1023-1031.

Chapin, F. S., K. Autumn, and F. Pugnaire. 1993. Evolution of suites of traits in response to environmental stresses. The American Naturalist **142**:78-92.

Chave, J., R. Condit, H. C. Muller-Landau, S. C. Thomas, P. S. Ashton, S. Bunyavejchewin, L. L. Co, H. S. Dattaraja, S. J. Davies, S. Esufali, C. E. N. Ewango, K. J. Feeley, R. B. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, T. B. Hart, C. HernÃ¡ndez, S. P. Hubbell, A. Itoh, S. Kiratiprayoon, J. V. LaFrankie, S. Loo de Lao, J.-R. m. Makana, M. N. S. Noor, A. R. Kassim, C. n. Samper, R. Sukumar, H. S. Suresh, S. Tan, J. Thompson, M. D. C. Tongco, R. Valencia, M. Vallejo, G. Villa, T. Yamakura, J. K. Zimmerman, and E. C. Losos. 2008. Assessing Evidence for a Pervasive Alteration in Tropical Tree Communities. PLoS Biol **6**:e45.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. Ecology Letters **12**:351-366.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual review of ecology and systematics **31**:343-366.

Chib, S. and B. P. Carlin. 1999. On MCMC Sampling in Hierarchical Longitudinal Models. Statistics and Computing **9**:17-26.

Clark, D. A. and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs **62**:315-344.

Clark, J. S. 2010. Individuals and the variation needed for high species diversity in forest trees. Science **327**:1129-1132.

Clark, J. S., J. Mohan, M. Dietze, and I. Ibanez. 2003a. Coexistence : how to identify trophic trade-offs ? Ecology **84**:17-31.

Clark, J. S., J. Mohan, M. Dietze, and I. Ibanez. 2003b. Coexistence: How to identify trophic trade-offs. Ecology **84**:17-31.

Collet, C., M. Fournier, F. Ningre, A. P.-I. Hounzandji, and T. Constant. 2011. Growth and posture control strategies in Fagus sylvatica and Acer pseudoplatanus saplings in response to canopy disturbance. Annals of Botany **107**:1345-1353.

Collinet, F. 1997. Essai de regroupements des principales espèces structurantes d'une forêt dense humide d'après l'analyse de leur structuration spatiale (Forêt de Paracou-Guyane). Université Claude Bernard Lyon.

Coomes, D. A. and P. J. Grubb. 2000. Impacts of Root Competition in Forests and Woodlands: A Theoretical Framework and Review of Experiments. Ecological Monographs **70**:171-207.

Coops, N., T. Hilker, M. Wulder, B. t. St-Onge, G. Newnham, A. Siggins, and J. Trofymow. 2007. Estimating canopy structure of Douglas-fir forest stands from discrete-return LiDAR. Trees - Structure and Function **21**:295-310.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. Ter Steege, H. D. Morgan, M. G. A. Van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany **51**:335-380.

Cornwell, W. K. and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs **79**:109-126.

Craine, J. 2009. Resource Strategies of Wild Plants. Princeton University Press

Craine, J. M. 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of ecology **93**:1041-1052.

Damgaard, C. and A. Fayolle. 2010. Measuring the importance of competition: a new formulation of the problem. Journal of ecology **98**:1-6.

Davies, S. J. 2001. Tree mortality and growth in 11 sympatric Macaranga species in Borneo. Ecology **82**:920-932.

Dawkins, H. C. 1958. The management of natural tropical highforests with special reference to Uganda. Imperial Forestry Institute, University of Oxford Institute **Paper 34**:p.155.

Dietze, M. C., M. S. Wolosin, and J. S. Clark. 2008. Capturing diversity and interspecific variability in allometries: A hierarchical approach. Forest Ecology and Management **256**:1939-1948.

Donohue, K., D. Messiqua, E. H. Pyle, M. S. Heschel, and J. Schmitt. 2000. Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade-avoidance responses in Impatiens capensis. Evolution **54**:1956-1968.

Du, X., S. Zhou, and R. S. Etienne. 2011. Negative density dependence can offset the effect of species competitive asymmetry: A niche-based mechanism for neutral-like patterns. Journal of Theoretical Biology **278**:127-134.

Engelbrecht, B. M. J. and H. M. Herz. 2001. Evaluation of different methods to estimate understorey light conditions in tropical forests. Journal of tropical Ecology **17**:207-224.

Falkowski, M. J., A. M. S. Smith, A. T. Hudak, P. E. Gessler, L. A. Vierling, and N. L. Crookston. 2006. Automated estimation of individual conifer tree height and crown diameter via Two-dimensional spatial wavelet analysis of lidar data. Canadian Journal of Remote Sensing **32**:153-161.

Falster, D. S. and M. Westoby. 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. Journal of ecology **93**:521-535.

Favrichon, V. 1995. Modèle matriciel déterministe en temps direct. Application à l'étude de la dynamique d'un peuplement forestier tropical humide (Guyane française). Claude Bernard, Lyon 1, Lyon.

Fine, P. V. A., Z. J. Miller, I. Mesones, S. Irazuzta, H. M. Appel, M. H. H. Stevens, I. Sääksjärvi, J. C. Schultz, and P. D. Coley. 2006. The growth defence trade-off and habitat specialization by plants in Amazonian forests. Ecology **87**:150-162.

Fisher, J. B. and D. E. Hibbs. 1982. Plasticity of tree architecture: specific and ecological variations found in Aubreville's model. American Journal of Botany **69**:690-702.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs Copyright 1999: Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, New York; (http://www.rem.sfu.ca/forestry/index.htm or http://www.ecostudies.org).

Freckleton, R. P. and A. R. Watkinson. 2001. Asymmetric competition between plant species. Functional Ecology **15**:615-623.

Freckleton, R. P., A. R. Watkinson, and M. Rees. 2009. Measuring the importance of competition in plant communities: Forum. Journal of ecology **97**:379-384.

Gause, G. F. 1934. The struggle for existence. MD: Williams & Wilkins, Baltimore.

Gilbert, I. R., P. G. Jarvis, and H. Smith. 2001. Proximity signal and shade avoidance differences between early and late successional trees. Nature **411**:792-795.

Givnish, T. J. 1988. Adaptation to sun and shade: A whole-plant perspective. Australian Journal of Plant Physiology **15**:63-92.

Gourlet-Fleury, S. 1998. Indices de compétition en forêt dense tropicale humide : étude de cas sur le dispositif sylvicole expérimental de Paracou. Annals of forest science **55**:623-654.

Gourlet-Fleury, S., L. Blanc, N. Picard, P. Sist, J. Dick, R. Nasi, M. D. Swaine, and E. Forni. 2005. Grouping species for predicting mixed tropical forest dynamics : looking for a strategy. Annals of forest science **62**:785-796.

Gourlet-Fleury, S., J.-M. Guehl, and O. Laroussinie, editors. 2004. Ecology and management of a neotropical rainforest. Lessons drawn from Paracou, a long-term experimental research site in French Guiana. Elsevier.

Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters **9**:399-409.

Grime, J. P. 2001. Plant strategies, Vegetation processes and Ecosystem Properties. 2nd edition, Chichester.

Grime, J. P., J. C. Crick, and J. E. Rincon. 1986. The ecological significance of plasticity. Pages 5-29 *in* D. H. Jennings and A. J. Trewavas, editors. Plasticity in plants, Pindar, Scarborough, UK.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews **52**:107-145.

Hammond, S. T. and K. J. Niklas. 2009. Emergent properties of plants competing in silico for space and light: Seeing the tree from the forest. Am. J. Bot. **96**:1430-1444.

Harja, D., G. Vincent, R. Mulia, and M. van Noordwijk. 2012. Tree shape plasticity in relation to crown exposure. Trees - Structure and Function **26**:1275-1285.

Henry, H. A. L. and L. W. Aarssen. 1999. Interpretation of stem diameter-height allometry in trees: biomechanical constraints, neighbour effects or biased regressions? . Ecology Letters **3**:89-97.

Herault, B., B. Bachelot, L. Poorter, V. Rossi, F. Bongers, J. Chave, C. E. T. Paine, F. Wagner, and C. Baraloto. 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species. Journal of ecology **99**:1431-1440.

Herault, B., J. Ouallet, L. Blanc, F. Wagner, and C. Baraloto. 2010. Growth responses of neotropical trees to logging gaps. Journal of applied ecology **47**:821-831.

Hikosaka, K. 2005. Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. Ann Bot **95**:521-533.

Hirose, T., M. J. A. Werger, T. L. Pons, and J. W. A. Rheenen. 1988. Canopy structure and leaf nitrogen distribution in a stand of Lysimachia vulgaris L. as influenced by stand density. Oecologia **77**:145-150.

Horn, H. 1971. The adaptive geometry of trees. Princeton University Press, NJ, USA.

Hubbell, P. S., editor. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Hubbell, S. P. 1979. Tree Dispersion, Abundance, and Diversity in a Tropical Dry Forest. Science **203**:1299-1309.

Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Functional Ecology **19**:166-172.

Hubbell, S. P., R. B. Foster, S. T. O'Brien, d. K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. Science **283**:554-557.

Hulshof, C. M. and N. G. Swenson. 2009. Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. Functional Ecology **24**:217-223.

Hutchinson, G. E. 1957. Concluding remarks. Pages 415-427 *in* Cold Spring Harbor Symposia on Quantitative Biology

Ishida, A., A. Uemura, N. Yamashita, M. Shimizu, T. Nakano, and A. L. Hoe. 2003. Leaf physiological adjustments to changing lights: Partitioning the heterogeneous resources across tree species. Pages 225-239 *in* T. Okuda, N. Manokaran, Y. Matsumo, K. Niiyama, S. C. Thomas, and P. S. Ashton, editors. Pasoh Ecology of a Lowland Rain Forest in Southeast Asia. Springer-Verlag, Tokyo - Berlin - Heidelberg - New York.

Jennings, S. B., N. D. Brown, and D. Sheil. 1999. Assessing forest canopies and understorey illumination : canopy closure, canopy clover and other measures. Forestry **72**:59-73.

John, R. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proc. Natl Acad. Sci. USA **104**:864-869.

John, R., J. W. Dalling, K. E. Harms, J. B. Yavitt, R. F. Stallard, M. Mirabello, S. P. Hubbell, R. Valencia, H. Navarrete, M. Vallejo, and R. B. Foster. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences **104**:864-869.

Jung, V., C. Violle, C. Mondy, L. Hoffmann, and S. Muller. 2010. Intraspecific variability and trait-based community assembly. Journal of ecology **98**:1134-1140.

Kearney, M., S. J. Simpson, D. Raubenheimer, and B. Helmuth. 2010. Modelling the ecological niche from functional traits. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:3469-3483.

Kikuzawa, K. 2003. Phenological and morphological adaptations to the light environment in two woody and two herbaceous plant species. Functional Ecology **17**:29-38.

Kikvidze, Z., M. Suzuki, and R. Brooker. 2011. Conceptualizing importance: response to Freckleton and Rees. Trends in Ecology & Evolution **26**:499-500.

King, D. A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. American Journal of Botany **81**:948-957.

King, D. A. and D. B. Clark. 2004. Inferring growth rates from leaf display in tropical forest saplings. Journal of tropical Ecology **20**:351-354.

King, D. A., S. J. Davies, and N. S. M. Noor. 2006. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. Forest Ecology and Management **223**:152-158.

King, D. A., S. J. Davies, M. N. N. Supardi, and S. Tan. 2005. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. Functional Ecology **19**:445-453.

King, D. A., E. G. Leigh, R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Relationships between branch spacing, growth rate and light in tropical forest saplings. Functional Ecology **11**:627-635.

Kneitel, J. M. and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters **7**:69-80.

Kohyama, T. and M. Hotta. 1990. Significance of allometry in tropical saplings. Functional Ecology **4**:515-521.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. Science **322**:580-582.

Laurans, M., O. Martin, E. Nicolini, and G. Vincent. 2012. Functional traits and their plasticity predict tropical trees regeneration niche even among species with intermediate light requirements. Journal of ecology **100**:1440-1452.

Lecerf, A. and E. Chauvet. 2008. Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. Basic and Applied Ecology **9**:598-605.

Leibold, M. A. and M. A. McPeek. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology **87**:1399-1410.

Lhotka, J. M. and E. F. Loewenstein. 2006. Indirect measures of predicting light transmittance along a gradient of riparian forest canopy structures. Forest Ecology and Management.

Lida, Y., L. Poorter, F. J. Sterck, A. R. Kassim, T. Kubo, M. D. Potts, and T. S. Kohyama. 2012. Wood density explains architectural differentiation across 145 co-occurring tropical tree species. Functional Ecology **26**:274-282.

Lieberman, M. and D. Lieberman. 1989. Forests are not just swiss cheese : canopy stereogeometry of non-gaps in tropical forests. Ecology **70**:550-552.

Little, J. D. C. 1961. A Proof of the Queueing Formula L = λ W. Operations Research **9**:383-387.

Lorimer, C. G. 1983. A test of the accuracy of shade-tolerance classifications based on physiognomic and reproductive traits. Canadian Journal of Botany **61**:1595-1598.

Lortie, C. J. and L. W. Aarssen. 1996. The specialization hypothesis for phenotypic plasticity in plants. International Journal of Plant Science **157**:484-487.

Lusk, C. H. 2002. Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. Oecologia **132**:188-196.

Lusk, C. H., Y. Onoda, R. Kooyman, and A. Gutiérrez-Girón. 2010. Reconciling species-level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. New Phytologist **186**:429-438.

Lusk, C. H., P. B. Reich, R. A. Montgomery, D. D. Ackerly, and J. Cavender-Bares. 2008. Why are evergreen leaves so contrary about shade? Trends in Ecology & Evolution **23**:299-303.

Macarthur, R. and R. Levins. 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. The American Naturalist **101**:377-385.

Markesteijn, L., L. Poorter, F. Bongers, H. Paz, and L. Sack. 2011. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. New Phytologist **191**:480-495.

Martinez-Garza, C. and H. A. F. Howe. 2005. Developmental strategy or immediate responses in leaf traits of tropical tree species? International Journal of Plant Sciences **166**:41-48.

Mc Gill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution **21**:178-185.

Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. Ecology Letters **13**:838-848.

Molino, J.-F. and D. Sabatier. 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. Science **294**:1702-1704.

Moravie, M.-A., M. Durand, and F. Houllier. 1999. Ecological meaning and predictive ability of social status, vigour and competition indices in a tropical rain forest (India). Forest Ecology and Management **17**:221-240.

Morneau, F. 2007. Effets d'un gradient d'engorgement sur la structure et la dynamique d'une forêt tropicale humide. Ecole du Génie Rural, des Eaux et des Forêts.

Muth, C. C. and F. A. Bazzaz. 2003. Tree canopy displacement and neighbourhood interactions. Canadian Journal of forest research **33**:1323-1330.

Nagelkerke, C. and S. J. Menken. 2013. Coexistence of Habitat Specialists and Generalists in Metapopulation Models of Multiple-Habitat Landscapes. Acta Biotheoretica:1-14.

Navas, M.-L., B. Ducout, C. Roumet, J. Richarte, J. Garnier, and E. Garnier. 2003. Leaf life span, dynamics and construction cost of species from Mediterranean old-fields differing in successional status. New Phytologist **159**:213-228.

Nicotra, A., R. L. Chazdon, and S. V. B. Iriarte. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecology **80**:1908-1926.

Nicotra, A., R. L. Chazdon, and C. D. Schlichting. 1997. Patterns of genotypic variation and phenotypic plasticity of light response in two tropical *Piper* (Piperaceae) species. American Journal of Botany **84**:1542-1552.

Nicotra, A. B., O. K. Atkin, S. P. Bonser, A. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, M. D. Purugganan, C. L. Richards, F. Valladares, and M. van Kleunen. 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Science **15**:684-692.

Niinemets, Ü. 1997. Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. Functional Ecology **11**:518-531.

Niinemets, Ü. 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecological Research **25**:693-714.

Oldeman, R. A. A. and J. van Dijk. 1991. Diagnosis of the temperament of tropical trees. Pages 21-63 *in* A. Gomez-Pompa, T. C. Whitmore, and M. Hadley, editors. Rain Forest Regeneration and Management. UNESCO, Paris.

Onoda, Y., F. Schieving, and N. P. R. Anten. 2008. Effects of light and nutrient availability on leaf mechanical properties of *Plantago major*: a conceptual approach. Annals of Botany **101**:727-736.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest Models Defined by Field Measurements: Estimation, Error Analysis and Dynamics. Ecological Monographs **66**:1-43.

Pachepsky, E., J. L. Bown, A. Eberst, U. Bausenwein, P. Millard, G. R. Squire, and J. W. Crawford. 2007. Consequences of intraspecific variation for the structure and function of ecological communities Part 2: Linking diversity and function. Ecological Modelling **207**:277-285.

Paine, C. E. T., C. Baraloto, J. Chave, and B. Hérault. 2010. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. Oikos **120**:720-727.

Patino, S., N. M. Fyllas, T. R. Baker, R. Paiva, C. A. Quesada, A. J. B. Santos, M. Schwarz, H. ter Steege, O. L. Phillips, and J. Lloyd. 2012. Coordination of physiological and structural traits in Amazon forest trees. Biogeosciences **9**:775-801.

Pearcy, R. W. and F. Valladares. 1999. Resource acquisition by plants : the role of crown architecture.*in* M. C. Press, J. D. Scholes, and M. G. Barjer, editors. Physiological plant ecology. Blackwell science.

Pearcy, R. W., F. Valladares, S. J. Wright, and E. L. De Paulis. 2004. A functional analysis of the crown architecture of tropical forest *Psychotria* species : do species cary in light capture efficiency and consequently in carbon gain and growth ? Oecologia **139**:163-177.

Pedersen, R. Ã. s., O. M. BollandsÃ¥s, T. Gobakken, and E. NÃ¦sset. 2012. Deriving individual tree competition indices from airborne laser scanning. Forest Ecology and Management **280**:150-165.

Pfennig, D. W., A. M. Rice, and R. A. Martin. 2006. Ecological opportunity and phenotypic plasticity interact to promote character displacement and species coexistence. Ecology **87**:769-779.

Poorter, H. and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water : a quantitative review. Australian Journal of Plant Physiology **27**:595-607.

Poorter, L. 1999. Growth response of 15 rain-forest tree species to a light gradient : the relative importance of morphological and physiological traits. Functional Ecology **13**:396-410.

Poorter, L. and E. Arets. 2003. Light environment and tree strategies in a Bolivian tropical moist forest: an evaluation of the light partitioning hypothesis. Plant Ecology **166**:295-306.

Poorter, L. and F. Bongers. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology **87**:1733-1743.

Poorter, L., F. Bongers, F. Sterck, and H. Wöll. 2005. Beyond the regeneration phase : differenciation of height light trajectories among tropical tree species. Journal of ecology **93**:256-267.

Poorter, L., I. McDonald, A. Alarcón, E. Fichtler, J.-C. Licona, M. Peña-Claros, F. Sterck, Z. Villegas, and U. Sass-Klaassen. 2010. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytologist **185**:481-492.

Poorter, L. and D. Rozendaal. 2008. Leaf size and leaf display of thirty-eight tropical tree species. Oecologia **158**:35-46.

Poorter, L. and M. J. A. Werger. 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. American Journal of Botany **86**:1464-1473.

Poorter, L., S. J. Wright, H. Paz, D. D. Ackerly, R. Condit, G. Ibarra-Manriquez, K. E. Harms, J. C. Licona, M. Martinez-Ramos, S. J. Mazer, H. C. Muller-Landau, M. Pena-Claros, C. O. Webb, and I. J. Wright. 2008. Are functional traits good predictors of demographic rates ? Evidence from five neotropical forests. Ecology **89**:1908-1920.

Popma, J., F. Bongers, and M. J. A. Werger. 1992. Gap-dependence and leaf characteristics of trees in a tropical lowland rain forest in Mexico. Oikos **63**:207-214.

Portsmuth, A. and U. Niinemets. 2007. Structural and physiological plasticity in response to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. Functional Ecology **21**:61-77.

Posada, J. M., R. SievÃ¤nen, C. Messier, J. Perttunen, E. Nikinmaa, and M. J. Lechowicz. 2012. Contributions of leaf photosynthetic capacity, leaf angle and self-shading to the maximization of net photosynthesis in Acer saccharum: a modelling assessment. Annals of Botany **110**:731-741.

R Development Core Team. 2011. R : A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rees, M., D. Z. Childs, and R. P. Freckleton. 2012. Assessing the role of competition and stress: a critique of importance indices and the development of a new approach. Journal of ecology **100**:577-585.

Reich, P., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation : traits, spectra, and strategies. International Journal of Plant Science **164**:143-164.

Reich, P. B., C. Uhl, M. B. Walters, and D. S. Ellsworth. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. Oecologia **86**:16-24.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs **62**:365-392.

Riéra, B. and D. Alexandre. 1988. Surface des chablis et temps de renouvellement en forêt dense tropicale. Acta Oecologica **9**:211-220.

Rozendaal, D. M. A., V. H. Hurtado, and L. Poorter. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Functional Ecology **20**:207-216.

Rüger, N., U. Berger, S. P. Hubbell, G. Vieilledent, and R. Condit. 2011. Growth strategies of tropical tree species: disentangling light and size effects. PloS One **6**:e25330.

Rüger, N., C. Wirth, S. J. Wright, and R. Condit. 2012. Functional traits explain light and size response of growth rates in tropical tree species. Ecology **93**:2626-2636.

Rutishauser, E., D. Barthélémy, L. Blanc, and N. Eric-André. 2011. Crown fragmentation assessment in tropical trees: Method, insights and perspectives. Forest Ecology and Management **261**:400-407.

Sabatier, D., M. Grimaldi, M.-F. Prévost, J. Guillaume, M. Gordon, M. Dosso, and P. Curmi. 1997. The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. Plant Ecology **131**.

Schmitz, O. J., F. R. Adler, and A. A. Agrawal. 2003. Linking individual-scale trait plasticity to community dynamics. Ecology **84**:1081-1082.

Schwinning, S. and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia **113**:447-455.

Seiwa, K., K. Kikuzawa, T. Kadowaki, S. Akasaka, and N. Ueno. 2006. Shoot life span in relation to successional status in deciduous broad-leaved tree species in a temperate forest. New Phytologist **169**:537-548.

Semchenko, M., M. Lepik, L. Götzenberger, and K. Zobel. 2012. Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? Journal of ecology **100**:459-466.

Shiodera, S., J. S. Rahajoea, and T. Kohyama. 2008. Variation in longevity and traits of leaves among co-occurring understorey plants in a tropical montane forest. Journal of tropical Ecology **24**:121-133.

Shirakawa, H. and K. Kikuzawa. 2009. Crown hollowing as a consequence of early shedding of leaves and shoots. Ecological Research **24**:839-845.

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology & Evolution **19**:605-611.

Sokal, R. R. and F. J. Rohlf. 2010. Biometry: the principles and practice of statistics in biological research. Freeman, New York.

Southwood, T. R. E., V. K. Brown, and P. M. Reader. 1986. Leaf palatability, life expectancy and herbivore damage. Oecologia **70**:544-548.

Sterck, F. 1999. Crown development in tropical rain forest trees in gaps and understorey. Plant Ecology **143**:89-98.

Sterck, F., F. Bongers, and D. M. Newbery. 2001. Tree architecture in a Bornean lowland rain forest : intraspecific and interspecific patterns. Plant Ecology **153**:279-292.

Sterck, F., L. Markesteijn, F. Schieving, and L. Poorter. 2011. Functional traits determine trade-offs and niches in a tropical forest community. Proceedings of the National Academy of Sciences **108**:20627-20632.

Sterck, F., M. Martinez-Ramos, G. Dyer-Leal, J. Rodrigez-Velasquez, and L. Poorter. 2003. The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest. Functional Ecology **17**:194-200.

Sterck, F., L. Poorter, and F. Schieving. 2006a. Leaf traits determine the growth-survival trade-off across rain forest tree species. The American Naturalist **167**:758-765.

Sterck, F., F. Schieving, A. Lemmens, and T. L. Pons. 2005. Performance of trees in forest canopies : explorations with a bottom-up functional-structural plant growth model. New Phytologist **166**:827-843.

Sterck, F. J. and F. Schieving. 2007. 3-D growth patterns of trees : effect of carbon economy, meristem activity, and selection. Ecological Monographs **77**:405-420.

Sterck, F. J., H. A. Van Gelder, and L. Poorter. 2006b. Mechanical branch constraints contribute to life-history variation across tree species in a Bolivian forest. Journal of ecology **94**:1192-1200.

Strauss-Debenedetti and F. A. Bazzaz. 1991. Plasticity and acclimation to light in tropical Moraceae of different sucessional positions. Oecologia **87**:377-387.

Sultan, S. E. 2001. Phenotypic plasticity for fitness components in polygonum species of contrasting ecological breadth. Ecology **82**:328-343.

Sultan, S. E. 2003. Phenotypic plasticity in plants : a case study in ecological development. Evolution and Development **5**:25-33.

Sultan, S. E., A. M. Wilczek, S. D. Hann, and B. J. Brosi. 1998. Contrasting ecological breadth of co-occurring annual Polygonum species. Journal of ecology **86**:363-383.

Swenson, N. G. 2013. The assembly of tropical tree communities – the advances and shortcomings of phylogenetic and functional trait analyses. Ecography **36**:264-276.

Synnot, T. J. 1979. A manual of permanent plot procedure for tropical rainforests. Commonwealth Forestry Institute, University of Oxford.

Takahashi, K., T. Seino, and T. Kohyama. 2001. Responses to canopy openings in architectural development of saplings in eight deciduous broad-leaved tree species. Canadian Journal of forest research **31**:1336-1347.

Takashima, A., A. Kume, and S. Yoshida. 2006. Methods for estimating understory light conditions using crown projection maps and topographic data. Ecological Research **21**:560-569.

Temesgen, H. and K. Gadow. 2004. Generalized height–diameter models—an application for major tree species in complex stands of interior British Columbia. European Journal of Forest Research **123**:45-51.

Thomas, S. C. and F. A. Bazzaz. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology **80**:1607-1622.

Thomas, S. C. and W. E. Winner. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. Tree physiology **22**:117-127.

Thompson, K., J. G. Hodgson, and K. J. Gaston. 1998. Abundance–range size relationships in the herbaceous flora of central England. Journal of ecology **86**:439-448.

Todd, K., F. Csillag, and P. M. Atkinson. 2003. Three-dimensional mapping of light transmittance and foliage distribution using lidar. Canadian Journal of Remote Sensing **29**:544-555.

Uriarte, M., C. D. Canham, J. Thompson, and J. K. Zimmerman. 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. Ecological Monographs **74**:591-614.

Valladares, F. 2003. Light heterogeneity and plants : from ecophysiology to species coexistence and biodiversity. Pages 439-471 *in* K. Esser, V. Lüttge, W. Beyschlag, and F. Hellwig, editors. Progress in Botany. Springer, Berlin.

Valladares, F. and U. Niinemets. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. Annual Review of Ecology, Evolution, and Systematics **39**:237-257.

Valladares, F., D. Sanchez-Gomez, and M. A. Zavala. 2006. Quantitative estimation of phenotypic plasticity : bridging the gap between the evolutionary concept and its ecological applications. Journal of ecology **94**:1103-1116.

Valladares, F., J. B. Skillman, and R. W. Pearcy. 2002. Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures : a case of morphological compensation. American Journal of Botany **89**:1275-1284.

Valladares, F., S. J. Wright, E. Lasso, K. Kitajima, and R. W. Pearcy. 2000. Plastic response to light of 16 congeneric shrubs from a panamanian rainforest. Ecology **81**:1925-1936.

van Breugel, M., P. van Breugel, P. Jansen, M. Martínez-Ramos, and F. Bongers. 2012. The relative importance of above- versus belowground competition for tree growth during early succession of a tropical moist forest. Plant Ecology **213**:25-34.

Veneklaas, E. J. and H. Poorter. 1998. Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. Pages 337-361 *in* H. Lambers, H. Poorter, and M. M. I. Van Nuren, editors. Inherent growth variation in plant growth.Physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden.

Vieilledent, G., B. Courbaud, G. Kunstler, J.-F. Dhôte, and J. S. Clark. 2010. Individual variability in tree allometries determines light resource allocation in forest ecosystems: a hierarchical Bayesian approach. Oecologia **163**:759-773.

Vile, D., B. Shipley, and E. Garnier. 2006. A STRUCTURAL EQUATION MODEL TO INTEGRATE CHANGES IN FUNCTIONAL STRATEGIES DURING OLD-FIELD SUCCESSION. Ecology **87**:504-517.

Vincent, G. 2001. Leaf photosynthetic capacity and nitrogen content adjustment to canopy openness in tropical forest tree seedlings. Journal of tropical Ecology **17**:495-509.

Vincent, G. 2006. Leaf life span plasticity in tropical seedlings grown under contrasting light regimes. Annals of Botany **97**:245-255.

Vincent, G., F. Azhima, L. Joshi, and J. R. Healey. 2011a. Are permanent rubber agroforests an alternative to rotational rubber cultivation? An agro-ecological perspective. Forests, Trees and Livelihoods **20**:85-109.

Vincent, G., H. De Foresta, and R. Mulia. 2002. Predictors of tree growth in a Dipterocarp-based agroforest : a critical assessment. Forest Ecology and Management **161**:39-52.

Vincent, G., J.-F. Molino, L. Marescot, K. Barkaoui, D. Sabatier, V. Freycon, and J. B. Roelens. 2011b. The relative importance of dispersal limitation and habitat preference in shaping distribution of saplings in a tropical moist forest : a case study along a combination of hydromorphic and canopy disturbance gradients. Annals of forest science **68**:357-370.

Vincent, G., D. Sabatier, L. Blanc, J. Chave, E. Weissenbacher, R. Pélissier, E. Fonty, J. F. Molino, and P. Couteron. 2012. Accuracy of small footprint airborne LiDAR in its predictions of tropical moist forest stand structure. Remote Sensing of Environment **125**:23-33.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. c. H. Albert, C. Hulshof, V. Jung, and J. Messier. In Press. The return of the variance: intraspecific variability in community ecology. Trends in Ecology and Evolution.

Violle, C. and L. Jiang. 2009. Towards a trait-based quantification of species niche. J Plant Ecol **2**:87-93.

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos **116**:882-892.

Wagner, F., B. Hérault, C. Stahl, D. Bonal, and V. Rossi. 2011. Modeling water availability for trees in tropical forests. Agricultural and Forest Meteorology **151**:1202-1213.

Walters, M. B. and P. B. Reich. 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants : do winter deciduous and broad-leaved evergreen species differ ? New Phytologist **143**:143-154.

Weiner, J. and S. Xiao. 2012. Variation in the degree of specialization can maintain local diversity in model communities. Theoretical Ecology **5**:161-166.

Weinig, C. 2000. Plasticity versus canalization: population differences in the timing of shade-avoidance responses. Evolution **54**:441-451.

Welden, C. W., S. W. Hewett, S. P. Hubbell, and R. B. Foster. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. Ecology **72**:35-50.

Welden, C. W. and W. L. Slauson. 1986. The Intensity of Competition Versus its Importance: An Overlooked Distinction and Some Implications. The quarterly review of biology **61**:23-44.

Westbrook, J. W., K. Kitajima, J. G. Burleigh, W. J. Kress, D. L. Erickson, and S. J. Wright. 2011. What Makes a Leaf Tough? Patterns of Correlated Evolution between Leaf Toughness Traits and Demographic Rates among 197 Shade-Tolerant Woody Species in a Neotropical Forest. American Naturalist **177**:800-811.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual review of ecology and systematics **33**:125-159.

Wildova, R., L. Gough, T. Herben, C. Hershock, and D. E. Goldberg. 2007. Architectural and growth traits differ in effects on performance of clonal plants: an analysis using a field-parameterized simulation model. Oikos **116**:836-852.

Williams, K., C. B. Field, and H. A. Mooney. 1989. Relationships among leaf construction cost, leaf longevity, and light environment in rain-forest plants of the genus Piper. The Amarican Naturalist **133**:198-211.

Wilson, B. F. 2000. Apical control of branch growth and angle in woody plants. American Journal of Botany **87**:601-607.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, U. Niinemets,

J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature **428**:821-827.

Wright, I. J., M. Westoby, and P. B. Reich. 2002. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. Journal of ecology **90**:534-543.

Wright, J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia **130**:1-14.

Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, S. Diaz, B. M. J. Engelbrecht, K. E. Harms, S. P. Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, and A. E. Zanne. 2010. Functional traits and the growth mortality trade-off in tropical trees. Ecology **91**:3664-3674.

Wright, S. J., H. C. Muller-Landau, R. Condit, and S. P. Hubbell. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. Ecology **84**:3174-3185.

# Annexes

## Protocole du suivi de croissance des juvéniles - Paracou 2007- 2009

Premier passage en juillet 2007 pour un premier lot d'individus puis novembre/décembre 2007 pour le second lot.

On mesure sur les individus sélectionnés : la hauteur totale, la hauteur première branche, l'encombrement du houppier, le nombre de branches d'ordre 1, le nombre de feuilles. On repère l'arbre de référence le plus proche la date du premier relevé le code de Dawkins. En outre ou mesure les caractéristiques suivantes :

Critères communs :

- ✓ Le niveau de ramification de l'individu est relevé (sauf pour BP, PC pour les quelles cela n'a pas grand sens)
- ✓ L'encombrement du houppier est mesuré dans deux directions perpendiculaires et inclut l'extension des feuilles
- ✓ Le nombre de branches et la hauteur de la première branche sont mesurés. A défaut la hauteur de la première feuille est notée, notamment pour les EG et DG et PG non ramifiés. Une branche comptabilisée est une branche portant des feuilles. Lorsque l'apex est visiblement mort, cela est précisé en observation.
- ✓ 1 à 4 axes sont marqués et suivis, dont un axe principal effectif ou désigné lorsqu' aucun n'est visible. Un scotch marqueur est placé à l'extrémité de chacun, le plus près possible du bourgeon terminal et des marqueurs de croissances sont comptés en amont et en aval de la marque.
- ✓ Le nombre total de feuilles, et le nombre de feuilles avant et après la marque des axes suivis sont relevés. Une feuille comptabilisée est une feuille complètement formée, ouverte et de plus d'1cm de limbe, mature ou non, chlorophyllienne ou non. Les feuilles immatures, et cicatrices foliaires sont indiquées comme telles dans le compte des feuilles des axes suivis. En Z1 (sous le scotch) on ne note pas les cicatrices mais uniquement les feuilles présentes.
- ✓ Le diamètre est mesuré dans la mesure du possible à 20cm, en évitant les irrégularités de la tige, juste au dessus d'un scotch marqueur et dans deux directions

perpendiculaires (l'une d'elle étant indiquée par le scotch).

- ✓ Un indice de Dawkins adapté aux juvéniles est défini comme suit :
  - Classe 1 : Pas de lumière directe (couronne non éclairée)
  - Classe 1,5 : Faible lumière latérale (couronne éclairée seulement d'un côté, pas ou peu de moyennes ou larges ouvertures dans la canopée).
  - Classe 2 : Lumière latérale moyenne (couronne éclairée seulement d'un côté : plusieurs petites ouverture ou une ouverture moyenne dans la canopée).
  - Classe 2,5 : Forte lumière latérale (couronne éclairée seulement d'un côté : exposée à au moins une ouverture de grande taille ou à des ouvertures de taille moyenne)
  - Classe 3 : Présence de lumière verticale (10 à 90 % de la projection verticale de la couronne est exposée à un éclairement vertical)
  - Classe 4 : Pleine lumière verticale (> 90 % de la projection verticale de la couronne est exposée à un éclairement vertical)
  - Classe 5 : Couronne complètement exposée à la lumière verticale et latérale dans un cône de 90 ° entourant la couronne. Cette classe n'est pas représentée chez les juvéniles en couvert forestier.

Paramètres mesurés et critères de choix :

- *Oxandra asbeckii* présente régulièrement de petites feuilles caduques sur l'axe principal. Leur comptage n'étant pas pertinent, on compte dans le cadre du suivi de croissance de cet axe le nombre de branches foliées en amont et en aval du marquage.
- *Virola michelii* émet des rameaux latéraux par étages ; on compte outre le nombre total de branches le nombre d'étages formés.
- *Symphonia sp1.* présente régulièrement des figures d'UC en croissance et non encore foliés. On mesure la longueur de la nouvelle UC lorsque c'est le cas d'un axe suivi. Cataphylles sur axe orthotrope quasi systématique et parfois sur ramification.
- *Licania alba* ne présente pas la plupart du temps d'axe principal à port droit, ce qui rend difficile la mesure de sa hauteur. On mesure donc cette hauteur au niveau de la base de la dernière branche /dernier relais sur l'axe principal. Ses feuilles étant d'une longueur conséquente, deux indices d'encombrement du houppier sont mesurés.

- *Tachigali melinonii* présente souvent un nombre important de cicatrices foliaires et de cataphylles au niveau de l'apex, ce qui le rend difficilement lisible. Ces cicatrices sont comptées à la loupe à main.

Les relais successifs posent problème pour le suivi des populations foliaires.

*Dicorynia guianensis, Qualea rosea, Eperua falcata* et *Eperua grandifolia* ne présentent pas de traits particuliers qui justifieraient la mesure de paramètres supplémentaires.

Remarque :

La hauteur est en général mesurée comme la hauteur totale de l'individu estimée à l'aplomb de l'axe SAUF pour VM : hauteur de l'axe principal (rameaux redressé peuvent être plus haut).

Table 11. Significance of sapling size effect for 14 species. Significance levels of this test are shown with. P<0.1, *P <0.05, ** P<0.01, ***P<0.001.

| Esp | CD | RCD | CSHAPE | CWMEAN | HD | IL A0 | IL BRHIGH | IL BRLOW | LLS | LMA | ULA | NBFEU | NB | Nb ETAGE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BP | * | - | - | * | - | - | - | - | - | - | - | * | * | NA |
| DG | * | - | - | * | - | - | - | - | - | * | * | - | * | NA |
| EF | * | - | - | * | - | - | - | - | * | - | * | * | * | NA |
| EG | * | - | - | * | - | - | - | - | - | - | * | * | * | NA |
| GH | * | - | - | * | - | - | - | - | - | - | - | * | * | NA |
| LA | * | - | - | * | - | - | - | - | - | * | * | * | * | NA |
| LP | * | - | - | * | - | - | - | - | - | * | * | * | * | NA |
| OA | * | - | - | * | - | - | * | - | - | * | * | * | * | NA |
| PC | * | - | - | * | - | - | - | - | - | - | * | * | * | NA |
| QR | * | - | - | * | - | - | - | - | * | * | * | * | * | NA |
| SR | * | - | - | * | * | - | * | - | - | * | - | * | * | NA |
| SS | * | - | - | * | - | - | - | - | - | * | - | * | * | NA |
| TM | * | - | - | * | - | * | - | - | - | - | * | * | * | NA |
| VM | * | - | - | * | * | - | - | - | * | * | * | * | * | * |

Table 12 : Correlation matrix of light-niche parameters, adult stature and median values (measured in low- (LI=1) and high-light (LI=3) conditions) and plasticity of functional traits of 14 tropical tree species. Pearson correlation coefficient are given and levels of significance are shown with P < 0.1, *P  < 0.05, ** P < 0.01, ***P < 0.001.

| **Variable** | **POP.RESP** | | Degree of specialization | | **Hmax** | | **Plasticity of GRDIA** | | **GRDIA_LI1** | | **LMA_LI1** | | **LLS_LI1** | | **ULA_LI1** | | **TLA_LI1** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **POP.RESP** | 1 | NA | 0.383 | | 0.108 | | 0.591 | * | 0.436 | | -0.591 | * | -0.531 | . | 0.037 | | 0.202 | |
| **Degree of specialization** | 0.383 | | 1 | NA | -0.306 | | 0.115 | | 0.179 | | -0.195 | | -0.188 | | -0.272 | | -0.169 | |
| **Hmax** | 0.108 | | -0.306 | | 1 | NA | 0.276 | | 0.073 | | -0.26 | | -0.227 | | 0.452 | | -0.053 | |
| **Plasticity of GRDIA** | 0.591 | * | 0.115 | | 0.276 | | 1 | NA | 0.704 | ** | -0.454 | | -0.521 | . | -0.046 | | 0.566 | * |
| **GRDIA_LI1** | 0.436 | | 0.179 | | 0.073 | | 0.704 | ** | 1 | NA | -0.455 | | -0.645 | * | -0.134 | | 0.695 | ** |
| **LMA_LI1** | -0.591 | * | -0.195 | | -0.26 | | -0.454 | | -0.455 | | 1 | NA | 0.841 | *** | -0.265 | | -0.094 | |
| **LLS_LI1** | -0.531 | . | -0.188 | | -0.227 | | -0.521 | . | -0.645 | * | 0.841 | *** | 1 | NA | -0.077 | | -0.146 | |
| **ULA_LI1** | 0.037 | | -0.272 | | 0.452 | | -0.046 | | -0.134 | | -0.265 | | -0.077 | | 1 | NA | -0.016 | |
| **TLA_LI1** | 0.202 | | -0.169 | | -0.053 | | 0.566 | * | 0.695 | ** | -0.094 | | -0.146 | | -0.016 | | 1 | NA |
| **RCD_LI1** | -0.545 | * | 0.021 | | -0.629 | * | -0.439 | | -0.112 | | 0.588 | * | 0.522 | . | -0.497 | . | 0.108 | |
| **CSHAPE_LI1** | -0.525 | . | 0.298 | | -0.462 | . | -0.395 | | -0.078 | | 0.351 | | 0.47 | . | -0.335 | | -0.005 | |
| **GRA0_LI1** | 0.504 | . | 0.078 | | 0.157 | | 0.31 | | 0.64 | * | -0.561 | * | -0.692 | ** | 0.094 | | 0.344 | |
| **LMA_LI3** | -0.613 | * | -0.345 | | -0.035 | | -0.418 | | -0.387 | | 0.928 | *** | 0.676 | ** | -0.228 | | -0.135 | |
| **LLS_LI3** | -0.376 | | -0.297 | | -0.343 | | -0.392 | | -0.563 | * | 0.74 | ** | 0.797 | *** | 0.003 | | -0.052 | |
| **ULA_LI3** | 0.171 | | -0.181 | | 0.411 | | -0.031 | | -0.127 | | -0.331 | | -0.137 | | 0.98 | *** | -0.049 | |
| **TLA_LI3** | 0.658 | * | 0.214 | | -0.309 | | 0.502 | . | 0.458 | . | -0.128 | | -0.216 | | -0.005 | | 0.616 | * |
| **RCD_LI3** | -0.127 | | 0.312 | | -0.355 | | 0.291 | | 0.455 | | 0.304 | | -0.04 | | -0.43 | | 0.316 | |
| **CSHAPE_LI3** | -0.248 | | 0.486 | . | -0.226 | | 0.093 | | 0.334 | | 0.145 | | 0.059 | | -0.282 | | 0.069 | |
| **GRA0_LI3** | 0.557 | * | 0.042 | | 0.214 | | 0.485 | . | 0.544 | * | -0.485 | . | -0.662 | ** | -0.017 | | 0.277 | |
| **Plasticity of LMA** | -0.167 | | -0.561 | * | 0.606 | * | 0.023 | | -0.002 | | -0.024 | | -0.268 | | 0.126 | | -0.181 | |
| **Plasticity of LLS** | -0.449 | | -0.336 | | -0.228 | | -0.511 | . | -0.609 | * | 0.83 | *** | 0.943 | *** | -0.114 | | -0.105 | |
| **Plasticity of RCD** | 0.593 | * | 0.165 | | 0.313 | | 0.763 | ** | 0.39 | | -0.5 | . | -0.571 | * | 0.119 | | 0.25 | |
| **Plasticity of CSHAPE** | 0.318 | | 0.223 | | 0.205 | | 0.513 | . | 0.323 | | 0.161 | | -0.021 | | -0.048 | | 0.257 | |
| **Plasticity of ULA** | 0.366 | | 0.508 | . | -0.025 | | -0.145 | | -0.316 | | -0.001 | | 0.18 | | 0.221 | | -0.24 | |
| **Plasticity of TLA** | 0.593 | * | 0.162 | | 0.068 | | 0.22 | | 0.172 | | -0.26 | | -0.372 | | 0.372 | | 0.189 | |
| **Plasticity of GRA0** | 0.409 | | 0.064 | | 0.161 | | 0.461 | . | 0.557 | * | -0.321 | | -0.58 | * | -0.215 | | 0.215 | |

| Variable | RCD_LI1 | | CSHAPE_LI1 | | GRA0_LI1 | | LMA_LI3 | | LLS_LI3 | | ULA_LI3 | | TLA_LI3 | | RCD_LI3 | | CSHAPE_LI3 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **POP.RESP** | -0.545 | * | -0.525 | . | 0.504 | . | -0.613 | * | -0.376 | | 0.171 | | 0.658 | * | -0.127 | | -0.248 | |
| **Degree of specialization** | 0.021 | | 0.298 | | 0.078 | | -0.345 | | -0.297 | | -0.181 | | 0.214 | | 0.312 | | 0.486 | . |
| **Hmax** | -0.629 | * | -0.462 | . | 0.157 | | -0.035 | | -0.343 | | 0.411 | | -0.309 | | -0.355 | | -0.226 | |
| **Plasticity of GRDIA** | -0.439 | | -0.395 | | 0.31 | | -0.418 | | -0.392 | | -0.031 | | 0.502 | . | 0.291 | | 0.093 | |
| **GRDIA_LI1** | -0.112 | | -0.078 | | 0.64 | * | -0.387 | | -0.563 | * | -0.127 | | 0.458 | . | 0.455 | | 0.334 | |
| **LMA_LI1** | 0.588 | * | 0.351 | | -0.561 | * | 0.928 | *** | 0.74 | ** | -0.331 | | -0.128 | | 0.304 | | 0.145 | |
| **LLS_LI1** | 0.522 | . | 0.47 | . | -0.692 | ** | 0.676 | ** | 0.797 | *** | -0.137 | | -0.216 | | -0.04 | | 0.059 | |
| **ULA_LI1** | -0.497 | . | -0.335 | | 0.094 | | -0.228 | | 0.003 | | 0.98 | *** | -0.005 | | -0.43 | | -0.282 | |
| **TLA_LI1** | 0.108 | | -0.005 | | 0.344 | | -0.135 | | -0.052 | | -0.049 | | 0.616 | * | 0.316 | | 0.069 | |
| **RCD_LI1** | 1 | NA | 0.796 | *** | -0.485 | . | 0.429 | | 0.241 | | -0.521 | . | -0.111 | | 0.482 | . | 0.401 | |
| **CSHAPE_LI1** | 0.796 | *** | 1 | NA | -0.404 | | 0.163 | | 0.063 | | -0.394 | | -0.343 | | 0.336 | | 0.694 | ** |
| **GRA0_LI1** | -0.485 | . | -0.404 | | 1 | NA | -0.444 | | -0.444 | | 0.125 | | 0.363 | | -0.136 | | -0.154 | |
| **LMA_LI3** | 0.429 | | 0.163 | | -0.444 | | 1 | NA | 0.639 | * | -0.308 | | -0.226 | | 0.301 | | 0.109 | |
| **LLS_LI3** | 0.241 | | 0.063 | | -0.444 | | 0.639 | * | 1 | NA | -0.049 | | 0.058 | | -0.089 | | -0.175 | |
| **ULA_LI3** | -0.521 | . | -0.394 | | 0.125 | | -0.308 | | -0.049 | | 1 | NA | 0.097 | | -0.435 | | -0.346 | |
| **TLA_LI3** | -0.111 | | -0.343 | | 0.363 | | -0.226 | | 0.058 | | 0.097 | | 1 | NA | 0.299 | | -0.16 | |
| **RCD_LI3** | 0.482 | . | 0.336 | | -0.136 | | 0.301 | | -0.089 | | -0.435 | | 0.299 | | 1 | NA | 0.697 | ** |
| **CSHAPE_LI3** | 0.401 | | 0.694 | ** | -0.154 | | 0.109 | | -0.175 | | -0.346 | | -0.16 | | 0.697 | ** | 1 | NA |
| **GRA0_LI3** | -0.621 | * | -0.585 | * | 0.904 | *** | -0.35 | | -0.361 | | 0.014 | | 0.408 | | -0.088 | | -0.222 | |
| **Plasticity of LMA** | -0.388 | | -0.549 | * | 0.13 | | 0.336 | | -0.079 | | 0.071 | | -0.34 | | -0.103 | | -0.238 | |
| **Plasticity of LLS** | 0.566 | * | 0.342 | | -0.692 | ** | 0.701 | ** | 0.775 | ** | -0.147 | | -0.131 | | -0.041 | | -0.099 | |
| **Plasticity of RCD** | -0.667 | ** | -0.647 | * | 0.311 | | -0.468 | . | -0.279 | | 0.151 | | 0.375 | | -0.083 | | -0.274 | |
| **Plasticity of CSHAPE** | -0.187 | | -0.15 | | -0.023 | | 0.182 | | 0.04 | | -0.089 | | 0.27 | | 0.35 | | 0.322 | |
| **Plasticity of ULA** | -0.203 | | -0.12 | | -0.079 | | -0.114 | | 0.147 | | 0.351 | | 0.349 | | -0.143 | | -0.179 | |
| **Plasticity of TLA** | -0.401 | | -0.633 | * | 0.35 | | -0.224 | | -0.094 | | 0.504 | . | 0.724 | ** | 0.009 | | -0.44 | |
| **Plasticity of GRA0** | -0.438 | | -0.432 | | 0.804 | *** | -0.223 | | -0.373 | | -0.204 | | 0.255 | | 0.024 | | -0.123 | |

| Variable | GRA0_LI3 | | Plasticity of LMA | | Plasticity of LLS | | Plasticity of RCD | | Plasticity of CSCHAPE | | Plasticity of ULA | | Plasticity of TLA | | Plasticity of GRA0 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **POP.RESP** | 0.557 | * | -0.167 | | -0.449 | | 0.593 | * | 0.318 | | 0.366 | | 0.593 | * | 0.409 | |
| **Degree of specialization** | 0.042 | | -0.561 | * | -0.336 | | 0.165 | | 0.223 | | 0.508 | . | 0.162 | | 0.064 | |
| **Hmax** | 0.214 | | 0.606 | * | -0.228 | | 0.313 | | 0.205 | | -0.025 | | 0.068 | | 0.161 | |
| **Plasticity of GRDIA** | 0.485 | . | 0.023 | | -0.511 | . | 0.763 | ** | 0.513 | . | -0.145 | | 0.22 | | 0.461 | . |
| **GRDIA_LI1** | 0.544 | * | -0.002 | | -0.609 | * | 0.39 | | 0.323 | | -0.316 | | 0.172 | | 0.557 | * |
| **LMA_LI1** | -0.485 | . | -0.024 | | 0.83 | *** | -0.5 | . | 0.161 | | -0.001 | | -0.26 | | -0.321 | |
| **LLS_LI1** | -0.662 | ** | -0.268 | | 0.943 | *** | -0.571 | * | -0.021 | | 0.18 | | -0.372 | | -0.58 | * |
| **ULA_LI1** | -0.017 | | 0.126 | | -0.114 | | 0.119 | | -0.048 | | 0.221 | | 0.372 | | -0.215 | |
| **TLA_LI1** | 0.277 | | -0.181 | | -0.105 | | 0.25 | | 0.257 | | -0.24 | | 0.189 | | 0.215 | |
| **RCD_LI1** | -0.621 | * | -0.388 | | 0.566 | * | -0.667 | ** | -0.187 | | -0.203 | | -0.401 | | -0.438 | |
| **CSHAPE_LI1** | -0.585 | * | -0.549 | * | 0.342 | | -0.647 | * | -0.15 | | -0.12 | | -0.633 | * | -0.432 | |
| **GRA0_LI1** | 0.904 | *** | 0.13 | | -0.692 | ** | 0.311 | | -0.023 | | -0.079 | | 0.35 | | 0.804 | *** |
| **LMA_LI3** | -0.35 | | 0.336 | | 0.701 | ** | -0.468 | . | 0.182 | | -0.114 | | -0.224 | | -0.223 | |
| **LLS_LI3** | -0.361 | | -0.079 | | 0.775 | ** | -0.279 | | 0.04 | | 0.147 | | -0.094 | | -0.373 | |
| **ULA_LI3** | 0.014 | | 0.071 | | -0.147 | | 0.151 | | -0.089 | | 0.351 | | 0.504 | . | -0.204 | |
| **TLA_LI3** | 0.408 | | -0.34 | | -0.131 | | 0.375 | | 0.27 | | 0.349 | | 0.724 | ** | 0.255 | |
| **RCD_LI3** | -0.088 | | -0.103 | | -0.041 | | -0.083 | | 0.35 | | -0.143 | | 0.009 | | 0.024 | |
| **CSHAPE_LI3** | -0.222 | | -0.238 | | -0.099 | | -0.274 | | 0.322 | | -0.179 | | -0.44 | | -0.123 | |
| **GRA0_LI3** | 1 | NA | 0.219 | | -0.675 | ** | 0.471 | . | 0.094 | | -0.065 | | 0.344 | | 0.912 | *** |
| **Plasticity of LMA** | 0.219 | | 1 | NA | -0.147 | | 0.109 | | 0.094 | | -0.37 | | 0.03 | | 0.173 | |
| **Plasticity of LLS** | -0.675 | ** | -0.147 | | 1 | NA | -0.57 | * | -0.04 | | 0.121 | | -0.257 | | -0.602 | * |
| **Plasticity of RCD** | 0.471 | . | 0.109 | | -0.57 | * | 1 | NA | 0.465 | . | -0.004 | | 0.4 | | 0.451 | |
| **Plasticity of CSHAPE** | 0.094 | | 0.094 | | -0.04 | | 0.465 | . | 1 | NA | -0.109 | | 0.097 | | 0.129 | |
| **Plasticity of ULA** | -0.065 | | -0.37 | | 0.121 | | -0.004 | | -0.109 | | 1 | NA | 0.583 | * | -0.244 | |
| **Plasticity of TLA** | 0.344 | | 0.03 | | -0.257 | | 0.4 | | 0.097 | | 0.583 | * | 1 | NA | 0.122 | |
| **Plasticity of GRA0** | 0.912 | *** | 0.173 | | -0.602 | * | 0.451 | | 0.129 | | -0.244 | | 0.122 | | 1 | NA |

Table 13. Model parameter values and significance. Alpha- is the mean of the fixed and the random effect of : the constant (alpha0g), the DBH effect (alpha1g), the CP effect (alpha2g), the logDBH effect (alpha3g) and the LBA effect (alpha4g). s- is the significance (if the 95%CI did not include 0, s=1) of : the constant (s0g), the DBH effect (s1g), the CP effect (s2g), the logDBH effect (s3g) and the LBA effect (sg).

| Sp | alpha0 | alpha1 | alpha2 | alpha3 | alpha4 | s0 | s1 | s2 | s3 | s4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Spmean | -2,12 | 0,50 | 0,16 | -0,02 | -0,21 | 1 | 1 | 1 | 1 | 1 |
| Abarema jupunba | -2,85 | 0,90 | 0,20 | -0,02 | -0,34 | 0 | 0 | 0 | 0 | 0 |
| Agonandra silvatica | -1,84 | 0,32 | 0,13 | -0,01 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Albizia pedicellaris | -1,69 | 0,26 | 0,26 | 0,00 | -0,37 | 0 | 0 | 0 | 1 | 0 |
| Amaioua guianensis | -2,31 | 0,53 | 0,15 | -0,03 | -0,16 | 0 | 0 | 0 | 0 | 0 |
| Amanoa congesta | -2,15 | 0,62 | 0,16 | -0,03 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Ambelania acida | -2,15 | 0,36 | 0,08 | -0,02 | 0,04 | 0 | 0 | 0 | 0 | 1 |
| Amphirrhox longifolia | -2,07 | 0,46 | 0,15 | -0,03 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Anacardium spruceanum | -2,38 | 0,53 | 0,10 | -0,01 | -0,18 | 0 | 0 | 0 | 0 | 0 |
| Anaxagorea dolichocarpa | -1,93 | 0,34 | 0,16 | -0,04 | -0,08 | 0 | 0 | 0 | 0 | 0 |
| Andira coriacea | -2,22 | 0,51 | 0,26 | -0,02 | -0,04 | 0 | 0 | 0 | 0 | 0 |
| Aniba citrifolia | -1,99 | 0,40 | 0,12 | -0,02 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Aniba taubertiana | -2,26 | 0,52 | 0,14 | -0,03 | -0,29 | 0 | 0 | 0 | 0 | 0 |
| Aniba williamsii | -2,18 | 0,54 | 0,17 | -0,02 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Annona foetida | -2,17 | 0,51 | 0,16 | -0,04 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Antonia ovata | -2,36 | 0,61 | 0,25 | -0,02 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Apeiba glabra | -2,24 | 0,73 | 0,20 | -0,04 | -0,38 | 0 | 0 | 0 | 0 | 0 |
| Aspidosperma album | -2,34 | 0,64 | 0,15 | -0,02 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Aspidosperma desmanthum | -1,78 | 0,34 | 0,18 | -0,02 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Aspidosperma excelsum | -2,30 | 0,59 | 0,17 | 0,02 | -0,42 | 0 | 0 | 0 | 0 | 0 |
| Aspidosperma spruceanum | -2,19 | 0,59 | 0,18 | -0,02 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Bocoa prouacensis | -1,53 | 0,12 | 0,12 | -0,01 | -0,10 | 0 | 1 | 0 | 1 | 1 |
| Brosimum guianense | -1,53 | 0,14 | 0,19 | -0,01 | -0,12 | 0 | 0 | 0 | 0 | 0 |
| Brosimum rubescens | -2,20 | 0,53 | 0,18 | -0,02 | -0,32 | 0 | 0 | 0 | 0 | 0 |
| Brosimum utile | -1,90 | 0,48 | 0,23 | -0,04 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Buchenavia grandis | -1,76 | 0,23 | 0,13 | 0,00 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Byrsonima laevigata | -1,99 | 0,61 | 0,21 | -0,04 | -0,29 | 0 | 0 | 0 | 0 | 0 |
| Carapa procera | -1,33 | 0,24 | 0,15 | -0,01 | -0,27 | 0 | 0 | 0 | 0 | 0 |
| Caryocar glabrum | -1,86 | 0,36 | 0,09 | -0,01 | -0,28 | 0 | 0 | 0 | 0 | 0 |
| Casearia sylvestris | -2,17 | 0,51 | 0,14 | -0,03 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Catostemma fragrans | -0,86 | -0,32 | 0,12 | 0,03 | -0,18 | 1 | 1 | 0 | 1 | 0 |
| Cecropia obtusa | -2,54 | 0,83 | 0,11 | -0,02 | -0,32 | 0 | 0 | 0 | 0 | 0 |
| Cecropia sciadophylla | -2,46 | 0,57 | 0,17 | 0,02 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Chaetocarpus schomburgkianus | -1,38 | 0,12 | 0,14 | -0,01 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Chaunochiton kappleri | -1,86 | 0,46 | 0,14 | -0,03 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Cheiloclinium cognatum | -2,12 | 0,50 | 0,17 | -0,02 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Chimarrhis turbinata | -2,13 | 0,51 | 0,16 | -0,01 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Chrysophyllum argenteum | -1,71 | 0,15 | 0,08 | -0,01 | 0,00 | 0 | 0 | 0 | 0 | 0 |
| Chrysophyllum cuneifolium | -1,53 | 0,31 | 0,16 | -0,03 | -0,23 | 0 | 0 | 0 | 0 | 0 |

| Sp | alpha0 | alpha1 | alpha2 | alpha3 | alpha4 | s0 | s1 | s2 | s3 | s4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Chrysophyllum pomiferum | -1,50 | 0,18 | 0,12 | 0,00 | -0,32 | 0 | 0 | 0 | 0 | 0 |
| Chrysophyllum prieurii | -2,04 | 0,41 | 0,22 | -0,02 | -0,02 | 0 | 0 | 0 | 0 | 1 |
| Chrysophyllum sanguinolentum | -2,51 | 0,70 | 0,17 | -0,03 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Coccoloba mollis | -2,14 | 0,45 | 0,11 | -0,01 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Conceveiba guianensis | -2,45 | 0,77 | 0,19 | -0,04 | -0,48 | 0 | 0 | 0 | 0 | 1 |
| Cordia sagotii | -2,26 | 0,49 | 0,16 | -0,01 | -0,16 | 0 | 0 | 0 | 0 | 0 |
| Couepia bracteosa | -2,82 | 0,86 | 0,16 | -0,04 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Couepia caryophylloides | -1,65 | 0,28 | 0,21 | -0,01 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Couepia guianensis | -1,71 | 0,35 | 0,17 | -0,01 | -0,33 | 0 | 0 | 0 | 0 | 0 |
| Couepia habrantha | -1,95 | 0,45 | 0,14 | -0,01 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Couepia obovata | -2,09 | 0,50 | 0,16 | -0,01 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Couma guianensis | -2,61 | 0,73 | 0,10 | -0,03 | 0,01 | 0 | 0 | 0 | 0 | 0 |
| Couratari calycina | -1,97 | 0,52 | 0,19 | -0,03 | -0,29 | 0 | 0 | 0 | 0 | 0 |
| Couratari guianensis | -1,80 | 0,27 | 0,20 | 0,00 | -0,08 | 0 | 0 | 0 | 0 | 0 |
| Couratari multiflora | -1,72 | 0,19 | 0,16 | -0,01 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Coussarea machadoana | -2,16 | 0,52 | 0,13 | -0,03 | -0,17 | 0 | 0 | 0 | 0 | 0 |
| Dacryodes nitens | -1,92 | 0,37 | 0,12 | -0,02 | -0,11 | 0 | 0 | 0 | 0 | 0 |
| Dendrobangia boliviana | -2,46 | 0,73 | 0,21 | -0,03 | -0,16 | 0 | 0 | 0 | 0 | 0 |
| Dialium guianense | -2,21 | 0,55 | 0,17 | -0,01 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Dicorynia guianensis | -3,05 | 0,95 | 0,14 | -0,03 | -0,25 | 1 | 1 | 0 | 1 | 0 |
| Diospyros carbonaria | -2,11 | 0,49 | 0,16 | -0,03 | -0,18 | 0 | 0 | 0 | 0 | 0 |
| Diplotropis purpurea | -2,79 | 0,98 | 0,24 | -0,05 | -0,12 | 0 | 0 | 0 | 0 | 0 |
| Dipteryx odorata | -2,01 | 0,51 | 0,23 | -0,03 | -0,24 | 0 | 0 | 0 | 0 | 0 |
| Drypetes fanshawei | -2,05 | 0,44 | 0,20 | -0,03 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Drypetes variabilis | -1,73 | 0,15 | 0,19 | 0,00 | -0,10 | 0 | 0 | 0 | 0 | 0 |
| Duguetia calycina | -2,25 | 0,48 | 0,10 | -0,03 | -0,11 | 0 | 0 | 0 | 0 | 0 |
| Duroia aquatica | -2,22 | 0,52 | 0,17 | -0,04 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Duroia eriopila | -2,33 | 0,53 | 0,07 | -0,02 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Duroia longiflora | -0,86 | -0,21 | 0,13 | 0,01 | -0,08 | 0 | 1 | 0 | 0 | 0 |
| Ecclinusa guianensis | -1,86 | 0,28 | 0,17 | 0,00 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Ecclinusa ramiflora | -1,71 | 0,45 | 0,16 | -0,04 | -0,37 | 0 | 0 | 0 | 0 | 0 |
| Endlicheria melinonii | -1,99 | 0,49 | 0,22 | -0,03 | -0,32 | 0 | 0 | 0 | 0 | 0 |
| Enterolobium oldemanii | -2,78 | 0,75 | 0,06 | -0,02 | -0,05 | 0 | 0 | 0 | 0 | 0 |
| Enterolobium schomburgkii | -3,13 | 0,89 | 0,30 | -0,02 | -0,28 | 0 | 0 | 0 | 0 | 0 |
| Eperua falcata | -1,68 | 0,26 | 0,14 | -0,01 | -0,19 | 1 | 1 | 0 | 1 | 0 |
| Eperua grandiflora | -2,32 | 0,67 | 0,25 | -0,02 | -0,10 | 0 | 0 | 1 | 0 | 0 |
| Eriotheca globosa | -2,23 | 0,67 | 0,09 | -0,02 | -0,54 | 0 | 0 | 0 | 0 | 1 |
| Eriotheca longitubulosa | -2,17 | 0,58 | 0,15 | -0,03 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Eschweilera congestiflora | -2,19 | 0,60 | 0,17 | -0,03 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Eschweilera coriacea | -2,03 | 0,39 | 0,19 | -0,02 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Eschweilera decolorans | -0,28 | -0,46 | 0,14 | 0,02 | -0,04 | 1 | 1 | 0 | 1 | 0 |
| Eschweilera grandiflora | -2,11 | 0,49 | 0,18 | -0,04 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Eschweilera pedicellata | -2,18 | 0,51 | 0,16 | -0,03 | -0,21 | 0 | 0 | 0 | 0 | 0 |

| Sp | alpha0 | alpha1 | alpha2 | alpha3 | alpha4 | s0 | s1 | s2 | s3 | s4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Eschweilera praeclara | -2,03 | 0,49 | 0,15 | -0,03 | -0,28 | 0 | 0 | 0 | 0 | 0 |
| Eschweilera sagotiana | -1,52 | 0,14 | 0,03 | -0,01 | -0,16 | 1 | 1 | 1 | 1 | 0 |
| Eschweilera simiorum | -2,14 | 0,50 | 0,15 | -0,04 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Eschweilera wachenheimii | -1,83 | 0,44 | 0,17 | -0,04 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Eugenia anastomosans | -1,99 | 0,43 | 0,15 | -0,03 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Eugenia cupulata | -2,07 | 0,44 | 0,14 | -0,03 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Eugenia exaltata | -2,04 | 0,38 | 0,12 | -0,02 | -0,11 | 0 | 0 | 0 | 0 | 0 |
| Eugenia patrisii | -2,09 | 0,43 | 0,07 | -0,02 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Eugenia pseudopsidium | -2,12 | 0,49 | 0,15 | -0,03 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Eugenia tetramera | -2,09 | 0,49 | 0,13 | -0,04 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Ficus piresiana | -2,47 | 0,76 | 0,24 | -0,01 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Garcinia benthamiana | -1,73 | 0,29 | 0,07 | -0,02 | -0,10 | 0 | 0 | 0 | 0 | 0 |
| Garcinia madruno | -2,46 | 0,74 | 0,18 | -0,04 | -0,26 | 0 | 0 | 0 | 0 | 0 |
| Glycydendron amazonicum | -1,85 | 0,30 | 0,14 | -0,01 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Goupia glabra | -1,67 | 0,38 | 0,33 | -0,01 | -0,43 | 0 | 0 | 1 | 0 | 1 |
| Guatteria guianensis | -2,33 | 0,57 | 0,21 | -0,03 | -0,16 | 0 | 0 | 0 | 0 | 0 |
| Guatteria schomburgkiana | -2,17 | 0,61 | 0,16 | -0,02 | -0,33 | 0 | 0 | 0 | 0 | 0 |
| Gustavia hexapetala | -1,61 | 0,21 | 0,07 | -0,02 | -0,17 | 0 | 0 | 0 | 0 | 0 |
| Hebepetalum humiriifolium | -2,35 | 0,84 | 0,14 | -0,05 | -0,32 | 0 | 0 | 0 | 0 | 0 |
| Heisteria densifrons | -2,45 | 0,61 | 0,14 | -0,03 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Helicostylis pedunculata | -2,40 | 0,74 | 0,28 | -0,05 | -0,29 | 0 | 0 | 0 | 0 | 0 |
| Helicostylis tomentosa | -1,82 | 0,32 | 0,15 | -0,02 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Henriettella flavescens | -1,97 | 0,45 | 0,14 | -0,02 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Hevea guianensis | -1,43 | 0,19 | 0,27 | -0,01 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Hieronyma oblonga | -1,88 | 0,45 | 0,20 | -0,03 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Hirtella bicornis | -1,69 | 0,42 | 0,25 | -0,03 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Hirtella glandulosa | -1,89 | 0,45 | 0,14 | -0,02 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Hirtella racemosa | -2,10 | 0,47 | 0,15 | -0,03 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Humiriastrum subcrenatum | -1,54 | 0,23 | 0,12 | 0,00 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Inga alba | -2,16 | 0,58 | 0,15 | -0,02 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Inga cayennensis | -2,25 | 0,55 | 0,12 | -0,01 | -0,26 | 0 | 0 | 0 | 0 | 0 |
| Inga graciliflora | -2,13 | 0,49 | 0,14 | -0,03 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Inga gracilifolia | -1,45 | 0,12 | 0,13 | 0,01 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Inga jenmanii | -2,79 | 0,93 | 0,18 | -0,03 | -0,61 | 0 | 0 | 0 | 0 | 1 |
| Inga loubryana | -1,45 | 0,35 | 0,20 | -0,02 | -0,55 | 0 | 0 | 0 | 0 | 1 |
| Inga melinonis | -3,47 | 1,33 | 0,18 | -0,05 | -0,43 | 0 | 0 | 0 | 0 | 0 |
| Inga pezizifera | -2,43 | 0,72 | 0,33 | 0,00 | -0,33 | 0 | 0 | 0 | 0 | 0 |
| Inga rubiginosa | -2,20 | 0,53 | 0,14 | 0,00 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Inga sarmentosa | -1,85 | 0,27 | 0,20 | 0,01 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Iryanthera hostmannii | -2,01 | 0,39 | 0,06 | -0,03 | -0,07 | 0 | 0 | 1 | 0 | 0 |
| Iryanthera sagotiana | -2,06 | 0,42 | 0,08 | -0,02 | -0,05 | 0 | 0 | 0 | 0 | 0 |
| Isertia coccinea | -1,98 | 0,42 | 0,16 | -0,03 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Jacaranda copaia | -2,21 | 0,50 | 0,34 | -0,02 | -0,11 | 0 | 0 | 1 | 0 | 0 |

| Sp | alpha0 | alpha1 | alpha2 | alpha3 | alpha4 | s0 | s1 | s2 | s3 | s4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Lacmellea aculeata | -2,05 | 0,45 | 0,16 | -0,04 | -0,16 | 0 | 0 | 0 | 0 | 0 |
| Laetia procera | -1,94 | 0,54 | 0,19 | -0,02 | -0,29 | 0 | 0 | 0 | 0 | 0 |
| Lecythis chartacea | -2,24 | 0,40 | 0,10 | 0,00 | -0,27 | 0 | 0 | 0 | 0 | 0 |
| Lecythis corrugata | -1,99 | 0,52 | 0,19 | -0,05 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Lecythis holcogyne | -2,15 | 0,52 | 0,16 | -0,01 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Lecythis persistens | -1,01 | -0,13 | 0,05 | 0,00 | -0,12 | 1 | 1 | 1 | 1 | 1 |
| Lecythis poiteaui | -1,05 | -0,16 | 0,09 | 0,01 | -0,02 | 0 | 1 | 0 | 0 | 1 |
| Lecythis zabucajo | -1,84 | 0,45 | 0,25 | -0,03 | -0,29 | 0 | 0 | 0 | 0 | 0 |
| Leonia glycycarpa | -2,35 | 0,58 | 0,21 | 0,00 | -0,32 | 0 | 0 | 0 | 0 | 0 |
| Licania alba | -2,07 | 0,49 | 0,12 | -0,03 | -0,12 | 0 | 0 | 0 | 0 | 1 |
| Licania canescens | -1,67 | 0,29 | 0,04 | -0,02 | -0,10 | 0 | 0 | 1 | 0 | 0 |
| Licania densiflora | -2,04 | 0,52 | 0,22 | -0,02 | -0,35 | 0 | 0 | 0 | 0 | 0 |
| Licania heteromorpha | -2,53 | 0,67 | 0,19 | -0,03 | -0,10 | 0 | 0 | 0 | 0 | 1 |
| Licania laxiflora | -1,63 | 0,26 | 0,11 | -0,01 | -0,07 | 0 | 0 | 0 | 0 | 0 |
| Licania licaniiflora | -2,39 | 0,68 | 0,15 | -0,02 | -0,33 | 0 | 0 | 0 | 0 | 0 |
| Licania longistyla | -2,48 | 0,65 | 0,18 | -0,01 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Licania membranacea | -3,58 | 1,24 | 0,16 | -0,05 | -0,12 | 1 | 1 | 0 | 1 | 0 |
| Licania micrantha | -2,65 | 0,69 | 0,14 | -0,03 | -0,08 | 0 | 0 | 0 | 0 | 0 |
| Licania ovalifolia | -1,87 | 0,26 | 0,13 | 0,00 | -0,08 | 0 | 0 | 0 | 1 | 0 |
| Licania parvifructa | -2,12 | 0,60 | 0,17 | -0,03 | -0,28 | 0 | 0 | 0 | 0 | 0 |
| Licania sprucei | -1,38 | -0,04 | 0,09 | 0,01 | -0,09 | 0 | 0 | 0 | 0 | 0 |
| Licaria cannella | -1,88 | 0,31 | 0,16 | 0,00 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Licaria martiniana | -2,25 | 0,53 | 0,16 | -0,02 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Lueheopsis rugosa | -2,10 | 0,48 | 0,18 | -0,04 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Mabea piriri | -2,15 | 0,58 | 0,23 | -0,04 | -0,40 | 0 | 0 | 0 | 0 | 0 |
| Macoubea guianensis | -3,17 | 0,95 | 0,09 | -0,03 | -0,02 | 0 | 0 | 0 | 0 | 0 |
| Mahurea palustris | -2,02 | 0,44 | 0,16 | -0,03 | -0,16 | 0 | 0 | 0 | 0 | 0 |
| Manilkara bidentata | -3,21 | 0,94 | 0,12 | -0,03 | -0,09 | 0 | 0 | 0 | 0 | 0 |
| Maquira guianensis | -2,14 | 0,49 | 0,16 | -0,04 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Maytenus oblongata | -2,96 | 0,94 | 0,09 | -0,04 | -0,32 | 0 | 0 | 0 | 0 | 0 |
| Miconia acuminata | -2,98 | 0,90 | 0,11 | 0,00 | -0,28 | 0 | 0 | 0 | 0 | 0 |
| Miconia tschudyoides | -1,11 | 0,21 | 0,34 | -0,01 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Micropholis egensis | -1,97 | 0,42 | 0,14 | -0,01 | -0,38 | 0 | 0 | 0 | 0 | 0 |
| Micropholis guyanensis | -2,16 | 0,48 | 0,20 | -0,01 | -0,26 | 0 | 0 | 0 | 0 | 0 |
| Micropholis longipedicellata | -2,19 | 0,54 | 0,16 | -0,01 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Micropholis melinoniana | -1,50 | 0,08 | 0,09 | 0,01 | -0,22 | 0 | 0 | 0 | 1 | 0 |
| Micropholis obscura | -2,18 | 0,48 | 0,18 | -0,01 | -0,26 | 0 | 0 | 0 | 0 | 0 |
| Micropholis venulosa | -1,00 | -0,15 | 0,11 | 0,01 | -0,27 | 0 | 0 | 0 | 1 | 0 |
| Minquartia guianensis | -2,31 | 0,55 | 0,16 | -0,03 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Moronobea coccinea | -1,99 | 0,48 | 0,14 | -0,02 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Mouriri crassifolia | -2,39 | 0,68 | 0,18 | -0,03 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Myrciaria floribunda | -2,08 | 0,49 | 0,15 | -0,02 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Naucleopsis guianensis | -2,11 | 0,47 | 0,15 | -0,03 | -0,19 | 0 | 0 | 0 | 0 | 0 |

| Sp | alpha0 | alpha1 | alpha2 | alpha3 | alpha4 | s0 | s1 | s2 | s3 | s4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Ocotea puberula | -2,47 | 0,66 | 0,19 | 0,00 | -0,24 | 0 | 0 | 0 | 0 | 0 |
| Ocotea subterminalis | -2,50 | 0,62 | 0,24 | -0,02 | -0,27 | 0 | 0 | 0 | 0 | 0 |
| Ormosia coutinhoi | -1,60 | 0,37 | 0,23 | -0,03 | -0,31 | 0 | 0 | 0 | 0 | 0 |
| Ouratea decagyna | -2,03 | 0,52 | 0,21 | -0,04 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Ouratea guianensis | -2,12 | 0,50 | 0,15 | -0,03 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Oxandra asbeckii | -2,04 | 0,44 | 0,05 | -0,04 | -0,07 | 0 | 0 | 1 | 0 | 1 |
| Pachira dolichocalyx | -0,67 | -0,37 | 0,25 | 0,03 | -0,16 | 1 | 1 | 0 | 1 | 0 |
| Parahancornia fasciculata | -2,19 | 0,55 | 0,16 | -0,02 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Parinari campestris | -4,42 | 1,75 | 0,11 | -0,06 | -0,43 | 1 | 1 | 0 | 1 | 0 |
| Parinari montana | -2,38 | 0,52 | 0,13 | -0,01 | -0,09 | 0 | 0 | 0 | 0 | 0 |
| Parinari rodolphii | -2,38 | 0,66 | 0,18 | -0,02 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Parkia nitida | -4,26 | 1,54 | 0,19 | -0,04 | -0,37 | 1 | 1 | 0 | 1 | 0 |
| Parkia pendula | -2,79 | 0,89 | 0,28 | -0,03 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Parkia ulei | -2,19 | 0,56 | 0,16 | 0,02 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Parkia velutina | -3,53 | 1,19 | 0,17 | -0,03 | -0,33 | 0 | 1 | 0 | 0 | 0 |
| Peltogyne paniculata | -2,05 | 0,49 | 0,16 | -0,02 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Perebea guianensis | -2,02 | 0,48 | 0,14 | -0,03 | -0,24 | 0 | 0 | 0 | 0 | 0 |
| Perebea mollis | -2,18 | 0,58 | 0,17 | -0,03 | -0,24 | 0 | 0 | 0 | 0 | 0 |
| Perebea rubra | -2,09 | 0,45 | 0,16 | -0,02 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Platonia insignis | -1,79 | 0,28 | 0,10 | -0,01 | 0,00 | 0 | 0 | 0 | 1 | 0 |
| Platymiscium pinnatum | -2,24 | 0,56 | 0,16 | -0,02 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Pogonophora schomburgkiana | -1,63 | 0,17 | 0,09 | 0,00 | -0,09 | 0 | 0 | 1 | 0 | 1 |
| Poraqueiba guianensis | -1,35 | 0,04 | 0,11 | 0,00 | -0,26 | 0 | 0 | 0 | 0 | 0 |
| Posoqueria latifolia | -2,12 | 0,37 | 0,10 | -0,02 | 0,00 | 0 | 0 | 0 | 0 | 0 |
| Pourouma bicolor | -1,98 | 0,39 | 0,17 | 0,00 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Pourouma melinonii | -1,89 | 0,49 | 0,11 | 0,02 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Pouteria ambelaniifolia | -2,13 | 0,48 | 0,17 | -0,02 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Pouteria bangii | -1,57 | 0,30 | 0,12 | -0,03 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Pouteria bilocularis | -2,00 | 0,41 | 0,16 | -0,02 | -0,08 | 0 | 0 | 0 | 0 | 0 |
| Pouteria cicatricata | -1,97 | 0,42 | 0,14 | -0,03 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Pouteria engleri | -2,32 | 0,73 | 0,19 | -0,03 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Pouteria eugeniifolia | -1,83 | 0,24 | 0,22 | -0,01 | -0,09 | 0 | 0 | 0 | 0 | 0 |
| Pouteria fimbriata | -2,16 | 0,45 | 0,15 | -0,02 | -0,17 | 0 | 0 | 0 | 0 | 0 |
| Pouteria flavilatex | -1,93 | 0,48 | 0,13 | -0,03 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Pouteria gongrijpii | -1,15 | 0,05 | 0,10 | -0,01 | -0,30 | 0 | 0 | 0 | 0 | 0 |
| Pouteria grandis | -2,03 | 0,40 | 0,12 | -0,02 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Pouteria guianensis | -2,54 | 0,77 | 0,16 | -0,04 | -0,31 | 0 | 0 | 0 | 0 | 0 |
| Pouteria hispida | -1,87 | 0,34 | 0,15 | -0,03 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Pouteria jariensis | -1,64 | 0,22 | 0,19 | 0,00 | -0,29 | 0 | 0 | 0 | 0 | 0 |
| Pouteria melanopoda | -2,56 | 0,69 | 0,23 | -0,02 | -0,34 | 0 | 0 | 0 | 0 | 0 |
| Pouteria sagotiana | -1,73 | 0,36 | 0,18 | -0,01 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Pouteria singularis | -2,83 | 0,69 | 0,13 | -0,02 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Pouteria torta | -1,14 | -0,02 | 0,11 | 0,00 | -0,10 | 0 | 0 | 0 | 0 | 0 |

| Sp | alpha0 | alpha1 | alpha2 | alpha3 | alpha4 | s0 | s1 | s2 | s3 | s4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Pouteria venosa | -2,18 | 0,52 | 0,16 | 0,00 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Pradosia cochlearia | -3,44 | 1,09 | -0,01 | -0,04 | -0,18 | 1 | 1 | 1 | 1 | 0 |
| Protium decandrum | -2,11 | 0,49 | 0,16 | -0,02 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Protium giganteum | -2,11 | 0,49 | 0,16 | -0,02 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Protium guianense | -2,08 | 0,48 | 0,16 | -0,02 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Protium opacum | -0,81 | -0,02 | 0,21 | 0,00 | -0,30 | 0 | 0 | 0 | 0 | 0 |
| Protium sagotianum | -2,11 | 0,42 | 0,16 | -0,02 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Protium subserratum | -2,96 | 1,00 | 0,21 | -0,01 | -0,48 | 0 | 0 | 0 | 0 | 0 |
| Protium tenuifolium | -2,38 | 0,61 | 0,20 | 0,00 | -0,27 | 0 | 0 | 0 | 0 | 0 |
| Pseudolmedia laevis | -2,01 | 0,32 | 0,15 | -0,01 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Pterocarpus officinalis | -1,70 | 0,38 | 0,24 | -0,02 | -0,28 | 0 | 0 | 0 | 0 | 0 |
| Qualea rosea | -2,46 | 0,60 | 0,23 | -0,02 | -0,16 | 0 | 0 | 0 | 0 | 0 |
| Quiina integrifolia | -2,09 | 0,50 | 0,17 | -0,02 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Quiina obovata | -1,67 | 0,33 | 0,19 | -0,03 | -0,18 | 0 | 0 | 0 | 0 | 0 |
| Rauvolfia paraensis | -1,90 | 0,33 | 0,16 | -0,02 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Recordoxylon speciosum | -3,14 | 1,08 | 0,22 | -0,04 | -0,39 | 1 | 1 | 0 | 1 | 1 |
| Rhodostemonodaphne grandis | -2,94 | 1,04 | 0,32 | -0,05 | -0,39 | 0 | 0 | 0 | 0 | 0 |
| Rhodostemonodaphne rufovirgata | -2,22 | 0,50 | 0,14 | -0,02 | -0,17 | 0 | 0 | 0 | 0 | 0 |
| Rollinia exsucca | -2,26 | 0,62 | 0,18 | -0,03 | -0,37 | 0 | 0 | 0 | 0 | 0 |
| Ruizterania albiflora | -3,32 | 1,06 | 0,18 | -0,03 | -0,09 | 0 | 1 | 0 | 0 | 0 |
| Sacoglottis guianensis | -1,81 | 0,32 | 0,17 | 0,00 | -0,10 | 0 | 0 | 0 | 0 | 0 |
| Sandwithia guyanensis | -1,94 | 0,31 | 0,09 | -0,02 | -0,09 | 0 | 0 | 0 | 0 | 0 |
| Schefflera decaphylla | -3,75 | 1,48 | 0,38 | -0,07 | -0,22 | 0 | 1 | 1 | 1 | 0 |
| Sextonia rubra | -2,48 | 0,48 | 0,17 | -0,01 | -0,06 | 0 | 0 | 0 | 1 | 0 |
| Simaba cedron | -1,66 | 0,15 | 0,08 | -0,01 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Simaba morettii | -2,23 | 0,58 | 0,18 | -0,03 | -0,16 | 0 | 0 | 0 | 0 | 0 |
| Simaba polyphylla | -2,39 | 0,53 | 0,12 | -0,02 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Simarouba amara | -3,41 | 1,46 | 0,23 | -0,07 | -0,37 | 0 | 1 | 0 | 1 | 0 |
| Siparuna cuspidata | -2,02 | 0,44 | 0,18 | -0,03 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Siparuna decipiens | -1,54 | 0,17 | 0,14 | -0,01 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Sloanea guianensis | -2,05 | 0,47 | 0,19 | -0,04 | -0,18 | 0 | 0 | 0 | 0 | 0 |
| Sterculia multiovula | -2,17 | 0,38 | 0,20 | -0,01 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Sterculia pruriens | -2,01 | 0,61 | 0,31 | -0,02 | -0,79 | 0 | 0 | 1 | 0 | 1 |
| Sterculia speciosa | -1,72 | 0,32 | 0,17 | -0,01 | -0,31 | 0 | 0 | 0 | 0 | 0 |
| Swartzia arborescens | -2,27 | 0,61 | 0,16 | -0,02 | -0,31 | 0 | 0 | 0 | 0 | 0 |
| Swartzia grandifolia | -1,95 | 0,38 | 0,13 | -0,03 | -0,11 | 0 | 0 | 0 | 0 | 0 |
| Swartzia guianensis | -2,23 | 0,45 | 0,13 | -0,03 | -0,06 | 0 | 0 | 0 | 0 | 0 |
| Swartzia panacoco | -2,33 | 0,63 | 0,09 | -0,03 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Swartzia polyphylla | -2,59 | 0,61 | 0,12 | -0,01 | -0,12 | 0 | 0 | 0 | 0 | 0 |
| Symphonia globulifera | -2,86 | 0,99 | 0,23 | -0,03 | -0,39 | 0 | 1 | 0 | 0 | 0 |
| Tabebuia insignis | -1,76 | 0,28 | 0,17 | -0,02 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Tabernaemontana attenuata | -1,78 | 0,37 | 0,18 | -0,04 | -0,21 | 0 | 0 | 0 | 0 | 0 |
| Tachigali bracteolata | -2,08 | 0,83 | 0,23 | -0,01 | -0,39 | 0 | 0 | 0 | 0 | 0 |

| Sp | alpha0 | alpha1 | alpha2 | alpha3 | alpha4 | s0 | s1 | s2 | s3 | s4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Tachigali melinonii | -4,77 | 2,11 | 0,33 | -0,08 | -0,40 | 1 | 1 | 0 | 1 | 0 |
| Tachigali paraensis | -2,68 | 0,93 | 0,21 | -0,01 | -0,28 | 0 | 0 | 0 | 0 | 0 |
| Talisia hexaphylla | -2,61 | 0,61 | 0,15 | -0,02 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Talisia praealta | -2,21 | 0,51 | 0,14 | -0,03 | -0,14 | 0 | 0 | 0 | 0 | 0 |
| Talisia simaboides | -1,99 | 0,35 | 0,16 | -0,02 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Tapura capitulifera | -2,72 | 0,67 | 0,07 | -0,02 | -0,06 | 0 | 0 | 0 | 0 | 0 |
| Tetragastris hostmannii | -2,33 | 0,72 | 0,13 | -0,04 | -0,20 | 0 | 0 | 0 | 0 | 0 |
| Theobroma subincanum | -1,47 | 0,12 | 0,07 | 0,00 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Thyrsodium guianense | -2,09 | 0,59 | 0,21 | -0,03 | -0,19 | 0 | 0 | 0 | 0 | 0 |
| Thyrsodium puberulum | -1,92 | 0,43 | 0,12 | -0,03 | -0,13 | 0 | 0 | 0 | 0 | 0 |
| Tovomita brasiliensis | -2,00 | 0,38 | 0,10 | -0,03 | -0,10 | 0 | 0 | 0 | 0 | 0 |
| Tovomita brevistaminea | -2,60 | 0,62 | 0,11 | -0,02 | -0,17 | 0 | 0 | 0 | 0 | 0 |
| Trattinnickia rhoifolia | -2,20 | 0,54 | 0,16 | 0,00 | -0,18 | 0 | 0 | 0 | 0 | 0 |
| Trichilia schomburgkii | -2,15 | 0,53 | 0,17 | -0,02 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Trymatococcus oligandrus | -1,98 | 0,36 | 0,04 | -0,02 | -0,11 | 0 | 0 | 0 | 0 | 0 |
| Unonopsis rufescens | -1,86 | 0,30 | 0,03 | -0,01 | -0,09 | 0 | 0 | 0 | 0 | 0 |
| Vantanea parviflora | -2,16 | 0,51 | 0,17 | -0,02 | -0,18 | 0 | 0 | 0 | 0 | 0 |
| Virola michelii | -2,01 | 0,56 | 0,22 | -0,02 | -0,29 | 0 | 0 | 0 | 0 | 0 |
| Virola surinamensis | -2,35 | 0,66 | 0,18 | -0,01 | -0,25 | 0 | 0 | 0 | 0 | 0 |
| Vismia sessilifolia | -2,21 | 0,59 | 0,15 | -0,03 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Vitex triflora | -2,14 | 0,44 | 0,12 | -0,03 | -0,12 | 0 | 0 | 0 | 0 | 0 |
| Vochysia guianensis | -2,02 | 0,44 | 0,14 | 0,00 | -0,23 | 0 | 0 | 0 | 0 | 0 |
| Votomita guianensis | -2,08 | 0,44 | 0,15 | -0,03 | -0,15 | 0 | 0 | 0 | 0 | 0 |
| Vouacapoua americana | -0,99 | 0,03 | 0,09 | 0,00 | -0,26 | 1 | 1 | 0 | 1 | 0 |
| Xylopia crinita | -2,58 | 0,66 | 0,19 | -0,02 | -0,22 | 0 | 0 | 0 | 0 | 0 |
| Xylopia frutescens | -1,62 | 0,46 | 0,18 | -0,01 | -0,41 | 0 | 0 | 0 | 0 | 0 |
| Xylopia nitida | -2,11 | 0,85 | 0,22 | -0,05 | -0,45 | 0 | 0 | 0 | 0 | 0 |
| Xylopia pulcherrima | -2,57 | 0,63 | 0,15 | -0,01 | -0,17 | 0 | 0 | 0 | 0 | 0 |
| Zygia tetragona | -1,78 | 0,32 | 0,10 | -0,02 | -0,17 | 0 | 0 | 0 | 0 | 0 |

Table 14. Species-specific absolute (CP_IMPabs and LBA_IMPabs) importance of resource competition. N indicates species abundance,Gpred_cp3, the predicted growth at CP3 and D95 the 95th percentile of DBH diameter (cm)

| Species | N | CP_imp$_{abs}$ | LBA_imp$_{abs}$ | Gpred_cp3 | D$_{95}$ |
|---|---|---|---|---|---|
| Abarema jupunba | 21 | 0,055 | 0,051 | 0,3 | 48,4 |
| Agonandra silvatica | 5 | 0,026 | 0,023 | 0,14 | 34,6 |
| Albizia pedicellaris | 12 | 0,065 | 0,05 | 0,25 | 91,9 |
| Amaioua guianensis | 7 | 0,025 | 0,014 | 0,09 | 13,6 |
| Amanoa congesta | 2 | 0,042 | 0,032 | 0,25 | 48,4 |
| Ambelania acida | 49 | 0,012 | 0,003 | 0,05 | 16,4 |
| Amphirrhox longifolia | 8 | 0,023 | 0,016 | 0,06 | 13,6 |
| Anacardium spruceanum | 23 | 0,022 | 0,02 | 0,16 | 29,7 |
| Anaxagorea dolichocarpa | 8 | 0,021 | 0,005 | 0,02 | 12,8 |
| Andira coriacea | 27 | 0,064 | 0,006 | 0,23 | 62 |
| Aniba citrifolia | 3 | 0,023 | 0,013 | 0,12 | 13,6 |
| Aniba taubertiana | 12 | 0,02 | 0,022 | 0,05 | 25,8 |
| Aniba williamsii | 8 | 0,035 | 0,027 | 0,16 | 23,2 |
| Annona foetida | 2 | 0,025 | 0,017 | 0,07 | 11,3 |
| Antonia ovata | 14 | 0,064 | 0,018 | 0,26 | 68,6 |
| Apeiba glabra | 26 | 0,043 | 0,045 | 0,19 | 40,4 |
| Aspidosperma album | 5 | 0,037 | 0,027 | 0,22 | 42,8 |
| Aspidosperma desmanthum | 10 | 0,034 | 0,022 | 0,13 | 25,1 |
| Aspidosperma excelsum | 3 | 0,063 | 0,084 | 0,45 | 23,1 |
| Aspidosperma spruceanum | 6 | 0,045 | 0,028 | 0,23 | 36,2 |
| Bocoa prouacensis | 354 | 0,02 | 0,009 | 0,09 | 42 |
| Brosimum guianense | 41 | 0,035 | 0,011 | 0,11 | 30,4 |
| Brosimum rubescens | 34 | 0,038 | 0,035 | 0,17 | 35,8 |
| Brosimum utile | 7 | 0,041 | 0,019 | 0,12 | 25 |
| Buchenavia grandis | 9 | 0,024 | 0,021 | 0,12 | 50,3 |
| Byrsonima laevigata | 4 | 0,051 | 0,038 | 0,23 | 28,8 |
| Carapa procera | 155 | 0,034 | 0,033 | 0,2 | 40,4 |
| Caryocar glabrum | 35 | 0,019 | 0,029 | 0,14 | 63,5 |
| Casearia sylvestris | 3 | 0,025 | 0,02 | 0,1 | 11,6 |
| Catostemma fragrans | 115 | 0,021 | 0,017 | 0,1 | 30,6 |
| Cecropia obtusa | 10 | 0,032 | 0,05 | 0,31 | 24,1 |
| Cecropia sciadophylla | 3 | 0,062 | 0,026 | 0,45 | 26,9 |
| Chaetocarpus schomburgkianus | 117 | 0,027 | 0,014 | 0,13 | 41,1 |
| Chaunochiton kappleri | 13 | 0,031 | 0,017 | 0,17 | 32,8 |
| Cheiloclinium cognatum | 2 | 0,034 | 0,021 | 0,15 | 11,9 |
| Chimarrhis turbinata | 2 | 0,039 | 0,028 | 0,23 | 11,6 |
| Chrysophyllum argenteum | 22 | 0,012 | 0 | 0,05 | 24,6 |
| Chrysophyllum cuneifolium | 8 | 0,031 | 0,024 | 0,13 | 17,7 |
| Chrysophyllum pomiferum | 22 | 0,024 | 0,034 | 0,14 | 55,2 |
| Chrysophyllum prieurii | 86 | 0,045 | 0,002 | 0,16 | 48,3 |

| Species | N | CP_imp$_{abs}$ | LBA_imp$_{abs}$ | Gpred_cp3 | D$_{95}$ |
|---|---|---|---|---|---|
| Chrysophyllum sanguinolentum | 63 | 0,035 | 0,028 | 0,17 | 50,4 |
| Coccoloba mollis | 17 | 0,023 | 0,016 | 0,15 | 22,3 |
| Conceveiba guianensis | 57 | 0,037 | 0,051 | 0,15 | 29,3 |
| Cordia sagotii | 6 | 0,032 | 0,018 | 0,15 | 20,1 |
| Couepia bracteosa | 40 | 0,035 | 0,022 | 0,18 | 40,8 |
| Couepia caryophylloides | 21 | 0,05 | 0,025 | 0,22 | 43 |
| Couepia guianensis | 26 | 0,038 | 0,039 | 0,19 | 36,5 |
| Couepia habrantha | 8 | 0,034 | 0,024 | 0,22 | 39,1 |
| Couepia obovata | 2 | 0,042 | 0,029 | 0,25 | 26 |
| Couma guianensis | 17 | 0,023 | 0,001 | 0,2 | 45,9 |
| Couratari calycina | 2 | 0,041 | 0,033 | 0,18 | 19,8 |
| Couratari guianensis | 7 | 0,047 | 0,01 | 0,21 | 31 |
| Couratari multiflora | 146 | 0,027 | 0,014 | 0,09 | 39,9 |
| Coussarea machadoana | 11 | 0,024 | 0,017 | 0,12 | 17,7 |
| Dacryodes nitens | 4 | 0,021 | 0,01 | 0,1 | 26,8 |
| Dendrobangia boliviana | 10 | 0,052 | 0,021 | 0,23 | 34,4 |
| Dialium guianense | 2 | 0,047 | 0,03 | 0,27 | 18,4 |
| Dicorynia guianensis | 148 | 0,035 | 0,033 | 0,22 | 62,8 |
| Diospyros carbonaria | 2 | 0,027 | 0,016 | 0,1 | 20,9 |
| Diplotropis purpurea | 6 | 0,068 | 0,018 | 0,3 | 55,8 |
| Dipteryx odorata | 4 | 0,053 | 0,029 | 0,2 | 41,8 |
| Drypetes fanshawei | 5 | 0,031 | 0,021 | 0,08 | 23,6 |
| Drypetes variabilis | 11 | 0,034 | 0,01 | 0,12 | 36,5 |
| Duguetia calycina | 51 | 0,016 | 0,009 | 0,07 | 14,7 |
| Duroia aquatica | 3 | 0,024 | 0,016 | 0,05 | 12,4 |
| Duroia eriopila | 4 | 0,013 | 0,015 | 0,12 | 14,9 |
| Duroia longiflora | 41 | 0,022 | 0,007 | 0,09 | 27,7 |
| Ecclinusa guianensis | 4 | 0,033 | 0,024 | 0,13 | 37,6 |
| Ecclinusa ramiflora | 8 | 0,029 | 0,035 | 0,11 | 21,9 |
| Endlicheria melinonii | 6 | 0,042 | 0,033 | 0,15 | 24,4 |
| Enterolobium oldemanii | 10 | 0,013 | 0,006 | 0,16 | 43,6 |
| Enterolobium schomburgkii | 13 | 0,074 | 0,037 | 0,25 | 69 |
| Eperua falcata | 1086 | 0,028 | 0,02 | 0,13 | 61,4 |
| Eperua grandiflora | 285 | 0,077 | 0,016 | 0,35 | 63,3 |
| Eriotheca globosa | 19 | 0,021 | 0,07 | 0,22 | 43,1 |
| Eriotheca longitubulosa | 2 | 0,032 | 0,024 | 0,16 | 41 |
| Eschweilera congestiflora | 62 | 0,034 | 0,025 | 0,15 | 27,2 |
| Eschweilera coriacea | 137 | 0,037 | 0,013 | 0,15 | 36,8 |
| Eschweilera decolorans | 92 | 0,026 | 0,004 | 0,11 | 41,1 |
| Eschweilera grandiflora | 2 | 0,028 | 0,017 | 0,06 | 12 |
| Eschweilera pedicellata | 4 | 0,029 | 0,02 | 0,11 | 17,1 |
| Eschweilera praeclara | 3 | 0,025 | 0,025 | 0,09 | 14,4 |
| Eschweilera sagotiana | 1111 | 0,006 | 0,014 | 0,08 | 47 |

| Species | N | $CP\_imp_{abs}$ | $LBA\_imp_{abs}$ | Gpred_cp3 | $D_{95}$ |
|---|---|---|---|---|---|
| Eschweilera simiorum | 3 | 0,023 | 0,019 | 0,07 | 11,2 |
| Eschweilera wachenheimii | 8 | 0,03 | 0,013 | 0,1 | 23,1 |
| Eugenia anastomosans | 2 | 0,024 | 0,017 | 0,07 | 17,3 |
| Eugenia cupulata | 3 | 0,023 | 0,014 | 0,09 | 12,2 |
| Eugenia exaltata | 22 | 0,02 | 0,01 | 0,09 | 23,1 |
| Eugenia patrisii | 9 | 0,011 | 0,012 | 0,07 | 17,9 |
| Eugenia pseudopsidium | 2 | 0,024 | 0,018 | 0,08 | 15,4 |
| Eugenia tetramera | 7 | 0,02 | 0,021 | 0,06 | 12,7 |
| Ficus piresiana | 2 | 0,091 | 0,052 | 0,48 | 40,1 |
| Garcinia benthamiana | 54 | 0,011 | 0,009 | 0,09 | 18,1 |
| Garcinia madruno | 35 | 0,038 | 0,03 | 0,18 | 23,6 |
| Glycydendron amazonicum | 14 | 0,025 | 0,017 | 0,1 | 33,3 |
| Goupia glabra | 72 | 0,087 | 0,06 | 0,28 | 63,3 |
| Guatteria guianensis | 2 | 0,042 | 0,018 | 0,16 | 14,2 |
| Guatteria schomburgkiana | 11 | 0,043 | 0,046 | 0,26 | 31,9 |
| Gustavia hexapetala | 197 | 0,012 | 0,015 | 0,07 | 20,9 |
| Hebepetalum humiriifolium | 47 | 0,033 | 0,041 | 0,22 | 37,3 |
| Heisteria densifrons | 8 | 0,022 | 0,02 | 0,08 | 15,6 |
| Helicostylis pedunculata | 13 | 0,056 | 0,032 | 0,16 | 27,5 |
| Helicostylis tomentosa | 9 | 0,026 | 0,013 | 0,1 | 32,2 |
| Henriettella flavescens | 4 | 0,029 | 0,022 | 0,15 | 15 |
| Hevea guianensis | 68 | 0,06 | 0,029 | 0,19 | 39,3 |
| Hieronyma oblonga | 3 | 0,04 | 0,024 | 0,16 | 41,3 |
| Hirtella bicornis | 54 | 0,059 | 0,026 | 0,23 | 32,7 |
| Hirtella glandulosa | 10 | 0,032 | 0,027 | 0,18 | 36,3 |
| Hirtella racemosa | 2 | 0,024 | 0,017 | 0,08 | 17,8 |
| Humiriastrum subcrenatum | 17 | 0,031 | 0,019 | 0,25 | 53,8 |
| Inga alba | 2 | 0,042 | 0,034 | 0,27 | 31 |
| Inga cayennensis | 9 | 0,031 | 0,036 | 0,24 | 21,3 |
| Inga graciliflora | 4 | 0,023 | 0,019 | 0,08 | 13,1 |
| Inga gracilifolia | 6 | 0,034 | 0,018 | 0,25 | 39,2 |
| Inga jenmanii | 24 | 0,045 | 0,084 | 0,25 | 37,8 |
| Inga loubryana | 56 | 0,047 | 0,068 | 0,21 | 34,9 |
| Inga melinonis | 10 | 0,057 | 0,072 | 0,35 | 32 |
| Inga pezizifera | 3 | 0,132 | 0,072 | 0,54 | 15,4 |
| Inga rubiginosa | 5 | 0,041 | 0,04 | 0,32 | 22,8 |
| Inga sarmentosa | 5 | 0,056 | 0,02 | 0,3 | 29,8 |
| Iryanthera hostmannii | 162 | 0,009 | 0,005 | 0,06 | 24,3 |
| Iryanthera sagotiana | 144 | 0,014 | 0,005 | 0,1 | 27,5 |
| Isertia coccinea | 3 | 0,025 | 0,017 | 0,06 | 12,5 |
| Jacaranda copaia | 50 | 0,08 | 0,013 | 0,23 | 33,3 |
| Lacmellea aculeata | 32 | 0,025 | 0,013 | 0,06 | 19,7 |
| Laetia procera | 14 | 0,05 | 0,041 | 0,26 | 53,3 |

| Species | N | $CP\_imp_{abs}$ | $LBA\_imp_{abs}$ | Gpred_cp3 | $D_{95}$ |
|---|---|---|---|---|---|
| Lecythis chartacea | 13 | 0,018 | 0,026 | 0,11 | 50,8 |
| Lecythis corrugata | 6 | 0,033 | 0,019 | 0,09 | 28,8 |
| Lecythis holcogyne | 2 | 0,041 | 0,027 | 0,23 | 11,7 |
| Lecythis persistens | 1084 | 0,008 | 0,009 | 0,05 | 25,3 |
| Lecythis poiteaui | 80 | 0,015 | 0,002 | 0,06 | 35,3 |
| Lecythis zabucajo | 15 | 0,053 | 0,034 | 0,18 | 43,7 |
| Leonia glycycarpa | 2 | 0,067 | 0,054 | 0,36 | 25,8 |
| Licania alba | 765 | 0,023 | 0,012 | 0,13 | 38,7 |
| Licania canescens | 145 | 0,008 | 0,009 | 0,1 | 31 |
| Licania densiflora | 6 | 0,048 | 0,04 | 0,18 | 23,9 |
| Licania heteromorpha | 412 | 0,043 | 0,012 | 0,19 | 32,2 |
| Licania laxiflora | 39 | 0,022 | 0,008 | 0,15 | 34,9 |
| Licania licaniiflora | 9 | 0,037 | 0,043 | 0,23 | 51,5 |
| Licania longistyla | 3 | 0,048 | 0,035 | 0,25 | 21,2 |
| Licania membranacea | 254 | 0,044 | 0,017 | 0,26 | 40,4 |
| Licania micrantha | 123 | 0,028 | 0,009 | 0,15 | 41,5 |
| Licania ovalifolia | 57 | 0,026 | 0,009 | 0,15 | 54 |
| Licania parvifructa | 5 | 0,042 | 0,036 | 0,23 | 31,1 |
| Licania sprucei | 66 | 0,015 | 0,008 | 0,08 | 23 |
| Licaria cannella | 17 | 0,033 | 0,024 | 0,15 | 34,3 |
| Licaria martiniana | 4 | 0,036 | 0,023 | 0,18 | 20,1 |
| Lueheopsis rugosa | 3 | 0,027 | 0,017 | 0,06 | 14 |
| Mabea piriri | 30 | 0,039 | 0,036 | 0,1 | 20,1 |
| Macoubea guianensis | 16 | 0,021 | 0,003 | 0,21 | 47,5 |
| Mahurea palustris | 2 | 0,029 | 0,016 | 0,12 | 12,7 |
| Manilkara bidentata | 37 | 0,027 | 0,011 | 0,18 | 52,8 |
| Maquira guianensis | 2 | 0,022 | 0,015 | 0,04 | 21,4 |
| Maytenus oblongata | 20 | 0,02 | 0,037 | 0,17 | 40,4 |
| Miconia acuminata | 19 | 0,045 | 0,061 | 0,5 | 15,1 |
| Miconia tschudyoides | 21 | 0,116 | 0,038 | 0,43 | 23,4 |
| Micropholis egensis | 27 | 0,029 | 0,041 | 0,16 | 51,6 |
| Micropholis guyanensis | 44 | 0,042 | 0,03 | 0,18 | 37,5 |
| Micropholis longipedicellata | 2 | 0,041 | 0,03 | 0,25 | 34,1 |
| Micropholis melinoniana | 20 | 0,016 | 0,021 | 0,1 | 51,4 |
| Micropholis obscura | 7 | 0,039 | 0,029 | 0,17 | 51 |
| Micropholis venulosa | 21 | 0,018 | 0,024 | 0,09 | 41,2 |
| Minquartia guianensis | 3 | 0,027 | 0,019 | 0,09 | 17,6 |
| Moronobea coccinea | 137 | 0,033 | 0,03 | 0,22 | 52,1 |
| Mouriri crassifolia | 97 | 0,039 | 0,022 | 0,18 | 37,2 |
| Myrciaria floribunda | 2 | 0,031 | 0,025 | 0,15 | 22,7 |
| Naucleopsis guianensis | 3 | 0,023 | 0,016 | 0,07 | 13,9 |
| Ocotea puberula | 2 | 0,065 | 0,044 | 0,4 | 19,6 |
| Ocotea subterminalis | 14 | 0,052 | 0,032 | 0,19 | 21,7 |

| Species | N | $CP\_imp_{abs}$ | $LBA\_imp_{abs}$ | Gpred_cp3 | $D_{95}$ |
|---|---|---|---|---|---|
| Ormosia coutinhoi | 10 | 0,046 | 0,033 | 0,15 | 16,9 |
| Ouratea decagyna | 4 | 0,04 | 0,021 | 0,13 | 20,5 |
| Ouratea guianensis | 3 | 0,026 | 0,021 | 0,12 | 30,9 |
| Oxandra asbeckii | 461 | 0,007 | 0,006 | 0,05 | 15,4 |
| Pachira dolichocalyx | 66 | 0,047 | 0,017 | 0,14 | 31,6 |
| Parahancornia fasciculata | 3 | 0,04 | 0,028 | 0,22 | 53,8 |
| Parinari campestris | 43 | 0,035 | 0,073 | 0,34 | 63,7 |
| Parinari montana | 22 | 0,027 | 0,01 | 0,17 | 57,5 |
| Parinari rodolphii | 2 | 0,051 | 0,032 | 0,3 | 63,2 |
| Parkia nitida | 23 | 0,06 | 0,062 | 0,36 | 65,6 |
| Parkia pendula | 7 | 0,087 | 0,042 | 0,36 | 36,6 |
| Parkia ulei | 2 | 0,074 | 0,051 | 0,59 | 19,7 |
| Parkia velutina | 17 | 0,055 | 0,056 | 0,36 | 56,2 |
| Peltogyne paniculata | 2 | 0,034 | 0,025 | 0,16 | 14,8 |
| Perebea guianensis | 2 | 0,025 | 0,023 | 0,11 | 16,9 |
| Perebea mollis | 2 | 0,035 | 0,027 | 0,16 | 34,2 |
| Perebea rubra | 4 | 0,028 | 0,021 | 0,1 | 29,5 |
| Platonia insignis | 39 | 0,021 | 0 | 0,17 | 74,9 |
| Platymiscium pinnatum | 4 | 0,033 | 0,026 | 0,16 | 28,8 |
| Pogonophora schomburgkiana | 487 | 0,017 | 0,009 | 0,11 | 21,8 |
| Poraqueiba guianensis | 62 | 0,018 | 0,024 | 0,09 | 29,9 |
| Posoqueria latifolia | 67 | 0,018 | 0 | 0,09 | 22,6 |
| Pourouma bicolor | 8 | 0,044 | 0,03 | 0,25 | 26,7 |
| Pourouma melinonii | 10 | 0,057 | 0,053 | 0,7 | 26,4 |
| Pouteria ambelaniifolia | 35 | 0,037 | 0,024 | 0,18 | 38,6 |
| Pouteria bangii | 21 | 0,021 | 0,02 | 0,1 | 22,3 |
| Pouteria bilocularis | 23 | 0,032 | 0,009 | 0,14 | 27,5 |
| Pouteria cicatricata | 4 | 0,023 | 0,018 | 0,09 | 15,8 |
| Pouteria engleri | 12 | 0,054 | 0,039 | 0,3 | 67,5 |
| Pouteria eugeniifolia | 38 | 0,044 | 0,01 | 0,15 | 56,9 |
| Pouteria fimbriata | 30 | 0,029 | 0,017 | 0,13 | 34,6 |
| Pouteria flavilatex | 3 | 0,027 | 0,014 | 0,17 | 27,4 |
| Pouteria gongrijpii | 51 | 0,016 | 0,028 | 0,1 | 31,9 |
| Pouteria grandis | 6 | 0,022 | 0,02 | 0,11 | 42,5 |
| Pouteria guianensis | 51 | 0,031 | 0,033 | 0,15 | 35,7 |
| Pouteria hispida | 6 | 0,023 | 0,012 | 0,06 | 35,7 |
| Pouteria jariensis | 9 | 0,039 | 0,032 | 0,16 | 29,1 |
| Pouteria melanopoda | 15 | 0,049 | 0,038 | 0,18 | 55,3 |
| Pouteria sagotiana | 2 | 0,047 | 0,02 | 0,25 | 17,3 |
| Pouteria singularis | 16 | 0,025 | 0,015 | 0,14 | 43,3 |
| Pouteria torta | 44 | 0,02 | 0,009 | 0,1 | 34,6 |
| Pouteria venosa | 4 | 0,044 | 0,032 | 0,29 | 18 |
| Pradosia cochlearia | 174 | 0,002 | 0,02 | 0,14 | 51,8 |

| Species | N | CP_imp$_{abs}$ | LBA_imp$_{abs}$ | Gpred_cp3 | D$_{95}$ |
|---|---|---|---|---|---|
| Protium decandrum | 2 | 0,031 | 0,024 | 0,15 | 13,5 |
| Protium giganteum | 2 | 0,036 | 0,025 | 0,19 | 35,7 |
| Protium guianense | 6 | 0,034 | 0,022 | 0,17 | 21,2 |
| Protium opacum | 32 | 0,047 | 0,036 | 0,2 | 29,2 |
| Protium sagotianum | 4 | 0,029 | 0,024 | 0,11 | 30,4 |
| Protium subserratum | 9 | 0,082 | 0,099 | 0,49 | 23,4 |
| Protium tenuifolium | 3 | 0,066 | 0,048 | 0,38 | 21,6 |
| Pseudolmedia laevis | 3 | 0,027 | 0,013 | 0,11 | 27,2 |
| Pterocarpus officinalis | 52 | 0,053 | 0,033 | 0,19 | 40,2 |
| Qualea rosea | 151 | 0,056 | 0,021 | 0,22 | 75,9 |
| Quiina integrifolia | 3 | 0,033 | 0,024 | 0,15 | 12,7 |
| Quiina obovata | 7 | 0,037 | 0,019 | 0,14 | 22,2 |
| Rauvolfia paraensis | 4 | 0,029 | 0,014 | 0,1 | 33,6 |
| Recordoxylon speciosum | 153 | 0,056 | 0,055 | 0,27 | 54,5 |
| Rhodostemonodaphne grandis | 15 | 0,082 | 0,054 | 0,27 | 25,8 |
| Rhodostemonodaphne rufovirgata | 4 | 0,026 | 0,017 | 0,13 | 23,7 |
| Rollinia exsucca | 2 | 0,037 | 0,042 | 0,17 | 15,5 |
| Ruizterania albiflora | 18 | 0,056 | 0,015 | 0,35 | 81,1 |
| Sacoglottis guianensis | 12 | 0,041 | 0,013 | 0,22 | 55 |
| Sandwithia guyanensis | 94 | 0,014 | 0,008 | 0,07 | 14,2 |
| Schefflera decaphylla | 12 | 0,141 | 0,043 | 0,48 | 34,7 |
| Sextonia rubra | 62 | 0,032 | 0,007 | 0,14 | 82,4 |
| Simaba cedron | 182 | 0,011 | 0,011 | 0,04 | 18,6 |
| Simaba morettii | 13 | 0,041 | 0,02 | 0,19 | 49,8 |
| Simaba polyphylla | 8 | 0,022 | 0,015 | 0,12 | 29,2 |
| Simarouba amara | 4 | 0,092 | 0,079 | 0,51 | 56,5 |
| Siparuna cuspidata | 5 | 0,028 | 0,016 | 0,08 | 14,1 |
| Siparuna decipiens | 14 | 0,024 | 0,011 | 0,09 | 22,1 |
| Sloanea guianensis | 14 | 0,032 | 0,015 | 0,09 | 19,4 |
| Sterculia multiovula | 5 | 0,036 | 0,022 | 0,11 | 45,3 |
| Sterculia pruriens | 95 | 0,077 | 0,105 | 0,26 | 60,5 |
| Sterculia speciosa | 33 | 0,035 | 0,034 | 0,16 | 41,8 |
| Swartzia arborescens | 5 | 0,034 | 0,036 | 0,17 | 16,8 |
| Swartzia grandifolia | 12 | 0,02 | 0,009 | 0,06 | 14,5 |
| Swartzia guianensis | 53 | 0,02 | 0,005 | 0,06 | 17,4 |
| Swartzia panacoco | 27 | 0,018 | 0,016 | 0,14 | 43,1 |
| Swartzia polyphylla | 7 | 0,025 | 0,014 | 0,16 | 16,1 |
| Symphonia globulifera | 56 | 0,07 | 0,064 | 0,35 | 69,8 |
| Tabebuia insignis | 2 | 0,029 | 0,02 | 0,1 | 61,7 |
| Tabernaemontana attenuata | 10 | 0,027 | 0,017 | 0,07 | 17,8 |
| Tachigali bracteolata | 12 | 0,148 | 0,136 | 0,96 | 52 |
| Tachigali melinonii | 27 | 0,173 | 0,113 | 0,77 | 66,7 |
| Tachigali paraensis | 9 | 0,103 | 0,074 | 0,66 | 72,4 |

| Species | N | CP_imp$_{abs}$ | LBA_imp$_{abs}$ | Gpred_cp3 | D$_{95}$ |
|---|---|---|---|---|---|
| Talisia hexaphylla | 23 | 0,027 | 0,013 | 0,11 | 20,3 |
| Talisia praealta | 12 | 0,025 | 0,012 | 0,1 | 26,5 |
| Talisia simaboides | 9 | 0,024 | 0,016 | 0,06 | 27,9 |
| Tapura capitulifera | 49 | 0,013 | 0,006 | 0,12 | 38,3 |
| Tetragastris hostmannii | 3 | 0,028 | 0,023 | 0,17 | 35,2 |
| Theobroma subincanum | 84 | 0,012 | 0,022 | 0,1 | 25,5 |
| Thyrsodium guianense | 15 | 0,048 | 0,024 | 0,21 | 33,7 |
| Thyrsodium puberulum | 3 | 0,022 | 0,013 | 0,11 | 21,4 |
| Tovomita brasiliensis | 12 | 0,015 | 0,008 | 0,06 | 12,5 |
| Tovomita brevistaminea | 9 | 0,019 | 0,016 | 0,1 | 15,3 |
| Trattinnickia rhoifolia | 2 | 0,047 | 0,03 | 0,32 | 23,8 |
| Trichilia schomburgkii | 4 | 0,038 | 0,026 | 0,19 | 13,2 |
| Trymatococcus oligandrus | 47 | 0,006 | 0,009 | 0,06 | 21,4 |
| Unonopsis rufescens | 48 | 0,006 | 0,008 | 0,08 | 16,9 |
| Vantanea parviflora | 3 | 0,034 | 0,02 | 0,15 | 34,5 |
| Virola michelii | 37 | 0,056 | 0,04 | 0,26 | 39,8 |
| Virola surinamensis | 3 | 0,053 | 0,04 | 0,32 | 78,7 |
| Vismia sessilifolia | 6 | 0,03 | 0,016 | 0,15 | 27,4 |
| Vitex triflora | 2 | 0,018 | 0,01 | 0,06 | 12,7 |
| Vochysia guianensis | 2 | 0,037 | 0,032 | 0,25 | 60,7 |
| Votomita guianensis | 12 | 0,023 | 0,012 | 0,06 | 13,9 |
| Vouacapoua americana | 240 | 0,018 | 0,028 | 0,15 | 56,4 |
| Xylopia crinita | 7 | 0,039 | 0,025 | 0,17 | 15,3 |
| Xylopia frutescens | 9 | 0,055 | 0,067 | 0,34 | 17,6 |
| Xylopia nitida | 14 | 0,062 | 0,067 | 0,3 | 33 |
| Xylopia pulcherrima | 3 | 0,036 | 0,021 | 0,2 | 19,6 |
| Zygia tetragona | 21 | 0,016 | 0,014 | 0,08 | 24,2 |

Table 15. Effect of an abundance filter on the medians of CP (CP_impabs) and LBA (LBA_impabs) absolute importance and on correlations (Pearson r and P-value) between CP_impabs and LBA_impabs with predicted growth rate at CP3 (Gpred_cp3, cm.y$^{-1}$) and observed maximum dbh (D95, cm).

| Abundance treshold | Number of species | Number of trees | Median of CP_imp$_{abs}$ (cm.y$^{-1}$) | Median of LBA_imp$_{abs}$ (cm.y$^{-1}$) | CP model parameter vs. LBA model parameter | P | CP_imp$_{abs}$ vs. LBA_imp$_{abs}$ | P | CP_imp$_{abs}$ vs. GpredCP3 | P | CP_imp$_{abs}$ vs. D95 | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 282 | 13510 | 0,0325 | 0,021 | -0,413 | 0 | 0,71 | 0 | 0,848 | 0 | 0,313 | 0 |
| 5 | 192 | 13239 | 0,032 | 0,02 | -0,403 | 0 | 0,682 | 0 | 0,836 | 0 | 0,361 | 0 |
| 10 | 142 | 12841 | 0,031 | 0,0195 | -0,412 | 0 | 0,674 | 0 | 0,865 | 0 | 0,373 | 0 |
| 20 | 101 | 12252 | 0,028 | 0,017 | -0,432 | 0 | 0,654 | 0 | 0,905 | 0 | 0,416 | 0 |
| 50 | 54 | 10733 | 0,027 | 0,0155 | -0,513 | 0 | 0,652 | 0 | 0,886 | 0 | 0,575 | 0 |
| 100 | 27 | 8925 | 0,023 | 0,014 | -0,256 | 0,2 | 0,472 | 0,013 | 0,897 | 0 | 0,612 | 0,001 |
| 200 | 11 | 6539 | 0,02 | 0,012 | 0,167 | 0,62 | 0,261 | 0,439 | 0,963 | 0 | 0,51 | 0,109 |

| Abundance treshold | Number of species | Number of trees | LBA_impabs vs. GpredCP3 | P | LBA_impabs vs. D95 | P | GpredCP3 vs. D95 | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 282 | 13510 | 0,768 | 0 | 0,246 | 0 | 0,344 | 0 |
| 5 | 192 | 13239 | 0,76 | 0 | 0,265 | 0 | 0,399 | 0 |
| 10 | 142 | 12841 | 0,763 | 0 | 0,313 | 0 | 0,441 | 0 |
| 20 | 101 | 12252 | 0,732 | 0 | 0,38 | 0 | 0,547 | 0 |
| 50 | 54 | 10733 | 0,646 | 0 | 0,402 | 0 | 0,681 | 0 |
| 100 | 27 | 8925 | 0,607 | 0 | 0,587 | 0 | 0,698 | 0 |
| 200 | 11 | 6539 | 0,411 | 0,21 | 0,779 | 0,01 | 0,551 | 0,079 |

# Liste des figures et tables

## Figures

## Tables

## Résumé

Ce travail de thèse explore la signification écologique des variations inter et intraspécifiques de la croissance et des traits fonctionnels des espèces d'arbres de forêt tropicale guyanaise en relation avec les conditions d'éclairement. Nous démontrons que le syndrome de traits associé à la niche de régénération (durée de vie des feuilles plus longue et surface massique plus grande pour les espèces les plus tolérantes à l'ombre) est valide pour 14 espèces non pionnières et non strictement sciaphiles. La plasticité de la surface massique exprimée au stade juvénile chez les espèces les moins spécialisées pourrait refléter une adaptation à l'hétérogénéité de l'éclairement rencontrée au stade jeune et au cours des stades ontogéniques successifs. Les analyses multivariées mettent en évidence un lien étroit entre la durée de vie des feuilles, la profondeur relative du houppier et la niche de régénération. La plasticité de la profondeur du houppier observée chez les espèces les plus héliophiles ne peut pas être interprétée comme une réponse d'évitement de l'auto-ombrage. Nous montrons qu'elle correspond plutôt à un changement des taux de croissance et de mortalité des feuilles et des branches imposé par les conditions d'éclairement et se produisant à l'échelle de la plante entière. En ce qui concerne la variabilité intraspécifique de la croissance des arbres adultes, nous avons observé une faible contribution de la compétition pour la lumière et un effet important de l'espèce. Nos résultats indiquent que ce patron de réponse résulte de la partition des espèces le long du gradient lumineux vertical et de la forte abondance d'espèces de petite taille peu sensibles à la compétition du fait de leur adaptation aux conditions lumineuses du sous-bois. La différentiation de niche de régénération et la stratification verticale des arbres adultes étayent l'hypothèse d'une partition de niche vis à vis de la ressource lumineuse dans les trois dimensions de la forêt tropicale humide.

**Mots clés** : stature adulte, perturbation de la canopée, durée de vie des feuilles, vitesse de croissance, différentiation de niche, plasticité phénotypique, forêt tropicale humide.

## Abstract

This study explores the ecological significance of inter- and intraspecific variations of growth and functional traits found in tropical tree species of French Guiana in relation to light regime. We demonstrate that the syndrome of leaf traits associated with light -niche (longer life span, higher leaf mass per area of more shade tolerant species) holds among a set of 14 species comprising no pioneer nor any shade specialist species. Our results further suggest that plasticity of leaf mass per area expressed at the sapling stage may reflect adaptation to the spatial heterogeneity of light conditions encountered both at the sapling stage and across ontogenetic stages. Multivariate analysis provides evidence of a close linkage between leaf lifespan, relative crown depth and light-niche optimum. The plasticity in relative crown depth observed in shade-intolerant species can not be interpreted in terms of self-shading avoidance. Rather, crown depth adjustment was found to be a consequence of changes in growth rates and mortality rates of leaves and branches imposed by current light conditions and occurring at the whole-plant level. At the adult stage, our results point to competition for light making an unexpectedly low contribution to individual tree growth variations, contrasting with a major effect of species identity. We argue that this pattern of variation is likely to result from the vertical niche partitioning of species and the high abundance of small-statured species that are moderately responsive to light competition (consistent with their adaptation to understorey conditions). Light-niche differentiation of juvenile trees and vertical stratification of adult trees provide strong evidence for light niche partitioning in the three-dimensional space of tropical forests.

**Keywords** : adult stature, canopy disturbance, leaf lifespan, growth rate, morphology, niche differentiation, phenotypic plasticity, tropical moist forest.