UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LE RÔLE DES PROPRIÉTÉS DU SOL DANS LA DISTRIBUTION DES PALMIERS DU GENRE *ATTALEA* (PALMAE) ET DES CATIONS ÉCHANGEABLES DE LA RÉGION DU BAS TAPAJÓS (AMAZONIE BRÉSILIENNE)

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RÉSUMÉ

L'agriculture sur brûlis le long d'un front de colonisation du Bas Tapajós (Pará, Brésil) favorise l'émergence d'une double situation d'exposition au risque pour les communautés. D'une part, le brûlis occasionne le transfert du mercure inorganique du sol vers le milieu aquatique utilisé par les populations humaines; de l'autre, les grands palmiers arborescents du genre *Attalea* dont la fréquence est stimulée par l'agriculture sur brûlis sont des indicateurs importants de l'aléa de la Trypanosomiase américaine, car ses vecteurs, les triatomes (Hemiptera : Triatominae), nichent principalement dans la matière organique qui s'accumule dans leurs couronnes. Notre étude a comme objectif de déterminer comment la distribution des espèces du genre *Attalea* (Palmae) est liée aux propriétés édaphiques d'un front de colonisation de la région du Bas Tapajós, dans le bassin amazonien. Nous avons identifié 3 espèces d'*Attalea* et un quatrième palmier considéré comme pouvant être une variété acaule d'*Attalea speciosa* (*A.* sp. nain). Nos résultats montrent qu'*A. phalerata* préfère des sols aux teneurs en cations disponibles plus élevées et moins acides. *A. maripa* est inversement distribué à *A. phalerata* et se limite aux sols les plus pauvres en cations disponibles et plus acides. Malgré que la distribution de *A. speciosa* n'a pas varié fortement avec les propriétés édaphiques mesurées, nos données indiquent que *A.* sp. nain serait associée à des sols aux teneurs plus élevées en chlore ainsi qu'à des caractéristiques minéralogiques spécifiques des Alfisols. L'effet important des cations majeurs échangeables sur la présence et l'absence des espèces d'*Attalea* nous a amené à étudier comment ces nutriments sont associés aux propriétés physicochimiques du sol. Nos résultats montrent que le Ca^{2+} échangeable est corrélé aux oxyhydroxydes de fer associés aux limons fins (2-10 μm). Le K^{+} échangeable est principalement associé à des réserves non échangeables de K_{tf}. Le Mg^{2+} échangeable, de taille intermédiaire, est d'une part fortement lié aux facteurs du sol qui contrôlent le Ca^{2+} échangeable, mais est aussi significativement associé au Mg_{tf} non échangeable. Nos résultats suggèrent de privilégier le rôle individuel de chacun des cations échangeables ainsi qu'une catégorisation granulométrique détaillée pour la recherche en écologie végétale. De plus, la présence de quantités appréciables de Mg_{tf} et de K_{tf} indique que l'altération des minéraux joue un rôle significatif dans le cycle des éléments nutritifs de ces forêts de terre ferme amazonienne. Enfin, ces découvertes complètent les connaissances actuelles sur le cycle du mercure de la région considérant le rôle capital des cations échangeables dans son relargage du sol.

MOTS CLÉS : palmier, *Attalea*, cations, sol, texture, minéralogie, Trypanosomiase américaine

INTRODUCTION

En dépit des controverses liées au suivi de la tendance mondiale du déclin des forêts tropicales (Hansen *et coll.*, 2008), il a été estimé que 2,36 % des forêts tropicales humides mondiales ont été déboisées entre 2000 et 2005 (Steininger *et coll.*, 2008). Le Brésil est en avant-plan, responsable de 47,8 % de la perte totale de ce biome. Le déboisement a principalement lieu aux marges de l'Amazonie, le long d'un « arc de déforestation » généré par l'expansion de la production bovine et de soja (Malhi *et coll.*, 2008). Bien qu'entre les mois de juillet 2005 et 2009, les taux de déforestation en Amazonie brésilienne aient diminué de 36 % en raison de la chute du prix du soja, une augmentation de la force de la monnaie brésilienne, ainsi qu'une réglementation gouvernementale active, la menace à ces forêts uniques demeure toutefois une préoccupation réelle (Fearnside, 2009 ; Malhi *et coll.*, 2008 ; Nepstad *et coll.*, 2009 ; Soares-Filho *et coll.*, 2006).

Malgré la gravité des conséquences mondiales du réchauffement climatique et d'une perte importante de la biodiversité, les effets néfastes de la déforestation de l'Amazonie sont considérablement plus percutants pour ses habitants (Foley *et coll.*, 2007 ; Rodrigues *et coll.*, 2009). Par ailleurs, si la plupart de la déforestation actuelle est attribuée à l'agriculture industrielle, les populations les plus vulnérables demeurent celles qui dépendent le plus des ressources locales pour leur subsistance (Cohenca, 2005). Cette réalité est d'autant plus troublante quand nous considérons les relations qui existent entre la santé de ces populations largement défavorisées et l'environnement (Foley *et coll.*, 2007). Par exemple, des effets neurologiques et cardiovasculaires issus d'une exposition chronique au méthylmercure ont été liés à la consommation de poissons principalement contaminés par l'érosion du mercure inorganique des sols soumis à l'agriculture sur brûlis (Dolbec *et coll.*, 2000 ; Fillion *et coll.*, 2006 ; Lebel *et coll.*, 1998 ; Lucotte *et coll.*, 2004). Les altérations écologiques associées à la déforestation ont aussi augmenté le risque de contamination de l'agent pathogène de la malaria dans la région amazonienne par le biais d'une augmentation des sites de reproduction de son vecteur, *Anopheles (Nyssorhynchus) darlingi* Root 1926 (Vittor *et coll.*, 2009). De plus, l'émergence et la réémergence de plusieurs viroses dues à des virus comme la fièvre jaune, le Mayaro et l'Oropouche ont aussi été principalement liées à la déforestation (Briceño-León, 2007).

Bien que la Trypanosomiase américaine soit principalement associée aux régions subtropicales de l'Amérique latine, les cas humains d'infections par *Trypanosoma (Schizotrypanum) cruzi* Chagas 1909 sont en hausse depuis les années 1970 en Amazonie brésilienne (Abad-Franch *et coll.*, 2009 ; Coura *et coll.*, 2002 ; Valente *et coll.*, 1999). Cette augmentation est attribuable à la déforestation récente du milieu rural qui accroît les risques de contact entre les humains, les animaux domestiques et les insectes vecteurs de l'agent pathogène de la Trypanosomiase américaine, les triatomes (Hemiptera : Triatominae) (Briceño-León, 2007 ; Coura *et coll.*, 1999 ; Coura *et coll.*, 2002 ; Sanchez-Martin *et coll.*, 2006 ; Valente *et coll.*, 1998 ; Vasconcelos *et coll.*, 2001). Sa relation étroite avec le changement drastique du paysage qui a lieu le long des fronts de colonisation amazoniens et la précarité des conditions de vie des petits agriculteurs exige une vigilance accrue en zone rurale (Briceño-León et Galván, 2007 ; Pinto *et coll.*, 2008).

L'exposition au parasite de la Trypanosomiase américaine se fait principalement par un contact cutané ou muqueux avec les excréments de plusieurs espèces de triatomes hématophages (Coura *et coll.*, 2002 ; Nóbrega *et coll.*, 2009). Malgré le fait qu'à ce jour aucune des espèces de Triatominae, les insectes vecteurs du parasite, n'a été rapportée comme colonisant les habitations en Amazonie brésilienne, les espèces du genre *Rhodnius* sont principalement associées à des palmiers en milieu forestier humide (Abad-Franch *et coll.*, 2005 ; Aguilar *et coll.*, 2007 ; Coura *et coll.*, 2002 ; Gaunt et Miles, 2000 ; Miles *et coll.*, 1983 ; Romaña *et coll.*, 1999). En fait, les caractéristiques structurales de certains palmiers, dont ceux du genre *Attalea,* sont particulièrement favorables à la colonisation par ces insectes (Abad-Franch *et coll.*, 2005 ; Naiff et Naiff, 1998 ; Romaña *et coll.*, 1999 ; Teixeira *et coll.*, 2001 ; Valente *et coll.*, 1999). De plus, ces palmiers sont fréquents près des habitations humaines où ils peuvent former des populations denses, car leur mode de germination cryptogé est extrêmement bien adaptée à l'agriculture sur brûlis (Jackson, 1974) et difficilement contrôlable par les habitants locaux non mécanisés (Anderson *et coll.*, 1991 ; Romaña *et coll.*, 1999). Ainsi, les grands palmiers arborescents du genre *Attalea* sont ciblés comme préoccupation majeure pour la santé des communautés amazoniennes vivant d'une agriculture de subsistance (Abad-Franch *et coll.*, 2009 ; Romaña *et coll.*, 1999).

La présente étude s'inscrit dans le programme « Poor Land Use, Poor Health » (PLUPH) au sein duquel un groupe de recherche international réalise des travaux portant principalement sur les risques à la santé humaine liés à la gestion inappropriée du territoire (PLUPH, 2010). Ce projet est la suite au projet canado-brésilien CARUSO responsable de la découverte d'une relation étroite entre la déforestation du milieu et l'exposition au mercure des populations riveraines d'un front de colonisation du Bas Tapajós (CARUSO, 2004 ; Lucotte *et coll.*, 2004). Le programme PLUPH cherche à renforcer les connaissances sur les conditions d'exposition au mercure et aux insectes vecteurs de *T. cruzi* responsable de la Trypanosomiase américaine afin de savoir s'il existe synergie ou antagonisme entre les deux problèmes chez les communautés d'agriculteurs de cette région. Simultanément, le projet explore l'impact qu'un changement dans le mode d'agriculture pourrait avoir sur ces menaces environnementales par l'entremise de projets pilotes en agroforesterie. Mis à part les nombreuses recherches dans le domaine des sciences naturelles, ce programme innove par son approche interdisciplinaire. Il cherche à intégrer les perspectives de santé, sociales, religieuses, économiques et politiques dans une vision holistique de la santé environnementale. Finalement, par l'entremise d'indicateurs générés par les recherches, ce projet proposera un modèle intégratif des relations entre la sensibilité de l'écosystème et la vulnérabilité des populations humaines. Ce modèle intégrateur facilitera la prise de décision par les organismes gouvernementaux responsables du développement et de la santé des populations du Bas Tapajós.

La région du Tapajós est un front de colonisation actif du Pará (Brésil), un des trois États amazoniens où environ 85 % de la déforestation de l'Amazonie a lieu (Margulis, 2004). Malgré que les communautés autochtones de la région ont dû s'adapter à plusieurs vagues migratoires, la dernière, déclenchée par le programme d'intégration nationale brésilien dans les années 1970, a créé une situation précaire dans laquelle les communautés demeurent particulièrement vulnérables à la dégradation environnementale qui y a lieu (Briceño-León et Galván, 2007 ; Farella, 2005 ; Fearnside, 1984). Même si ces communautés défavorisées d'un point de vue socioéconomique sont majoritairement favorables à la mécanisation du travail agricole dans l'espoir que ces technologies améliorent leurs conditions de vie, l'agriculture industrielle qui pénètre actuellement la région risque plutôt de stimuler leur déplacement vers des zones toujours inexploitées (Fearnside, 2002). Cette tendance est par ailleurs renforcée par l'installation d'un terminal portuaire de soja Cargill à Santarém ainsi que du projet d'asphaltage de l'autoroute BR-163 entre Santarém et Cuiabá dans le cadre du programme national « *Avança Brasil* ». Cette pression sur la forêt et ses habitants perpétue à la fois l'apport du mercure dans le milieu aquatique et le risque d'une augmentation de la prévalence de la Trypanosomiase américaine. Effectivement, le développement durable de la région, essentiel à la protection des écosystèmes et des populations vulnérables qu'elle abrite, exige un changement de cap.

Si l'objectif premier du présent travail est de fournir des indicateurs édaphiques de la distribution hétérogène des palmiers, biotopes principaux des triatomes, pour la prédiction de l'aléa dans la région, l'étude s'est déroulée en association étroite avec les objectifs des projets des autres étudiants du programme PLUPH. En fait, les travaux de terrain de recherche ont débuté après un séminaire d'intégration à Santarém pendant une semaine en septembre 2008. Une quinzaine d'étudiants brésiliens, canadiens et suisse ont entamé leurs contributions respectives à ce projet d'envergure durant cette période d'environ 40 jours. La campagne de récolte de données de la présente recherche a été coordonnée avec celles de deux autres étudiants s'intéressant à la modélisation de l'érosion du sol

(Durante Tagliari, 2009) et le déplacement du mercure inorganique vers le milieu aquatique (non publié). D'autres étudiants du projet compléteront cette étude avec des données phytosociologiques sur les palmiers, l'effet de la luminosité sur le développement des espèces et les taux d'infestations par les triatomes.

Les objectifs spécifiques de cette recherche sont les suivants :

1. Identifier les espèces de palmiers du genre *Attalea* présent sur le territoire des quatre communautés de São Tomé, Demanda, Agrovila et Nova Estrela (Bas Tapajós, Pará, Brésil).

2. Déterminer comment les propriétés édaphiques du sol peuvent expliquer la distribution des espèces du genre *Attalea* dans la zone d'étude.

3. Proposer des indicateurs édaphiques de la présence des espèces de palmiers du genre *Attalea* qui serviront à prédire les zones à risque dans le cas de la Trypanosomiase américaine dans le Bas Tapajós.

4. Identifier comment les cations majeurs échangeables, principaux déterminants de la variation dans la distribution spatiale des espèces d'*Attalea* observés, sont associés aux propriétés physicochimiques du sol.

Le mémoire est présenté sous la forme de deux chapitres rédigés en articles scientifiques pour publication dans les revues *Journal of Tropical Ecology* et *Geoderma*. L'auteur de ce mémoire a conçu la recherche et a effectué l'échantillonnage, les analyses et la rédaction des textes. Toutefois, les coauteurs ont joué un rôle d'appui dans les diverses phases de réalisation des chapitres scientifiques. Le premier chapitre s'intitule *Effects of edaphic factors on the distribution of palms of the Attalea (Palmae) genus in the Lower Tapajós River Basin (Brazilian Amazon),* et traite principalement des trois premiers objectifs. Le deuxième chapitre, *Distribution of the exchangeable major cations in upland soils of the Lower Tapajós River Basin (Brazilian Amazon),* présente les relations existantes entre les teneurs en cations et les facteurs du sol de la région. Ce chapitre se limite au quatrième objectif et propose à la fois des pistes méthodologiques innovatrices pour une future recherche en écologie tropicale.

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CHAPITRE I

L'IMPACT DES PROPRIÉTÉS ÉDAPHIQUES SUR LA DISTRIBUTION DES PALMIERS DU GENRE *ATTALEA* (PALMAE) DANS LA RÉGION DU BAS TAPAJÓS (AMAZONIE BRÉSILIENNE)

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Résumé

Les grands palmiers arborescents du genre *Attalea* (Palmae) dont la fréquence est stimulée par l'agriculture sur brûlis sont des indicateurs importants de l'aléa de la Trypanosomiase américaine car ses vecteurs, les triatomes (Hemiptera : Triatominae), nichent principalement dans la matière organique qui s'accumule dans leurs couronnes. Quoique l'architecture de diverses espèces de palmiers ait été associée à des taux d'infestation importants de triatomes, l'écologie des espèces du genre *Attalea* est peu étudiée. Notre étude a comme objectif de déterminer comment la distribution des espèces du genre *Attalea* est liée aux propriétés édaphiques du sol d'un front de colonisation de la région du Bas Tapajós, dans le bassin amazonien. Nous avons identifié 3 espèces d'*Attalea* et un quatrième palmier considéré comme pouvant être une variété acaule d'*Attalea speciosa* (*A.* sp. nain). Les palmiers et le sol ont été échantillonnés sur 43 parcelles divisés sur 14 transects et répartis dans 4 communautés d'agriculteurs de subsistance dans les environs du Lac Araipa. Nos résultats montrent qu'*A. phalerata* préfère des sols aux teneurs en cations disponibles relativement plus élevées et moins acides. *Attalea* maripa est inversement distribué à *A. phalerata* et se limite aux sols les plus pauvres en cations disponibles et plus acides. Même si la distribution de *A. speciosa* n'a pas varié fortement avec les propriétés édaphiques mesurées, nos données indiquent que *A.* sp. nain serait associée à des sols aux teneurs plus élevées en chlore ainsi qu'à des caractéristiques minéralogiques spécifiques des Alfisols. Des mécanismes physiologiques sont proposés pour expliquer la distribution hétérogène de ces espèces en fonction des variations édaphiques. Bien que des recherches supplémentaires soient nécessaires afin de régionaliser les résultats, nous proposons des indicateurs édaphiques de la distribution des palmiers du genre *Attalea* pouvant servir à cartographier l'aléa de la Trypanosomiase américaine dans le Bas Tapajós.

Mots-Clés : *Attalea,* palmier, distribution, sol, cation, pH, minéral, Triatominae, Trypanosomiase américaine, aléa

CHAPTER I

EFFECTS OF EDAPHIC FACTORS ON THE DISTRIBUTION OF PALMS OF THE *ATTALEA* (PALMAE) GENUS IN THE LOWER TAPAJÓS RIVER BASIN (BRASILIAN AMAZON)

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Abstract

Large arborescent palms of the genus *Attalea* (Palmae) suited to slash and burn agriculture are important indicators of the risk of contracting the American Trypanosomiasis because its vectors, triatomine insects (Hemiptera: Triatominae), nest primarily in the organic matter that accumulates in their crowns. While the architecture of several palm species has been linked to important triatomine infestation rates, the ecology of *Attalea* sp. remains poorly understood. Our study aims at determining how the distribution of *Attalea* sp. is related to edaphic soil properties in the Lower Tapajós River region, Amazon Basin. We identified 3 *Attalea* species and a fourth palm considered as an acaulescent variety of *Attalea speciosa* (*A*. sp. dwarf). Palms and soils were sampled from 43 lots along 14 transects distributed throughout 4 subsistence farming communities near Lake Araipa. Our results showed that *A. phalerata* prefers soils with a relatively higher content of available cations and of lower acidity. *Attalea maripa* is inversely distributed to *A. phalerata* and is limited to soils poorest in available cations and of higher acidity. While the distribution of *A. speciosa* is not strongly related to the measured edaphic variables, evidence suggests that *A*. sp. dwarf is associated to higher levels of soil chlorine content and mineralogical features specific to Alfisols. Physiological mechanisms are proposed to explain how these related palms species have developed diverging responses to edaphic variations. While more research is required to extend our findings to the region, we propose simple edaphic *Attalea* palm species distribution indicators that may be useful to the mapping of the American Trypanosomiasis transmission risk along the Lower Tapajós River.

Keywords: *Attalea* palm species, distribution, soil, cation, pH, mineral, Triatominae, American Trypanosomiasis, risk

1.1 Introduction

The American Trypanosomiasis (Chagas disease) is a chronic parasitic disease caused by *Trypanosoma* (*Schizotrypanum*) *cruzi* Chagas 1909 (Chagas, 1909) that currently affects between 8 and 10 million Latin Americans (Miles *et al.*, 1983 ; Schofield *et al.*, 2006 ; Whitlaw and Chaniotis, 1978 ; World Health Organization, 2010). Human populations are mainly exposed to the parasite via bloodsucking triatomine insects (Hemiptera: Triatominae). Even though recent prevention measures based on the elimination of domiciliated triatomine species from households have managed to curb the disease's global incidence by 73% in South America in the last 10-15 years, cases of *T. cruzi* infection have been increasing since the 1970's in the Amazon basin, where it is now considered endemic (Abad-Franch *et al.*, 2009 ; Pinto *et al.*, 2008 ; World Health Organization, 2010). This localized increase has been attributed to drastic environmental changes induced by the relatively recent human activity that has occurred in the region (Briceño-León, 2007 ; Romaña, 2007 ; Romaña *et al.*, 2003).

While Amazonian triatomines have not been reported as domiciliated in households, several studies have showed that palm trees have become the principal ecotope of several sylvatic species (Diotaiuti and Dias, 1984 ; Miles *et al.*, 1983 ; Romaña *et al.*, 1999 ; Teixeira *et al.*, 2001 ; Whitlaw and Chaniotis, 1978). Triatomine infestation is particularly favored by palm species that have specific architectural features (stem diameter, length and crown radius) that promote the accumulation of large quantities of decaying organic matter in their crowns (Abad-Franch *et al.*, 2005 ; Romaña *et al.*, 1999). This micro-environment provides these nest-dwelling insects with the buffered microclimate and constant food supply they require to survive in cleared forested areas. Large arborescent palms of the *Attalea* genus are specifically targeted as a health concern in subsistence farming communities of the humid tropics of the Americas (Abad-Franch *et al.*, 2009 ; Romaña, 2007 ; Romaña *et al.*, 1999 ; Whitlaw and Chaniotis, 1978). They are common near human settlements where they can freely form dense stands because their cryptogeal germination mode is extremely well suited to current slash and burn practices while rendering them practically immune to local extirpation efforts (Anderson *et al.*, 1991 ; Mitja and Ferraz, 2001). Abad-Franch *et al.* (2009) have reviewed numerous studies that confirm the presence of Triatominae in several *Attalea* species within the Brazilian Amazon.

While extensive research has been conducted on the biological and ecological determinants of triatomine infestation, relatively little has been done on the ecology of the palms on which these sylvatic species depend. However, a better understanding of palms of the *Attalea* genus is critical to the development of eco-epidemiological risk indicators for the American Trypanosomiasis (Abad-Franch *et al.*, 2009). Furthermore, by charting the distribution of these palms on a map, we can understand the biogeography of the risk of contracting this disease (Romaña, 2007). Nevertheless, because the morphological differences between palms of the *Attalea* genus may imply different infestation rates (Romaña *et al.*, 1999), this research must be conducted at the species level (Henderson *et al.*, 1995 ; Pintaud, 2008).

Several tropical forest studies in Amazonian uplands (*terra firme*) have shown that plant species are distributed heterogeneously along edaphic gradients (Jirka *et al.*, 2007 ; Sollins, 1998 ; Svenning *et al.*, 2004). However, species specific palm studies have mostly associated their distributions to broadly defined climatic and topographic categories (Montufar and Pintaud, 2006 ; Salm *et al.*, 2007 ; Vormisto *et al.*, 2004b) or finer scale forest dynamics (Cintra *et al.*, 2005 ; Fragoso, 1997) that have little relevance to the heavily modified landscapes that characterize modern human settlements in the Amazon. Of these, fewer still have determined the effects of soil properties on the distribution of palm species (Clark *et al.*, 1995 ; Svenning, 1999 ; Vormisto, 2002). While the existence of a strong relationship between soil properties and palm species composition at the mesoscale (10-100 km^2) is now well accepted (Costa *et al.*, 2009), a robust model for the species-level distribution of large arborescent palms is still needed.

The following study aims at determining how the distribution of palm species of the genus *Attalea* is related to edaphic soil properties in subsistence farming communities of the Lower Tapajós region within the Brazilian Amazon. This active colonization front is located in the state of Pará, one of three Amazonian states where approximately 85% of the deforestation in the Amazon has taken place (Farella *et al.*, 2007). Furthermore, the majority (68.3%) of the 442 autochthonous Chagas infection cases reported in the Brazilian Amazon between 1968 and 2005 have occurred in this state (Valente *et al.*, 2006). The massive colonization of the area by subsistence farmers following the implementation of Brazil's National Integration Program in the 1970s has created a precarious situation in which these disadvantaged communities are particularly vulnerable to environmental degradation (Briceño-León and Galván, 2007 ; Fearnside, 1984a).

1.2 Study area and methods

1.2.1 Study area

The present study was carried out in the Lower Tapajós region (Pará, Brazil), approximately 55 km downstream from Itaituba (fig. 1.1). The specific study area was chosen in accordance with the research goals of a larger interdisciplinary study on health risks related to poor land use (PLUPH, 2010). It was located in four neighboring communities (São Tomé, Demanda, Agrovila and Nova Estrela) along the Tapajós River, districts of Aveiro and Rurópolis (fig. 1.2).

The predominant soil types of the area are Oxisols and Ultisols (according to the USDA system) (Soil Survey Division Staff, 1999) or Latossolos Amarelos and Argissolos Velmelho-Amarelos (according to the Brazilian classification system) (EMBRAPA, 2007). These soils developed from continental sediments as a result of related geochemical processes on the Alter-do-Chão geological formation (Bravard and Righi, 1989). These highly weathered soils are generally acidic, have low cation exchange capacities and relatively high concentrations of available aluminum (Lucas *et al.*, 1996). Alfisols or Nitossolos according to the U.S. or Brazilian classifications, derived from relatively recent igneous intrusions of diabasic rock are also known to occur in the region and are significantly richer than both Oxisols and Ultisols (Fearnside, 1984b ; Jordan, 1985). While we interpreted the elevation range of the specific study area from a SRTM DEM as ranging from 0 to 125 m (Consortium for Spatial Information, 2010), the terrain consists of a complex series of highly dissected valleys with notable soil variations. The climate is hot and humid with an annual rainfall varying between 1800 and 2200 mm and interrupted by a drier season of approximately 3 months (Grupo de Trabalho Interministerial, 2006). The primary upland (*terra firme*) vegetation is classified as sub-montane open forest (*floresta ombrófila aberta submontana*) (EMBRAPA, 2007) with at least one *Attalea* palm species present in any given area (Pires and Prance, 1985). However, slash and burn agriculture, cattle herding on pastures and young secondary fallow-forests now dominate the landscape near human settlements.

1.2.2 Sampling sites

The study area was prospected prior to data collection to construct a non-random sampling design that would be representative of the distribution patterns of palms species prone to triatomine infestation (app. A) (Abad-Franch *et al.*, 2005 ; Romaña *et al.*, 1999). Sampling site selection based on observed floristic variations insures that the majority of the variability is sampled (Richards, 1996). Fourteen upland transects were identified on slopes along surface drainage flow axes (fig. 1.2) to accommodate the requirements of parallel soil erosion (Durante Tagliari, 2009) and mercury displacement studies (unpublished). The majority of transects (13/14) were placed on agricultural land to facilitate access and correspond to human settlements. The length of each transect (median 270.8 m, min.: 90.2 m, max.: 629.3 m) varied according to the length of the slope and accessibility. Each transect consisted of three lots (75 m by 25 m, *n=43*) (except for #5 with 4 lots) whose longer sides were oriented perpendicular to the site's surface drainage flow. The central lot of each transect was placed approximately halfway between the other two. Care was taken to insure that slope, vegetation cover, soil color and texture were constant within each lot. The location of each lot and its elevation were georeferenced. In all cases, permission to work on each site was solicited from landowners before sampling.

1.2.3 Sampling and analyses

1.2.3.1 Palm community survey

Palms species occurring in the study area were identified during the initial survey of the area. Only species of the *Attalea* genus were retained for further analysis because they are considered strong indicators of the presence of triatomines (Abad-Franch *et al.*, 2005 ; Romaña *et al.*, 1999). Palm species were identified according to Henderson *et al.* (1995) and *Attalea* specimens were confirmed according to a more recent taxonomic treatment by Glassman (1999). Staminate inflorescences from several *Attalea* specimens were observed under a magnifying glass to support field identification of this complex group. Voucher fruit and flower specimens were placed in the herbarium of the Universidade Federal do Pará (UFPA) in Santarém, Pará.

1.2.3.2 Topography

The mean of three elevation recordings per lot was calculated. Slope was also estimated using three categories (near plateau, sloping, steep). Lots showing signs of seasonal flooding along streams (soil and vegetation changes at the bottom of a slope) were recorded (constant drainage or periodic water saturation) as a rough indicator of soil water potential (Costa *et al.*, 2009). While raw elevation values were used as a continuous environmental variable, slope and soil water potential were binary-coded as dummy variables (Legendre and Legendre, 1998).

1.2.3.3 Soil properties

Several studies have shown that slash and burn agriculture increases the density of *Attalea* spp. palm stands by eliminating most of the species with which they compete with for light (Anderson *et al.*, 1991 ; Barot *et al.*, 2005 ; Salm, 2005). However, the low seed dispersal capacity and the persistence of *Attalea* spp. in modified landscapes indicates that their presence and absence in an area is more related to the pre-anthropic state of the soil than to the relatively recent chemical changes induced by slash and burn agriculture (Anderson *et al.*, 1991 ; Fragoso, 1997 ; Sávio Pimentel and Tabarelli, 2004). Furthermore, unless purposefully eradicated via land grading or herbicides, it has been estimated that it might take at least 50 years of annual cutting and burning before a stand of *Attalea speciosa* is decimated (Anderson *et al.*, 1991 ; May *et al.*, 1985b). The relatively recent colonization of our study area precludes this possibility (Farella *et al.*, 2007). Therefore, we assume that any relationship between the presence and absence of *Attalea* spp. and soil properties should be strongest with variables that indicate pre-anthropic conditions. We controlled for the effects of human intervention by sampling at a depth of 50-55 cm because soil chemical variables were found to vary less there than nearer to the surface as a result of slash and burn agriculture (Alegre *et al.*, 1988 ; Farella *et al.*, 2007 ; Makeschin *et al.*, 2008). Furthermore, because most soil properties at the 50-55 cm depth correlate with those near the surface in primary forests, they are indicative of the edaphic variations that existed near the surface prior to human intervention (Béliveau, 2007 ; Silver *et al.*, 2000). Nevertheless, thorough studies of the African oil palm *Elaeis guineensis* (Binkley and Vitousek, 1989), the observation of *Attalea cohune* stump holes of between 0.5-1.0 m (Furley, 1975) and *A. speciosa*'s reputedly deep and extensive root system (Balick and Pinheiro, 1993) all suggest that soil properties at the 50-55 cm depth have an important effect on the presence and growth of large arborescent palms (Fisher *et al.*, 2000).

We collected three soil samples per lot from a depth of 50-55 cm, 25 m apart from each other, along a line perpendicular to the transect slope. Areas with abnormal characteristics (ex: decomposing trees, manure, erosion) were screened before sampling. Duplicates at each sample point were extracted from a 50 cm deep hole using a 100 cm^3 stainless steel percussion sampler. The first duplicate was oven-dried at 45°C and then weighted while the second was frozen to interrupt microbial activity.

Sample analyses were performed at the Biodôme of Montreal as well as the GÉOTOP, the Earth and atmospheric sciences and the Geography departments of the Université du Québec à Montréal (Canada). Depending on the soil variable, samples of a same lot were pooled either before or after laboratory analysis to overcome spatial variability (Sollins, 1998). Detailed laboratory methods for most variables are described in chapter 2. Only those specific to the present study are described herein.

Oven-dried samples were lightly crushed and sieved at 2mm. The weight of the >2mm fraction of each sample was measured and used to calculate the average percentage of gravel, herein referred to as stoniness (dry weight of >2mm fraction/dry weight of sample) (Peverill *et al.*, 1999). The pH of each sample was determined with a glass electrode at a soil to nanopure water solution ratio of 1:2. Because pH is the product of a negative logarithmic transformation of H^+ ion concentration conventionally applied without an adequate statistical basis, results were back transformed (10^{-pH}) to H^+ values for statistical analysis (Murphy, 1982). Reported mean pH values (and corresponding asymmetric confidence limits) for each lot were calculated using the following equation: -log (mean $[H^+]$) to avoid the bias introduced by standard mean pH calculations. The analysis of Mn^{2+}, Fe^{2+}, Al^{3+} was performed idem as for Ca^{2+}, Mg^{2+} and K^+ (chap. 2). The following detection limits were used: Mn^{2+}= 0.046, Fe^{2+}= 0.174 mg/l, Al^{3+}=1.24 mg/l. The sequential extraction of four forms of phosphorus: P_{ex} (exchangeable), P_{cdb}, P_{apa} (apatite) and P_{org} (organic), was performed on frozen samples alongside iron and aluminum oxyhydroxide analyses according to an analytical procedure developed by Lucotte and d'Anglejan (1985). Phosphorus fractions were measured by colorimetry with a Bran and Luebbe Traacs 800 auto-analyzer.

The following quantitative soil properties were retained for data analysis: density, redness rating (Torrent *et al.*, 1980), soil texture (0-2 μm, 2-50 μm, 0.05-2 mm), stoniness (Fisher *et al.*, 2000), available H^+ ions (pH), total available base cations (Ca^{2+}, Mg^{2+}, K^+), Al^{3+}, total C, total N, C:N, Fe & Al oxyhydroxides (referred to in this article as Fe_{cdb} and Al_{cdb}) and four forms of phosphorus (P_{ex}, P_{cdb}, P_{apa}, P_{org}). Both the proportion of eight clay minerals (illite, kaolinite, quartz, feldspar-K, plagioclase, calcite, dolomite, hematite) and the concentrations of several elements (in total form) essential to plant growth (C_{tf}, Cl_{tf}, Cu_{tf}, Fe_{tf}, K_{tf}, Mg_{tf}, Mn_{tf}, Na_{tf}, P_{tf}, S_{tf}, Si_{tf} and Zn_{tf}) derived from the fine soil fraction (0-20 μm) were analyzed as well.

1.2.3.4 Human activity

An interview was conducted with each of the farmers responsible for the plots on which the sampling transects were placed to confirm the assumption that human activity does not alter the presence or absence of *Attalea* spp. at our sampling scale. We gathered information concerning land use history and palm tree management in order to verify if any changes in the presence or absence of *Attalea* spp. had occurred since initial land clearing. All interviews were conducted with the aid of a local field assistant to overcome language barriers. The questionnaire used is presented in appendix C.

Additionally, thirty farmers of the study area were interviewed to provide us with a broader understanding of local palm tree management practices (Guentert, 2010).

1.2.4 Data analysis

According to niche theory, species are predicted to have unimodal distributions along environmental gradients (Legendre and Legendre, 1998). Canonical correspondence analysis (CCA) was chosen because we are interested in testing in what way species presence-absence data is related to large ecological gradients that frequently generate the absence of species (app. D). Statistical analysis was performed using JMP 7.0.1 (SAS Institute inc.) and Canoco for Windows 4.54 (Microcomputer Power).

Considering the misleading effects of a low sample to environmental variables ratio (43:45) in CCA, variables were split into two environmental matrices (henceforth labeled EM1 and EM2) (McCune, 1997). EM1 was composed of commonly sampled edaphic properties (tab. 1.2) while EM2 included soil variables that are novel or rarely sampled in tropical plant ecology studies (Sollins, 1998). Environmental variables were centered and standardized by CANOCO before performing multivariate analyses. Variance partitioning allowed us to determine if EM2 variables provided an alternative understanding of the species composition (Leps and Smilauer, 2003).

A detrended correspondence analysis (DCA) was first computed for both EM1 and EM2. The DCA was detrended by segments and environmental variables were projected onto the ordination. Constrained ordinations (CCA) where then performed with a bi-plot scaling focused on inter-species distances (Leps and Smilauer, 2003). The significance of all canonical axes was tested using a Monte-Carlo permutation test under the reduced model ($\alpha=0.001$). Considering the exploratory nature of our study, stepwise CCAs were then performed on each environmental matrix to identify variables that best relate to species composition ($\alpha=0.05$ was used as the cut-off point) (Palmer, 1993). A species-environment model for each environmental matrix was built from these and used to test variance partitioning.

Group differences for environmental variables were tested using nonparametric statistics because most data series did not meet the requirements for normality and homoscedasticity even when transformed for nonlinearity (Scherrer, 1984). Differences in the distribution of samples grouped according to the presence and absence of a species were tested using the Wilcoxon-Man-Whitney test. Environmental variables that showed heterogeneous sample distributions for the presence of all studied species (Kruskal-Wallis test) were further tested to determine which groups differed significantly using the Noether test ($\alpha' = 0.00417$). Finally, species pairs with significantly different distributions along a same environmental variable were analyzed using recursive partitioning to determine optimal splitting values. The relative accuracy of variables as discriminatory indicators was determined by calculating the percentage of misplaced samples that occurred during recursive partitioning using the following equation:

$$\%\ \text{misplaced samples} = \frac{(n \text{ of misplaced lots} - n \text{ of lots harboring both species}) \times 100}{n \text{ of lots harboring either species}}$$

While Bonferroni corrections were not performed in order to prevent a needless increase of Type II error, the Kruskal-Wallis test was used to screen for important variables prior to multiple group comparison thereby reducing the risk of a Type I error in subsequent tests (Cabin and Mitchell, 2000). Similarly, we heed to Type I errors during the comparison of environmental variables for the presence and absence of species by considering the relative strength (significant; 0.05, highly significant; 0.01 and very highly significant; 0.001) of the resulting p-values (Gotelli and Ellison, 2004). Under this scenario, very highly significant differences are considered robust.

1.3 Results

1.3.1 Palm species

The following palm species were observed in the study area (common names are given in brackets): *Attalea maripa* (Aubl.) Mart. 1845 (inajá), *A. speciosa* Mart. 1826 (babaçu), *A. phalerata* Mart. ex Spreng. 1825 (urucuri), *Oenocarpus distichus* Martius 1823 (bacaba), *Mauritia flexuosa* L. f. 1782 (buriti), *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. 1824 (macaúba) and *Astrocaryum vulgare* Mart. 1824 (tucumã). Only the first three observed species were retained for analysis (see app. B for pictures). Furthermore, populations of a sexually mature acaulescent *Attalea* (*A.* sp. dwarf) were observed in São Tomé and Nova Estrela (common names include coquinho, coco baixinho, coco dende and pindoba). *A*ttalea sp. dwarf has a morphology and growth pattern that corresponds well with those of *A. speciosa* (Glassman, 1999 ; Henderson *et al.*, 1995) while being particularly concurrent with Markley's (1971) observations of the species within the Tapajós region and those of Mitja and Ferraz (2001) in southern Pará. *A*ttalea sp. dwarf has an identical leaf (leaflets regularly arranged and spreading in the same plane) and flower (inflorescence born among the leaves on relatively long peduncles sometimes becoming pendulous in fruit, staminate flowers with 2-3 flattened incurved petals (one petal always larger than the other) and 24-28 tightly coiled and twisted stamens) morphology as *A. speciosa* but becomes reproductively mature without the prior development of an aboveground stem. The stem of *A.* sp. dwarf only rarely develops, attaining at most 2 meters in height, while both brachi and fruit (1-3 seeded, ellipsoid-oblong sometimes pointed, 6-9 cm long and 3-4 cm in diameter) were smaller than those of *A. speciosa* specimens within the study area. The possibility of a misidentification with other stemless *Attalea* species such as *Attalea eichleri* (Drude) Henderson, Galeano, and Bernal 1995, *Attalea attaleoides* (Barb. Rodr.) Wess.Boer 1965 and *Attalea spectabilis* Mart. 1826 or published hybrids such as *Orbignya* × *teixeirana* (Bondar) Balick, Pinheiro and Anderson 1987 (between *A. speciosa* and *A. eichleri*) and *Attalea dahlgreniana* (Bondar) Henderson, Galeano, and Bernal 1995 (between *A. speciosa* and *A. maripa*) was excluded following a detailed examination of staminate flowers (Balick *et al.*, 1987 ; Glassman, 1978, 1999 ; Henderson *et al.*, 1995 ; Pintaud, 2008). In some areas, both *A. speciosa* and *A.* sp. dwarf occurred simultaneously but they were more commonly observed as distinct populations. In some instances, it was impossible to differentiate between *A. speciosa* and *A.* sp. dwarf in mixed stands (probably as a result of intergradations), while in others, morphological differences were more pronounced between them. Finally, reproductively mature *A.* sp. dwarf stands were observed in both forests and open areas. While the smaller crown size and height of *A.* sp. dwarf may bestow it with a lower or null risk of triatomine infestation (Abad-Franch *et al.*, 2005), it was included in our study to provide a better understanding of the environmental conditions that regulate this species' risk of infestation.

At least one *Attalea* species was present at any given area regardless of elevation, slope and land use. *Attalea maripa* was the dominant palm species (34/43 of surveyed lots) and was generally absent only where *A. phalerata* was present (9/10 lots) (fig. 1.2 and app. A). Alternatively, *A. phalerata* and both *A. speciosa* varieties were distributed in stands whose limits were clearly visible in the landscape. While *A. maripa* was frequently the only species present in a given area, *A. phalerata* was frequently observed alongside other *Attalea* species. Whenever *A. speciosa* was present, it always cohabited with either *A. maripa* or *A. phalerata*.

1.3.2 Influence of human activity on palm species distribution

Most farmers (12/14) could reliably describe the land use history of their lots. They cleared their lots a median of 16.5 years prior to sampling. One half of transects were placed in agricultural lots first cleared 20 or more years ago and one was placed in a mature forest. Most farmers (11/12) had cultivated between one and three food crop cycles before seeding permanent grass pastures for cattle herding. Pastures had been sown for a median of 7.3 years (3 to 17 years of age).

The presence of *Attalea* palms is generally considered a nuisance to both food crops and pastures. Farmers mostly attributed yield loss to the shading that these palms produced while others believed that *Attalea* sp. dry-up and compact the soil. Several farmers considered that *A. maripa* is particularly problematic with regards to the latter. While all farmers manage palm densities in their lots, practices differ widely. Mature palms are often felled with an ax or a chainsaw before burning. However, *A. speciosa* palms are sometimes sparred because colonists from Maranhão occasionally harvest their fruits. Otherwise, only the leaves of these large palms are of notable use for the building of roofs and shelters (app. B). Some farmers cut the fronds of stemless or short *Attalea* palms after a burn to reduce crop shading even though they understand that these will grow back unless their stems are severed. Furthermore, those that resort to felling mature *Attalea* palms only cut a proportion of the standing specimens because their highly fibrous stems are both difficult to sever and can easily damage chainsaw blades. Only four farmers whose plots we sampled considered that palm densities had diminished since the initial clearing while the majority (8/13) noticed that populations had actually increased. Farmers never manage to extirpate a species or a variety from their plots and no one observed the establishment of a new species since initial land clearing.

1.3.3 Palm community distribution patterns

The summary of DCA and CCA for EM1 and EM2 are presented in table 1.1. The *F* ratio is much higher for the first axes of each matrix than trace (higher) axes indicating that they explain most of the species composition data. The variance explained by all the significant environmental axes (CCA) is slightly less or even more than that expressed by the respective species composition axes (DCA) implying that the measured environmental variables do effectively explain species composition.

The marginal effects of environmental variables under CCA show that several of them are correlated (tab. 1.2). A correlation between two or more variables is probable when their λ 1 values are similar. Correlations can be corroborated with the Spearman ρ correlation matrix (tab. 1.3). Several of these correlations are to be expected due to compositional (e.g.: cations and Ca^{2+}) and causal (e.g.: cations and pH, sand and density) relationships. Stepwise selection of variables reduced explanatory variables to 3 (cations, pH, density) for EM1 and to 7 (Zn_{tf}, Ca_{tf}, Fe_{cdb}, Cl_{tf}, Fe_{tf}, Na_{tf}, Mg_{tf}) for EM2 ($p<0,05$). The ordination diagram illustrates the same species composition gradients as identified during DCA and the relationship of selected environmental variables to them (fig. 1.3a). The length of an environmental variable's arrow is proportional to the strength of its correlation to the axes. A longer arrow therefore implies a stronger influence on species composition. Two major environmental gradients can be distinguished along the plotted axes. Cations as well as corresponding soil pH and Ca_{tf} content primarily differentiate the three species but more specifically *A. maripa* and *A. phalerata*. Zn_{tf} follows the same trend. Alternatively, several essential soil nutrients in total form and Fe_{cdb} differentiate *A. speciosa* and *A.* sp. dwarf and then again, but only to a lesser extent, *A. maripa* and *A. phalerata*. Redundant environmental variables removed by stepwise selection that had significant marginal effects and/or were correlated ($r_S \geq 0.600$, $p<0.001$) to at least one of the retained variables are presented with non-bold row headings on the correlation matrix (tab. 1.3).

The CCA of the ten stepwise selected variables explains 85.3% of the total species data variability. The three canonical axes explain respectively 40.2%, 15.8% and 12,6% of the variance. When Mg_{tf}, Fe_{tf} and Ca_{tf} (collinear with Na_{tf}, Fe_{cdb} and cation content respectively) were removed to lower inflation factors below 5, 74.5% of the total species variability could still be explained by the remaining variables. These results testify that the chosen combination of environmental variables is sufficient to explain most of the species composition. The majority of the variance is expressed by the first canonical axis and a considerable amount of expected noise remains unexplained. A variance partition analysis showed that most (50.3%) of the species data variability could be explained by variables from either EM1 or EM2. Then again, each matrix explained a considerable amount of variability not accounted for by the other (8.4% and 26.6% respectively).

As the selection of variables to be removed during the CCA automatic selection process is somewhat attributable to chance, the marginal effects of the removed environmental values were examined in order to consider their usefulness as explanatory variables (Leps and Smilauer, 2003). Seven environmental variables (P_{ex}, kaolinite, quartz, silt, plagioclase, feldspar-K and Cr_{tf}) with relatively high marginal effects (0.09-0.15) were automatically removed during stepwise selection even though they did not correlate well ($r_S<0.600$) with any of the selected variables. While these variables cannot be used interchangeably with selected variables in our model for lack of correlation, they were used to build an alternative one. Environmental variables of the alternative model are passively projected onto the ordination of the main model (fig. 1.3b). A CCA revealed that the alternative model explained

55.0% of the total species composition variability (eigenvalues: 0.306, 0.173, 0.071). Most of the variability was explained by the first axis (24.6%) while 13.9% was explained by the second. The first axis is highly significant (F-ratio: 11.428, *p*=0.006) while the second one is significant (F-ratio: 7.895, *p*=0.012). With the exception of a strong inverse correlation between kaolinite and quartz (r_S=-0.976, *p*=0.001), the seven variables of the alternative model are not correlated with each other.

The median values as well as results from the Wilcoxon-Mann-Whitney test of differences of the most relevant environmental variables according to the presence and absence of each species are presented in appendix D. The layout of significant results among species corresponds well with the major trends highlighted by the CCA ordination diagram, confirming that stepwise selection identified the most appropriate environmental variables.

Thirteen environmental variables were detected as significantly differentiating the distributions of at least one species. These variables include all those discriminating very highly significantly between the presence and absence of *A. maripa* and *A. phalerata* (app. D) as well as Cl_{tf}, C:N, Fe_{cdb} and P_{cdb}. Complementary Noether tests identified which species differed significantly from each other for each of these variables (fig. 1.4a-m). A species' distribution was in no case distinct from all others. *Attalea maripa* was generally associated to *A. speciosa* while *A. phalerata* was to *A.* sp. dwarf but these two pairs did not significantly differ from each other. *Attalea speciosa* and *A.* sp. dwarf were only significantly segregated along a Cl_{tf} gradient.

Optimal splitting values for environmental variables discriminating between *A. maripa* and *A. phalerata* populations are presented in table 1.4. *Attalea speciosa* and *A.* sp. dwarf are best discriminated at a Cl_{tf} splitting value of 80 ppm (with 15.0 % misplaced samples).

1.4 Discussion

1.4.1 Morphological plasticity of *Attalea speciosa*

The identification of an acaulescent variety of *A. speciosa* (*A.* sp. dwarf) (App. B.10-12) in our study area coincides with Anderson and Balick's (1988) observations of an exceptionally high degree of morphological variability within this species. This variability is best exemplified by *A. speciosa*'s high propensity to hybridize naturally with other *Attalea* species (Balick *et al.*, 1987 ; Henderson *et al.*, 1995). Markley (1971) anecdotally mentioned the existence of "semi-dwarfed" populations in his extensive report on the species but no other evidence supporting the existence of a stemless *A. speciosa* variety was found in the literature. In fact, earlier research suggests that even under optimal light conditions, *A. speciosa* does not normally attain sexual maturity before developing a 2 to 3 meter aboveground stem (Anderson, 1983 ; Anderson and Balick, 1988 ; Barot *et al.*, 2005). Anderson and Balick (1988) mostly attribute the high variability of this species to its occurrence under extremely variable ecological conditions over a wide geographic range. Indeed, this highly adaptive behavior with regards to edaphic conditions is well expressed in our study. When both *A. speciosa* and *A.* sp. dwarf are considered as a single species, the ecological amplitude of this species is much larger than those of the other *Attalea* spp. we sampled (fig. 1.4a-m). However, the morphological variations that we have observed cannot be the result of the vast geographic discrepancies that Anderson and Balick (1988) mention because both *A. speciosa* and *A.* sp dwarf occur simultaneously in our study area. Hybridization is not a plausible explanation either because *A.* sp. dwarf does not match published hybrid descriptions (Balick *et al.*, 1987 ; Glassman, 1999), was not consistently observed in mixed stands with at least two potential source species and had staminate inflorescences identical to those of *A. speciosa* (Anderson and Balick, 1988).

Rather, if *A.* sp. dwarf is a variety of *A. speciosa*, the high phenotypic plasticity of this species might be understood as a response to environmental variations. Nonetheless, while *Attalea* stem growth is highly dependant on light availability (Barot *et al.*, 2005), the consistent lack of tall *A.* sp. dwarf palms on sites that harbor tall specimens from other *Attalea* species indicates that this environmental variable cannot explain the morphological differences between *A. speciosa* and *A.* sp. dwarf. Furthermore, the occasional presence of mixed *A. speciosa* and *A.* sp. dwarf stands further suggests that these variations might be occurring at a scale smaller than our sampling units. Considering that we selected lot sites as to minimize internal slope, vegetation cover, soil color and texture variations, soil chemistry disparities offer the most plausible explication for this divergence (chap. 2).

1.4.2 The edaphic requirements of *Attalea* palms

1.4.2.1 *Attalea maripa* and *A. phalerata*

Stands of either *A. maripa* or *A. phalerata* were present at all locations throughout the study area. Our results showed that *A. phalerata* prefers soils with a relatively higher content of available cations and of higher pH (figs. 1.3a, 1.4a-c). *Attalea maripa* is inversely distributed to *A. phalerata* and is limited to soils poorest in available cations and of lower pH (figs. 1.3a, 1.4a-c). The relationship between these two variables is well understood and their fundamental role in tropical plant distribution has been shown elsewhere (Oliveira-Filho *et al.*, 1994). Ca_{tf} correlates very highly significantly with these edaphic variables and shows the same significant inverse distribution for both species (tab. 1.3a, fig. 1.4f). However, a parallel study showed that unlike magnesium and potassium, the soils of our study area do not contain significant quantities of non-exchangeable calcium (chap. 2). Therefore, Ca_{tf} is essentially solely composed of the exchangeable calcium fraction detected by our Ca^{2+} measurement. Consequently, whenever both variables are pertinent, only Ca^{2+} will be considered herein. Furthermore, while Zn_{tf} differentiates both species as strongly as Ca_{tf} (tab. 1.2), its role in species composition could not be inferred due to its high redundancy with cation content and pH, two variables whose ecological roles are well known.

Attalea phalerata's dependence on higher soil cation and higher pH can be understood as either a physiological predisposition for a higher nutrient demand or an intolerance of a high available aluminum concentration. These ions are highly correlated to pH and commonly related to plant species distribution patterns (Sollins, 1998). However, the consistent absence of *A. maripa* from those soils richest in cations suggests that its distribution cannot simply be explained by a tolerance for very acid soils. Calcifuge species also tend to have a low ability to solubilize and acquire phosphorus and iron in less acid soils (Lambers *et al.*, 2008). Additionally, P_{ex} and P_{cdb} values are significantly lower where *A. maripa* is absent (figs. 1.4i and k). Significantly higher levels of phosphorus adsorbing minerals such as Fe_{cdb} where *A. phalerata* grows might allow it to outcompete *A. maripa* in these cation rich environments by rapidly removing available P from the soil solution (Chacon *et al.*, 2006 ; Richards, 1996).

While both sand and clay variations were not related to the distributions of *A. maripa* and *A. phalerata*, silt content was significantly higher wherever the latter was present. However, while silt content was not correlated to the other measured variables, it was redundant in explaining species composition. Unfortunately, the role of silt content on plant growth has been poorly discussed in the literature (chap. 2). Nevertheless, several studies have reported the presence of *A. phalerata* in white water floodplains (*várzeas*) (Carim *et al.*, 2008 ; de Queiroz and Machado, 2007 ; Miranda *et al.*, 2008), known to be significantly richer in both silt and clay content than either upland (*terra firme*) or clear water flooded forests (*igapó*) (Haugaasen and Peres, 2006). These alluvial soils are also much richer in all major cations as they are replenished yearly via seasonal flooding. Coincidentally, studies also suggest that *A.*

speciosa and *A. maripa* are largely restricted to well drained upland ecosystems (Anderson *et al.*, 1991 ; Barot *et al.*, 2005 ; Scariot *et al.*, 1989 ; Svenning, 2001 ; Zent and Zent, 2004). Nevertheless, Fragoso (1997) mentioned that *A. maripa* stands were regularly found adjacent to wetlands in Maracá Island (Roraima, Brazil), while others also observed them on the large seasonally flooded island of Marajó (80 kilometers downstream of Belém, Pará, Brazil) (Santos and Jardim, 2006 ; Valente *et al.*, 1998). This suggests that *A. maripa* may be more tolerant of shallow water tables than *A. speciosa*. In our study, sites harboring *A. phalerata* either showed signs of occasional flooding by streams or were relatively (when compared to other *Attalea* ssp.) close to large water bodies suggesting that *A. phalerata* might be specifically adapted to poorly drained environments. In as much, while *A. maripa* is capable of extending its distribution into flooded areas, it is probably more easily outcompeted by *A. phalerata* in these less acid environments because of the low phosphorus availability associated with the higher Fe_{cdb} levels present there (Chacon *et al.*, 2006 ; Richards, 1996). However, more research into the hydrological requirements of *Attalea* species in a greater range of soil conditions and in particular, those of clear water systems, is required to confirm this phenomenon. In any case, even though white water floodplains are zones of poor triatomine diversity (Abad-Franch *et al.*, 2009), they should not be considered free of large arborescent *Attalea* spp. or consequently, American Trypanosomiasis vectors (Pinto *et al.*, 2008 ; Valente *et al.*, 1998). Moreover, considering that *A. phalerata*, which appears to thrive in such environments, tends to grow leaving old leaf bases attached to its trunk, infestation rates for this species might actually be higher than those of smoother stemmed *Attalea* species of comparable height and crown size (Barrett, 1991).

1.4.2.2 *Attalea speciosa*

Assuming that *A.* sp. dwarf is a variety of *A. speciosa*, the fact that all environmental variables associated with *A.* sp. dwarf are not significant for *A. speciosa* shows that as a single species, the distribution of *A. speciosa* is not strongly influenced by edaphic soil properties. Unfortunately, other than an unsuccessful attempt at detecting phenological differences between *A. speciosa* populations growing on three different soil types (Araújo *et al.*, 1996), no studies of the physiological or morphological adaptability of natural stands of this species to edaphic variations have been published. Nevertheless, two notable studies relating the effects of fertilization on the germination and initial growth of *A. speciosa* support the relatively high physiological amplitude we have observed for this species in regards to the major soil nutrients (Anderson and Anderson, 1983 ; Lambers *et al.*, 2008 ; Pinheiro, 1997). *Attalea speciosa*'s high physiological amplitude supports the hypothesis that this species' relatively widespread distribution might have largely resulted from its dissemination by indigenous peoples for whom this plant was once extremely useful (May *et al.*, 1985a). Then again, other factors that we did not measure in this study might be more important in explaining the presence and absence of this species.

Even though the species-environment relations for *A. speciosa* and *A.* sp. dwarf lack the strength of those of *A. maripa* and *A. phalerata*, our results nonetheless show that environmental differences exist between them. *Attalea* sp. dwarf is present in areas that are relatively less acid and richer in K^+ and Mg^{2+} (app. D). Consequently, this palm is regularly found in association with *A. phalerata*. *Attalea* sp. dwarf is also associated with higher levels of several essential elements in total form (Cl_{tf}, Na_{tf} and to a lesser extent Mg_{tf} and K_{tf}), three 2:1 minerals (illite, K-feldspar, plagioclase feldspar) rich in all of the former except Cl_{tf} as well as higher quartz and lower kaolinite content (app. D) (Mengel and Kirkby, 2001). These values indicate that the soils where *A.* sp. dwarf is present contain relatively larger nutrient reserves than those of the surrounding area. Furthermore, the availability of these nutrient reserves is facilitated by the relatively higher pH of the soils where *A.* sp. dwarf grows (Mengel and Kirkby, 2001). Additionally, the higher quartz to kaolinite ratio (2.67:1 compared to an average of 0.39:1) of the fine soil fraction of these sites is indicative of relatively reduced soil weathering (Schulze, 1989). This corroborates with the presence of larger Na_{tf}, Mg_{tf} and K_{tf} reserves at these sites, giving us reason to suspect that these soils might be of younger basaltic origin (Alfisols). While the relatively low Fe_{cdb} values (médian of 313.72 µmol/g) observed where *A.* sp. dwarf grows contrast with those expected for Alfisols, the sieving we performed prior to analysis might have caused us to significantly under evaluate the presence of iron oxides because they regularly occur in these soils as large well-crystallized particles (Richards, 1996).

Of the edaphic variables that are associated to the distributions of *A. speciosa* and *A.* sp. dwarf, Cl_{tf} is the only one that significantly differentiated between the two (fig. 1.4l). Chlorine is particular in that it is not present in the original rock material, rather originating from atmospheric deposition (Jobbagy and Jackson, 2001 ; Öberg, 2003). It is present in the soil as chloride (Cl^-), a very mobile negatively charged ion, but is usually found in larger quantities bound to organic matter, forming stocks that can later be mineralized (Johansson *et al.*, 2003). Chlorine's association with organic matter was observed in our study as a correlation between Cl_{tf} and C_{tf}. Similarly, its lack of correlation with the other soil properties we measured confirms its unique nature as an atmospheric input.

Although essential to photosynthetic activity, Chlorine is not a limiting nutrient to most plants because the small quantities required are constantly being replenished by precipitation and dry deposition. However, studies have shown that significant quantities of chloride are required for the adequate stomatal functioning of two members of the *Palmaceae* (*Cocos nucifera* and *Elaeis guineensis*) where it acts as a mobile counterion to K^+ (Mengel and Kirkby, 2001 ; Von Uexküll, 1985 ; Xu *et al.*, 1999). Both species have been known to develop growth depression and wilting symptoms under chlorine deficiency. The significantly higher K^+ and Cl_{tf} values observed where *A.* sp. dwarf grows suggest that chloride might also play an important role in *Attalea* physiology. Then again, the tendency for *A. speciosa* to develop acaulescent stands where Cl_{tf} and K^+ values are higher is counterintuitive in regards to the expected growth improvements these ions would generate. However, research showing that the African oil palm (*E. guineensis*) stores large amounts of K^+ in its stem has provided us with a tentative explication (Ng *et al.*, 2003). Insofar as the physiological response to K^+ of *E. guineensis* is comparable to that of *Attalea* species, we propose that the high morphological plasticity of *A. speciosa* frees it of the need to accumulate K^+ storage tissues in its stem when the soil environment is rich in both potassium and chloride. Under this scenario, specimens growing on these richer soils could allocate considerably less energy to competing for and stocking soil nutrient resources while more effectively allocating more to the essential and costly aim of sexual reproduction (Anderson *et al.*, 1991 ; Barot *et al.*, 2005 ; Cunningham, 1997). Further research into the physiology, and phenology of this species (including dwarf or acaulescent forms) as well as its response to both macro- and micronutrients is needed before more substantial hypotheses are brought forth. These studies should ideally be performed in a controlled environment to verify causality, but also on a long-term basis to identify growth responses that are critical to sexual maturation (Sollins, 1998).

1.5 Conclusion

Results from the present study confirm previous reports of a significant relationship between palm species distribution and edaphic properties in Amazonian rainforests (Clark *et al.*, 1995 ; Costa *et al.*, 2009 ; Svenning, 1999 ; Vormisto, 2002). *Attalea phalerata* prefers soils with a relatively higher content of available cations and of lower acidity. *Attalea maripa* is inversely distributed to *A. phalerata* and is limited to soils poorest in available cations and of higher acidity. The higher levels of available and iron oxyhydroxide bound phosphorus within the distributional limits of *A. phalerata* may explain its competitive advantage over *A. maripa*. Furthermore, its preference for soils with high silt content is consistent with its widespread presence in white water floodplains of the Amazon Basin.

While the distribution of *A. speciosa* was not strongly associated to soil properties, its probable expression a distinct variety, *A.* sp. dwarf, was related to a secondary mineral gradient indicative of long-term soil nutrient reserves. Curiously, *A.* sp. dwarf showed morphological and phenological traits that exceeded those normally expected for this highly plastic species under conditions of unlimited access to light. Stands of this stemless palm were frequently associated with *A. phalerata* but also preferred soils richer in sodium, magnesium and potassium reserves. These soils also had a higher 2:1 clay mineral content while the relatively reduced weathering of quartz at these sites indicates that they are probably Alfisols. Most notably, the chlorine content of soils harboring *A. speciosa* and *A.* sp. dwarf differed significantly suggesting that Cl^- may play a critical physiological role as a counterion to potassium in these *Palmaceae*.

Considering the relatively large edaphic gradients we encountered in our study area, the omnipresence of large arborescent palms of the genus *Attalea* indicates that the ecotypes required by triatomines are probably present near all human settlements of the Lower Tapajós region. As several environmental and social factors combine to determine a communities' risk of contracting the American Trypanosomiasis, we believe that *Attalea* palm species contribute differently to the formation of regional hot spots. Therefore, the prediction of their distribution ranges is vital to the development of a comprehensive eco-epidemiological risk management tools for the American Trypanosomiasis. While parallel Triatominae population studies will determine the infestation risk associated with each palm species in our study area, the relationships we observed between *Attalea spp.* and edaphic soil gradients suggests that the presence and absence of these species can be predicted from soil maps. Bearing in mind that *A. maripa* and *A. phalerata* showed a clear inverse distribution pattern (they only occurred simultaneously in 1/43 lots, one being absent only when the other was present) (fig. 1.2), we propose that a simple splitting value may be used to predict their distributions. This is best performed with total cation content followed by Ca^{2+} and Al^{3+} (tab. 1.4). Although prone to more error than the latter (9.3%), the simplicity involved in measuring pH is ample reason for selecting it as an acceptable indicator as well. Even though the distribution of *A. speciosa* was not strongly related to soil properties, evidence suggests that its morphology is at least significantly influenced by it within its distributional limits. Considering that these growth forms can contribute differently to an American Trypanosomiasis transmission risk model, we propose the use of Cl_{tf} in predicting the expression of *A. speciosa* and the stemless *A.* sp. dwarf. Although the physiological importance of chlorine has not been confirmed in the *Attalea*, stemmed *A. speciosa* specimens tend to occur where Cl_{tf} is lower than 80 ppm (with 15.0 % misplaced samples).

Evidently, the effect of the presence of a palm species on the transmission of the American Trypanosomiasis will have to be understood in light of several factors (such as land management and local household practices) (Black *et al.*, 2007 ; Feliciangeli *et al.*, 2007) before a functional risk map is proposed (Abad-Franch *et al.*, 2009). Nonetheless, as these simple indicators result from work in an area showing relatively large edaphic soil variations for the Brazilian Amazon, they may be effective at a regional level as well. However, the validity of these indicators should be tested in other areas before using them as broad palm distribution prediction tools (Costa *et al.*, 2009) because the diversity and dominance of species (Vormisto *et al.*, 2004a), as well as the importance of different ecological factors (Bohlman *et al.*, 2008) can change between both regions and scales (Normand *et al.*, 2006 ; Terborgh and Andresen, 1998).

1.6 Tables and figures

Figure 1.1 Location map of the study region. Water bodies are in black, forested areas are in grey and unforested areas are in white. The specific study area is framed in white.

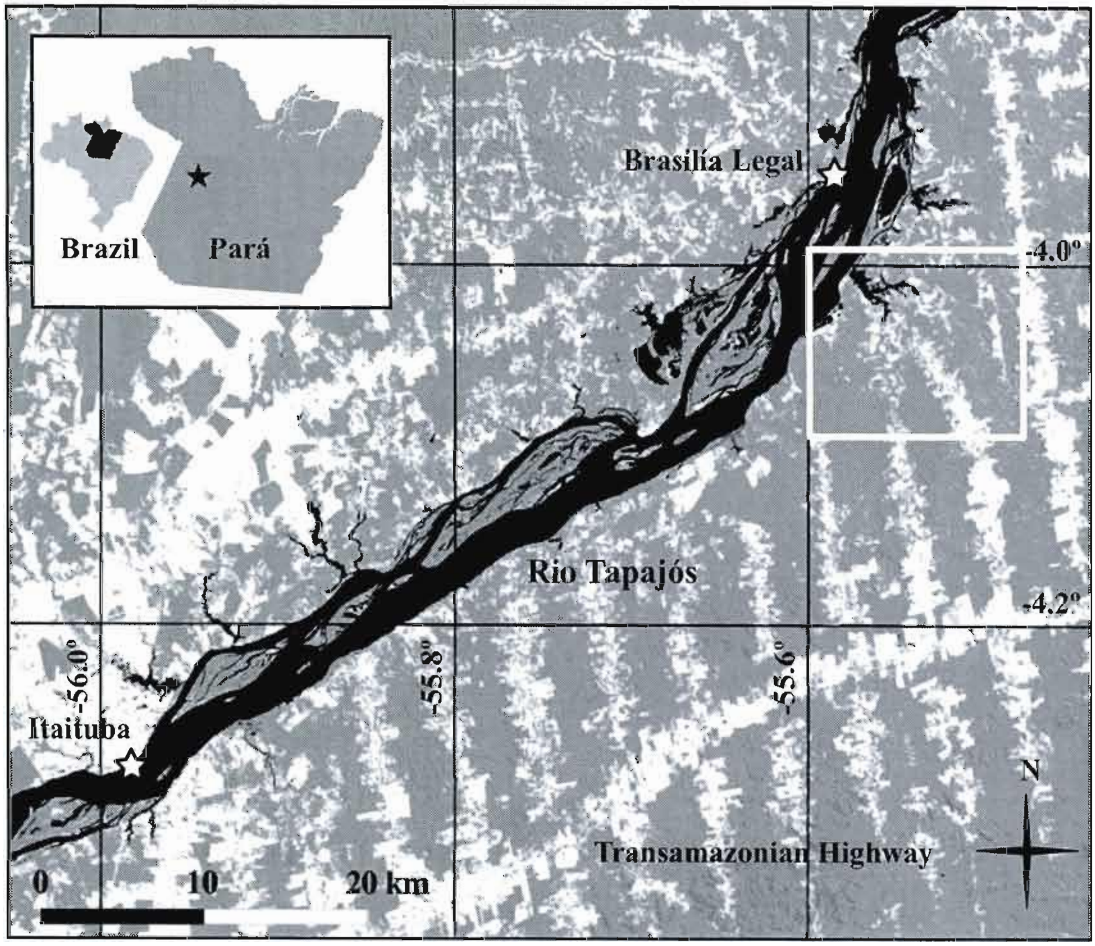


Figure 1.2 Distribution map of palm species and varieties sampled near the four neighboring communities of São Tomé, Demanda, Agrovila and Nova Estrela (Lower Tapajós, Pará, Brazil). The grey zones are water bodies and upland streams (predicted from a SRTM DEM) are identified by dashed lines. Presence and absence data is only given for each sample lot. *Attalea maripa* is identified by the symbol □, *A. phalerata* is identified by the symbol O, *A. speciosa* is identified by the symbol × and *A.* sp. dwarf is identified by the symbol +. Community centers are identified by the symbol ☆.

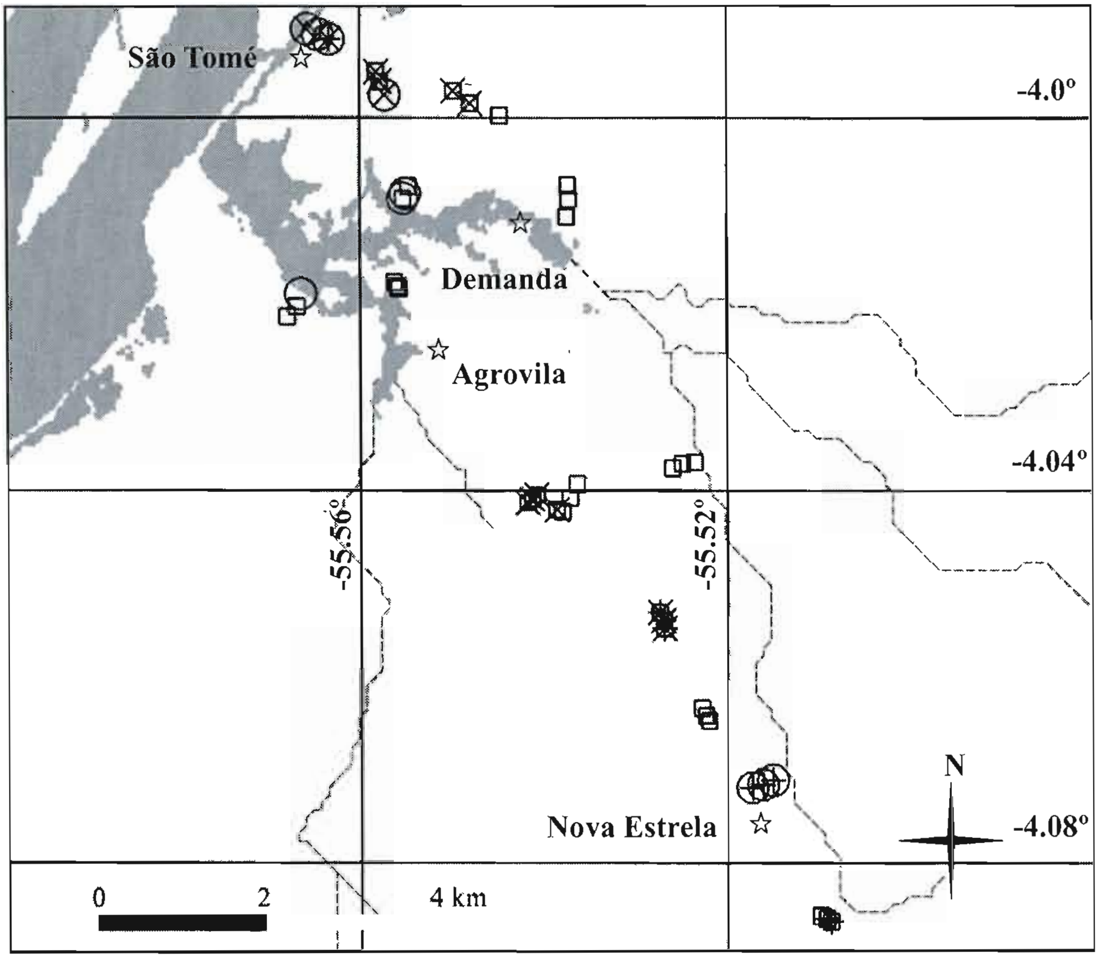
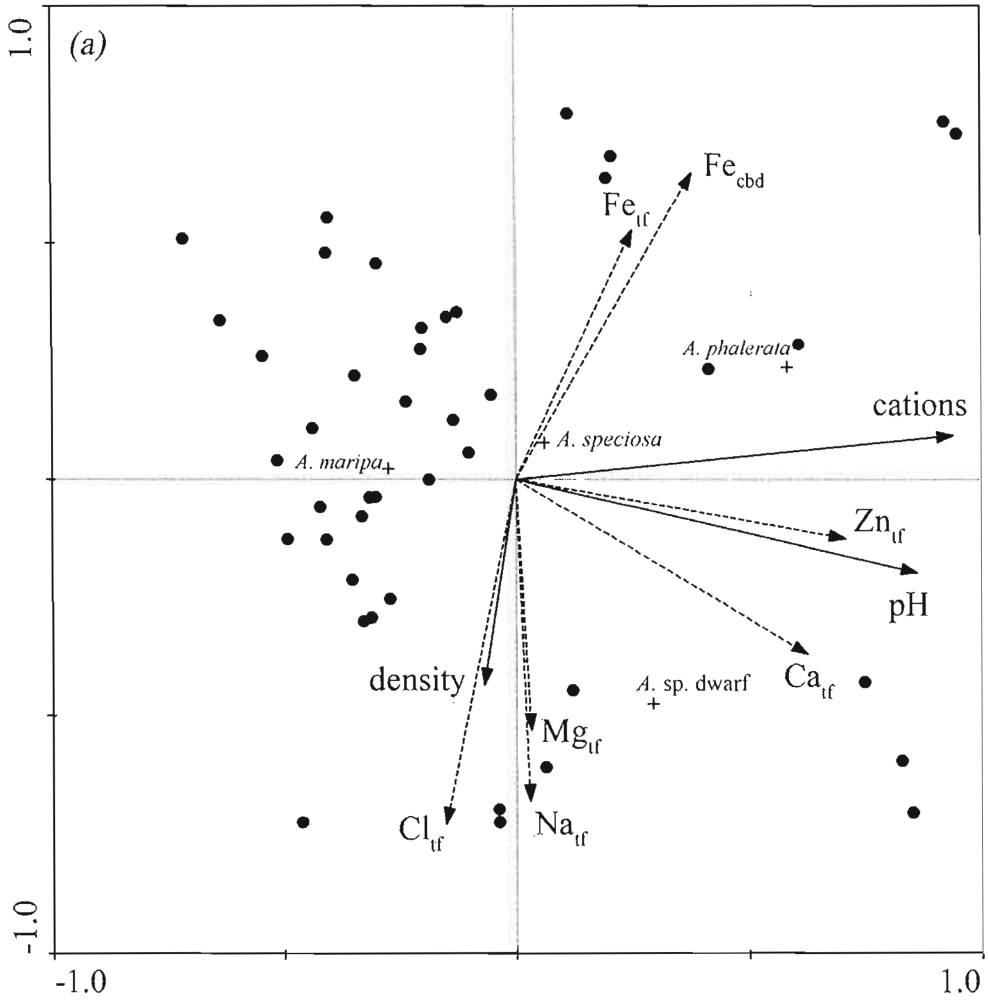


Figure 1.3 Ordination biplots yielded by a canonical correspondence analysis (CCA) of the presence and absence of palms species of the genus *Attalea* sampled near the four neighboring communities of São Tomé, Demanda, Agrovila and Nova Estrela (Lower Tapajós, Pará, Brazil). The diagrams show the relationships between palm species and environmental variables for stepwise selected (*a*) and alternative model (*b*) variables. The stepwise selected variables are those that best explain the distribution of palm species. The alternative model is composed of environmental variables with considerable marginal effects, uncorrelated to stepwise selected variables and eliminated by the automatic CCA stepwise selection process. Environmental variables of the alternative model are projected passively onto the stepwise selected variable biplot. Samples are identified with the symbol • and species are identified with the symbol +. Variables from the environmental matrix 1 are represented as continuous arrows. Variables from the environmental matrix 2 are represented as discontinuous arrows.



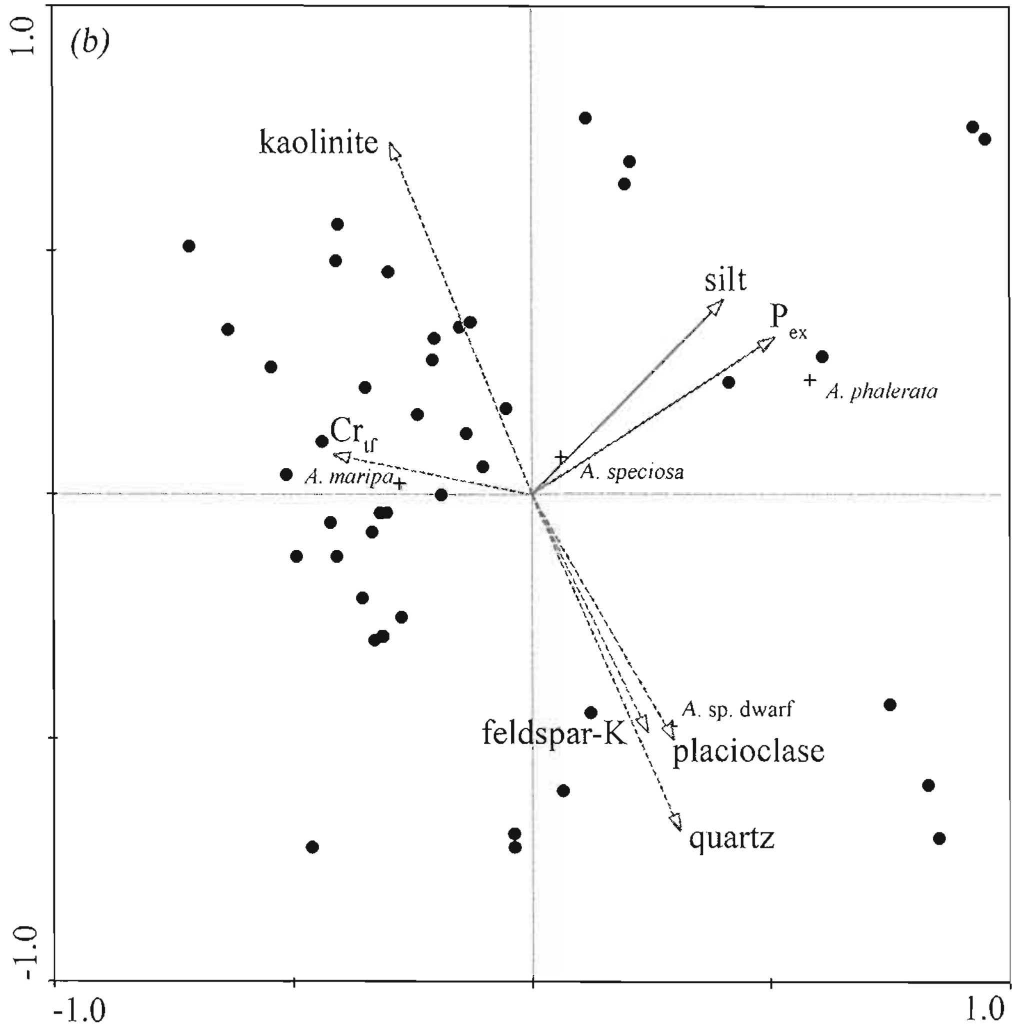
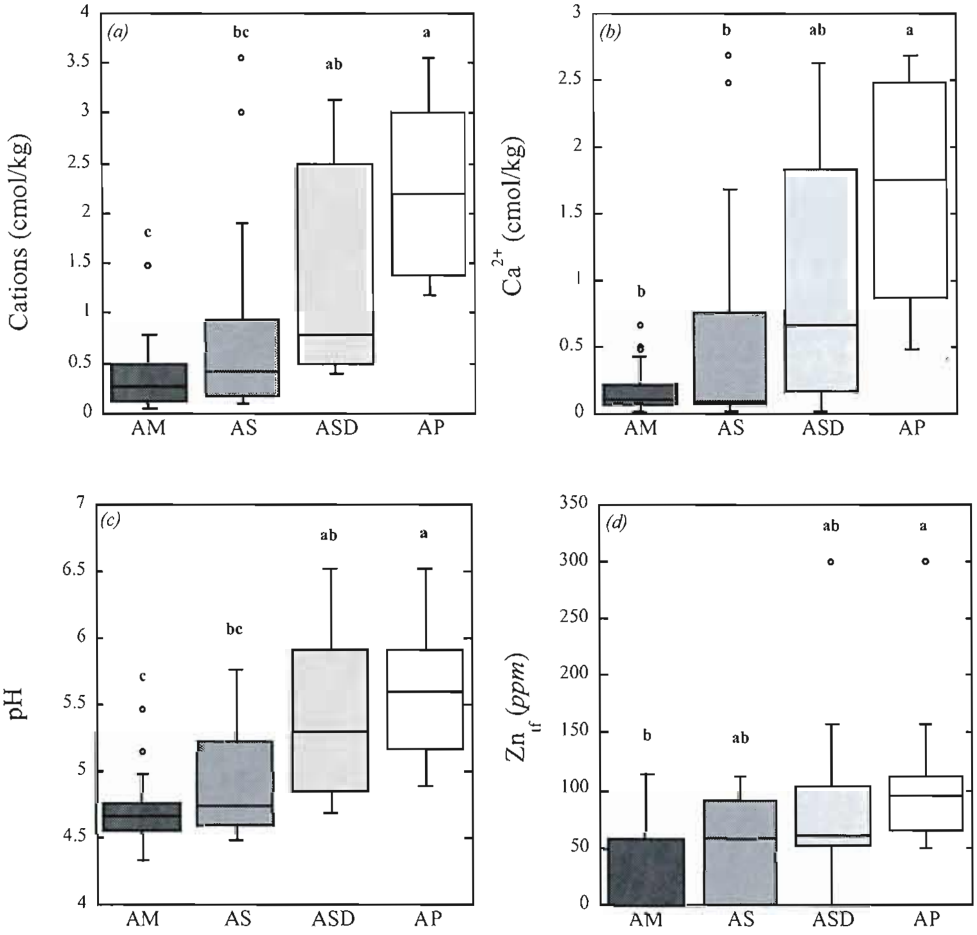
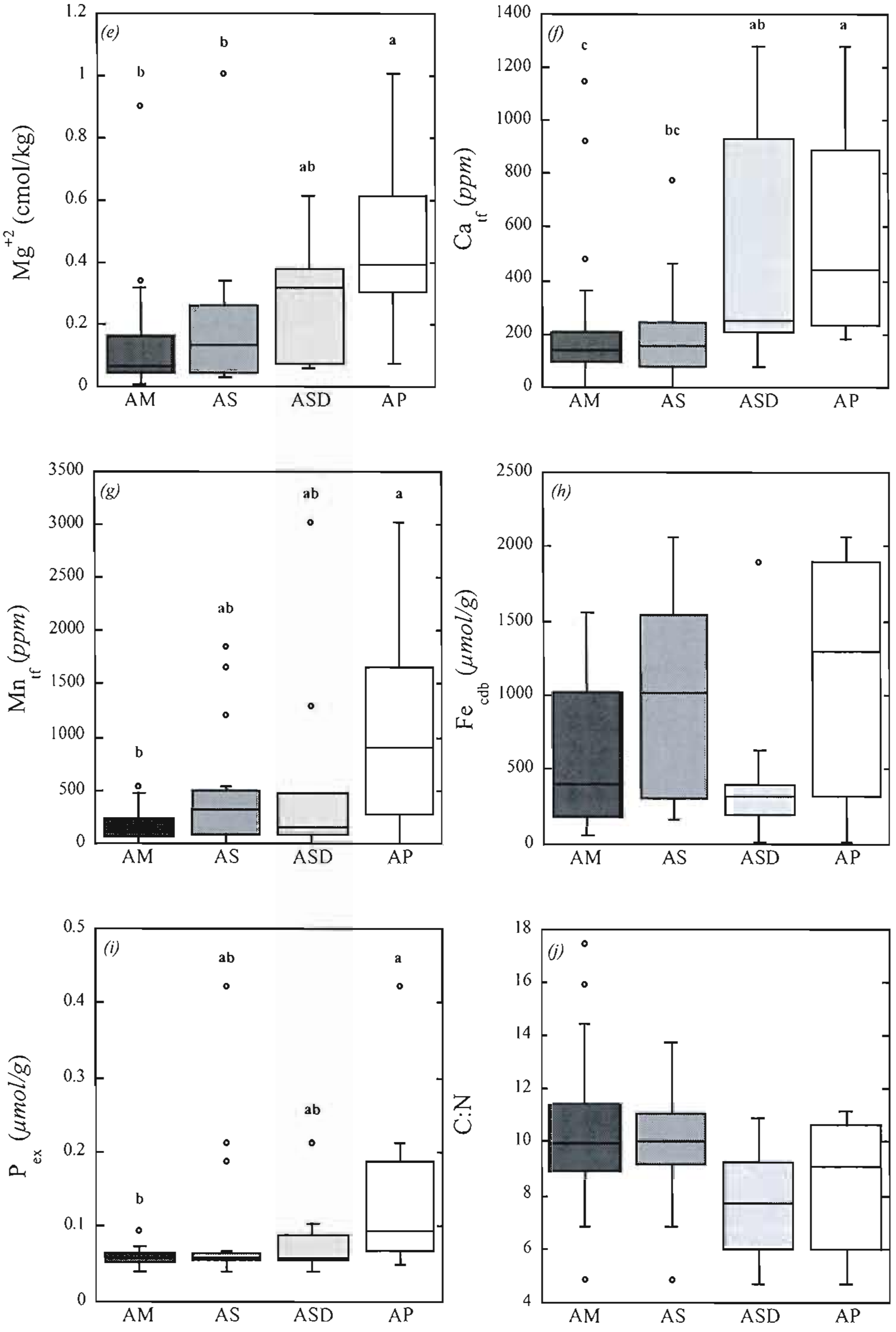
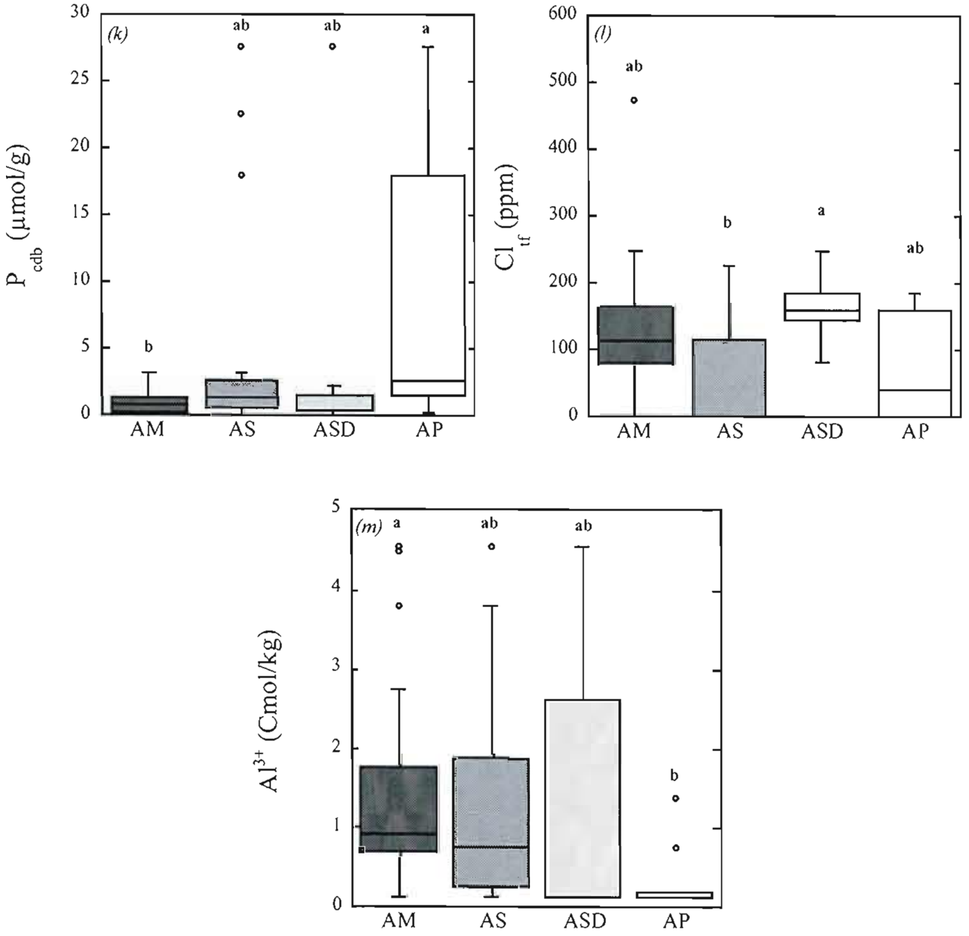

(b)
1.0
-1.0
-1.0
1.0
kaolinite
silt
P_{ex}
A. phalerata
Cr_{tr}
A. maripa
A. speciosa
A. sp. dwarf
feldspar-K
placioclase
quartz

Figure 1.4 Box plots of environmental variables for each *Attalea* palm species and variety sampled near the four neighboring communities of São Tomé, Demanda, Agrovila and Nova Estrela (Lower Tapajós, Pará, Brazil). Only stepwise selected and alternative model variables identified by the Kruskal-Wallis test as having at least one significantly different rank sum per species presence groups ($p<0.05$) are presented. AM, *Attalea maripa*; AS, *A. speciosa*; ASD, *A.* sp. dwarf; AP, *A. phalerata.* Significantly different groups were determined using the Noether test and identified by bold letters.




(e)
Mg^{+2} (cmol/kg)
0
0.2
0.4
0.6
0.8
1
1.2
b
b
ab
a
AM
AS
ASD
AP
(f)
Ca_{tf} (ppm)
0
200
400
600
800
1000
1200
1400
c
bc
ab
a
AM
AS
ASD
AP
(g)
Mn_{tf} (ppm)
0
500
1000
1500
2000
2500
3000
3500
b
ab
ab
a
AM
AS
ASD
AP
(h)
Fe_{cdb} (µmol/g)
0
500
1000
1500
2000
2500
AM
AS
ASD
AP
(i)
P_{ex} (µmol/g)
0
0.1
0.2
0.3
0.4
0.5
b
ab
ab
a
AM
AS
ASD
AP
(j)
C:N
4
6
8
10
12
14
16
18
AM
AS
ASD
AP


(k)
P_cdb (µmol/g)
0
5
10
15
20
25
30
b
ab
ab
a
AM
AS
ASD
AP
(l)
Cl_tf (ppm)
0
100
200
300
400
500
600
ab
b
a
ab
AM
AS
ASD
AP
(m)
Al3+ (Cmol/kg)
0
1
2
3
4
5
a
ab
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AP

Table 1.1 Results of detrended (DCA) and constrained (CCA) canonical analyses testing the effect two edaphic variable matrices on the distribution of palms species of the genus *Attalea* sampled near the four neighboring communities of São Tomé, Demanda, Agrovila and Nova Estrela (Lower Tapajós, Pará, Brazil).

		Environmental matrix 1					Environmental matrix 2				
	Axes	1	2	3	4	Total inertia	1	2	3	4	Total inertia
DCA	Eigenvalues	0.66	0.13	0.02	0	1.244	0.66	0.13	0.02	0	1.244
	Lengths of gradient	2.71	1.27	1.39	0		2.71	1.27	1.39	0	
	Species-environment correlations	0.9	0.67	0.66	0		0.93	0.95	0.94	0	
	Cumulative percentage variance										
	of species data	53.2	63.4	65.3	0		53.2	63.4	65.3	0	
	of species-environment relation	62.8	79.4	0	0		53.0	73.0	0	0	
	Sum of all eigenvalues					1.244					1.244
	Sum of all canonical eigenvalues					0.849					1.079
CCA	Eigenvalues	**0.54**	**0.220**	0.09	0.22	1.244	**0.58**	**0.28**	**0.22**	0.09	1.244
	Species-environment correlations	0.91	0.88	0.54	0		0.93	0.95	0.9	0	
	Cumulative percentage variance										
	of species data	43.6	61.2	68.2	85.5		46.4	68.7	86.7	93.7	
	of species-environment relation	63.8	89.7	100.0	0		53.5	79.2	100.0	0	
	Sum of all eigenvalues					1.244					1.244
	Sum of all canonical eigenvalues					0.849					1.079
	Test of significance of canonical axes										
	F-ratio	20.073	11.862	5.73			13.836	11.421	21.760		
	P-value	0	0	0.770			0	0	0.01		
	Test of significance of all canonical axes										
	Trace	0.85					1.08				
	F-ratio	3.49					4.03				
	P-value	0					0				

Environmental matrix 1 is composed of commonly sampled edaphic properties and environmentental matrix 2 is composed of novel or rarely sampled soil variables. CCA eigenvalues for significant canonical axes are given in bold.

Table 1.2 Results of an automatic stepwise canonical correspondence analysis testing the effect of edaphic variables on the distribution of palms species of the genus *Attalea* sampled near the four neighboring communities of São Tomé, Demanda, Agrovila and Nova Estrela (Lower Tapajós, Pará, Brazil).

		Marginal effects			Conditional effects		
		λ 1	*p*	F	λ A	*p*	F
EM 1	**cations**	**0.45**	***0.001***	**23.27**	**0.45**	***0.002***	**23.37**
	Ca^{2+}	0.41	*0.001*	20.42	0.00	*0.996*	0.01
	pH	**0.38**	***0.001***	**18.35**	**0.06**	***0.012***	**3.44**
	Mg^{2+}	0.26	*0.001*	10.77	0.04	*0.104*	2.09
	P_{ex}	0.15	*0.005*	5.85	0.01	*0.676*	0.46
	C:N	0.15	*0.008*	5.79	0.03	*0.126*	1.90
	K^{+}	0.13	*0.013*	4.60	0.03	*0.104*	2.14
	Silt	0.12	*0.011*	4.29	0.03	*0.158*	1.79
	Al^{3+}	0.09	*0.037*	3.38	0.02	*0.208*	1.60
	Density	**0.07**	***0.064***	**2.55**	**0.08**	***0.012***	**4.37**
	Sand	0.07	*0.061*	2.53	*collinear with texture data*		
	C total	0.07	*0.071*	2.44	0.01	*0.458*	0.79
	Redness rating	0.06	*0.078*	2.28	0.01	*0.592*	0.59
	N total	0.05	*0.142*	1.85	0.02	*0.252*	1.33
	Elevation	0.05	*0.156*	1.77	0.02	*0.202*	1.49
	Clay	0.05	*0.184*	1.66	0.01	*0.394*	0.91
	Soil water potential	0.02	*0.500*	0.77	0.02	*0.206*	1.52
	Slope	0.00	*0.936*	0.13	0.01	*0.648*	0.56
EM 2	**Zn_{tf}**	**0.26**	***0.002***	**10.92**	0.26	*0.00*	10.92
	Ca_{tf}	**0.26**	***0.002***	**10.59**	**0.09**	***0.01***	**5.00**
	Mn_{tf}	0.24	*0.001*	9.81	0.02	*0.20*	1.60
	Fe_{cdb}	**0.17**	***0.006***	**6.69**	**0.15**	***0.00***	**7.08**
	P_{cdb}	0.15	*0.012*	5.55	0.03	*0.12*	2.07
	Kaolinite	0.15	*0.008*	5.46	0.00	*0.71*	0.42
	Quartz	0.15	*0.005*	5.45	*collinear with mineralogy data*		
	Cl_{total}	**0.15**	***0.007***	**5.41**	**0.05**	***0.02***	**3.77**
	P_{apa}	0.14	*0.009*	5.31	0.01	*0.52*	0.73
	Cu_{tf}	0.14	*0.007*	5.03	0.00	*0.95*	0.09
	Fe_{tf}	**0.13**	***0.002***	**4.71**	**0.05**	***0.03***	**3.58**
	P_{tf}	0.12	*0.013*	4.45	0.07	*0.00*	9.18
	P_{org}	0.12	*0.012*	4.33	0.01	*0.55*	0.69
	Plagioclase	0.10	*0.019*	3.72	0.01	*0.51*	0.81
	Al_{cdb}	0.10	*0.280*	3.66	0.01	*0.80*	0.29
	Na_{tf}	**0.10**	***0.037***	**3.56**	**0.11**	***0.01***	**6.00**
	Feldspar-K	0.09	*0.030*	3.32	0.02	*0.26*	1.41
	Cr_{tf}	0.09	*0.049*	3.11	0.00	*0.47*	0.81
	Illite	0.07	*0.073*	2.46	0.01	*0.32*	1.15
	Mg_{tf}	**0.06**	***0.086***	**2.21**	0.06	***0.01***	**3.93**
	K_{tf}	0.06	*0.068*	2.20	0.02	*0.21*	1.63
	C_{tf}	0.05	*0.132*	1.88	0.03	*0.08*	2.59
	Dolomite	0.03	*0.342*	1.14	0.01	*0.23*	1.44
	S_{tf}	0.03	*0.356*	1.07	0.00	*0.82*	0.27
	Calcite	0.01	*0.348*	0.80	0.02	*0.21*	1.43
	Stoniness	0.01	*0.825*	0.32	0.02	*0.15*	1.73
	Hematite	0.01	*0.811*	0.31	0.02	*0.26*	1.41

EM, environmental matrix. EM 1 is composed of commonly sampled edaphic properties while EM 2 is composed of novel or rarely sampled soil variables. Variables per matrix are ordered according to descending marginal effects. Variables chosen during automatic stepwise selection are given in bold. A marginal effect is the variability in the palm species data that would be explained in a model using that edaphic variable as the only explanatory variable. A conditional effect is the effect that a variable brings to the model in addition to previouly selected variables.

Table 1.3 Spearman ρ correlation matrix of measured variables and environmental variables selected through an automatic stepwise canonical correspondence analysis testing the effect of edaphic variables on the distribution of palms species of the genus *Attalea* sampled near the four neighboring communities of São Tomé, Demanda, Agrovila and Nova Estrela (Lower Tapajós, Pará, Brazil).

	Cations	**pH**	**Zn_{tf}**	**Ca_{tf}**	**Fe_{cdb}**	**Cl_{tf}**	**Fe_{tf}**	**Na_{tf}**	**Density**	**Mg_{tf}**
Cations		**0.801** ***	0.541 ***	0.596 ***	0.297	-0.070	0.284	0.029	-0.025	0.159
Ca^{2+}	**0.884** ***	**0.705** ***	0.534 ***	0.583 ***	0.277	-0.165	0.237	-0.206	-0.014	-0.081
pH	**0.801** ***		0.460 **	**0.742** ***	0.082	0.112	0.080	0.156	0.011	0.149
Zn_{tf}	0.541 ***	0.460 **		0.228	0.370 *	-0.197	0.391 **	-0.198	-0.248	-0.228
Mg^{2+}	0.857 ***	**0.673** ***	0.496 ***	0.370 *	0.285	-0.054	0.287	0.162	-0.138	0.314 *
Ca_{tf}	0.596 ***	**0.742** ***	0.228		-0.276	0.397 ***	-0.302 *	0.295	0.420 **	0.294
Mn_{tf}	0.520 ***	0.395 **	**0.654** ***	0.089	**0.661** ***	-0.449 **	**0.728** ***	-0.392 **	-0.464 **	-0.317 *
Fe_{cdb}	0.297	0.082	0.370 *	-0.276		-0.569 ***	**0.953** ***	-0.556 ***	**-0.640** ***	-0.404 **
C:N	-0.412 **	-0.366 *	-0.110	-0.351 *	0.318 *	-0.112	0.251	-0.562 ***	-0.350 *	**-0.618** ***
P_{cdb}	0.439 **	0.292	0.527 ***	-0.087	**0.906** ***	-0.432 **	**0.884** ***	-0.457 **	-0.574 ***	-0.330 *
Cl_{tf}	-0.070	0.112	-0.197	0.397 **	-0.569 ***		-0.547 ***	**0.633** ***	0.530 ***	0.469 **
P_{apa}	0.368 **	0.196	0.457 **	-0.221	**0.902** ***	-0.493 ***	**0.881** ***	-0.483 **	**-0.631** ***	-0.344 *
Cu_{tf}	0.329 *	0.262	0.548 ***	-0.165	**0.817** ***	-0.509 ***	**0.838** ***	**-0.625** ***	**-0.739** ***	-0.528 ***
Fe_{tf}	0.284	0.080	0.391 **	-0.302 *	**0.953** ***	-0.547 ***		-0.535 ***	**-0.712** ***	-0.429 **
K^{+}	0.362 *	0.251	-0.086	0.328 *	-0.311 *	0.322 *	-0.345 *	**0.636** ***	0.448 **	**0.709** ***
P_{tf}	0.197	0.219	0.418 **	-0.095	**0.706** ***	-0.368 *	**0.685** ***	-0.524 ***	-0.545 ***	-0.487 ***
P_{org}	0.209	0.044	0.231	-0.315 *	**0.772** ***	-0.415 **	**0.708** ***	-0.347 *	-0.542 ***	-0.218
Al_{cdb}	0.157	-0.023	0.284	-0.403 **	**0.950** ***	-0.520 ***	**0.944** ***	-0.556 ***	**-0.728** ***	-0.447 **
Na_{tf}	0.029	0.156	-0.198	0.295	-0.556 ***	**0.633** ***	-0.535 ***		0.518 ***	**0.877** ***
Al^{3+}	-0.370 *	-0.461 **	-0.530 ***	-0.348 *	-0.162	0.306 *	-0.172	0.534 ***	0.160	**0.614** ***
Density	-0.025	0.011	-0.248	0.420 **	**-0.640** ***	0.530 ***	**-0.712** ***	0.518 ***		0.461 **
Sand	-0.229	-0.054	-0.326 *	0.366 *	**-0.847** ***	0.500 ***	**-0.832** ***	0.399 **	**0.700** ***	0.226
C total	-0.049	-0.158	0.124	-0.428 **	**0.669** ***	-0.295	**0.640** ***	-0.463 **	**-0.643** ***	-0.376 *
Mg_{tf}	0.159	0.149	-0.228	0.294	-0.404 **	0.469 **	-0.429 **	**0.877** ***	0.461 **	
K_{tf}	0.064	0.053	-0.328 *	0.204	-0.428 **	0.481 **	-0.442 **	**0.853** ***	0.476 **	**0.968** ***
C_{tf}	-0.197	-0.045	-0.308 *	0.227	-0.523 ***	**0.662** ***	-0.472 **	0.556 ***	0.414 **	0.436 **
N total	0.245	0.040	0.236	-0.354 *	**0.742** ***	-0.346 *	**0.755** ***	-0.272	**-0.636** ***	-0.119
Clay	0.050	-0.106	0.242	-0.518 ***	**0.785** ***	-0.472 **	**0.811** ***	-0.523 ***	-0.077	-0.395 **
S_{tf}	-0.066	0.005	0.262	-0.299	0.538 ***	-0.225	**0.600** ***	-0.545 ***	-0.587 ***	-0.581 ***

Variables are ordered according to descending marginal effect. Weighted correlation values above +/- 0.600 are given in bold. Significant correlations are identified with asterisks. *= significant ($p<0.05$), **= highly significant ($p<0.01$), ***= very highly significant ($p<0.001$). Only available variables with at least 1 correlation value >0.600 are shown.

Table 1.4 Optimal splitting values for edaphic variables discriminating between *A. maripa* and *A. phalerata* populations sampled near the four neighboring communities of São Tomé, Demanda, Agrovila and Nova Estrela (Lower Tapajós, Pará, Brazil).

	S.V.		% M. S.
Cations	1.18	*cmol / kg*	0.0%
Al^{3+}	0.14	*cmol / kg*	4.7%
Mn_{tf}	615	*ppm*	7.0%
pH	4.85		9.3%
P_{ex}	0.07	*μmol/g*	9.3%
Zn_{tf}	87	*ppm*	11.6%
Mg^{2+}	0.21	*cmol / kg*	11.6%
P_{cdb}	2.04	*μmol/g*	14.0%
Ca_{tf}	180	*ppm*	23.3%

All splitting values except for Al^{3+} are smaller for *A. maripa*. S.V., splitting value; % M.S., percentage of misplaced samples.

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CHAPITRE II

RÉPARTITION DES CATIONS MAJEURS ÉCHANGEABLES DES SOLS DE TERRE FERME DU BAS TAPAJÓS (AMAZONIE BRÉSILIENNE)

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Résumé

Malgré la nature fortement lessivée des terres fermes du bassin amazonien, une variation importante des teneurs en cations persiste et contribue significativement à la distribution hétérogène des espèces végétales. Des sols de la région du Bas Tapajós ont été analysés à l'aide d'une catégorisation granulométrique détaillée ainsi que des analyses minéralogiques et chimiques de la fraction fine du sol (0-20 μm) afin de déterminer le rôle des facteurs du sol dans la variation des teneurs en cations majeurs échangeables. Quarante-trois parcelles ont été échantillonnés le long de 14 transects répartis dans la région du Lac Araipa. Nos résultats montrent une différence marquée entre les distributions des 3 cations échangeables majeurs. Bien que le Ca^{2+} échangeable soit le principal cation régissant la teneur totale de cations majeurs échangeables, les réserves de Ca_{tf} fixées sur les minéraux des sols de la région sont épuisées. Quoique peu associé aux variables mesurées, le Ca^{2+} échangeable est corrélé aux oxyhydroxydes de fer associés aux limons fins (2-10 μm) des sols. De plus, le carbone organique du sol entre en compétition avec le Ca^{2+} échangeable pour les sites d'échange. Le plus petit cation échangeable, K^+, est principalement associé à des réserves non échangeables de K_{tf}. Le Mg^{2+} échangeable, de taille intermédiaire, est d'une part plus fortement lié aux facteurs du sol qui contrôle le Ca^{2+} échangeable, mais est aussi significativement associé au Mg_{tf} non échangeables. La forte corrélation entre les réserves minérales de Mg_{tf} et de K_{tf} suggère qu'ils sont des composantes élémentaires de l'illite, présente en petites quantités à travers la région d'étude. Nos résultats suggèrent de privilégier le rôle individuel de chacun des cations échangeables plutôt que celui des cations échangeables totaux pour la recherche en écologie végétale. De plus, les méthodes granulométriques traditionnelles pourraient être modifiées afin de tenir compte du rôle crucial des limons dans la dynamique des nutriments des sols de cette région. Enfin, la présence de quantités appréciables de Mg_{tf} et de K_{tf} suggère que l'altération des minéraux joue un rôle significatif dans le cycle des éléments nutritifs de ces forêts de terre ferme amazonienne.

Mots-clés : cations majeurs, sol, terre ferme, texture, limon fin, élément total, minéralogie, oxyhydroxyde de fer, illite

CHAPTER II

DISTRIBUTION OF THE EXCHANGEABLE MAJOR CATIONS IN UPLAND SOILS OF THE LOWER TAPAJÓS RIVER BASIN (BRAZILIAN AMAZON)

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Abstract

Despite the highly weathered nature of upland soils of the Amazon Basin, important cation variations persist, contributing significantly to plant distribution patterns. Soils sampled from the Lower Tapajós region were analyzed using a refined textural classification scheme as well as mineralogical and chemical analyses of the fine soil fraction (0-20 µm) in order to determine how soil factors govern exchangeable major cation content. Forty-three lots were sampled along 14 transects within the Lake Araipa region. Our results showed a marked difference in the distributions of the exchangeable major cations. Even though exchangeable Ca^{2+} is the principal ion driving total cation content, the soils are depleted of non-exchangeable Ca_{tf} reserves. While poorly associated to the measured variables, exchangeable Ca^{2+} is associated to iron oxy-hydroxides present in the fine silt fraction (2-10 µm) of soils. However, organic carbon molecules compete with exchangeable Ca^{2+} for these limited iron oxy-hydroxide exchange sites. The smaller, highly soluble exchangeable K^+ cation is primarily associated to non-exchangeable K_{tf} reserves. Exchangeable Mg^{2+}, a cation of intermediate size, is associated to the same soil factors that control exchangeable Ca^{2+} while also significantly associated to non-exchangeable forms of Mg_{tf}. The strong correlation between non-exchangeable Mg_{tf} and K_{tf} suggests that they are basic components of illite clays, present in small amounts throughout the study area. Our results suggest that the role of individual exchangeable cations should be prioritized over the total exchangeable cation content of soils in plant ecology research. Furthermore, granulometric methods could be modified to account for the critical role that fine silts play in the region's soil nutrient dynamics. Finally, the presence of appreciable amounts of non-exchangeable Mg_{tf} and K_{tf} suggest that mineral weathering might have a significant role in the nutrient cycling of upland forests.

Keywords: major cations, soil, upland, texture, fine silt, total element, mineralogy, iron oxy-hydroxide, illite

2.1 Introduction

Soil properties play an essential role in the distribution of plant species within the Amazon basin (Sollins, 1998). Although the highly weathered nature of old Amazonian upland (*terra firme*) soils has led to the bulk loss of their cation reserves (Lucas *et al.*, 1996), changes in species distribution are frequently associated to nutrient gradients (chap. 1) (Barthold *et al.*, 2008). However, the environmental factors responsible for these gradients remain poorly understood in these tropical regions. Various mechanisms have been proposed to explain the distribution of the different soils types of these warm and heavily weathered environments. For instance, geochemical processes along toposequences are responsible for the development of soils of contrasting physicochemical properties. The richer Oxisols are located at the top of slopes, while a loss of clays has contributed to the formation of poorer Ultisols in intermediate positions, down to Spodosols at the bottom of slopes under high alteration conditions (Bravard and Righi, 1989). Additionally, the presence of fertile pockets of Alfisols, derived from relatively recent igneous intrusions of diabasic rock, further increase the heterogeneity of this matrix of soils (Fearnside, 1984 ; Jordan, 1985). Nonetheless, research on upland soils has shown that soil nutrient variations are not restricted to the taxonomic units that have been developed to classify them (Fearnside, 1984). Rather, the presence of important variations in local conditions require that soil nutrient fluctuations also be understood at more detailed scales than those of currently available soil maps for the Brazilian Amazon. As the bulk of the soil's nutrients are present as relatively mobile exchangeable ions available to plants, a combination of more persistent soil factors interact to retain this local patchwork. These include various physical properties such as soil texture and clay mineralogy, but also variations in the content of certain elements such as carbon (C) and nitrogen (N). In some cases, cations fixed to the mineral structure of a soil may act as long-term nutrient reserves, slowly contributing to the available exchangeable cation pool as they are weathered. A better understanding of how these physical and chemical properties interact to control nutrient availability will necessarily contribute to a better understanding of the distribution of plant species within the Brazilian Amazon.

While the relationship between clay and nutrient content has been frequently assessed in tropical plant ecology, studies have generally been limited to conventional soil texture measurements that divide the soil into a composite of three fractions according to particle size: sand, silt and clay. Coarse soil fractions (>50 μm) are essentially composed of quartz, a sterile, poorly weatherable mineral both devoid of plant nutrients (except Si) and incapable of adsorbing or storing them (Mengel and Kirkby, 2001). As such, the importance of these fractions to plant life is essentially restricted to their contribution to physical soil properties (Soares *et al.*, 2005). However, fine soil fractions (0-20 µm), and clays (0-2 µm) in particular, are composed of the bulk of both primary silicates and secondary minerals well known to represent the principal sources and exchange sites for cations (Mengel and Kirkby, 2001). Consequently, total clay content is regularly used as an estimator of soil cation content. However, recent studies have revealed that total clay content does not always correlate well with soil cation content (Silver *et al.*, 2000) while some tropical plant ecologists have observed strong relationships between plant distributions and soil cation content without the expected textural correlations (Costa *et al.*, 2009). While the lack of correlation between clay and cation content is sometimes attributed to poor sampling methodology (Sollins, 1998 ; Teixeira *et al.*, 1984), we suspect that other fractions capable of cation exchange can otherwise overshadow the role of clay-sized particles on cation retention. In fact, Soares *et al.* (2005) and Mengel *and al.* (1998) have shown that in some soils, both sands and silts not only contribute significantly to the effective cation exchange capacity but can even play a critical role in the replenishment of certain cations in the soil solution.

When a positive relationship between soil texture and cation content occurs, it is a result of the specific physical and chemical features of the minerals that constitute those particle size classes. However, size is sometimes the only characteristic common to two particles within a same size class. Under these circumstances, variations in the soil's mineralogy may play a more important role on total cation content than does its clay content. For instance, certain clay minerals such as 2:1 phyllosilicates have a disproportionate bearing on a soil's nutrient cycle because of their high propensity to adsorb and store cations. Alternatively, others such as kaolinite, a 1:1 layer clay predominant in weathered soils have virtually no permanent charge (Schulze, 1989). Soils with a high content of this clay mineral remain relatively infertile albeit their potentially high clay content. With this in mind, finer scaled physical and chemical analyses aimed at detecting the role of a soil's mineralogy in the heterogeneous disposition of nutrients may shed new light into our limited understanding of the spatial distribution of plants in upland soils of the Amazon Basin.

2.2 Study area and methods

2.2.1 Study area

The present study was carried out in the Lower Tapajós region (state of Pará, Brazil), approximately 55 km downstream from the city of Itaituba (fig. 2.1). The specific study area was chosen in accordance with the research goals of a larger interdisciplinary study on health risks associated to land management (PLUPH, 2010). It was located in four neighboring communities (São Tomé, Demanda, Agrovila and Nova Estrela) near Lake Araipa along the Tapajós River, districts of Aveiro and Rurópolis (fig. 2.2).

The predominant soil types of the area are Oxisols and Ultisols (according to the USDA system) (Soil Survey Division Staff, 1999) or Latossolos Amarelos and Argissolos Velmelho-Amarelos (according to the Brazilian classification system) (EMBRAPA, 2007). These soils developed from continental sediments as a result of related geochemical processes on the Alter-do-Chão geological formation (Bravard and Righi, 1989). These highly weathered soils are generally acidic, have low cation exchange capacities and relatively high concentrations of exchangeable aluminum (Lucas *et al.*, 1996). Alfisols or Nitossolos according to the U.S. or Brazilian classifications, derived from relatively recent igneous intrusions of diabasic rock are also known to occur in the region and are significantly richer than both Oxisols and Ultisols (Fearnside, 1984 ; Jordan, 1985). While we interpreted the elevation range of the specific study area from a SRTM DEM as ranging from 0 to 125 m (Consortium for Spatial Information, 2010), the terrain consists of a complex series of highly dissected valleys with notable soil variations. The climate is warm and humid with an annual rainfall varying between 1800 and 2200 mm and interrupted by a drier season lasting approximately 3 months (Grupo de Trabalho Interministerial, 2006). The primary upland vegetation is classified as sub-montane open forest (*floresta ombrófila aberta submontana*) (EMBRAPA, 2007) with at least one *Attalea* palm species present in any given area (Pires and Prance, 1985). However, slash and burn agriculture, cattle herding on pastures and young secondary fallow-forests now dominate the landscape near human settlements.

2.2.2 Sampling sites

Soil sampling sites were selected in accordance with the requirements of parallel palm ecology (chap. 1), soil erosion (Durante Tagliari, 2009) and mercury displacement studies (unpublished). Fourteen transects where identified on slopes along surface drainage flow axes (fig. 2.2) on upland soils. The majority of transects (13/14) were placed on agricultural land to facilitate access and correspond to human settlements. The length of each transect (median 270.8 m, min.: 90.2 m, max.: 629.3 m) varied according to the length of the slope and accessibility. Each transect consisted of three lots (75 m by 25 m, *n=43*) (except for #5 with 4 lots) whose longer sides were oriented perpendicular to the site's surface drainage flow. The central lot of each transect was placed approximately halfway between the other two. Care was taken to insure that slope, vegetation cover, soil color and texture were constant within each lot. The location of each lot and its elevation were georeferenced using a Garmin eTrex Venture HC handheld GPS device. In all cases, permission to work on each site was solicited from landowners before sampling.

2.2.3 Soil sampling and analyses

While slash and burn agriculture has a significant impact on soil chemistry, these changes are less important in deeper horizons (Alegre *et al.*, 1988 ; Farella *et al.*, 2007 ; Makeschin *et al.*, 2008). Considering that we were primarily interested in the soil's natural properties, we controlled for the effects of human intervention by limiting our analysis to samples taken at a depth of 50-55 cm.

In September 2008, we collected three soil samples per lot from a depth of 50-55 cm, 25 m apart from each other, along a line perpendicular to the transect slope because soil physical and chemical properties tend to be more homogeneous along topographic contour lines (Chauvel *et al.*, 1987). Areas with abnormal characteristics (ex: decomposing trees, manure, erosion) were screened before sampling. Duplicates at each sample point were extracted from a 50 cm deep hole using a 100 cm^3 stainless steel percussion sampler (Blake and Hartge, 1986). The first duplicate was air-dried on site while approximately 30 g of the second was subsampled and frozen to interrupt microbial activity. Sample analyses were performed at the Biodôme of Montreal as well as the GÉOTOP, the Earth and atmospheric sciences and the Geography departments of the Université du Québec à Montréal (Canada). Depending on the soil variable, samples of a same lot were pooled either before or after laboratory analysis to overcome spatial variability (Binkley and Vitousek, 1989 ; Montanari *et al.*, 2008 ; Sollins, 1998 ; Teixeira *et al.*, 1984).

Air-dried samples were oven-dried at 45 °C until a stable weight was attained. Average bulk density (dry weight/100 cm^3) for each lot was calculated. Dried samples were then lightly crushed using a mortar and pestle and sieved at 2 mm. Soil color, texture, exchangeable major cations (Ca^{2+}, Mg^{2+}, K^+), mineralogy and total elements were determined from the <2 mm fraction.

Dry color of each sample was assessed using a Munsell color chart under artificial light (fluorescent lamps). Redness rating (RR) was calculated using the following formula adapted from Torrent and Barron (1993) to include hues in the Y range:

$$RR = (15-H)*C/V$$

where V and C are the values for value and chroma respectively. H is the numerical value of hue so that for 10R, H is 0, for 10YR, H is 10 and for 5Y, H is 15.

Particle size analysis was performed on one sample per lot using laser diffraction with a Fritsch Analysette 22 Compact laser particle sizer according to a protocol adapted from Sheldrick (1985). Sample preparation involved exposing fifty grams of soil to a weak hydrogen peroxide solution (5 ml of 30% H_2O_2 diluted in 250 ml of distilled H_2O) for 24 hours (agitated twice for 5 min) to digest organic matter. The sample was then deflocculated with 225 ml of a sodium pyrophosphate ($Na_4P_2O_7$) solution (30 g $Na_4P_2O_7$ / 2250 ml of distilled H_2O) for at least 12 hours (agitated once for 5 min). The resulting soil solution was sieved using a 63 μm mesh. The coarse fraction (>63 μm) was oven-dried at 105 °C and finally dry-sieved using a motorized sieve shaker. The dry weights of the following sand factions were determined: 63, 125, 250, 500 and 1000 μm. Laser diffractions of two diluted subsamples (lower and upper ends of the soil solution profile) of the agitated fine fraction solution (<63 μm) were performed (measuring range: 0.3-46 μm, ultrasonics on, stirrer speed: 3, sample dilution absorption: 7%, measurement scans: 10 and 1 clean fill before and after each measurement). Eight soil texture fractions (0-2, 2-10, 10-20, 20-50, 50-125, 125-250, 250-500 and 500-2000 μm) were extrapolated from a particle curve combining the average of the two fine fraction particle curves with a particle curve constructed from the sand fraction weights using Analysette 22 32-bit for Windows (Fritsch).

Analysis of exchangeable major cations (Ca^{2+}, Mg^{2+}, K^+) was performed on composite samples made from an equal volume of the <2 mm soil fraction of three replicates from each lot. Dry weight was first measured after oven drying composite samples at 105 °C. Exchangeable major cations were then extracted with a 1:10 soil solution of $BaCl_2$ rotated at 25 RPM for 2 hours and finally measured by atomic absorption (Hendershot *et al.*, 1993). Results were corrected according to the detection limits of each major cation (Ca^{2+}=0.038 mg/l, Mg^{2+}=0.024 mg/l, K^+=0.030 mg/l) while cmol kg/l values were calculated based on their respective molecular weights.

Mineralogy was determined from the fine soil fraction (0-20 μm) of the same sample used to determine the soil texture of each lot whenever possible. This relatively broad particle fraction was chosen in order to measure the bulk of primary silicates and secondary clay minerals that play a role in plant growth (Mengel and Kirkby, 2001). A total element analysis was also performed on these sieved fine soil samples because this fraction's chemical make-up is particularly involved in the replenishment of the soil solution. Each sample was initially wet-sieved manually with nanopure H_2O to remove the >63 µm soil fraction. The residual solution was then sieved to 20 µm on a magnetic stirrer until water passing through it was clear. X-ray diffraction analysis (Siemens D-5000 diffractometer) was performed on a dried subsample of the suspended 0-20 µm soil solution. The solution was then left to dry at room temperature for several weeks. Some samples were decanted when clear to hasten the drying process. Dried soil samples were formed into pellets with a Spex X-Pess press. Total element analysis was performed using a wavelength dispersive X-ray fluorescence spectrometer (S-4 Pioneer).

Frozen soil samples were vacuum dried to remove interstitial water. Samples were then lightly crushed using a mortar and pestle and sieved at 2 mm before being reduced to a fine powder with a steel percussion grinder. Ten representative samples were analyzed by coulometry to confirm the absence of carbonate in soils of the study area. Total C and total N of all samples was then determined by combustion with a Carlo-Erba analyzer (model NA-1500) (Verardo D.J *et al.*, 1990). Iron and aluminum oxy-hydroxide content of one sample per lot (referred to in this article as Fe_{cdb} and Al_{cdb}) were extracted with citrate-dithionate-bicarbonate and measured by atomic absorption (Lucotte and d'Anglejan, 1985).

2.2.4 Data analysis

Statistical analysis was performed using JMP 7.0.1 (SAS Institute inc.), Canoco for Windows 4.54 (Microcomputer Power) and Progiciel R 4.1. Maps were prepared using Quantum GIS 1.0.2 LTS and GRASS 6.4 while tables and graphs (except ordination plots produced using Canoco) were created using Excel 2008 (Microsoft inc.) and KaleidaGraph 4.04 (Synergy Software) respectively.

The atomic ratio of C:N was calculated according to Peverill *et al.* (1999). Of the 29 elements detected during total element analysis, only the values of the total forms of each of the three exchangeable cations under study (Ca^{2+}, Mg^{2+}, K^+) were retained. Of the 8 minerals detected, calcite and dolomite content were not analyzed because more than 45% of their sample values were zero. Variables were linearized before conducting multiple linear regressions. Variables expressed in percentage (texture, mineralogy) were coded using the arcsine transformation [$y' = \text{arcsine}\sqrt{(y/100)}$] (Legendre and Legendre, 1998). All other environmental variables were transformed logarithmically [$y' = \ln(100y)$].

The data set was scanned to detect outlying samples using multivariate correlations. The effect of the removal of outliers on linear regressions was evaluated by observing changes in the F ratio calculated before a stepwise multiple regression fit. Two samples originating from unique environments (a creek bed and a rocky outcrop respectively) with extreme values for several variables were subsequently removed (fig. 2.2). Furthermore, two additional samples with zeros values for Ca_{tf} were removed from analyses involving this variable (fig. 2.2).

A principal component analysis (PCA) of the exchangeable major cations was performed. Pearson product-moment correlations were computed between them. The relative contribution of each exchangeable major cation to total exchangeable cation ($Ca^{2+} + Mg^{2+} + K^{+}$) content was determined from the transformed values.

The difference between the total content of an element and its exchangeable form was tested to ensure that the observed total content values represented non-exchangeable forms fixed to the mineral structure. Exchangeable cation values (cmol/kg) were converted into ppm using the following equation:

$$f(x) = x \text{ cmol/kg x meq x } 10 \qquad \text{where meq} = \text{atomic weight (g) / valence}$$

The total elemental content (ppm) of a soil was estimated by multiplying values by the weight percentage of fine soil (0-20 μm) extracted from each sample. Differences in the distribution of exchangeable major cations (Ca^{2+}, Mg^{2+} and K^{+}) and major cations fixed to the minerals (Ca_{tf}, Mg_{tf} and K_{tf} respectively) were tested using the matched pairs Wilcoxon Sign-Rank test because total content variables did not satisfy normality and homoscedasticity requirements. Total content variables that did not show a significant difference with their exchangeable cation forms were removed from subsequent analyses.

Spearman ρ correlations were computed between the retained total element content variables. Potential outliers were removed to confirm correlations. A group of samples with relatively small values of both Mg_{tf} and K_{tf} was identified. Multiple Bonferroni-adjusted Wilcoxon-Man-Whitney tests were conducted with the explanatory variables (k=18, p=0.0028) to identify variables associated to them.

Spearman ρ correlations were also computed to identify explanatory variables that were significantly correlated to the exchangeable major cations. Correlations for exchangeable Ca^{2+} ($k=16$) were considered significant when $p<0{,}0031$ while exchangeable Mg^{2+} and exchangeable K^{+} were when

$p<0.0029$.

Refined silt and sand fractions were plotted against an increasing soil clay content axis using a weighted curve fit (60% smoothing factor). Spearman ρ correlations between the exchangeable major cations and all particle sizes were performed.

Finally, multiple regressions were performed for each of the exchangeable major cations. Models were built using a stepwise variable selection of environmental variables ($p<0.05$ as an entering and keeping level). Normality of the predicted–observed residuals was verified with a Shapiro-Wilk W test.

2.3 Results

2.3.1 Exchangeable major cations

Both the mean and the standard deviations of each exchangeable major cation are identified in figure 2.3. The relative contributions of each exchangeable major cation to the total exchangeable cation content ($Ca^{2+} + Mg^{2+} + K^{+}$) of the <2 mm soil fraction are presented in the same figure. Results of the PCA and the Pearson product moment correlations for the three exchangeable major cations are given in figure 2.4. The ranges of each of the exchangeable major cations observed are given in appendix D. Exchangeable Ca^{2+} and exchangeable Mg^{2+} are very highly significantly correlated and responsible for the bulk (89.16%) of the total exchangeable cation content of soils. Exchangeable K^{+} is distributed differently albeit being very significantly associated to exchangeable Mg^{2+}.

2.3.2 Major cations fixed to the mineral structure of soils

Results of the test of difference between the exchangeable (<2 mm soil fraction) and total (0-20 μm soil fraction) content of each major cation are given in figure 2.5. Exchangeable Ca^{2+} (<2 mm soil fraction) and Ca_{tf} fixed to minerals (0-20 μm soil fraction) did not differ significantly. The very highly significant correlation between Mg_{tf} and K_{tf} fixed to minerals (0-20 μm soil fraction) is illustrated in figure 2.6. Samples ($n=11$) with extremely small Mg_{tf} (≤96 ppm) and K_{tf} values (≤441 ppm) were significantly associated with soils of low density (median=1.11 g/cm^3, $p<0.0001$), high clay (median=48.03%, $p<0.0001$), high Al_{cdb} (median=565.30 μmol/kg, $p=0.0002$) and low sand content (median=16.00%, $p=0.0023$).

2.3.3 Soil texture

Variations in silt and sand soil fractions along a clay content gradient are illustrated in figure 2.7. Spearman ρ correlations for each are given in table 2.1.

2.3.4 Soil property relationships

Spearman ρ correlations between exchangeable major cations of the <2 mm soil fraction and all explanatory soil variables other than texture (tab. 2.1) are given in table 2.2. Both the medians and the ranges of these explanatory variables are presented in appendix D. Multiple linear regression models forecasting the content of each of the exchangeable major cations are given in table 2.3. The first model presented for each exchangeable major cation (tab. 2.3, models 1a, 2a and 3a) is composed of those explanatory variables that best forecast it. When applicable, alternative models (tab. 2.3, models 1b and 2b) provide an indication of the substitutability of those variables. A correlation matrix including most of the measured explanatory variables is provided in appendix E.

2.4 Discussion

2.4.1 Variations in the distributions of each of the exchangeable major cations

While exchangeable Ca^{2+} is the principal ion driving the content of total major cations in the <2 mm fraction of soils of the studied region, exchangeable Mg^{2+} also plays a considerable role (fig. 2.3). These two ions are however very highly significantly correlated to each other, further reducing the role of exchangeable K^{+} on total major soil cation content (figs. 2.3 and 2.4). Exchangeable Ca^{2+} and exchangeable Mg^{2+} are also significantly correlated to soil pH suggesting that the concentration of these ions is what largely determines soil acidity (chap. 1). Albeit being highly significantly correlated to exchangeable Mg^{2+}, the highly contrasting distribution of exchangeable K^{+} with regards to total cation content might have a unique influence on plant distribution patterns.

2.4.2 The relevance of nutrient reserves to the exchangeable major cation content of soils

The high exchangeable Mg^{2+}:Mg_{tf} and exchangeable K^+:K_{tf} ratios indicate that important quantities of these nutrients are bound to the fine soil fraction (0-20 μm) in forms unavailable to plants (fig. 2.5). These deposits may be acting as long term exchangeable Mg^{2+} and exchangeable K^+ sources and/or sinks that can be slowly accessed via plant mediated weathering mechanisms (Berner and Berner, 2005 ; Kelly *et al.*, 1998). On the other hand, the lack of a significant difference between Ca_{tf} and exchangeable Ca^{2+} is in agreement with prior work on similarly highly weathered soils of the Brazilian *cerrado* (Marques *et al.*, 2004). While the bulk of exchangeable Ca^{2+} present in the <2 mm soil fraction may have originated from the soils' initial weathering, the lack of non-exchangeable forms of Ca_{tf} suggest that its current calcium budget is now governed by biotic processes (Vitousek and Sanford Jr, 1986). Indeed, tropical plant communities have adapted to these extremely poor soils by developing highly efficient nutrient recycling mechanisms in which the bulk of nutrients are stored in the aboveground biomass. In these closed systems, nutrients that return to the soil solution via throughfall and litterfall decomposition are either temporarily bound to mineral cation exchange sites and organic matter and/or immediately re-adsorbed by bacteria, mychorrizae and plant roots (Richards, 1996).

The very highly significant correlation between Mg_{tf} and K_{tf} of the fine soil fraction (0-20 μm) indicates that they are not only governed by the same soil factors but perhaps components of a single clay species. In fact, these elements are most strongly correlated to illite (app. E), a non-expanding phyllosilicate whose chemical composition, while prone to considerable ion substitution, includes both magnesium and potassium:

$$(K,H_3O)(Al,Mg,Fe)_2(Si,Al)_4O_{10}[(OH)_2,(H_2O)]$$

Curiously, while K_{tf} of the fine soil fraction (0-20 μm) was both significantly correlated to exchangeable K^+ of the <2 mm soil fraction (tab. 2.2) and its strongest predictive parameter (tab. 2.3, models 3a), Mg_{tf} (0-20 μm) was not significantly associated to exchangeable Mg^{2+} (<2 mm soil fraction) (tab. 2.2) and only a second order regressor (tab. 2.3, models 2b). However, if illite is the main depository of magnesium and potassium in soils within our study area, this divergence can be understood in terms of this clay mineral's structure. As illite's interlayer space is mainly occupied by exchangeable K^+, this ion becomes more readily available during weathering than exchangeable Mg^{2+}, restricted to octahedral sites (Mengel and Kirkby, 2001 ; Schulze, 1989). Furthermore, while illite's interlayer space is specific to ions of a similar radius such as K^+, both Al^{3+} and Fe^{3+} commonly substitute Mg^{2+}. This behavior probably blurs any clear relationship between the soil's exchangeable (<2 mm soil fraction) and non-exchangeable (0-20 μm) magnesium cation content (tab. 2.2 and tab. 2.3, models 2a-b). Rather, the very highly significant correlation between exchangeable Mg^{2+} and exchangeable Ca^{2+} (<2 mm soil fraction) (fig. 2.4) suggests that Mg^{2+} might be controlled by the same physical and chemical soil factors as Ca^{2+} (tab. 2.3, models 1a-b and 2a-b). Alternatively, the pH variations, largely determined by the relatively important exchangeable Ca^{2+} soil concentrations, might also exert a strong influence on availability of exchangeable Mg^{2+} regardless of the fine soil fraction's (0-20 μm) non-exchangeable Mg_{tf} reserves (chap. 1).

2.4.3 The relevance of fine silts to the exchangeable major cation content of soils

Clay particles play a fundamental role in the retention and exchange of soil cations as opposed to sands, largely composed of the sterile quartz mineral (Mengel and Kirkby, 2001). As a result, clay content is frequently used as an indicator of soil fertility, while sandy soils of poor clay content are symptomatic of nutrient poor soils. While this model is deprived of the contribution of silt to nutrient dynamics, it has the benefit of providing a simple physical indication of soil fertility. However, in our study, exchangeable major cation content (<2 mm soil fraction) does not vary strongly in accordance with conventional soil texture fractions (0-2, 2-50 and 500-2000 μm) (tab. 2.1). Furthermore, we observed a decrease in the exchangeable K^+ ion content of the <2mm soil fraction in response to an increasing clay gradient. These findings nonetheless support recent observations within both the nearby Tapajós National Forest (Silver *et al.*, 2000) and elsewhere (Hall *et al.*, 2004). While Silver *et al.* (2000) showed a strong correlations between nitrogen, phosphorus and clay content, they hypothesized that other factors than texture must be exerting a strong influence on the content of exchangeable major cations.

While some alternative mechanisms will be proposed later, the refined silt and sand measurements we achieved with laser diffraction sheds light on important relationships between cations and texture that were otherwise obscured by conventional soil texture analyses. Firstly, the fine silt fraction (2-10 μm), while significantly correlated to clays, is the fraction most strongly associated to exchangeable Ca^{2+} and Mg^{2+} of the <2 mm soil fraction (tab. 2.1). This suggests that fine silts (2-10 μm) may effectively outweigh clays (0-2 μm) in regulating the availability of the bulk of cations in soils whose clay fraction is highly weathered and dominated by relatively inert quartz and 1:1 clay particles such as kaolinite. In fact, considering that cation adsorption and exchange take place at the surface of particles and that smaller particles provide a relatively greater surface area than larger ones, the fine silt fraction does contribute to soil fertility in a similar manner as do clay sized particles (0-2 μm). The role of fine silts in cation retention is further supported by the fact that several primary silicates (e.g. micas and feldspars) and secondary minerals of known significance to plant growth are between 2 and 10 μm in size (Mengel and Kirkby, 2001). Interestingly, the fine silt fraction of the soils we studied increased linearly with clays up to approximately 30% (r^2=0.3456) after which it varied independently (fig. 2.7a). This unique pattern can exert a strong alternative effect on soil cation content because fine silts are a relatively important soil component in the area we studied. Further research focused on identifying and quantifying the relative distribution of mineral species throughout the clay and silt fractions we determined would help us better understand the rôle of soil texture in the availability of cations of highly weathered tropical soils.

The importance of fine silts (0-20 μm) to the distribution of exchangeable major cations suggests that alternatives to the conventional soil texture classification scheme could better reflect soil fertility. As we examined our data for clues, we noticed that when fractions 2-10 and 10-20 μm were consolidated, the relationship of the resulting fraction to the cation content of the <2 mm soil fraction did not change. Additionally, while the proportion of particles between 20 and 500 μm decreased similarly along the clay gradient, coarse sand content (500-2000 μm) remained nearly constant while contributing relatively little to total sand content (figs. 2.7a-b). These trends suggest that in the absence of technologically intensive particle sizing technologies such as laser diffraction, simpler methods (hydrometer, pipette) could be used to provide an alternative tripartite particle sizing scheme such as 0-2, 2-20 and 20-500 μm from which we may more precisely estimate the exchangeable major cation content of soils within the Lower Tapajós region.

2.4.4 Soil factors as determinants of the exchangeable major cation content of soils

2.4.4.1 Calcium

The exchangeable Ca^{2+} of the <2 mm soil fraction was poorly associated to the measured soil factors (tabs. 2.1-2.3) albeit its relatively large concentration gradient across the study area (fig. 2.3). This suggests that exchangeable Ca^{2+} is retained within a closed system largely governed by plant mediated biological processes (Burnham, 1989 ; Herrera, 1985). Nonetheless, a combination of associated soil factors predicted 39.7% of exchangeable Ca^{2+} variations (tab. 2.3, models 1a-b). Exchangeable Ca^{2+} was most strongly and positively regressed to the fine silt (2-10μm) soil fraction followed by the iron oxy-hydroxide (Fe_{cdb}) content of the <2 mm soil fraction. While Fe_{cdb} was correlated to soil clay content (app. E), it was more strongly so to the fine silt fraction (r=0.8647, p<0.0001) indicating that an important proportion of the soil's iron oxy-hydroxides may be present as concretions on particles of this size (Allen and Hajek, 1989). Under this scenario, these concretions are the prominent features adsorbing exchangeable Ca^{2+} in the soil before being taken up again by the biota (Herrera, 1985).

While the exchangeable Ca^{2+} ion content of soils was positively regressed to fine silts and iron oxy-hydroxides, it was negatively associated to C concentrations and C:N ratios of the <2 mm soil fraction (app. 5). This observation suggests that organic compounds may indeed be competitively adsorbed onto iron oxy-hydroxides as shown in previous studies (Kaiser and Guggenberger, 2000 ; Schwertmann and Taylor, 1989). Therefore, in situations where C content is important, the role of iron oxy-hydroxides in cation retention and exchange is effectively reduced.

2.4.4.2 Magnesium

Of the three major cations we studied, the exchangeable Mg^{2+} of the <2 mm soil fraction was best forecasted by the measured soil factors (tab. 2.3). Exchangeable Mg^{2+} variations primarily occurred in association with the fine silt soil content (r^2=0.41) and at a rate more than twice that of exchangeable Ca^{2+}. The increased susceptibility of exchangeable Mg^{2+} to soil property variations could result from its relatively lower solubility, inadvertently rendering it more susceptible to leaching when not adsorbed. Alternatively, redness rating (r^2=0.33), a visual indicator for the presence of iron oxy-hydroxides, could replace fine silt content in our exchangeable Mg^{2+} models without a major loss in the proportion of the variance explained. Additionally, while the r^2 of Fe_{cdb} of the <2 mm soil fraction was relatively lower at 0.22, it explained the variance of exchangeable Mg^{2+} at a rate only slightly higher than for exchangeable Ca^{2+} (r^2=0.15). These results imply that it is the iron oxy-hydroxides bound to the fine silts that are primarily involved in the retention of the bulk of exchangeable cations (Ca^{2+} + Mg^{2+}) in the soil. Similarly, the secondary negative regression of the C:N ratio with exchangeable Mg^{2+} implies the same mechanisms as for Ca^{2+}. However, unlike exchangeable Ca^{2+}, non-exchangeable forms of Mg_{tf} present in the fine soil fraction (0-20 μm) appear to play a considerable, albeit secondary role in forecasting the exchangeable Mg^{2+} of the <2 mm soil fraction. This suggests that the ongoing weathering of Mg_{tf} ions fixed to minerals (0-20 μm soil fraction) may still be contributing to the replenishment of the soils' exchangeable Mg^{2+} of the <2 mm soil fraction.

Nevertheless, the extremely small Mg_{tf} values of the fine soil fraction (0-20 μm) we observed in very clayey soils and exchangeable Mg^{2+}'s high correlation to exchangeable Ca^{2+} suggest that the bulk of the soils' exchangeable Mg^{2+} (<2 soil fraction) is mostly recharged via plant mediated nutrient cycling mechanisms (Vitousek and Sanford Jr, 1986).

2.4.4.3 Potassium

The unique distribution of the exchangeable K^+ of the <2 mm soil fraction throughout the study area is symptomatic of its particularly strong relationship to non-exchangeable K_{tf} ions fixed to the minerals of the fine soil fraction (0-20 μm) (tab. 2.3). With an exchangeable to non-exchangeable ratio of approximately 1 :400, the soil's exchangeable K^+ supply is clearly dependent on relatively important mineral reserves (fig. 2.5). Even though the bulk of the K_{tf} present in soil minerals has no bearing on plant growth, research has shown that a non-exchangeable fraction located in the interlayers of clay and silt sized layer silicates such as illite does play a substantial role in supplying plants with exchangeable K^+ (Mengel and Kirkby, 2001 ; Mengel *et al.*, 1998). While this exchangeable K^+ reserve might be kept near equilibrium in healthy forest ecosystems via the mineral adsorption of exchangeable K^+ inputs via throughfall and litterfall decomposition, its role in plant growth is nonetheless crucial. This is particularly true for soils dominated by kaolinite clays as in the case of our study area, where exchangeable K^+ in soil solution is particularly prone to leaching (app. D). Ultimately, even though the salt-based extraction of exchangeable K^+ we performed has been justly criticized as a poor indicator of K^+ availability due to its inability to measure this non-exchangeable fraction present in clay interstices and available to plants, our results coincide with others in showing a positive relationship between the total and exchangeable forms of K^+ (Martin and Sparks, 1983). Furthermore, the observation of extremely low levels of K_{tf} fixed to minerals of the fine fraction (0-20 μm) of soils with the highest clay contents clearly illustrates that we must be cautious of not blindly associating a high clay content to soil fertility. Fortunately, this oversimplification can be avoided by regularly supplementing soil texture data with a more detailed analysis of the minerals involved.

2.5 Conclusion

Even though the nutrient pools of Amazonian uplands have been largely depleted through extensive weathering, we have observed important major cation variations at the local scale. While exchangeable Ca^{2+} and exchangeable Mg^{2+} of the <2 mm soil fraction are distributed similarly across the landscape, effectively controlling total soil cation content, exchangeable K^+ behaves rather differently. On the one hand, the larger exchangeable Ca^{2+} cations are retained in the soil by oxy-hydroxides associated to the fine silt fraction. Under this scenario, C competes with Ca^{2+} for available exchange sites. Alternatively, the smaller, highly soluble exchangeable K^+ ions are primarily associated to relatively important non-exchangeable reserves of K_{tf} fixed to the mineral structure of the fine soil fraction (0-20 μm). Exchangeable Mg^{2+}, of medium size, was strongly associated to the same soil factors that control exchangeable Ca^{2+} while also being significantly associated to its non-exchangeable forms present in the fine soil fraction (0-20 μm). Curiously, the strong correlation between non-exchangeable Mg_{tf} and non-exchangeable K_{tf} suggests that they are basic components of illite clays, present in small amounts throughout the study region.

While the mineralogical, elemental and refined soil texture analyses we conducted improved our understanding of local soil cation variations in the Lower Tapajós region, it also generated some important considerations for future research in tropical plant ecology. First, important differences between the distributions of some cations of the <2 mm soil fraction such as exchangeable K^+ indicate that each may have a unique effect on species distribution. The role of each cation on plant distribution should therefore be prioritized over that of total cation content or effective CEC in studies associating plant distribution with soil factors. Secondly, even though clay sized particles play a fundamental role in the nutrient dynamics of most soils, fine silts can play an even greater role in upland soils of the Amazon Basin. Conventional granulometric methods should be modified to account for this fraction because its effect is currently blurred by the conventional soil texture classification scheme. Finally, while our total element analysis of the fine soil fraction (0-20 μm) revealed that soils in the vicinity of Lake Araipa are depleted of fixed Ca_{tf}, appreciable amounts of Mg_{tf} and K_{tf} remain within its mineral structure. These nutrient reserves might play a critical role in the distribution of certain plant species capable of accessing them via specialized weathering mechanisms. Particular attention should be given to the non-exchangeable potassium fraction present in clay interstices whose role in plant growth is well known but commonly neglected by conventional salt-based cation extraction procedures. Indeed, several improvements to the sampling and analysis of soils within the field of tropical plant ecology are required before we can expect to consistently detect strong plant responses to soil factors in our experiments.

2.6 Tables and figures

Figure 2.1 Location map of the study region. Water bodies are in black, forested areas are in grey and unforested areas are in white. The specific study area is framed in white.

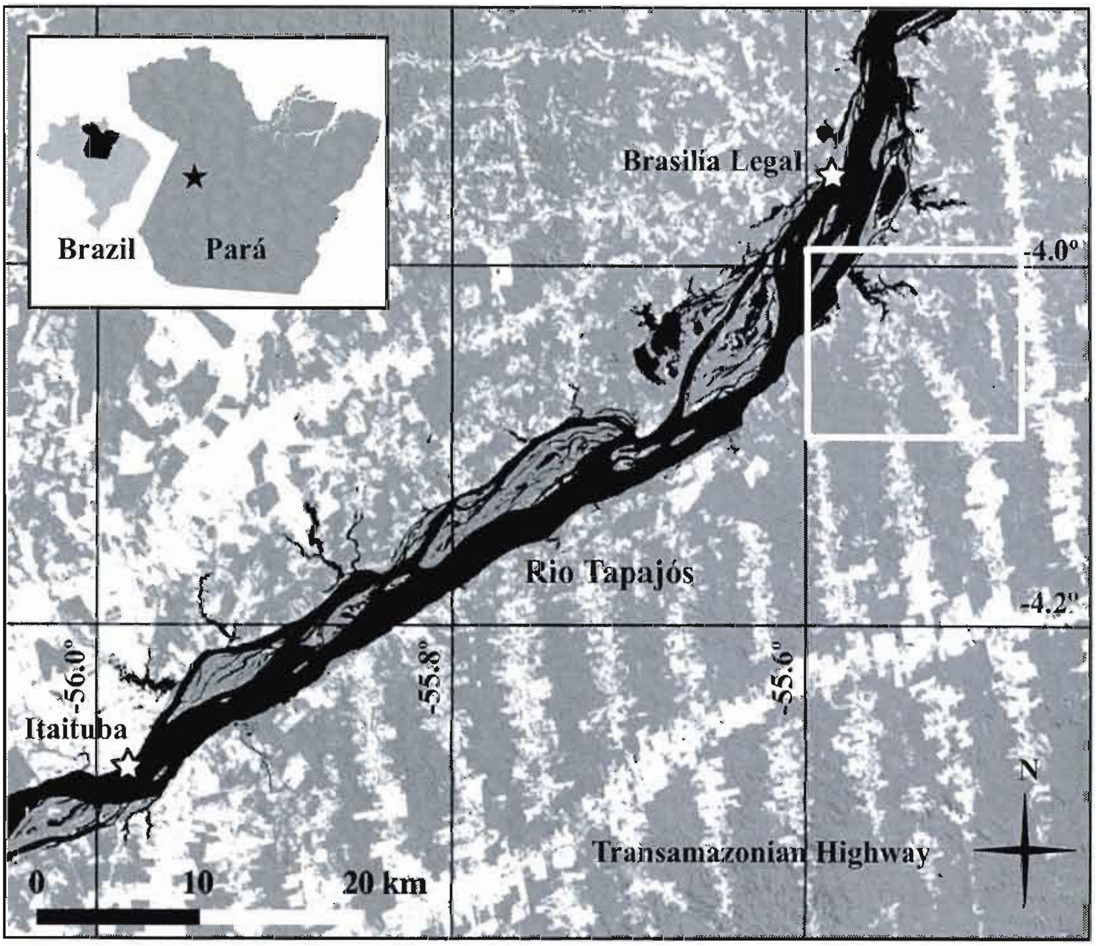

Figure 2.2 Location map of soil sampling plots within the specific study area near Lake Araipa along the Lower Tapajós River (Pará, Brazil). Water bodies are in black, forested areas are in grey and unforested areas are in white. Upland streams (predicted from a SRTM DEM) are identified by dashed lines. Transects are identified by their respective numbers and sampled lots are identified with symbols. Retained samples are identified with the symbol O. Outliers removed during data analysis are identified with the symbol ✕ and samples with zero values for Ca$_{tf}$ are identified with the symbol ●.

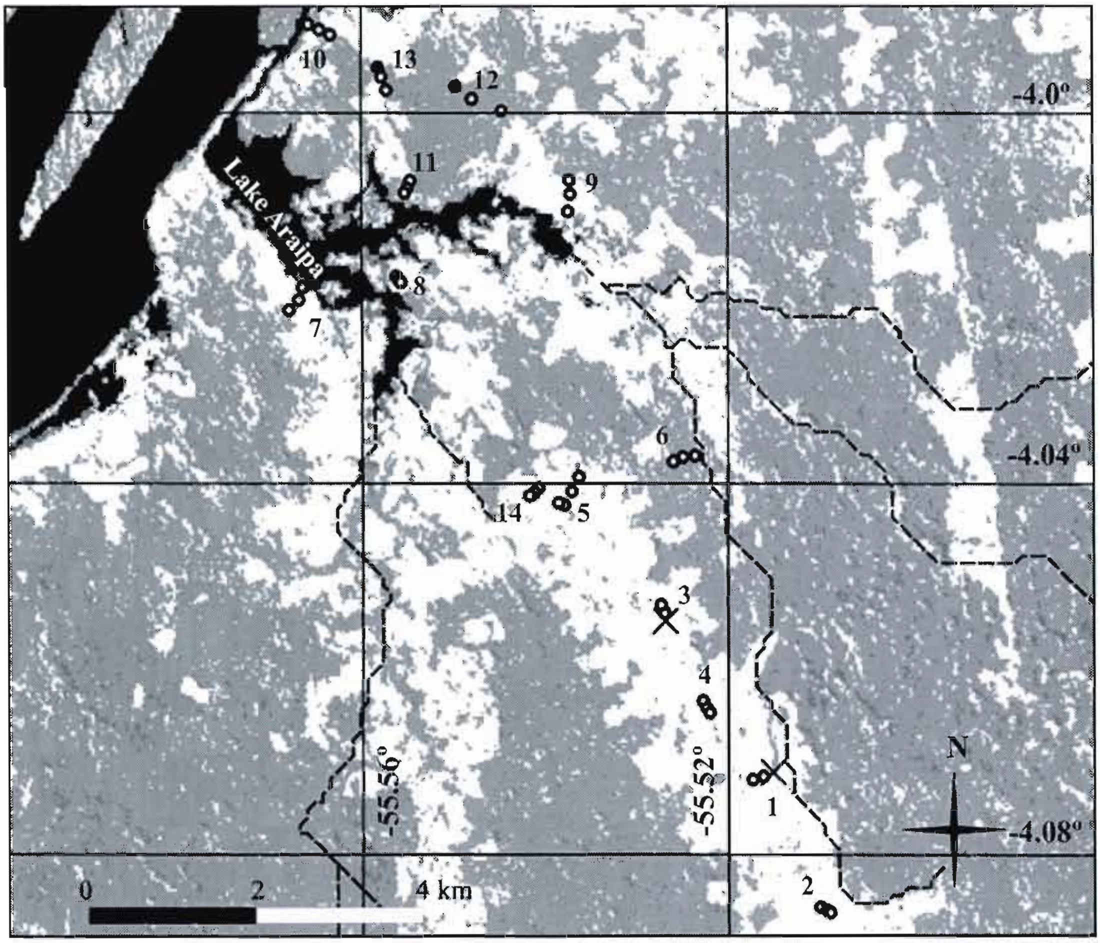

Figure 2.3 Mean exchangeable major cation content of soils (<2 mm fraction) sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil) and their respective standard error intervals. The average contribution of each exchangeable major cation to total exchangeable cation ($Ca^{2+} + Mg^{2+} + K^{+}$) content is given in bold.

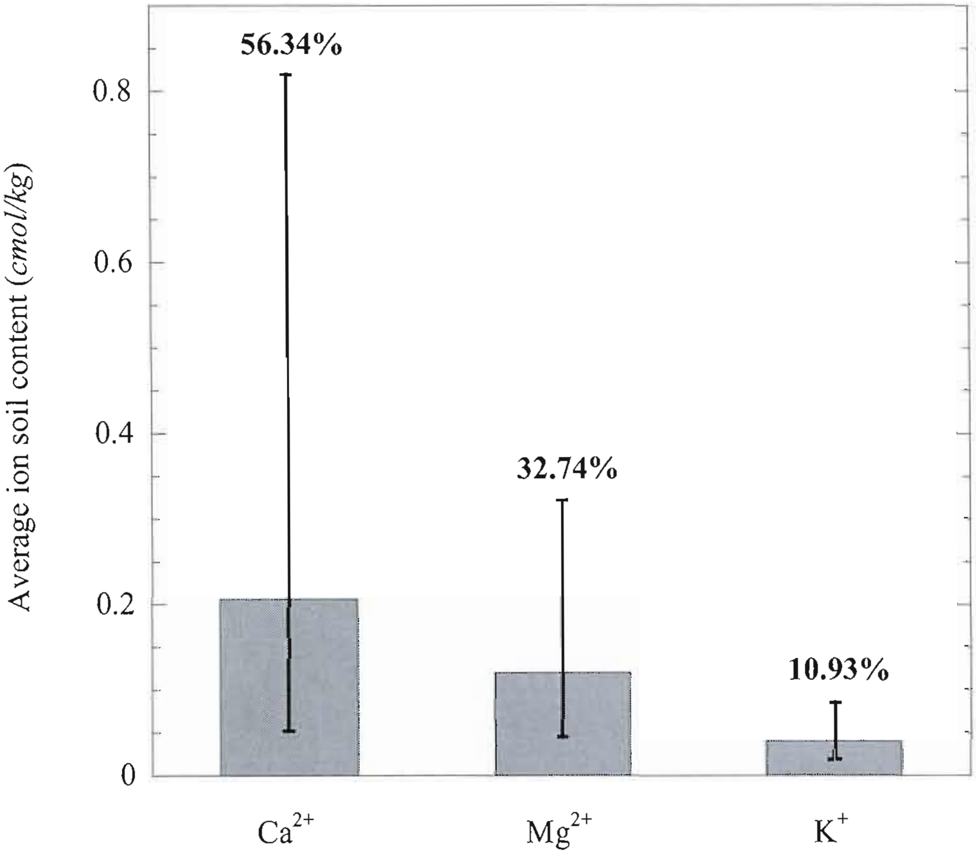

Figure 2.4 Principal component analysis (PCA) ordination of the exchangeable Ca^{2+}, Mg^{2+} and K^+ content of soils (<2 mm soil fraction) sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil). Significant correlations are identified with a bold line while non-significant correlations are identified with a dotted line. Pearson moment correlations (r_s) are given for each pair with probabilities in brackets.

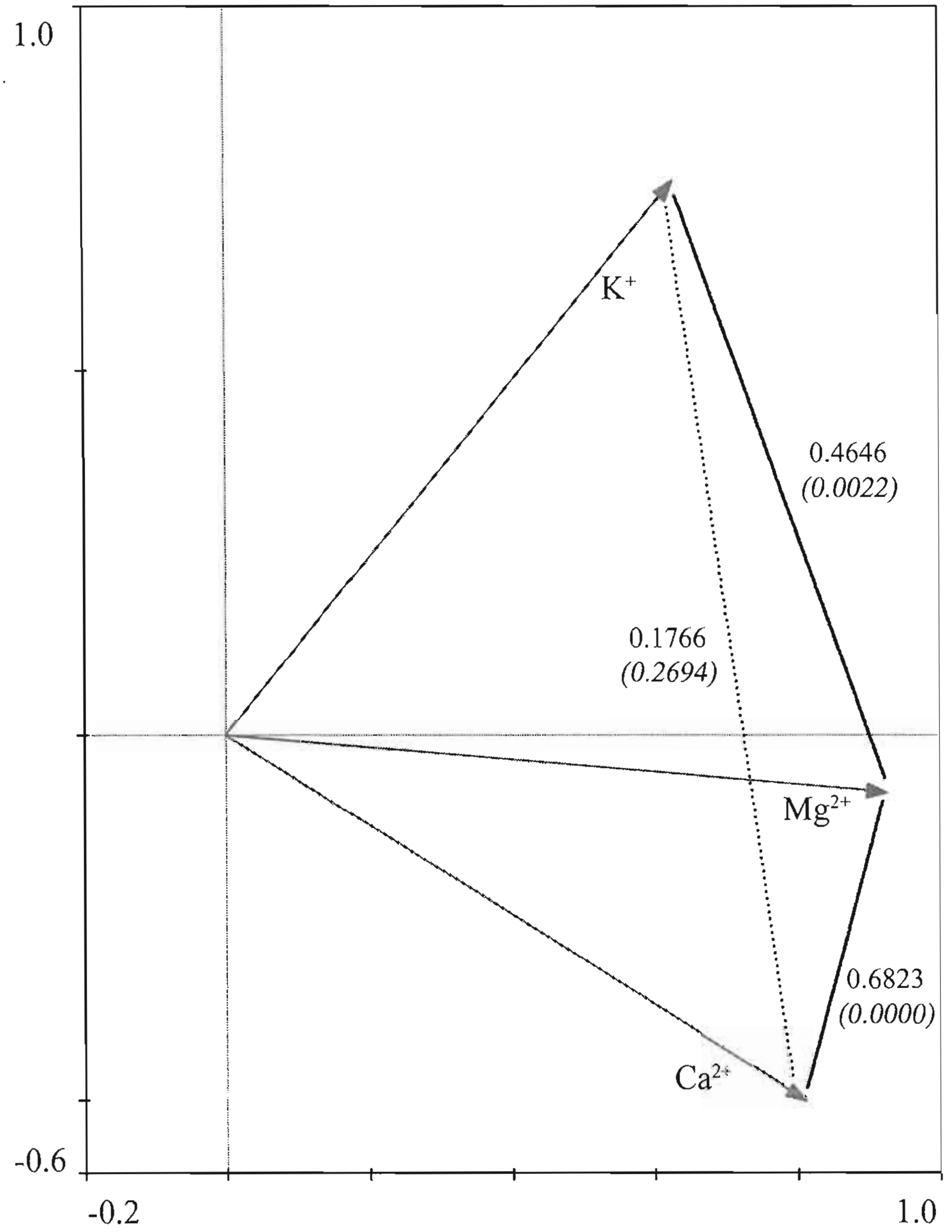

Figure 2.5 Box-plots comparing the distributions of exchangeable (<2 mm soil fraction) and total (0-20 μm soil fraction) *(a)* calcium, *(b)* magnesium and *(c)* potassium of soils sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil). The data was plotted on a logarithmic scale to show the distribution of lower values. Pairs were tested for significant differences using the Wilcoxon-Man-Whitney test. Results are identified in bold letters. A significant difference indicates that non-ionic forms of the element are present in the soil.

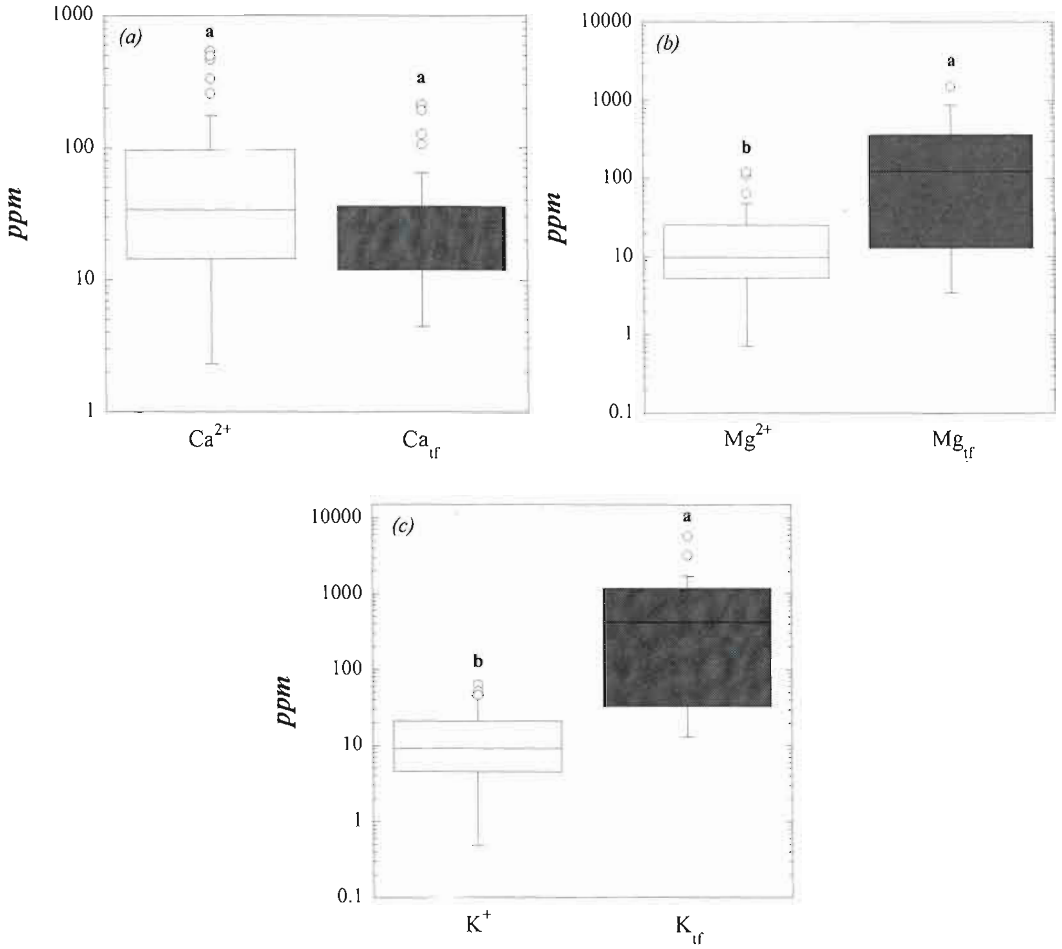

Figure 2.6 Correlation between the total magnesium (Mg_{tf}) and potassium (K_{tf}) content of the soil fine fraction (0-20 μm) of soils sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil). Samples ($n = 11$) with extremely small Mg_{tf} (max.=96ppm) and K_{tf} values (max.=441ppm) are identified with the symbol O while the remaining samples are identified with the symbol ●. The Spearman ρ correlation (r_s) and its associated probability are given on the graph. The correlation was not significantly altered when the two variables with the highest values we removed.

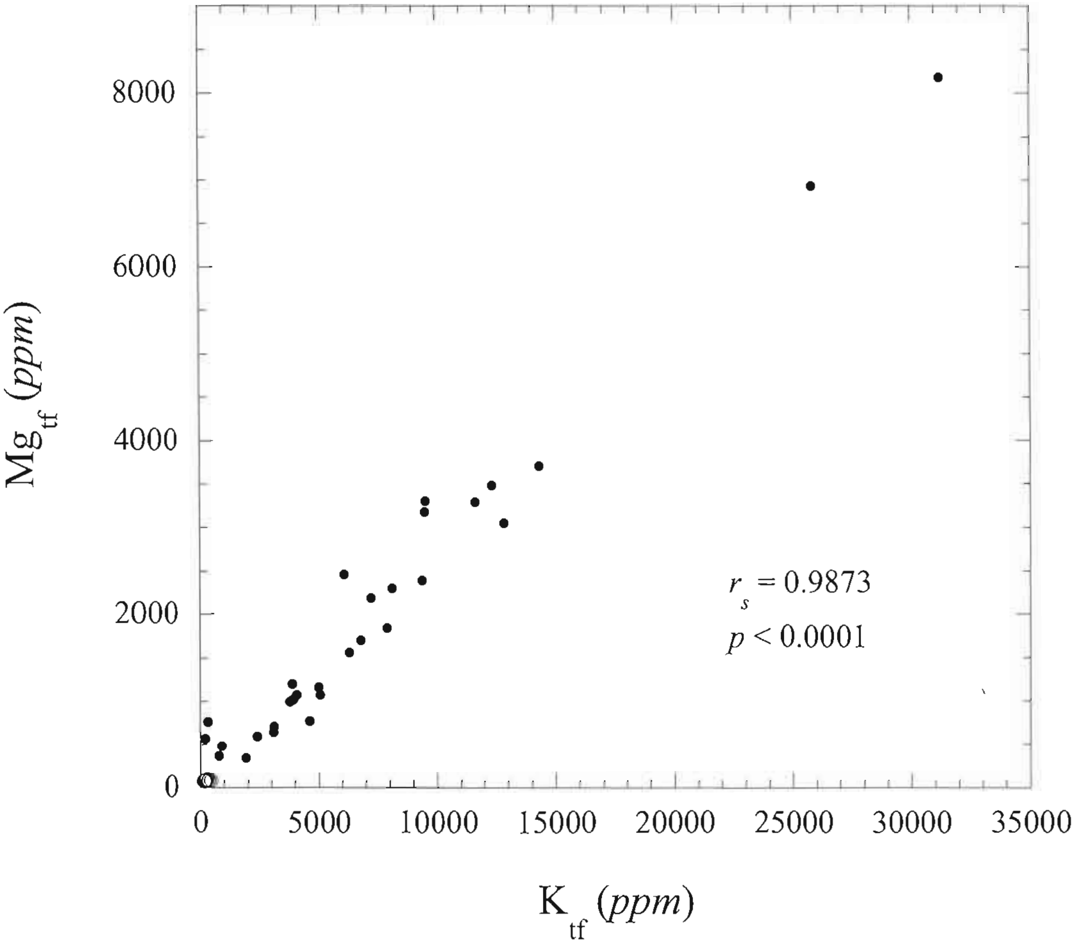

Figure 2.7 Variations in *(a)* silt and *(b)* sand soil fractions along a clay content gradient sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil)

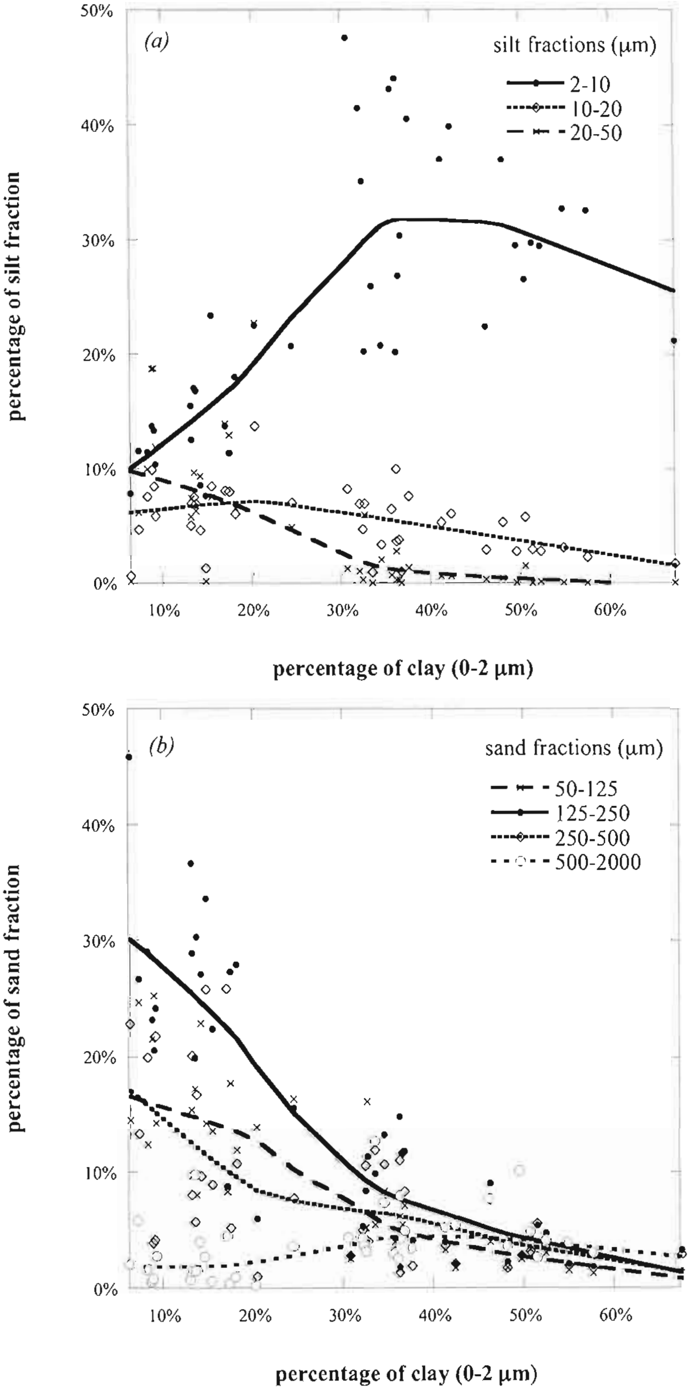

Table 2.1 Spearman ρ correlation matrix of soil texture fractions as they relate to clay and the exchangeable major cation content of the <2 mm fraction of soils sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil)

Texture class	Size (μm)	Clay	Ca^{2+}	Mg^{2+}	K^{+}
Clay	0-2		0.1427 *(0.3735)*	0.2317 *(0.1449)*	**-0.4402** ***(0.0040)***
Silt	2-50	0.2449 *(0.1227)*	0.1873 *(0.2410)*	0.4082 *(0.0081)*	0.0563 *(0.7268)*
fine	2-10	**0.7176** ***(0.0000)***	0.4016 *(0.0093)*	**0.5700** ***(0.0001)***	-0.1434 *(0.3712)*
medium	10-20	-0.4176 *(0.0066)*	0.0510 *(0.7517)*	0.1824 *(0.2537)*	0.3846 *(0.0130)*
coarse	20-50	**-0.7103** ***(0.0000)***	-0.0865 *(0.5906)*	-0.0983 *(0.5409)*	**0.4303** ***(0.0050)***
Sand	50-2000	**-0.8648** ***(0.0000)***	-0.2415 *(0.1283)*	**-0.4340** ***(0.0046)***	0.2887 *(0.0672)*
very fine	50-125	**-0.8463** ***(0.0000)***	-0.3000 *(0.0567)*	-0.3794 *(0.0144)*	0.3464 *(0.0265)*
fine	125-250	**-0.8195** ***(0.0000)***	-0.2571 *(0.1046)*	-0.3936 *(0.0109)*	0.2767 *(0.0799)*
medium	250-500	**-0.6082** ***(0.0000)***	-0.1019 *(0.5260)*	-0.3418 *(0.0287)*	0.1598 *(0.3184)*
coarse	500-2000	0.4003 *(0.0095)*	0.2641 *(0.0952)*	0.0718 *(0.6556)*	-0.0486 *(0.7628)*

Significant Bonferonni-adjusted correlations ($p<0.0056$ for clay and $p<0.005$ for excahngeable cation content) are given in bold.

Table 2.2 Spearman ρ correlation matrix of soil factors as they relate to the exchangeable major cation content of the <2 mm fraction of soils sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil)

	Ca^{2+}	Mg^{2+}	K^{+}
k	*13*	*14*	*14*
p	*0.0038*	*0.0036*	*0.0036*
density	-0.1028	-0.2089	**0.4615**
	(0.5333)	*(0.1900)*	***(0.0024)***
redness rating	0.3151	**0.5604**	0.2929
	(0.0507)	***(0.0001)***	*(0.0631)*
C total	-0.0221	0.1631	-0.3315
	(0.8939)	*(0.3084)*	*(0.0342)*
N total	0.1990	**0.5507**	-0.0855
	(0.2246)	***(0.0002)***	*(0.5949)*
C:N	-0.2808	**-0.4578**	**-0.4993**
	(0.0834)	***(0.0026)***	***(0.0009)***
Al_{cdb}	0.2089	0.2798	-0.3967
	(0.2018)	*(0.0764)*	*(0.0102)*
Fe_{cdb}	0.3747	0.3977	-0.3051
	(0.0188)	*(0.0100)*	*(0.0525)*
feldspar-K*	0.2527	0.4341	0.0749
	(0.1207)	*(0.0046)*	*(0.6418)*
hematite*	0.3228	0.4172	-0.1812
	(0.0450)	*(0.0067)*	*(0.2569)*
illite*	-0.0397	0.2817	0.3289
	(0.8105)	*(0.0744)*	*(0.0357)*
kaolinite*	0.0729	-0.2322	-0.3146
	(0.6593)	*(0.1440)*	*(0.0451)*
plagiocene*	0.0214	0.1288	0.2525
	(0.8973)	*(0.4223)*	*(0.1112)*
quartz*	-0.0595	0.1834	0.3432
	(0.7189)	*(0.2509)*	*(0.0280)*
Mg_{tf}*		0.2890	
		(0.0669)	
K_{tf}*			**0.6818**
			(0.0000)

Probabilities are given in brackets. Significant Bonferroni-adjusted correlations are given in bold. Mg_{tf} and K_{tf} are the total forms of magnesium and potassium respectively. Variables derived from the fine soil fraction (0-20 µm) are identified with asterisks. k, number of variables; p, Bonferonni-adjusted probability.

Table 2.3 Multiple regression models relating the exchangeable major cation content of the <2 mm soil fraction to soil factors sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil)

Model	Regression								r^2_{adjusted}	*SE*	*F*	*p*
1a	$\ln(\mathrm{Ca}^{2+})$ =	7.07 ± 1.78	+ 7.16 ± 1.52	arcsin√fine silt	- 2.09 ± 0.5	ln(C)	+ 10.37 ± 4.81	arcsin√hematite	0.397	1.04	9.77	0.0001
	r^2_{partial}			0.19		0.18		0.07				
1b	$\ln(\mathrm{Ca}^{2+})$ =	14.33 ± 5.62	+ 0.55 ± 0.19	$\ln(\mathrm{Fe}_{\mathrm{cdb}})$	- 2.50 ± 0.8	ln(C:N)			0.257	1.15	7.90	0.0014
	r^2_{partial}			0.15		0.14						
2a	$\ln(\mathrm{Mg}^{2+})$ =	12.87 ± 2.66	+ 5.00 ± 0.65	arcsin√fine silt	- 1.74 ± 0.4	ln(C:N)	- 1.07 ± 0.44	arcsin√kaolinite	0.685	0.54	29.96	0.0000
	r^2_{partial}			0.41		0.25		0.05				
2b	$\ln(\mathrm{Mg}^{2+})$ =	-4.64 ± 1.00	+ 4.73 ± 0.73	arcsin√fine silt	+ 0.34 ± 0.1	$\ln(\mathrm{Mg}_{\mathrm{tf}})$	+ 8.15 ± 2.77	arcsin√hematite	0.627	0.59	23.40	0.0000
	r^2_{partial}			0.41		0.16		0.08				
3a	$\ln(\mathrm{K}^{+})$ =	-5.67 ± 1.56	+ 0.27 ± 0.1	$\ln(\mathrm{K}_{\mathrm{tf}})$	+ 0.6 ± 0.2	ln(redness rating)			0.485	0.73	19.83	0.0000
	r^2_{partial}			0.44		0.07						

The ± symbol denotes the standard errors of each regression parameter. r^2, proportion of the variance explained; *SE*, standard error of estimates.

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CONCLUSION

Bien que les communautés du front de colonisation du Bas Tapajós sont peu préoccupées par les conséquences mondiales de la déforestation de l'Amazonie (Lecours, 2010), le mode actuel d'exploitation de cet écosystème est responsable d'altérations précoces de leur santé (Dolbec *et coll.*, 2000 ; Lebel *et coll.*, 1998). D'une part, les communautés riveraines dépendantes de la pêche sont exposées au mercure qui s'échappe des sols en culture (Lucotte *et coll.*, 2004). De l'autre, les activités humaines qui permettent des ouvertures de la forêt (agriculture sur brûlis, extractivisme, foresterie, élevage, etc.) créent involontairement les conditions idéales pour l'émergence de la Trypanosomiase américaine (Briceño-León, 2007 ; Romaña, 2007). De toute évidence, la santé des populations est intimement liée à la qualité de l'environnement. Par contre, le défi reste à savoir comment modifier les pratiques actuelles afin de maintenir des écosystèmes capables de fournir les services écologiques sur lesquels dépend la santé des habitants locaux et de leurs progénitures (Costanza *et coll.*, 1997). Bien que dans cette perspective holistique, les résultats de la présente recherche soient plutôt modestes, c'est par l'entremise du programme interdisciplinaire PLUPH que nous pouvons les reconnaître à leur juste valeur.

Afin de réduire l'aléa de la Trypanosomiase américaine en Amazonie, le développement de mesures préventives exige que le cycle de transmission de *Trypanosoma cruzi* soit abordé dans son ensemble (Abad-Franch *et coll.*, 2009). Même si dans leur ensemble, les palmiers du genre *Attalea* dominent toutes les clairières de notre zone d'étude, une variation architecturale importante tant au niveau de l'espèce que de la variété laisse paraître que la distribution des populations de triatomes, et donc de l'aléa de la Trypanosomiase américaine, est répartit de façon hétérogène (Abad-Franch *et coll.*, 2005 ; Romaña *et coll.*, 1999). Bien que des recherches parallèles à même le programme PLUPH élucideront la relation entre les triatomes et les palmiers du genre *Attalea*, l'effet important d'un gradient de cations échangeables sur la présence d'*A. maripa* et *A. phalerata* que nous avons observé indique la possibilité de prédire la distribution de ces palmiers à partir de données édaphiques régionales. Mise en commun avec les autres résultats du programme PLUPH, ces informations pourraient faciliter l'identification de zones à moindre risque à privilégier pour le développement. D'autant plus, la prédiction de l'emplacement de points chauds permettrait aux agences de santé de focaliser leurs interventions sanitaires sur les régions où l'aléa est plus grand. C'est dans cette optique que nous avons proposé des indicateurs édaphiques de la présence des trois espèces de palmiers présentes dans notre région d'étude.

Ceci étant dit, le manque de relation forte entre la distribution de *A. speciosa* et la multiplicité de variables édaphiques analysée dans le présent ouvrage complique significativement la modélisation de sa distribution. Pourtant, cette observation n'est pas nouvelle : tandis que certains anticipent une relation plus saillante entre ce palmier et des propriétés édaphiques comme la profondeur de la nappe phréatique (Anderson *et coll.*, 1991 ; Grogan et Galvão, 2006), d'autres proposent qu'il ait plutôt été dispersé intentionnellement par les indigènes qui peuplaient jadis le basin amazonien (May *et coll.*, 1985). Dans ce dernier cas, la prédiction de sa distribution est grandement limitée, car nous avons très peu d'informations sur l'emplacement et les pratiques des communautés précoloniales de cette région. De plus, la remarquable plasticité morphologique de l'espèce *A. speciosa* soulève un deuxième problème parce que les différentes variétés sous lesquelles elle se manifeste sont probablement associées à des index d'infestation distincts. Étrangement, notre recherche indique qu'une forme naine de l'espèce *A.* sp. dwarf, qui a la particularité d'atteindre sa maturité sexuelle sans avoir a développé un tronc aérien, serait associée au Cl_{tf} ainsi qu'à des propriétés minéralogiques spécifiques des Alfisols. Cette découverte témoigne du potentiel d'une démarche scientifique visant à comprendre la distribution d'espèces végétales en fonction des propriétés édaphiques tout en implorant davantage de recherches sur la physiologie des palmiers du genre *Attalea*.

Quoique le rôle majeur des cations échangeables sur la distribution d'espèces de palmiers ne nous ait pas surpris, le manque de relation forte entre les cations échangeables et la teneur en argiles des sols était à l'encontre de la plupart des articles scientifiques sur le sujet (Sollins, 1998). L'inaptitude de ce facteur facilement mesurable en tant qu'indicateur de la présence de certaines espèces de palmiers nous a incité à mieux comprendre les processus physico-chimiques impliqués. C'est ainsi que nous avons déterminé que les cations échangeables de calcium, magnésium et potassium sont distribués différemment dans les sols. De plus, cette mosaïque élaborée de nutriments suggère l'existence de gradients cationiques secondaires pouvant être associés à certaines espèces végétales.

Dans un deuxième temps, notre démarche analytique innovatrice nous a permis d'observer que des réserves de potassium et de magnésium fixées dans la structure minérale de ces sols hautement minéralisés ont un rôle actif dans le relargage de cations échangeables. Cela dit, les cations échangeables de calcium et de magnésium sont davantage retenus dans le sol par des oxyhydroxydes de fer associés aux limons fins (2-10 µm). En effet, le contenu important de limons fins des sols de la région serait responsable de la faible relation que nous avons observée entre les cations échangeables et l'argile. D'ailleurs si cette découverte nous a portés à réfléchir sur certaines prémisses et méthodes de l'écologie tropicale contemporaine, elle contribue également à l'avancement de nos connaissances sur le mercure, car ce dernier occupe les mêmes sites d'échange que les cations de calcium et de magnésium échangeables (Roulet *et coll.*, 1998). Malheureusement, seulement une autre recherche menée au début du programme CARUSO par Poirier (2004) a exposé la granulométrie des sols de la région plus en détails, incluant des fractions plus fines que celles délimitant de manière classique les argiles, les limons et les sables. Un effort que la portée de nos résultats démontre comme étant dorénavant nécessaire pour le programme PLUPH.

Il serait d'ailleurs intéressant de vérifier si le volume relativement plus important de matière organique que nous avons observé dans les couronnes d'*A. phalerata* lui confère un taux d'infestation supérieur par les triatomes (app. B). Considérant que les propriétés physicochimiques des zones à plus fortes teneurs en oxyhydroxydes de fer où *A. phalerata* prolifère présupposent que ces zones sont aussi à risque d'une perte relativement plus grande de mercure à la suite de brûlis, nous serions en mesure de constater l'émergence de milieux particulièrement sensibles à la déforestation (Farella *et coll.*, 2007 ; Roulet *et coll.*, 1999). Juxtaposé à une carte des populations humaines plus vulnérables, l'emplacement de ces zones nous permettrait de prédire les points chauds d'exposition au mercure et à la Trypanosomiase américaine. Par contre, ces endroits, à la fois plus fertiles et moins acides sont probablement aussi ceux les plus convoités par les petits agriculteurs (Fearnside, 1984). Des solutions de remplacement à l'agriculture sur brûlis tel que l'agroforesterie, pouvant prédire à la fois l'érosion du mercure et la présence des palmiers du genre *Attalea*, leur seraient alors d'autant plus indispensables.

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APPENDICE A

CARTES DE LOCALISATION DES DIFFÉRENTES ESPÈCES DE PALMIERS DU GENRE *ATTALEA* SUSCEPTIBLES D'HÉBERGER DES TRIATOMES DANS LA RÉGION D'ÉTUDE

Figure A. 1 Carte de distribution des espèces et variétés de palmiers recensés du genre *Attalea* dans les communautés de São Tomé, Demanda, Agrovila et Nova Estrela (Pará, Brésil). Les zones grises sont les plans d'eau et les ruisseaux (prédites à partir d'une DEM SRTM) sont identifiés par des lignes discontinues. La présence d'une espèce ou d'une variété est donnée à chaque point d'échantillonnage. L'espèce *Attalea maripa* est identifiée par le symbole □, l'espèce *A. phalerata* est identifiée par le symbole O, l'espèce *A. speciosa* est identifiée par le symbole × et le palmier *A.* sp. nain est identifié par le symbole +. La zone délimitée par un cadre noir est agrandie à la figure A.2.

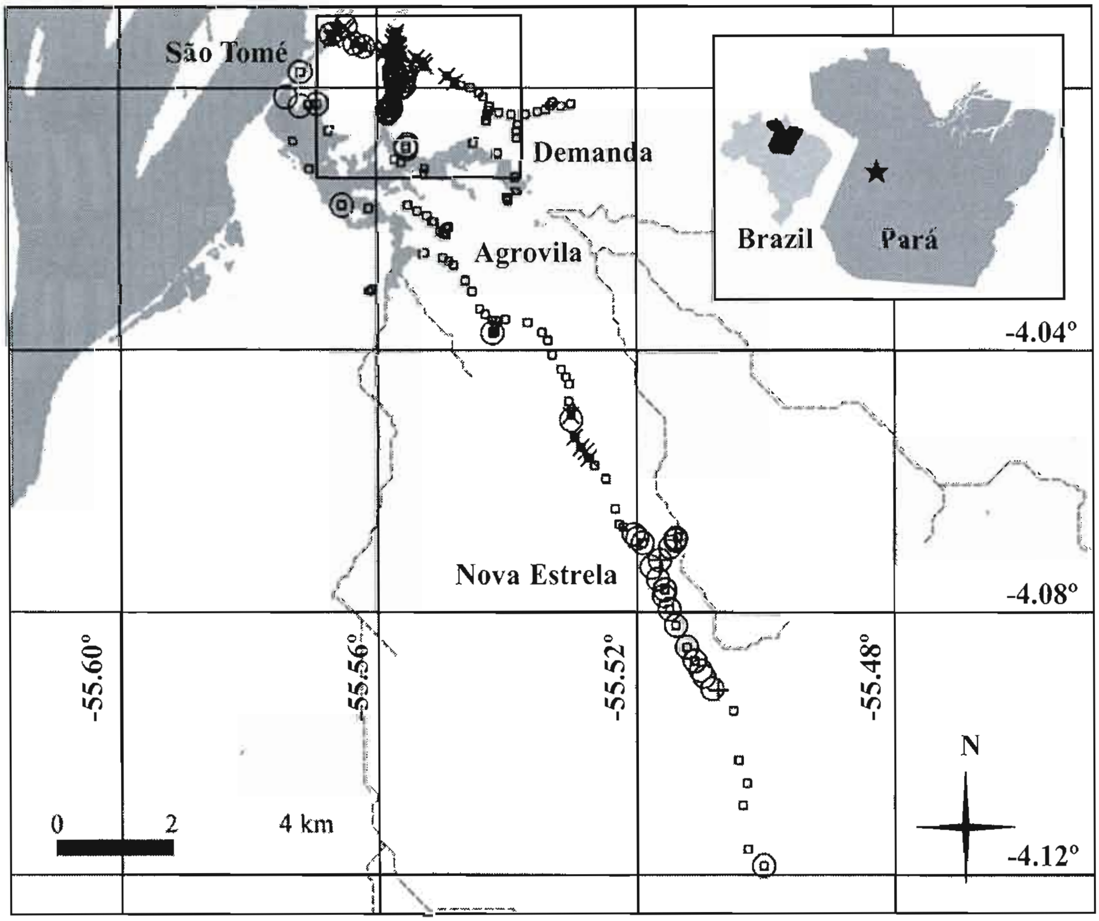
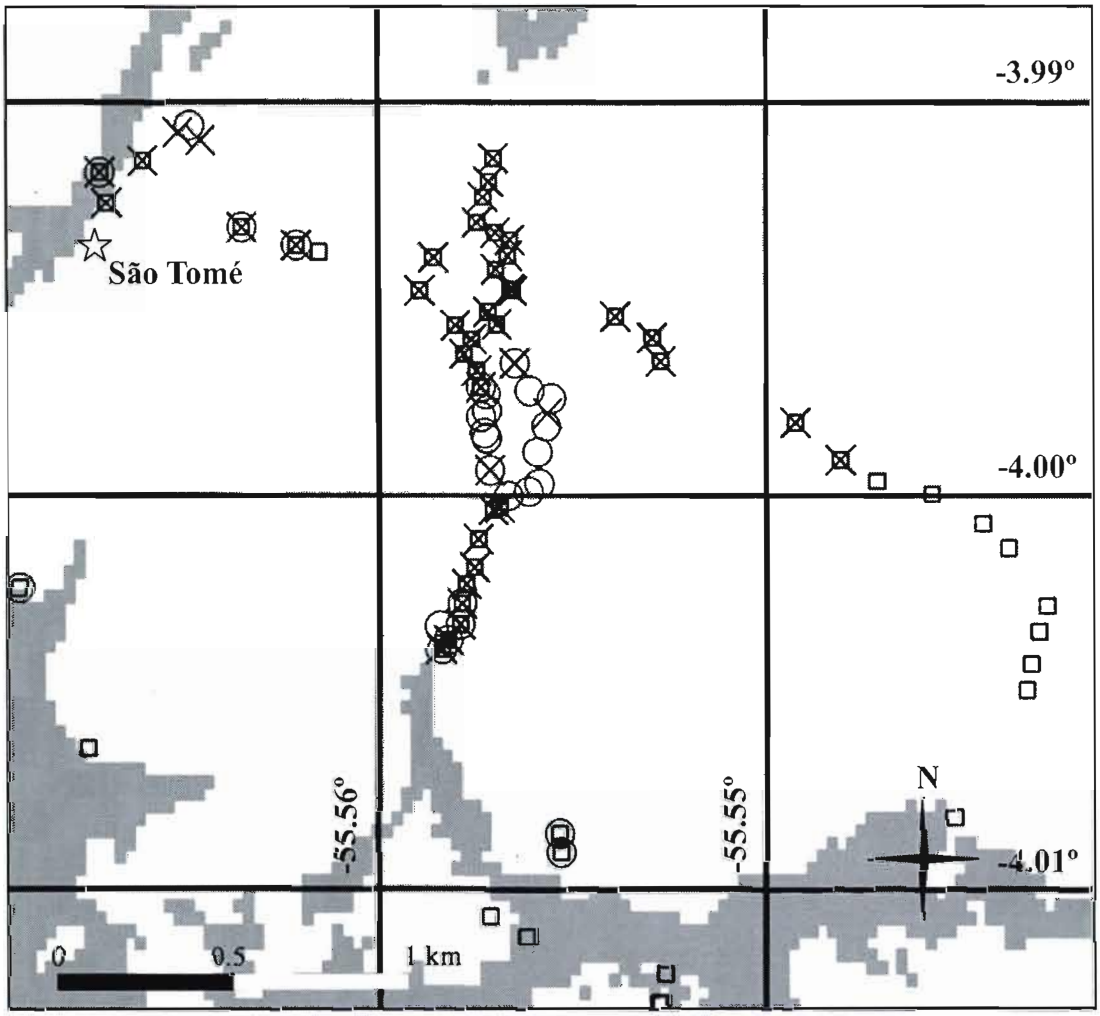


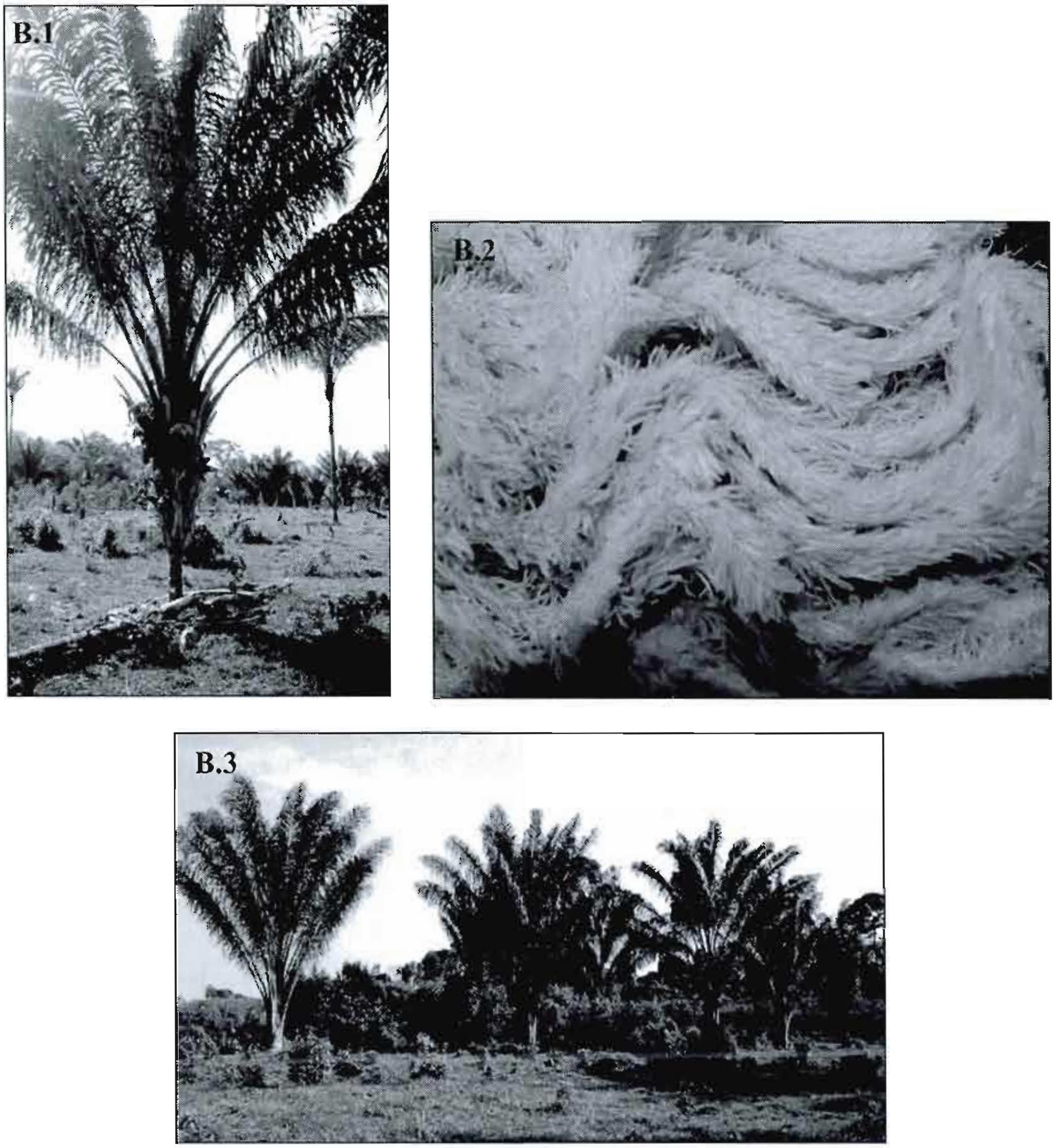
Figure A. 2 Carte de distribution des espèces et variétés de palmiers recensés à proximité de la communauté de São Tomé (Pará, Brésil). Les zones grises sont les plans d'eau. Le centre de la communauté de São Tomé est identifié par le symbole ☆. La présence d'une espèce ou d'une variété est donnée à chaque point d'échantillonnage. L'espèce *Attalea maripa* est identifiée par le symbole ☐, l'espèce *A. phalerata* est identifiée par le symbole ○, l'espèce *A. speciosa* est identifiée par le symbole × et le palmier *A.* sp. nain est identifié par le symbole +.



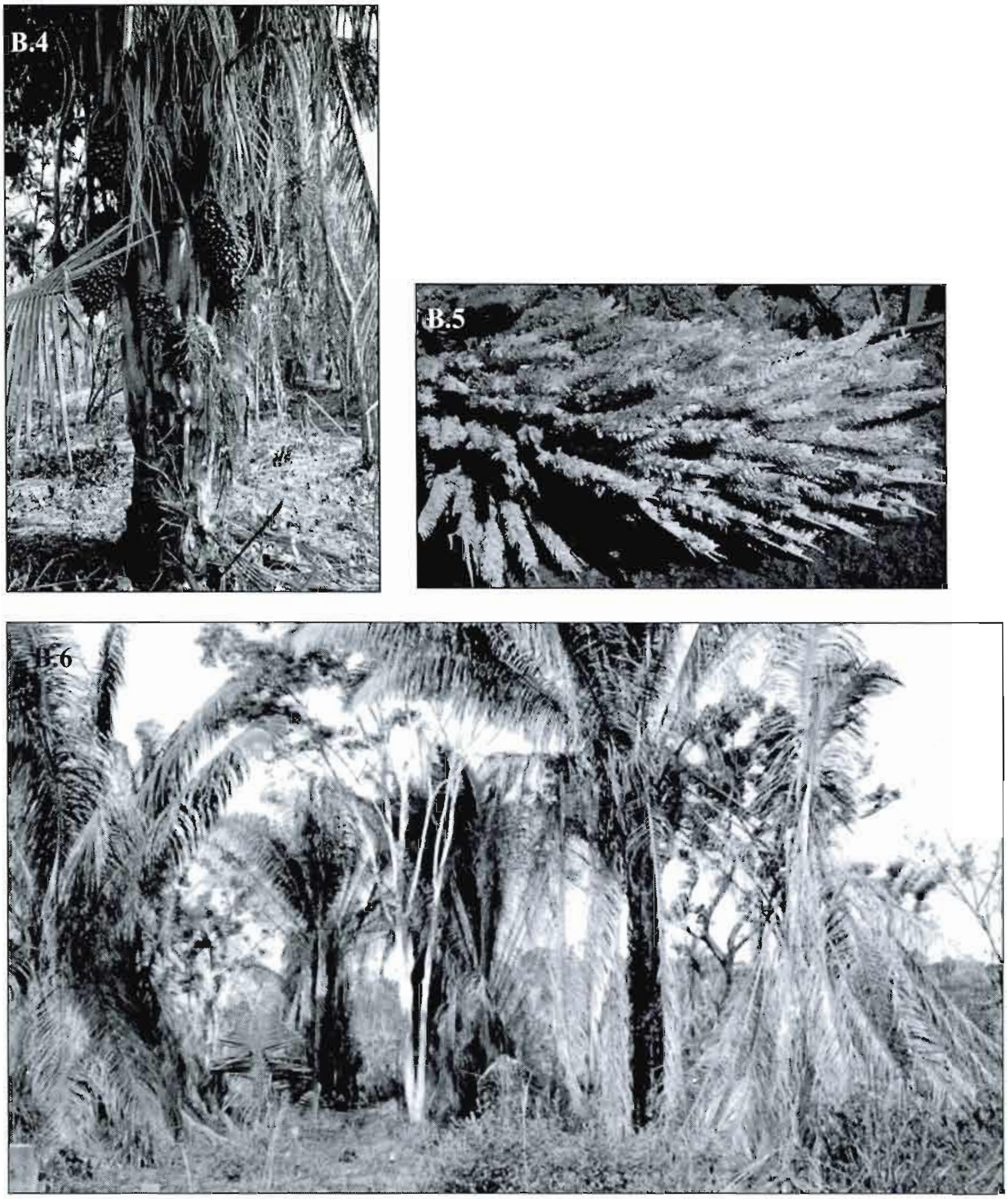
APPENDICE B

PHOTOGRAPHIES PRISES DURANT LES TRAVAUX DE TERRAIN

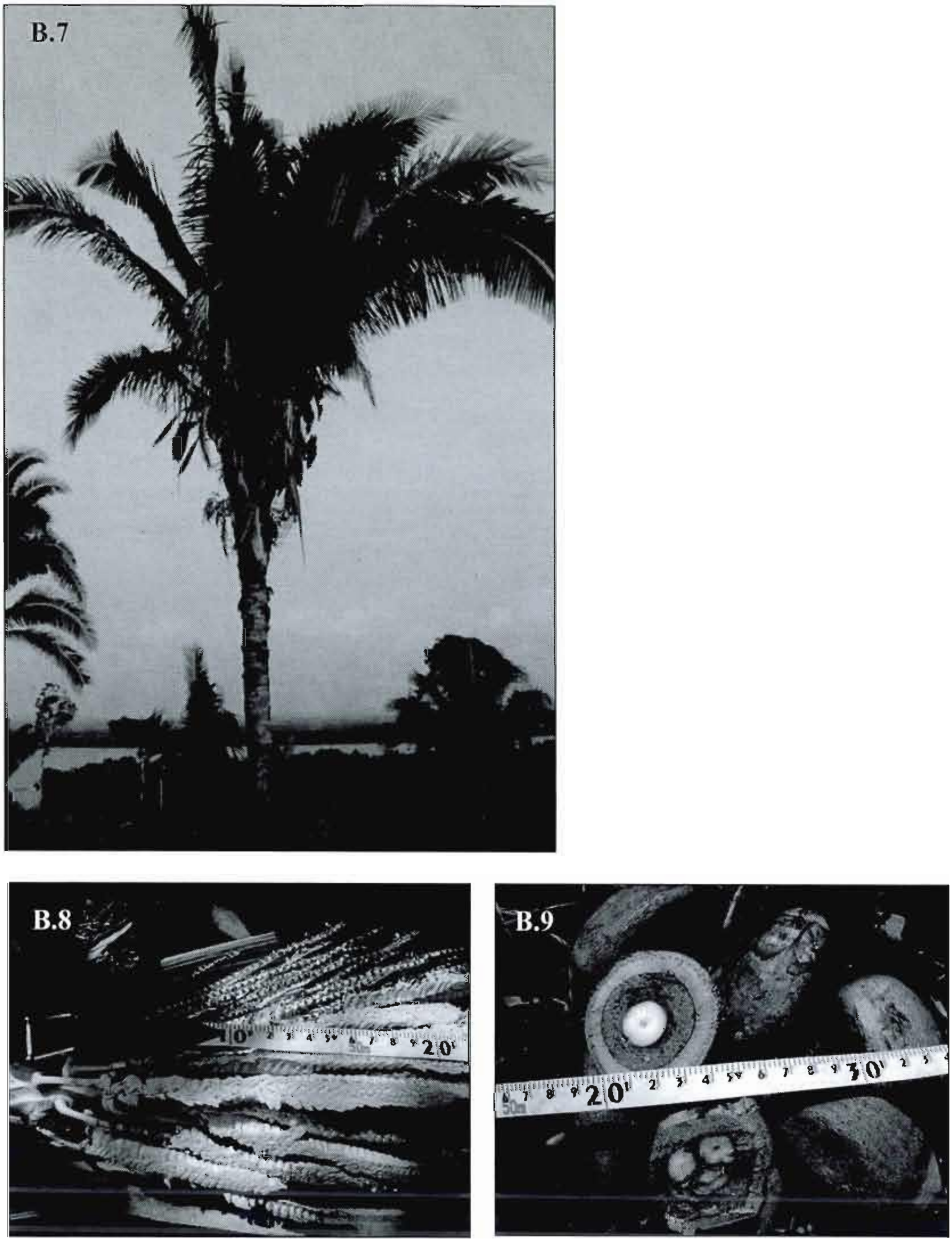
Figure B. 1-14 Photos des espèces et variétés de palmiers du genre *Attalea* de la région d'étude



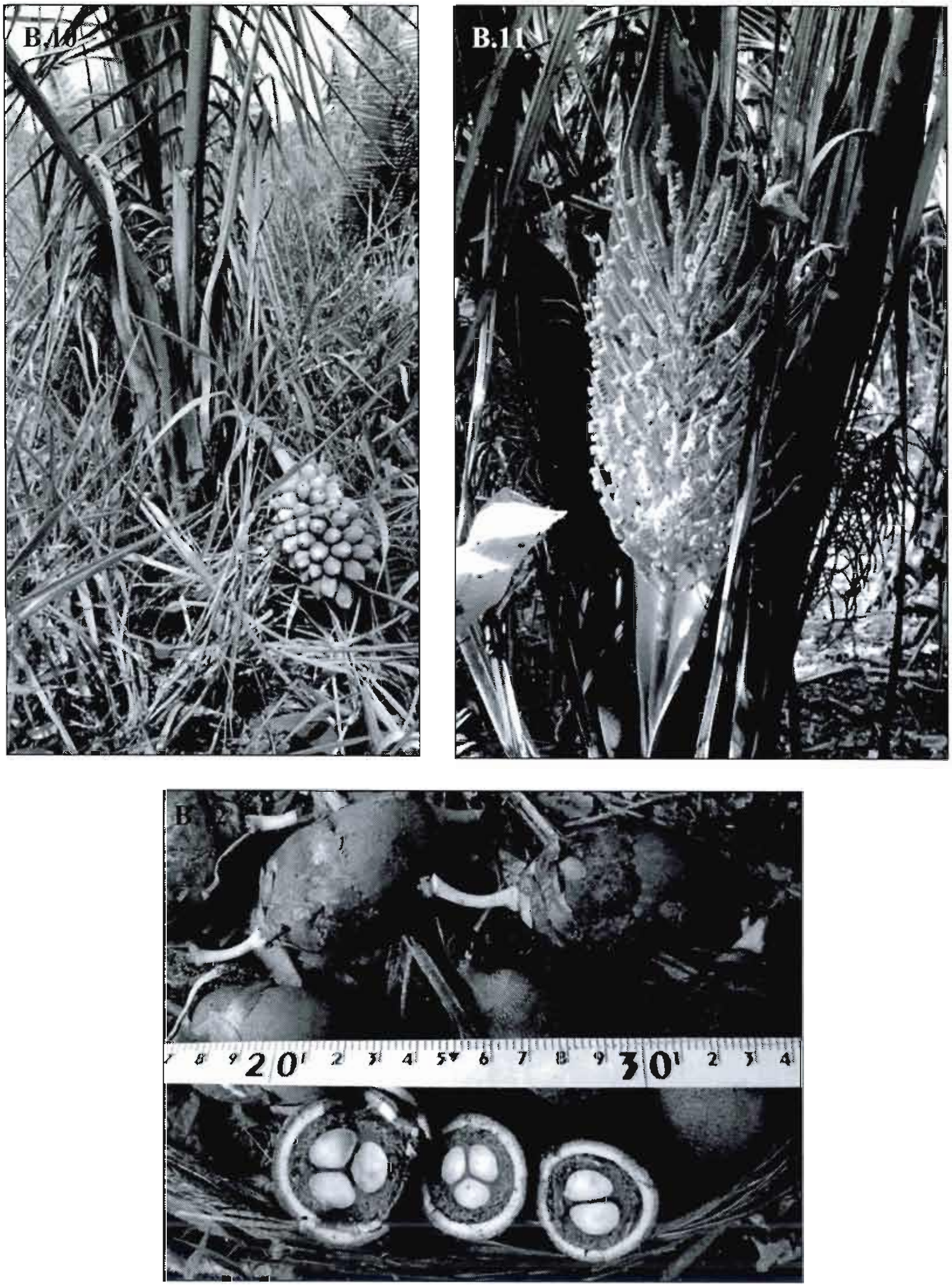
Attalea maripa (inajá). (B.1) spécimen mature, (B.2) fleurs mâles immatures, (B.3) un regroupement en pâturage.



Attalea phalerata (urucuri). (B.4) spécimen mature, (B.5) fleurs mâles immatures, (B.6) un regroupement en pâturage.



Attalea speciosa (babaçu). (B.7) spécimen mature, (B.8) fruits, (B.9) fleurs mâles immatures.



Attalea sp. nain (coquinho, coco baixinho, coco dende and pindoba). (B.10) spécimen mature, (B.11) fleurs mâles matures, (B.12) fruits.

B.13

(B.13) un regroupement d'*Attalea* sp. nain en pâturage, (B.14) toit de maison à base de palmes tissées. Palmes de *A. speciosa* à gauche et palmes de *A. maripa* à droite. Bien que les palmes des deux espèces servent à la fabrication de toits, ceux de la première sont favorisées en raison de la distribution uniforme des folioles le long de leurs pétioles.

APPENDICE C

QUESTIONNAIRE SUR L'HISTORIQUE DES PARCELLES ET LA GESTION DES PALMIERS PRÉSENTÉ À CHACUN DES PRODUCTEURS DES PARCELLES SUR LESQUELLES L'ÉCHANTILLONNAGE A EU LIEU

NOME DO PRODUCTOR :

TRANSECT & # LOT :

PONTO GPS :

1) Faz quanto tempo que vocês moram aqui?

2) Você é de onde? Qual e sua região de origem?

3) Como era aqui a vegetação antes quando chegaram aqui?

4) A quanto tempo foi desmatado essa parcela?

5) Tênia babaçus, inajás o urucuris na floresta primaria?

6) Hoje tem mais o menos palmeiras que nos primeiros anos?

7) O que foi feito na parcela a partir da primeira corte?

8) A área foi queimada ou não?

9) Como você lida com babaçu e inajá que resistem a queima ou que brotam depois da queima?

c) Como você faz?

d) Por que?

e) Que proporção das palmeiras continuam, apesar da intervenção?

10) Vocês usam as palmeiras? Por que?

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APPENDICE D

SOMMAIRE DES VALEURS MÉDIANES DES VARIABLES ENVIRONNEMENTALES SELON LA PRÉSENCE ET L'ABSENCE D'ESPÈCES DU GENRE *ATTALEA*.

Table D.1 Summary of median values for environmental variables according to the presence and absence of palms species of the genus *Attalea* samp near Lake Araipa along the Lower Tapajós River (Pará, Brazil)

			Total			*Attalea maripa*		*Attalea sp. var. speciosa*		*Attalea sp. var. nanus*		*Attalea phalerata*	
						present	absent	present	absent	present	absent	present	absent
		n=		*43*		*34*	*9*	*15*	*28*	*9*	*34*	*10*	*33*
				-	+								
EM1	**cations**	*cmol/kg*	0.32	*0.04*	*3.54*	0.26	2.48 ***	0.31	0.41	0.78	0.26 **	2.19	0.24 ***
	Ca^{2+}	*cmol/kg*	0.17	*0.01*	*2.69*	0.10	1.84 ***	0.18	0.09	0.65	0.14	1.76	0.09 ***
	pH		4.74	*6.52*	*4.33*	4.67	5.72 ***	4.74	4.74	5.29	4.67 **	5.59	4.65 ***
	Mg^{2+}	*cmol/kg*	0.08	*0.01*	*1.01*	0.07	0.37 ***	0.08	0.13	0.32	0.08 *	0.39	0.06 ***
	P_{ex}	*µmol/g*	*0.06*	*0.04*	*0.42*	0.06	0.10 ***	0.06	0.06	0.06	0.06	0.09	0.06 ***
	C:N		9.78	*4.71*	*17.46*	9.94	9.24	9.57	10.04	7.68	10.21 **	9.10	10.04
	K^+	*cmol/kg*	0.02	*0.00*	*0.16*	0.02	0.03	0.02	0.01	0.12	0.02 **	0.04	0.02
	silt	%	32.59	*8.61*	*58.82*	32.29	46.49	31.79	35.76	32.59	32.48	47.94	32.26 *
	Al^{3+}	*cmol/kg*	0.76	*0.11*	*4.54*	0.91	0.12 ***	0.80	0.76	0.14	0.77	0.12	0.84 ***
	density	*g / cm3*	1.35	*0.97*	*1.68*	1.42	1.25	1.44	1.21 *	1.52	1.33	1.25	1.44
	sand	%	34.46	*1.98*	*85.1*	39.65	15.99	41.48	16.06 *	45.3	32.4	15.12	39.8
	C total	%	0.69	*0.15*	*1.92*	0.64	0.71	0.56	0.78	0.33	0.73 *	0.73	0.63
	N total	%	0.07	*0.03*	*0.12*	0.06	0.07	0.06	0.08 *	0.05	0.07	0.08	0.06
	clay	%	32.32	*5.89*	*67.29*	32.42	31.96	22.28	32.52	18.00	33.85	33.74	32.32
EM2	**Zn$_{tf}$**	*ppm*	50	*0*	*301*	0	95 ***	25	57	60	0	94	0 ***
	Ca_{tf}	*ppm*	175	*0*	*1280*	137	461 ***	178.5	153	245	149 **	442	129 ***
	Mn_{tf}	*ppm*	156	*0*	*3020*	96	1200 **	107.5	316	158	133.5	907.5	88 ***
	Fe$_{cdb}$	*µmol/g*	544.94	*17.35*	*2061.47*	397.33	1328.77	383.99	1008.23 *	313.72	671.19	1287.64	389.69 *
	P_{cdb}	*µmol/g*	0.68	*0*	*27.64*	0.65	2.86 **	0.64	1.35	0.39	0.87	2.49	0.64 **
	kaolinite	%	68.14	*3.22*	*87.41*	67.63	68.14	67.41	68.14	23.96	68.77 **	66.94	68.28
	quartz	%	26.88	*6.63*	*92.86*	26.53	27.50	27.19	26.17	63.86	25.30 **	28.55	26.17
	Cl_{tf}	*ppm*	101	*0*	*474*	110	0	125.5	0 *	160	88 **	40	112
	P_{apa}	*µmol/g*	0.25	*0*	*5.18*	0.13	0.44	0.13	0.31	0.11	0.25	0.44	0.13 *
	Cu_{tf}	*ppm*	68	*0*	*779*	62	274 *	62	178	55	102.5	218.5	60 *
	Fe$_{tf}$	*ppm*	65000	*2730*	*152000*	59550	102000	52350	113000 *	59100	84050	97750	59400
	P_{tf}	*ppm*	493	*115*	*3400*	469.5	663	450	504	418	501.5	638	463
	P_{org}	*µmol/g*	3.202	*0*	*30.671*	3.06	6.46	3.22	2.92	2:20	3.24	7.01	2.92
	plagioclase	%	0.89	*0*	*2.22*	0.89	0.85	0.89	0.85	1.33	0.84 *	0.89	0.89
	Al_{cdb}	*µmol/g*	280.43	*14.39*	*766.16*	235.66	506.55	200.95	406.34 *	197.95	307.42	506.67	214.02
	Na_{tf}	*ppm*	189	*0*	*1370*	198.5	0	197	0	345	0 **	0	192
	feldspar-K	%	0.84	*0*	*3.07*	0.84	0.85	0.86	0.83	1.45	0.81 *	0.86	0.84
	Cr_{tf}	*ppm*	1.32	*0*	*2.21*	136	108 *	131.5	147	112	134.5	110	135
	Mg$_{tf}$	*ppm*	995	*79*	*13200*	1007.5	800	1045	762	2190	735	935	995
	K_{tf}	*ppm*	3870	*140*	*49000*	3885	2160	3885	302	6300	3090	3105	3870
	C_{tf}	*ppm*	0	*0*	*15800*	140	0	135	0	270	0	0	280
	S_{tf}	*ppm*	258	*114*	*667*	254	302	257.5	282	208	264	292	251

Median, minimum and maximum values of the total samples are given in the first column. Variables are grouped into two environmental matrices. EM1 includes commonly samples variables while EM2 includes both the minerological and total element content of soils. Variables are ordered according to their marginal effects. Labels of variables selected during automatic stepwise CCA are given in bold. A significant difference in the presence/absence ranking per species is identified with asterisks. *= significant ($p<0.05$), **= highly significant ($p<0.01$), ***= very highly significant ($p<0.001$). Variables uncorrelated (<0.600) to selected variables were omitted from the table.

APPENDICE E

MATRICES DE CORRÉLATIONS DE SPEARMAN ρ DES VARIABLES EXPLICATIVES DU SOL

Table E.1 Spearman ρ correlation matrix of explanatory soil variables sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil) (1/2)

	clay	silt	sand	density	RR	C total	N total	C:N	Al$_{cdb}$
clay		0.245 *(0.1227)*	**-0.865** ***(0.0000)***	**-0.720** ***(0.0000)***	**0.367** ***(0.0181)***	**0.624** ***(0.0000)***	**0.653** ***(0.0000)***	0.295 *(0.0612)*	**0.852** ***(0.0000)***
silt	0.245 *(0.1227)*		**-0.628** ***(0.0000)***	**-0.339** ***(0.0300)***	**0.362** ***(0.0201)***	**0.430** ***(0.0050)***	**0.607** ***(0.0000)***	-0.029 *(0.8584)*	**0.530** ***(0.0004)***
sand	**-0.865** ***(0.0000)***	**-0.628** ***(0.0000)***		**0.724** ***(0.0000)***	**-0.451** ***(0.0031)***	**-0.675** ***(0.0000)***	**-0.795** ***(0.0000)***	-0.163 *(0.3084)*	**-0.880** ***(0.0000)***
density	**-0.720** ***(0.0000)***	**-0.339** ***(0.0300)***	**0.724** ***(0.0000)***		-0.072 *(0.6553)*	**-0.628** ***(0.0000)***	**-0.623** ***(0.0000)***	**-0.310** ***(0.0489)***	**-0.714** ***(0.0000)***
RR	**0.367** ***(0.0181)***	**0.362** ***(0.0201)***	**-0.451** ***(0.0031)***	-0.072 *(0.6553)*		0.175 *(0.2751)*	**0.467** ***(0.0021)***	-0.206 *(0.1952)*	**0.443** ***(0.0037)***
C	**0.624** ***(0.0000)***	**0.430** ***(0.0050)***	**-0.675** ***(0.0000)***	**-0.628** ***(0.0000)***	0.175 *(0.2751)*		**0.813** ***(0.0000)***	**0.601** ***(0.0000)***	**0.744** ***(0.0000)***
N	**0.653** ***(0.0000)***	**0.607** ***(0.0000)***	**-0.795** ***(0.0000)***	**-0.623** ***(0.0000)***	**0.467** ***(0.0021)***	**0.813** ***(0.0000)***		0.088 *(0.5851)*	**0.768** ***(0.0000)***
C:N	0.295 *(0.0612)*	-0.029 *(0.8584)*	-0.163 *(0.3084)*	**-0.310** ***(0.0489)***	-0.206 *(0.1952)*	**0.601** ***(0.0000)***	0.088 *(0.5851)*		**0.372** ***(0.0167)***
Al$_{cdb}$	**0.852** ***(0.0000)***	**0.530** ***(0.0004)***	**-0.880** ***(0.0000)***	**-0.714** ***(0.0000)***	**0.443** ***(0.0037)***	**0.744** ***(0.0000)***	**0.768** ***(0.0000)***	**0.372** ***(0.0167)***	
Fe$_{cdb}$	**0.801** ***(0.0000)***	**0.591** ***(0.0000)***	**-0.896** ***(0.0000)***	**-0.621** ***(0.0000)***	**0.553** ***(0.0002)***	**0.647** ***(0.0000)***	**0.723** ***(0.0000)***	0.253 *(0.1103)*	**0.947** ***(0.0000)***
feldspar-K	0.299 *(0.0573)*	-0.102 *(0.5248)*	-0.173 *(0.2799)*	-0.145 *(0.3654)*	**0.426** ***(0.0055)***	0.035 *(0.8279)*	0.247 *(0.1197)*	-0.257 *(0.1049)*	0.071 *(0.6578)*
hematite	**0.463** ***(0.0023)***	0.215 *(0.1772)*	**-0.485** ***(0.0013)***	**-0.413** ***(0.0073)***	0.284 *(0.0723)*	**0.325** ***(0.0383)***	**0.520** ***(0.0005)***	-0.020 *(0.9023)*	**0.443** ***(0.0037)***
illite	0.001 *(0.9974)*	0.214 *(0.1800)*	-0.066 *(0.6841)*	-0.034 *(0.8330)*	0.281 *(0.0757)*	0.145 *(0.3653)*	**0.368** ***(0.0179)***	-0.292 *(0.0641)*	0.041 *(0.7994)*
kaolinite	**0.397** ***(0.0102)***	-0.015 *(0.9251)*	-0.267 *(0.0918)*	-0.235 *(0.1388)*	-0.160 *(0.3189)*	0.161 *(0.3136)*	0.003 *(0.9853)*	0.299 *(0.0573)*	0.287 *(0.0684)*
plagioclase	0.089 *(0.5813)*	0.217 *(0.1738)*	-0.077 *(0.6322)*	0.089 *(0.5821)*	0.300 *(0.0565)*	0.121 *(0.4514)*	0.227 *(0.1531)*	0.012 *(0.9414)*	0.123 *(0.4422)*
quartz	**-0.485** ***(0.0013)***	-0.022 *(0.8899)*	**0.345** ***(0.0272)***	0.276 *(0.0811)*	0.110 *(0.4918)*	-0.242 *(0.1277)*	-0.121 *(0.4521)*	-0.290 *(0.0663)*	**-0.361** ***(0.0205)***
Mg$_{tf}$	**-0.479** ***(0.0015)***	0.085 *(0.5963)*	**0.333** ***(0.0335)***	**0.481** ***(0.0015)***	0.185 *(0.2466)*	**-0.348** ***(0.0257)***	-0.082 *(0.6100)*	**-0.616** ***(0.0000)***	**-0.485** ***(0.0013)***
K$_{tf}$	**-0.463** ***(0.0023)***	0.013 *(0.9358)*	**0.365** ***(0.0191)***	**0.501** ***(0.0008)***	0.176 *(0.2716)*	**-0.339** ***(0.0304)***	-0.084 *(0.6013)*	**-0.578** ***(0.0001)***	**-0.471** ***(0.0019)***

Correlations were computed from a group of 41 samples. Probabilities are given in brackets. Significant correlations ($p<0.05$) are given in bold. RR, redness rating.

Table E.1 Spearman ρ correlation matrix of explanatory soil variables sampled near Lake Araipa along the Lower Tapajós River (Pará, Brazil) (2/2)

	Fe_{cdb}	feldspar-K	hematite	illite	kaolinite	plagioclase	quartz	Mg_{tf}	K_{tf}
clay	**0.801**	0.299	**0.463**	0.001	**0.397**	0.089	**-0.485**	**-0.479**	**-0.463**
	(0.0000)	*(0.0573)*	***(0.0023)***	*(0.9974)*	***(0.0102)***	*(0.5813)*	***(0.0013)***	***(0.0015)***	***(0.0023)***
silt	**0.591**	-0.102	0.215	0.214	-0.015	0.217	-0.022	0.085	0.013
	(0.0000)	*(0.5248)*	*(0.1772)*	*(0.1800)*	*(0.9251)*	*(0.1738)*	*(0.8899)*	*(0.5963)*	*(0.9358)*
sand	**-0.896**	-0.173	**-0.485**	-0.066	-0.267	-0.077	**0.345**	**0.333**	**0.365**
	(0.0000)	*(0.2799)*	***(0.0013)***	*(0.6841)*	*(0.0918)*	*(0.6322)*	***(0.0272)***	***(0.0335)***	***(0.0191)***
density	**-0.621**	-0.145	**-0.413**	-0.034	-0.235	0.089	0.276	**0.481**	**0.501**
	(0.0000)	*(0.3654)*	***(0.0073)***	*(0.8330)*	*(0.1388)*	*(0.5821)*	*(0.0811)*	***(0.0015)***	***(0.0008)***
RR	**0.553**	**0.426**	0.284	0.281	-0.160	0.300	0.110	0.185	0.176
	(0.0002)	***(0.0055)***	*(0.0723)*	*(0.0757)*	*(0.3189)*	*(0.0565)*	*(0.4918)*	*(0.2466)*	*(0.2716)*
C total	**0.647**	0.035	**0.325**	0.145	0.161	0.121	-0.242	**-0.348**	-0.339
	(0.0000)	*(0.8279)*	***(0.0383)***	*(0.3653)*	*(0.3136)*	*(0.4514)*	*(0.1277)*	***(0.0257)***	*(0.0304)*
N total	**0.723**	0.247	**0.520**	**0.368**	0.003	0.227	-0.121	-0.082	-0.084
	(0.0000)	*(0.1197)*	***(0.0005)***	***(0.0179)***	*(0.9853)*	*(0.1531)*	*(0.4521)*	*(0.6100)*	*(0.6013)*
C:N	0.253	-0.257	-0.020	-0.292	0.299	0.012	-0.290	**-0.616**	-0.578
	(0.1103)	*(0.1049)*	*(0.9023)*	*(0.0641)*	*(0.0573)*	*(0.9414)*	*(0.0663)*	***(0.0000)***	*(0.0001)*
Al_{cdb}	**0.947**	0.071	**0.443**	0.041	0.287	0.123	**-0.361**	**-0.485**	**-0.471**
	(0.0000)	*(0.6578)*	***(0.0037)***	*(0.7994)*	*(0.0684)*	*(0.4422)*	***(0.0205)***	***(0.0013)***	***(0.0019)***
Fe_{cdb}		0.050	**0.439**	-0.002	0.286	0.122	**-0.334**	**-0.417**	**-0.451**
		(0.7557)	***(0.0041)***	*(0.9922)*	*(0.0698)*	*(0.4481)*	***(0.0326)***	***(0.0068)***	***(0.0031)***
feldspar-K	0.050		**0.424**	0.254	-0.213	0.278	0.112	0.178	0.180
	(0.7557)		***(0.0057)***	*(0.1087)*	*(0.1818)*	*(0.0788)*	*(0.4854)*	*(0.2648)*	*(0.2609)*
hematite	**0.439**	**0.424**		0.035	0.036	0.219	-0.137	**-0.327**	-0.344
	(0.0041)	***(0.0057)***		*(0.8267)*	*(0.8246)*	*(0.1699)*	*(0.3923)*	***(0.0369)***	*(0.0276)*
illite	-0.002	0.254	0.035		-0.159	0.170	0.038	**0.550**	**0.571**
	(0.9922)	*(0.1087)*	*(0.8267)*		*(0.3200)*	*(0.2878)*	*(0.8145)*	***(0.0002)***	***(0.0001)***
kaolinite	0.286	-0.213	0.036	-0.159		-0.137	**-0.975**	**-0.447**	**-0.429**
	(0.0698)	*(0.1818)*	*(0.8246)*	*(0.3200)*		*(0.3944)*	***(0.0000)***	***(0.0034)***	***(0.0051)***
plagioclase	0.122	0.278	0.219	0.170	-0.137		0.061	0.083	0.102
	(0.4481)	*(0.0788)*	*(0.1699)*	*(0.2878)*	*(0.3944)*		*(0.7065)*	*(0.6050)*	*(0.5274)*
quartz	**-0.334**	0.112	-0.137	0.038	**-0.975**	0.061		**0.433**	0.407
	(0.0326)	*(0.4854)*	*(0.3923)*	*(0.8145)*	***(0.0000)***	*(0.7065)*		***(0.0047)***	*(0.0082)*
Mg_{tf}	**-0.417**	0.178	**-0.327**	**0.550**	**-0.447**	0.083	**0.433**		**0.967**
	(0.0068)	*(0.2648)*	***(0.0369)***	***(0.0002)***	***(0.0034)***	*(0.6050)*	***(0.0047)***		***(0.0000)***
K_{tf}	**-0.451**	0.180	**-0.344**	**0.571**	**-0.429**	0.102	**0.407**	**0.967**	
	(0.0031)	*(0.2609)*	***(0.0276)***	***(0.0001)***	***(0.0051)***	*(0.5274)*	***(0.0082)***	***(0.0000)***	

Correlations were computed from a group of 41 samples. Probabilities are given in brackets. Significant correlations ($p<0.05$) are given in bold. RR, redness rating.