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Original article

A trait database for Guianan rain forest trees permits intra- and inter-specific contrasts

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Abstract – We present a plant trait database covering autecology for rain forest trees of French Guiana. The database comprises more than thirty traits including autecology (e.g., habitat associations and reproductive phenology), wood structure (e.g., density and tension characteristics) and physiology at the whole plant (e.g., carbon and nitrogen isotopes) and leaf level (e.g., specific leaf area, photosynthetic capacity). The current database describes traits for about nine hundred species from three hundred genera in one hundred families. For more than sixty species, data on twelve morphological and ecophysiological traits are provided for individual plants under different environmental conditions and at different ontogenetic stages. The database is thus unique in permitting intraspecific analyses, such as the effects of ontogenetic stages or environmental conditions on trait values and their relationships.

plant traits / tropical forest / French Guiana / functional groups / plasticity / ontogeny

Résumé – Une base de données sur l'autécologie des arbres de la forêt tropicale de Guyane française. Nous présentons une base de données sur l'autécologie des arbres de la forêt tropicale de Guyane française. La base contient des données sur plus de trente traits concernant l'autécologie (par exemple, les préférences d'habitat et la phénologie reproductive), la structure du bois (par exemple, la densité et les caractéristiques du bois de tension) et la physiologie aux niveaux de la plante entière (par exemple, les isotopes du carbone et de l'azote) et de la feuille (par exemple, la surface spécifique ou la capacité photosynthétique). Dans son état actuel, la base décrit les traits d'environ neuf cents espèces de trois cents genres dans cent familles. Pour plus de soixante espèces, des données sur douze traits morphologiques et écophysiologiques sont fournis au niveau individuel pour des plants dans différentes conditions environnementales à différents stades ontogéniques. Cette base de données permet donc des analyses intraspécifiques, comme les effets des stades ontogéniques ou des conditions environnementales sur les valeurs des traits et leurs relations, ce en quoi elle n'a pas d'équivalent.

traits / forêt tropicale / Guyane française / groupes fonctionnels / plasticité / ontogénie

1. INTRODUCTION

Databases compiling species traits are important tools for plant ecologists to understand patterns of species abundance and distribution at a time of rapid loss of species diversity [10, 16, 17, 23, 24]. Recent studies have underlined at least four compelling research applications for such databases. First, trait databases can help us to understand basic strategies of resource use or biomass allocation among plants. Recent compilations [10, 34, 51, 52] illustrate how data from many different sources can be combined to confirm general conclusions of plant functioning that have been suggested from local datasets. Second, trait databases permit comparisons and contrasts of species diversity and plant functional types across natural environmental gradients, both within and among systems. For example, several studies demonstrate how trait values such as high foliar nutrient content are associated with particular environmental conditions such as high annual precipitation [33, 49, 50]. Third, trait databases are being used to select focal species for experimental communities to test relationships between species diversity, functional diversity and ecosystem function [21, 40], or to refine subsequent analyses for existing experiments [31]. More recently, a fourth objective has been underlined, to understand evolutionary patterns among trait associations, such as the origin of seed mass associations with other plant traits [27, 28].

In general, within-species analyses for continuous traits, such as leaf attributes, use a mean trait value for species, without consideration of the variability masked by that mean value. To address this gap, we propose a fifth application of trait databases of a particular construction, within-species analyses. We recognize three particular types of intra-specific variability that could influence the mean value of traits reported in most databases, noting that analyses of each of these levels of variation represent advances for the application of trait databases. First, the observed phenotype of many plant traits can be strongly influenced by genotype of individuals for which trait screening has been conducted; we refer to this as the effect of *genetic diversity*. For example, Balaguer et al. [1] found significant differences in biomass allocation patterns and foliar nutrient contents among *Quercus coccifera* seedlings from three Mediterranean ecotypes differing in isozyme patterns. A second level of intraspecific trait variability occurs based on

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the environmental conditions under which measurements are made; we refer to this as species *plasticity*. For example, foliar traits are often reported for 'sun leaves', but the definition of sun may include plants grown in pots under high transmission shadecloth and those in the field under open conditions [48]. In some cases, these environmental effects can interact with genotype effects so that the observed phenotype is the result of genotype × environment interactions; for example, in the study by Balaguer et al. [1], the three ecotype populations responded differently when grown in sun vs. shade. A third level of variation that may occur within species involves differences in trait values with plant size or developmental stage; we refer to this as *ontogenetic plasticity*. In a recent meta-analysis, for example, Thomas and Winner [47] report significant differences between saplings and adult trees of 35 tree species, for several photosynthetic traits.

In this paper, we present MARIWENN, a trait database for woody plant species of the Guiana Shield region of South America that has been constructed to permit both intra- and inter-specific contrasts. First, we describe the construction of the database and the sources of available data; in doing so, we contrast the design and potential uses of the database with those of other plant trait databases such as GLOPNET and LEDA. We then present some examples of analyses that can be conducted using the database, including the unique aspect of within species comparisons in addition to the contemporary interspecific contrasts.

2. CONTENT

We gathered plant trait data for more than nine hundred woody plant species from French Guiana, representing over three hundred genera in more than one hundred families. Many data sources appear only in the grey literature, and thus would not otherwise be easily accessible to all researchers. The first part of the database was built to be an exhaustive compilation of the results of research on general species traits. No standardization of the data was made at this step; the purpose was just to organize the data rigorously to allow users to find data sources and the methods employed. The result is a comprehensive synthesis of data covering fields from wood structure to reproductive phenology (Tab. I). The modular structure of the database allows new data to be entered as it is generated.

The second purpose of the database was to structure data of plant traits to allow multivariate analyses. Unlike the first approach, this framework requires normative rules of measure and organization of the data. Moreover, specific measures are required to structure the database. The trait list reflects the state of the art of research and may change according to demands and new discoveries (Tab. II). Unlike the GLOPNET [23] databases, MARIWENN contains trait values measured on individual plants. Each value is then linked to many other fields that permit more complex queries: details of measurements (protocol); its author (reference); the environment, described with two levels of detail (general environment such as glasshouse or canopy, and detailed environment indicating the soil or the topographic position, or light level); and the ontogenetic stage of the plant. The mean and standard deviation of the trait can be computed as requests are made, for each ontogenetic stage and each environment type. Filters are available to reduce the dataset to a chosen light level or detailed environment. This organization allows the retention of a large number of individuals or the isolation of particular environmental conditions, as a trade-off between sample size and variability among individuals.

The recorded traits are based on those described by Cornelissen et al. [7], without limitation (Tab. II). A priority of recent research has been leaf traits, including: specific leaf area, leaf area, laminar thickness, foliar carbon, nitrogen and phosphorus contents, and photosynthetic traits. An intensive campaign of measurement is being processed to enhance the database.

The botanical database is a straight adaptation of the checklist of the plants of the Guianas [3], including, where possible, a reference to the herbarium of Cayenne (IRD). Taxonomy is detailed down to the variety or subspecies, even though the standard level of detail is the species. Vernacular names are available as supplementary information. However, we caution the use of the database as a source of cross-referencing between scientific and common names because these links often vary between regions. The sites of field and experimental studies are referenced and their main characteristics detailed for each entry.

We chose to develop the database to maximize its versatility. No data related to the studied species are excluded a priori. The geographic limit is that of the botanical database which includes the plateau of the Guianas. The present content of the database is restricted to forest trees, but data from mangroves, savannas or non ligneous vegetation will be added as future research programs provide them.

3. USING THE DATABASE

All the published data are available through the Internet on http://ecofog.cirad.fr/Mariwenn. Unpublished data may be available in advance upon request of a password from the corresponding author. Future work will naturally be keeping data compilation up to date and also completing the trait records at plant level. We hope to gather individual data for most of the traits of the 100 most abundant woody species in French Guiana within two years.

Data can be obtained by species (all data available for a given species) or by topic (all species available for a given subject).

The web access is particularly easy to use but does not allow complex queries. Direct access using SQL queries is possible from the local network only, for technical and security reasons. Scientific collaborations are thus the easiest way to obtain complete access to the database, and interested researchers are invited to contact the corresponding author.

3.1. Examples of intraspecific analyses

In its current state, the database allows analyses within species for variation between environmental conditions, or between ontogenetic stages (see examples suggested in Tab. III). Current collections for trait screening are following half-sibling cohorts within species and will thus permit contrasts to be made to analyze 'genotype' or genotype × environment effects on trait values.

Table I. Traits that have been measured at the species level that can be used in interspecific comparisons within this database or in concert with other databases, across sites or biomes.

Trait	References
Ecophysiological data	
Nitrogen: Isotopic signature ($\delta^{15}N$) and leaf nitrogen concentration in various forest sites	[35–38]
Carbon: δ13C values and leaf carbon concentration at several sites	[4]
Photosynthesis-related ecophysiological parameters measured in glasshouse	[8]
Biomechanics	
Wood density at 12% moisture	[5]
Wood durability, impregnability; durability against termites and fungi	[14, 15]
Tension wood characteristics	[41]
Soil-vegetation relations	
Characterization of the edaphic preferences of species	[6, 30, 45]
Architecture and phenology	
Seedling morphology	[2]
Architectural patterns of trees	[18–20]
Vegetative phenology	[26]
Reproductive phenology	[9, 26, 42–44]
Reproduction	
Seeds and fruit characteristics	[2, 6, 12, 26, 42]
Pollen dispersal	[9]
Forest dynamics	
Pioneer species and soil seed bank	[29]
Response groups of species for light	[11]
Height groups: position of species in the vertical structure of the forest	[6]
Horizontal spatial structure of tree species	[6]

Table II. Traits describing species morphology and physiology that have been measured for individual plants for a given ontogenetic stage and under particular controlled environmental conditions, thereby permitting intra-specific analyses of species' plasticity across different environmental gradients, or ontogenetic shifts in trait values.

Trait	Unit	Measurement
Relative growth rate (RGR)	mg g^{-1} d^{-1}	After Hunt [22]
Root-shoot ratio	g g^{-1}	Root biomass/shoot biomass
Specific leaf area	cm^2 g^{-1}	leaf area/leaf biomass
Leaf blade surface area	cm^2	LICOR 3000 meter
SPAD chlorophyll estimation	SPAD units	Minolta SPAD-502 meter
Leaf thickness	µm	Mitutoyo caliper
Leaf dry matter content	mg g^{-1}	After Garnier et al. [13]
Leaf mass ratio	g g^{-1}	Leaf area/total biomass
Net assimilation rate (A_{max})	µmol CO_2 cm^{-2} s^{-1}	CIRAS-1 System
Dark respiration rate (Rd)	µmol CO_2 cm^{-2} s^{-1}	CIRAS-1 System
Stomatal conductance (Gs)	µmol CO_2 cm^{-2} s^{-1}	CIRAS-1 System
Foliar [d13C]	‰	Mass spectrometer [4]
Foliar [N]	%	CHN autoanalyzer
Foliar [P]	%	HF digest; colorimetry
Water use efficiency (WUE)	µmol H_2O mol^{-1} CO_2	A_{max}/Gs
Nitrogen efficiency index (NUE)	µg g^{-1} d^{-1}	Foliar [N]/RGR
Phosphorus efficiency index (PUE)	µg g^{-1} d^{-1}	Foliar [P]/RGR

Table III. Examples of intra-specific calculations of species' plasticity or performance response ratios, across different environmental gradients, that can be performed using the MARIWENN database.

Calculated index	Unit	Calculation
Response ratio - Light	%	$RGR_{hilite}/RGR_{lolite}$
Response ratio - Soil moisture	%	RGR_{hiSM}/RGR_{loSM}
Response ratio - Soil nutrients	%	RGR_{hiSN}/RGR_{loSN}
Plasticity in SLA	%	range of SLA/SLA_{max}
Plasticity in WUE	%	range of WUE/WUE_{max}
Plasticity in NUE	%	range of NUE/NUE_{max}
Plasticity in root-shoot allocation	$g\ g^{-1}$	range of RS/RS_{max}
Plasticity in leaf area ratio	$cm^2\ g^{-1}$	range of LAR/LAR_{max}

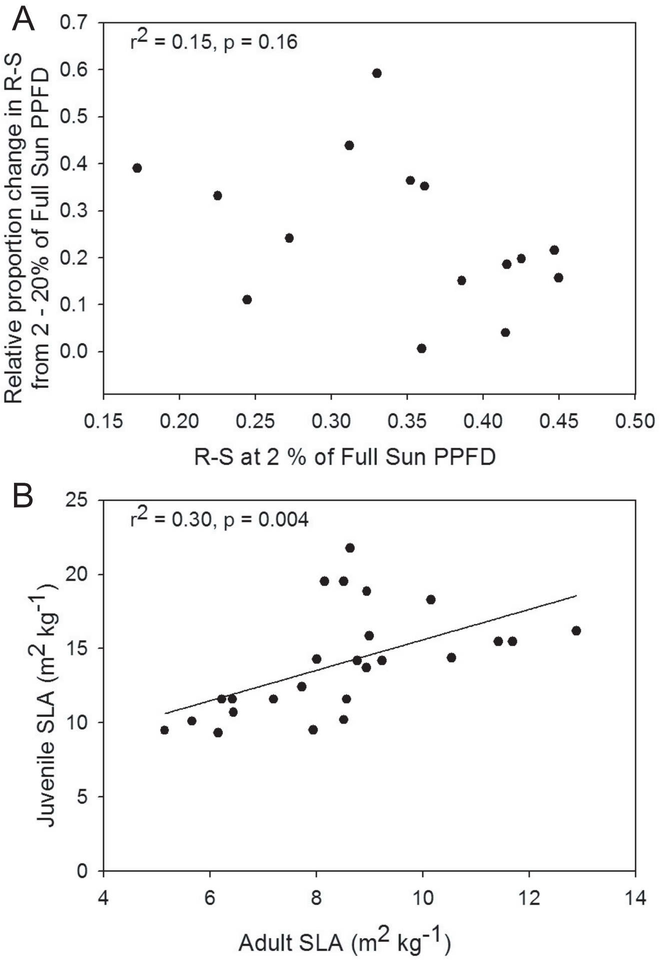

Figure 1. Examples of intra-specific analyses that can be conducted using the MARIWENN database. (A) Do species with particular mean values of a given trait exhibit greater breadth in trait values across a range of environmental conditions? In this example, we test whether species with low root-shoot ratio (R-S) have a larger range in R-S (relativized to maximum value; see Tab. II), across a light gradient varying from 2–20% of full sun. Data from C. Baraloto, unpublished. (B) Do species maintain trait values throughout developmental stages and/or size classes? In this example, we test whether mean values for SLA of sun leaves for 25 species change between juveniles and adult trees. Data from C. Baraloto and D. Bonal, unpublished.

Figure 1 illustrates two types of analyses that can be conducted using queries of the current database. The first example examines, for a given ontogenetic stage, if species-level trait breadth differs among species. In this case, the example addresses a species-level scenario for the hypothesis of Taylor and Aarssen [46] or Lortie and Aarssen [25] who suggest that a greater breadth of traits related to fitness should be exhibited by generalist species because they are exposed to selection under heterogeneous environments. If it is assumed that among tropical tree seedlings, the more specialized ecological guild is the light-demanding species, who generally have low root-shoot ratios [32], then we would predict a negative relationship between trait breadth and trait value in this case. However, no significant relationship was found for the species in the MARIWENN database (Fig. 1A).

The second example tests whether trait values, at a given environmental level (in this case leaves exposed to full sun) differ between developmental stages. Figure 1B shows a significant relationship between adult and juvenile specific leaf area (SLA). Nonetheless, a large degree of variation exists around this relationship, and many species pairs switch relative positions between stages. Moreover, as with the study of Thomas and Winner [47] or that of Roggy et al. [39], adult leaves have consistently lower SLA (or higher LMA).

3.2. Using these results to refine interspecific analyses

Each of the above examples shows how the intra-specific analyses can respond to particular research questions. In addition, we suggest that these types of analyses should serve as precursors to species-level analyses. When we find significant effects of environment or stage on mean trait values, this suggests that these factors need to be considered when conducting analyses among species. In the first example, (Fig. 1A), it is clear that the magnitude of shifts in root-shoot ratio between light environments differs among species (although not predictably based on a given trait value). This suggests that the results of multivariate analyses among species would be strongly dependent on the environmental conditions under which plants were grown for trait screening. Such variation may occur at what we have called the detailed environment, as in our example, or at what we have called the general environment.

For example, growing species in pots may influence the values of traits such as specific root length or root-shoot ratio (K. Kitajima, pers. comm.). The second example (Fig. 1B) indicates that for the 25 tropical tree species, multivariate analyses of foliar trait associations including specific leaf area (SLA, or its inverse, LMA), such as those conducted by Wright et al. [52], should control for the developmental stage of the plants measured in the database because species' values may shift rankings between stages.

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REFERENCES

[1] Balaguer L., Martinez-Ferri E., Valladares F., Perez-Corona M.E., Baquedano F.J., Castillo F.J., Manrique E., Population divergence in the plasticity of the response of *Quercus coccifera* to the light environment, Funct. Ecol. 15 (2001) 124–135.

[2] Baraloto C., Forget P.-M., Seed size, seedling morphology, and response to deep shade and damage in neotropical rain forest trees, Am. J. Bot. 94 (2007) 901–911.

[3] Boggan J., Funk V., Kelloff C., Hoff M., Cremers G., Feuillet C., Checklist of the Plants of the Guianas, 2nd ed., Museum of Natural History, Smithsonian Institution, Washington, D.C., 1997.

[4] Bonal D., Barigah T.S., Granier A., Guehl J.-M., Late-stage canopy tree species with extremely low delta C-13 and high stomatal sensitivity to seasonal soil drought in the tropical rainforest of French Guiana, Plant Cell Environ. 23 (2000) 445–459.

[5] Centre technique forestier tropical, Bois des DOM-TOM, 1989.

[6] Collinet F., Essai de regroupement des principales espèces structurantes d'une forêt dense humide d'après leur répartition spatiale (forêt de Paracou, Guyane), Thèse de doctorat, Université Claude Bernard-Lyon I, Lyon, 1997.

[7] Cornelissen J.H.C., Lavorel S., Garnier E., Diaz S., Buchmann N., Gurvich D.E., Reich P.B., Steege H.t., Morgan H.D., Heijden M.G.A.v.d., Pausas J.G., Poorter H., A handbook of protocols for standardised and easy measurement of plant functional traits worldwide, Aust. J. Bot. 51 (2003) 335–380.

[8] Coste S., Roggy J.-C., Imbert P., Born C., Bonal D., Dreyer E., Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance, Tree Physiol. 25 (2005) 1127–1137.

[9] Degen B., Dendrobase: Genetic system of tropical tree species, Silvolab, Kourou, 1999.

[10] Diaz S., Hodgson J.G., Thompson K., Cabido M., Cornelissen J.H.C., Jalili A., Montserrat-Marti G., Grime J.P., Zarrinkamar F., Asri Y., Band S.R., Basconcelo S., Castro-Diez P., Funes G., Hamzehee B., Khoshnevi M., Perez-Harguindeguy N., Perez-Rontome M.C., Shirvany F.A., Vendramini F., Yazdani S., Abbas-Azimi R., Bogaard A., Boustani S., Charles M., Dehghan M., de Torres-Espuny L., Falczuk V., Guerrero-Campo J., Hynd A., Jones G., Kowsary E., Kazemi-Saeed F., Maestro-Martinez M., Romo-Diez A., Shaw S., Siavash B., Villar-Salvador P., Zak M.R., The plant traits that drive ecosystems: Evidence from three continents, J. Veg. Sci. 15 (2004) 295–304.

[11] Favrichon V., Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise, Rev. Ecol. Terre Vie 49 (1994) 379–403.

[12] Forget P.-M., Dissémination et régénération naturelle de huit espèces d'arbres en forêt guyanaise, Ph.D. thesis, Université de Paris VI, 1988.

[13] Garnier E., Shipley B., Roumet C., Laurent G., A standardized protocol for the determination of specific leaf area and leaf dry matter content, Funct. Ecol. 15 (2001) 688–695.

[14] Gérard J., Narboni P., Une base de données sur les propriétés technologiques des bois, Bois For. Trop. 248 (1996) 65–70.

[15] Gérard J., Edi Kouassi A., Daigremont C., Détienne P., Fouquet D., Vernay M., Synthèse sur les caractéristiques technologiques de référence des principaux bois commerciaux africains, Série FORAFRI, CIRAD-Forêt, 1998.

[16] Grime J.P., Declining plant diversity: empty niches or functional shifts? J. Veg. Sci. 13 (2002) 457–460.

[17] Grime J.P., Thomson K., Hunt R., Hodgson J.G., Cornelissen J.H.C., Rorison I.H., Hendry G.A.F., Ashenden T.W., Askew A.P., Band S.R., Booth R.E., Bossard C.C., Campbell B.D., Cooper J.E.L., Davison A.W., Gupta P.L., Hall W., Hand D.W., Hannah M.A., Hillier S.H., Hodkinson D.J., Jalili A., Liu Z., Mackey J.M.L., Matthews N., Mowforth M.A., Neal A.M., Reader R.J., Reiling K., Ross-Fraser W., Spencer R.E., Sutton F., Tasker D.E., Thorpe P.C., Whitehouse J., Integrated screening validates primary axes of specialisation in plants, Oikos 79 (1997) 259–281.

[18] Hallé F., Oldeman R.A.A., Essai sur l'architecture et la dynamique de croissance des arbres tropicaux, 1970.

[19] Hallé F., Oldeman R.A.A., Tomlinson P.B., Tropical trees and forests – an architectural analysis, 1978.

[20] Heuret P., Analyse et modélisation de séquences d'événements botaniques : application à la compréhension des processus de croissance, de ramification et de floraison, Ph.D. thesis, Université de Nancy I, 2002.

[21] Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setala H., Symstad A.J., Vandermeer J., Wardle D.A., Effects of biodiversity on ecosystem functioning: A consensus of current knowledge, Ecol. Monogr. 75 (2005) 3–35.

[22] Hunt R., Plant growth analysis, The Institute of Biology's Studies in Biology, Edward Arnold, London, 1978.

[23] Knevel I.C., Bekker R.M., Bakker J.P., Kleyer M., Life-history traits of the northwest European flora: The LEDA database, J. Veg. Sci. 14 (2003) 611–614.

[24] Kuhn I., Durka W., Klotz S., BiolFlor – a new plant-trait database as a tool for plant invasion ecology, Divers. Distrib. 10 (2004) 363–365.

[25] Lortie C.J., Aarssen L.W., The specialization hypothesis for phenotypic plasticity in plants, Int. J. Plant Sci. 157 (1996) 484–487.

[26] Loubry D., Déterminisme du comportement phénologique des arbres en forêt tropicale humide de Guyane française, Ph.D. thesis, Université Paris 6, 1994.

[27] Moles A.T., Ackerly D.D., Webb C.O., Tweddle J.C., Dickie J.B., Westoby M., A brief history of seed size, Science 307 (2005) 576–580.

[28] Moles A.T., Ackerly D.D., Webb C.O., Tweddle J.C., Dickie J.B., Pitman A.J., Westoby M., Factors that shape seed mass evolution, Proc. Natl. Acad. Sci. USA 102 (2005) 10540–10544.

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

[30] Paget D., Étude de la diversité spatiale des écosystèmes forestiers guyanais : réflexion méthodologique et application, Ph.D. thesis, ENGREF, 1999.

[31] Petchey O.L., Hector A., Gaston K.J., How do different measures of functional diversity perform? Ecology 85 (2004) 847–857.

[32] Poorter L., Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits, Funct. Ecol. 13 (1999) 396–410.

[33] Reich P.B., Oleksyn J., Global patterns of plant leaf N and P in relation to temperature and latitude, Proc. Natl. Acad. Sci. USA 101 (2004) 11001–11006.

[34] Reich P.B., Ellsworth D.S., Walters M.B., Vose J.M., Gresham C., Volin J.C., Bowman W.D., Generality of leaf trait relationships: A test across six biomes, Ecology 80 (1999) 1955–1969.

[35] Roggy J.-C., Contribution des symbioses fixatrices d'azote à la stabilité de l'écosystème forestier tropical guyanais, Thèse Université C. Bernard Lyon I, 1998.

[36] Roggy J.-C., Prévost M.-F., Nitrogen-fixing legumes and silvigenesis in a rain forest in French Guiana: a taxonomic and ecological approach, New Phytol. 144 (1999) 283–294.

[37] Roggy J.-C., Prévost M.-F., Garbaye J., Domenach A.-M., Nitrogen cycling in the tropical rain forest of French Guiana: comparison of two sites with contrasting soil types using delta-15N, J. Trop. Ecol. 15 (1999) 1–22.

[38] Roggy J.-C., Prévost M.-F., Gourbiere F., Casabianca H., Garbaye J., Domenach A.-M., Leaf natural 15N abundance and total N concentration as potential indicators of plant N nutrition in legumes and pioneer species in a rain forest of French Guiana, Oecologia 120 (1999) 171–182.

[39] Roggy J.-C., Nicolini E., Imbert P., Caraglio Y., Bosc A., Heuret P., Links between tree structure and functional leaf traits in the tropical forest tree *Dicorynia guianensis* Amshoff (Caesalpiniaceae), Ann. For. Sci. 62 (2005) 553–564.

[40] Roscher C., Schumacher J., Baade J., Wilcke W., Gleixner G., Weisser W.W., Schmid B., Schulze E.D., The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community, Basic Appl. Ecol. 5 (2004) 107–121.

[41] Ruelle J., Anatomie comparative bois normal/bois de réaction et observation des relations structure/propriétés du bois de six espèces d'angiospermes de forêt tropicale humide et de trois espèces de gymnospermes de forêt tempérée, Nancy, 2003.

[42] Sabatier D., Fructification et dissémination en forêt guyanaise : l'exemple de quelques espèces ligneuses, Université des Sciences et Techniques du Languedoc, Montpellier, 1983.

[43] Sabatier D., Saisonnalité et déterminisme du pic de fructification en forêt guyanaise, Rev. Ecol. Terre Vie 40 (1985) 289–320.

[44] Sabatier D., Puig H., Phénologie et saisonnalité de la floraison et de la fructification en forêt dense guyanaise, Muséum National d'Histoire Naturelle, Paris, 1982.

[45] Sabatier D., Grimaldi M., Prévost M.-F., Guillaume J., Godron M., Dosso M., Curmi P., The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest, Plant Ecol. 131 (1997) 81–108.

[46] Taylor D.R., Aarssen L.W., An interpretation of phenotypic plasticity in *Agropyron repens*, Am. J. Bot. 75 (1988) 401–413.

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

[48] Whitmore T.C., A review of some aspects of tropical rain forest seedling ecology with suggestions for further inquiry, in: Swaine M.D. (Ed.), The ecology of tropical forest tree seedlings, UNESCO/ Parthenon Publishing, Paris 1996, pp. 3–39.

[49] Wright I.J., Westoby M., Leaves at low versus high rainfall: coordination of structure, lifespan and physiology, New Phytol. 155 (2002) 403–416.

[50] Wright I.J., Reich P.B., Westoby M., Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats, Funct Ecol. 15 (2001) 423–434.

[51] Wright I.J., Reich P.B., Cornelissen J.H.C., Falster D.S., Garnier E., Hikosaka K., Lamont B.B., Lee W., Oleksyn J., Osada N., Poorter H., Villar R., Warton D.I., Westoby M., Assessing the generality of global leaf trait relationships, New Phytol. 166 (2005) 485–496.

[52] Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F., Cavender-Bares J., Chapin T., Cornelissen J.H.C., Diemer M., Flexas J., Garnier E., Groom P.K., Gulias J., Hikosaka K., Lamont B.B., Lee T., Lee W., Lusk C., Midgley J.J., Navas M.-L., Niinemets U., Oleksyn J., Osada N., Poorter H., Poot P., Prior L., Pyankov V.I., Roumet C., Thomas S.C., Tjoelker M.G., Veneklaas E.J., Villar R., The worldwide leaf economics spectrum, Nature. 428 (2004) 821–827.