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**CALIBRATION DES FONCTIONS DE TRANSFERT ENTRE
ASSEMBLAGES PHYTOLITHIQUES, STRUCTURE DES
VEGETATIONS ET VARIABLES BIOCLIMATIQUES ACTUELLES,
POUR L'INTEGRATION DE LA DYNAMIQUE DES BIOMES
HERBACES DANS LES MODELES DE VEGETATION.**

THÈSE

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RESUME

Les formations herbacées actuellement dominantes en zone intertropicale sont mal discriminées par les marqueurs de végétation courants. Ainsi, la modélisation de la végétation et les reconstitutions des climats passés dans ces zones sont limitées. Les phytolithes sont des particules d'opale formées par précipitation de silice amorphe entre et/ou dans les cellules de nombreuses plantes vivantes, couramment utilisés pour tracer la dynamique des formations herbacées. Cependant, les calibrations entre assemblages phytolithiques, végétation et climat sont rares.

Cette thèse établit des fonctions de transfert entre indices phytolithiques, caractéristiques des formations herbacées intertropicales actuelles, et contraintes bio-climatiques, en vue de pouvoir intégrer les données phytolithiques à la méthode de biomisation pollinique permettant des reconstitutions de végétation. Ceci permettra d'améliorer et de valider certains modèles prédictifs de végétation.

En Afrique de l'Ouest, l'indice **I_{ph}** permet de différencier les savanes à graminées basses des savanes à graminées hautes. Une fonction de transfert, établie pour estimer l'évapotranspiration (AET/PET), offre de bons résultats, comparables et complémentaires aux estimations fournies par la biomisation pollinique.

L'indice **I_c** étudié sur un gradient altitudinal en Afrique de l'Est estime correctement la proportion des sous-familles graminéennes Pooideae et Panicoideae en zone intertropicale soit, potentiellement, la domination des Poaceae en C₄/C₃, jusqu'alors difficilement enregistrée.

Pour la première fois un marqueur de végétation, l'indice **D/P**, est calibré de façon quantitative en terme de LAI le long d'un transect forêt-savane.

Finalement, une analyse discriminante utilisant la totalité des assemblages permet de définir six biomes phytolithiques. Ces biomes intégrés à la méthode de biomisation pollinique, offriront des reconstructions paléo-environnementales plus précises, notamment les transitions désert/savane/forêt.

I. INTRODUCTION

I.1 Problématique

Ces dix dernières années (1990-1999) sont considérées comme les plus chaudes de ce siècle, si l'on se réfère aux données annuelles et aux données hivernales (IPCC, 2001). Des preuves évidentes de changements climatiques globaux se sont accumulées dans de nombreux systèmes (par exemple, fonte des glaces, déplacement géographique d'espèces végétales et animales et modifications biologiques dans le monde animal et végétal) que l'on ne saurait dissocier du réchauffement observé (IPCC, 2001). L'étude de l'impact des changements climatiques sur ces systèmes est aujourd'hui devenue prioritaire. Les seuls outils dont on dispose pour obtenir des estimations sur l'évolution future du climat sont les modèles numériques. Des modèles simples peuvent permettre une estimation quantitative approximative de certaines variables moyennées à l'échelle du globe mais il faut disposer de modèles climatiques plus élaborés pour effectuer des estimations précises notamment concernant les rétroactions Océan-Atmosphère-Végétation. Les modèles climatiques globaux ont su intégrer les relations océan-atmosphère (voir revue dans IPCC, 2001) et tendent aujourd'hui à tenir compte de l'effet des écosystèmes terrestres sur le climat global (e.g. Foley et al., 1998; Levis et al., 1999; Foley et al., 2000; Prentice et al., 2000a). Mais si les végétations actuelles sont de mieux en mieux simulées pour les conditions climatiques contemporaines, ces modèles doivent être nécessairement validés pour des changements équivalents à ceux qui sont prédits pour s'assurer de leur robustesse. La modélisation des climats passés permet de tester la sensibilité de ces modèles sous des conditions climatiques très différentes de celles qui ont été mesurées depuis seulement un siècle et utilisées pour calibrer les modèles. C'est l'objectif du programme international Paleoclimate Modelling Intercomparison Project (PMIP) qui fonctionne depuis plusieurs années (Joussaume & Taylor, 1995).

Les modèles de végétation impliquent des processus dont les caractéristiques de temps sont plus étendues que les processus atmosphériques, ce qui rend le couplage assez délicat. Les premiers couplages ont été asynchrones et ont impliqué des modèles de type BIOME (Prentice et al., 1992; Haxeltine & Prentice, 1996; Kaplan, 2001) qui prennent en compte de façon statique les contraintes climatiques (un biome végétal est un ensemble d'écosystèmes caractéristiques d'une zone biogéographique, nommé à partir de la végétation qui y prédomine et y est adaptée). Les modèles plus récents dit "dynamiques" comme LPJ (Sitch et al., 2003)

ou IBIS (Foley et al., 1996) mettent en jeu des processus tels que la compétition pour la lumière et les ressources en eau, la mortalité ou bien des perturbations (notamment les feux). Les modèles climatiques les plus récents sont actuellement capables de prendre en compte cette dynamique (Foley et al., 2000).

Le meilleur moyen de vérifier les prédictions des modèles est de les confronter à des archives fossiles pour des périodes de changements paléoclimatiques globaux. Il existe de nombreux marqueurs environnementaux qui ont été conservés sur plusieurs milliers ou millions d'années et qui peuvent permettre de valider ces modèles (isotopes du carbone, cernes d'arbres, charbons, pollens, macro-restes végétaux ...). Les méthodes les plus récentes de reconstruction des végétations à l'aide de ces marqueurs utilisent les mêmes concepts que les modèles de végétation précédemment cités, permettant ainsi une confrontation presque directe. C'est le cas notamment de la méthode de biomisation (Prentice et al., 1996; Prentice & Webb, 1998; Prentice et al., 2000a) qui permet d'estimer des biomes à l'aide de données polliniques. Cette méthode consiste à calculer des scores de type fonctionnel de plantes (que nous nommerons pfts, de l'anglais "Plant functional types") à partir de taxons polliniques. Ce concept est utilisé en écologie depuis de nombreuses années mais recoupe des notions différentes selon les auteurs (Smith et al., 1996). Nous considérons ici un pft comme un groupe d'espèces végétales ayant les mêmes exigences environnementales (climatiques et édaphiques); les pfts sont définis selon leur taille, la forme de leurs feuilles et leur phénologie (Prentice et al., 1992; Prentice et al., 1996)). Des biomes polliniques sont ensuite estimés par la combinaison d'un ou plusieurs pfts (Jolly et al., 1998). Cette méthode a fourni de très bons résultats pour la désignation des biomes forestiers. Cependant les biomes herbacés qui sont plus répandus sur les continents que les biomes forestiers sont mal caractérisés par les pollens. Ces derniers ne permettant pas une identification taxonomique plus précise que la famille Poaceae. Par ailleurs, les milieux chauds et secs, propices aux herbacées, sont des environnements oxydants qui ne permettent pas ou peu la conservation des grains de pollen.

Les formations herbacées couvrent 33% de la superficie des terres émergées, contre 24% pour les forêts (Demangeot, 1996). Elles regroupent par zone climatique: les toundras de la zone froide (6% de la superficie des terres émergées), les prairies de la zone tempérée (6%), les savanes de la zone inter-tropicale (11%) et les steppes des semi-déserts (10,5%)

(Demangeot, 1996). Parmi ces formations, certaines sont dominées par des graminées, annuelles ou pérennes, à cycle photosynthétique en C₃, d'autres par des graminées à cycle photosynthétique en C₄. Durant les périodes glaciaires qu'a connues la Terre, notamment le DMG (Dernier Maximum Glaciaire, 18000 ans avant l'actuel, en âge ¹⁴C), les formations herbacées étaient beaucoup plus répandues qu'à l'actuel. Par exemple, la végétation inter-tropicale auraient été beaucoup plus ouverte, avec une couverture herbacée importante (e.g. Elenga et al., 2000; Prentice et al., 2000b). Cette période, qui en zone inter-tropicale est synonyme de changements importants sur la pression partielle en CO₂ (pCO₂), la température ainsi que la fréquence des feux a favorisé l'expansion des graminées en C₄ dans les zones d'altitude (e.g. Street-Perrott et al., 1997; Huang et al., 1999; Wooller et al., 2000; Wooller et al., 2003).

Parmi les indicateurs complémentaires au pollen, le $\delta^{13}\text{C}$ de la matière organique, permet d'avoir une idée des proportions de plantes en C₃ et C₄ (e.g. Schwartz et al., 1986; Guillet et al., 1988; Mora & Pratt, 2002) mais aucunement sur la composante graminéenne. Des essais de mesures de $\delta^{13}\text{C}$ sur des fragments brûlés de graminées (Beuning & Scott, 2002) ont ouvert de nouvelles perspectives mais la méthode nécessite encore d'être validée puisque les résultats de Krull et al. (2003) tendent à infirmer cette méthode. L'étude des cuticules de graminées conservées dans les sédiments (Wooller et al., 2000; Marret et al., 2001; Ficken et al., 2002; Wooller et al., 2003) est également intéressante puisqu'elle fournit des indications taxonomiques au niveau de la sous-famille des Poaceae. Mais là encore, les travaux sont très peu nombreux et ne permettent pas d'appréhender les milieux oxydants où les cuticules sont rapidement dégradées. Des études récentes d'assemblages phytolithiques modernes et fossiles, provenant de sols et sédiments, montrent que les phytolithes peuvent être utilisés pour différencier les formations herbacées intertropicales, tempérées et méditerranéennes (e.g. Piperno, 1988; Fredlund & Tieszen, 1994; Alexandre et al., 1997b; Fredlund & Tieszen, 1997b; Alexandre et al., 1999; Barboni et al., 1999; Prebble et al., 2002; Delhon et al., 2003; Piperno & Jones, 2003). Le nombre de ce genre d'étude reste cependant faible et très peu de résultats quantitatifs sont proposés.

Nous proposons donc d'améliorer l'outil phytolithe, qui permet de caractériser la dynamique des formations herbacées, en calibrant des fonctions de transferts entre des assemblages phytolithiques modernes, la végétation et le climat afin d'intégrer ces données à la méthode de biomisation pollinique qui permet des reconstitutions de végétations. On pourra alors envisager d'intégrer ce marqueur aux méthodes de reconstitution des végétations qui utilisent

d'autre marqueurs telle que la méthode de biomisation pollinique (Jolly et al., 1998). Ceci permettra d'affiner les reconstructions paléo-environnementales pour permettre ensuite une validation plus pertinente des modèles de végétation sur des périodes passées.

I. 2 Les phytolithes, traceurs des formations herbacées

I. 2. 1 Les phytolithes

Les phytolithes sont des particules d'opale ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) (Jones & Seignit, 1696; Alexandre, 1996) qui se forment par précipitation de silice amorphe entre et dans les cellules de nombreuses plantes vivantes en sénescence (Piperno, 1988). C'est dans les graminées qu'ils sont particulièrement abondants, différents et distincts (Twiss et al., 1969; Twiss, 1983; Palmer et al., 1985; Twiss, 1987; Piperno, 1988; Mulholland, 1989; Twiss, 1992; Kondo et al., 1994). Les travaux précédemment cités montrent que trois des cinq sous-familles de Poaceae sont correctement différenciées par les types de phytolithes qu'elles produisent.

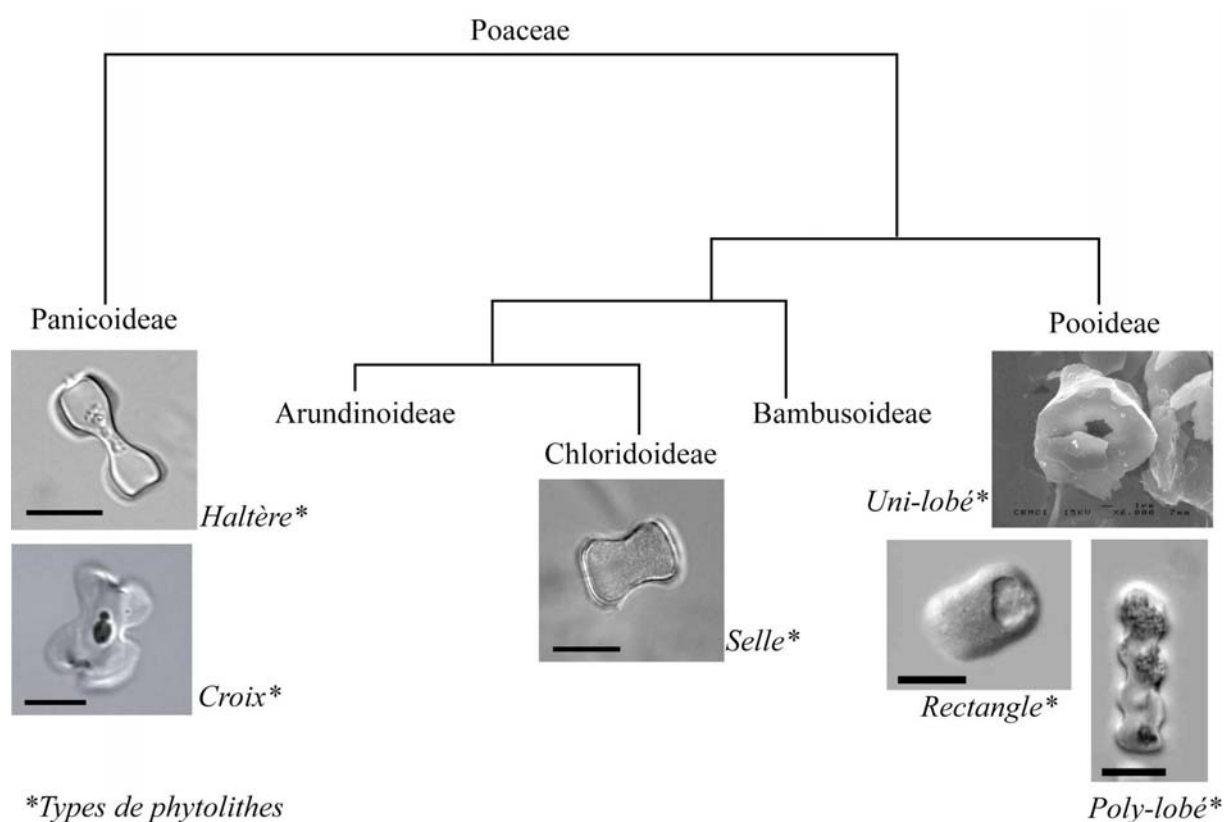


Figure I. 1 Classification des Poaceae selon (Watson et al., 1985; Watson & Dallwitz, 1992). et principaux types morphologiques de phytolithes produits par les sous-familles de graminées.

I. 2. 2. Les sous-familles de graminées

Les Panicoideae, constituent la première sous-famille. Ce sont essentiellement des graminées à cycle photosynthétique en C₄ (79% des genres selon Watson et al. (1985) et Watson et Dallwitz (1992)). Les Panicoideae en C₄ sont adaptées aux climats chauds et humides ou aux sols à forte teneur en eau disponible (Hartley, 1958; Teeri & Stowe, 1976; Tieszen et al., 1979; Cabido et al., 1997; Scott, 2002). Celles en C₃ sont inféodées aux zones ombragées des sous-bois tropicaux (Tieszen et al., 1979; Schwartz, 1991). Ces graminées sont d'une manière générale de grande taille (Watson et al., 1985; Watson & Dallwitz, 1992) et sont communément appelées "graminées hautes" par comparaison aux Chloridoideae qui sont dites des "graminées basses". Les Chloridoideae ont toutes un cycle photosynthétique en C₄ (Livingstone & Clayton, 1980; Watson et al., 1985; Watson & Dallwitz, 1992). Elles sont adaptées aux climats chauds et secs et aux sols pauvres en eau (Hartley, 1964; Tieszen et al., 1979; Livingstone & Clayton, 1980; Watson et al., 1985; Watson & Dallwitz, 1992). Les Pooideae (ou Festucoideae) sont des graminées en C₃ (Watson et al., 1985; Watson & Dallwitz, 1992), abondantes en zones tempérées et froides mais aussi présentes en altitude en zone inter-tropicale (Tieszen et al., 1979; Livingstone & Clayton, 1980; Tieszen et al., 1997; Scott, 2002; Winslow et al., 2003). Les Arundinoideae sont essentiellement des graminées en C₃ (92% des genres d'après Watson et al. (1985) et Watson et Dallwitz (1992)) et se retrouvent sous tout type de climat. Les Bambusoideae, cinquième sous-famille, sont des graminées en C₃, caractéristiques des zones tropicales et tempérées chaudes, essentiellement forestières (Watson et al., 1985; Watson & Dallwitz, 1992).

La figure I. 1. schématise la classification des Poaceae qui est adoptée dans cette thèse (Watson et al., 1985; Watson & Dallwitz, 1992). Sont aussi représentés les principaux types morphologiques de phytolithes (c.f. paragraphe suivant) produits par les sous-familles de graminées.

I. 2. 3. Classification taxonomique des phytolithes

Nous avons adopté dans ce mémoire la classification des phytolithes produites par les Poaceae proposée par Twiss (1969) et complétée des descriptions de Mulholland (1989), Kondo et al. (1994) et Fredlund et Tieszen (1994).

Quinze types de phytolithes ont été utilisés pour l'interprétation de nos assemblages modernes; neuf sont attribués aux Poaceae : les types "croix" (*cross*, en anglais) et "haltère" (*dumbbell*) sont produits essentiellement par les Panicoideae; le type "selle" (*saddle*) est

produit préférentiellement par les Chloridoideae; les types "uni-lobé" (*uni-lobate*), aussi appelé "roundel" (Mulholland, 1989) et "poly-lobés" (*poly-lobate*) et les "rectangle" (*rectangle*) sont produits en très grande majorité par les Pooideae; le type "pointe" (*point-shaped*), le type en "éventail" ou "cellule bulliforme silicifiée" (*fan-shaped*) ainsi que le type "allongé" (*elongate*) sont produits par les cinq sous-familles de Poaceae. Les sous-familles Bambusoideae et Arundinoideae produisent tous ces types de phytolithes avec, semble t'il, une dominance du type "selle" pour les Bambusoideae et du type "poly-lobé" pour les Arundinoideae. Ceci a été mis en évidence dans la classification des Poaceae de Watson et Dallwitz (1992) et remarqué dans nos assemblages.

Six types de phytolithes ne sont pas attribués à des Poaceae: le type "cône" (*conical*) est produit par les Cyperaceae (Le Cohu, 1973; Ollendorf, 1987; Kondo et al., 1994; Wallis, 2003); le "sphérique crénelé" (*crenate spherical*) est produit dans les feuilles des Palmae (Kondo et al., 1994; Runge, 1999; Runge, 2000; Vrydaghs & Doutrelepon, 2000), le "sphérique rugueux" (*rough spherical*) est produit dans les cellules du parenchyme du bois des dicotylédones ligneux (Scurfield et al., 1974; Kondo et al., 1994) ; les Pinaceae produisent un type que l'on peut retrouver dans les assemblages, nommé en anglais "*spherical with sockets*" par Delhon et al. (2003) ou bien "*spiny body*" par Kerns (2001) ou encore "*spiked type*" par Blinnikov et al. (2002), et qui peut être traduit par "sphérique irrégulier avec des pointes"; le "sphérique lisse" (*spherical smooth*) semble être produit par les dicotylédones ligneux ainsi que certaines monocotylédones herbacées (Piperno, 1988; Kondo et al., 1994). Ce type a aussi été observé dans les racines de certaines graminées (Alexandre et al., 2000).

Cette classification ne rend pas compte de la complexité des dénominations et de la disparité des termes employés dans la littérature rendant les comparaisons difficiles si des photographies ne viennent pas illustrer ces études. Les noms attribués à chacun des types étant sensiblement différents pour chacun de ces auteurs, les critères descriptifs proposés par l'ICPN (International Code For Phytolith Nomenclature) ont été utilisés. Cette nomenclature en préparation devrait être rapidement publiée.

I. 2. 4. Concept d'assemblages et d'indices phytolithiques

Un grand nombre d'études sur les phytolithes sont des descriptions de formes ou types (aussi nommés morphotypes) extraits de nombreux taxons végétaux, dans le but d'établir des classifications de références (Parry & Smithson, 1964; Sendulsky & Labouriau, 1966;

Geis, 1973; Scurfield et al., 1974; Brown, 1984; Kondo & Sase, 1986; Mulholland, 1989; Bozarth, 1992; Kaplan et al., 1992; Rapp & Mulholland, 1992; Kondo et al., 1994; Ball et al., 1996; Ball et al., 1999; Runge & Fimbel, 1999; Albert et al., 2000; Mbida et al., 2000; Runge, 2000; Vrydaghs & Doutrelepon, 2000; Kerns, 2001; Lu & Liu, 2003; Wallis, 2003). Ce genre d'étude, comparable à ce qui a été fait avec les pollens, est intéressant mais cependant de portée limitée. En effet, avant même que tous les genres et les espèces n'aient été encore étudiés, les résultats ont montré qu'un type de phytolithe pouvait être produit par différentes plantes et qu'une plante pouvait produire plusieurs types de phytolithes. C'est le phénomène de multiplicité et de redondance très bien expliqué par Fredlund et Tieszen (1994). Ceci montre qu'il est périlleux d'essayer d'attribuer un ou plusieurs types à un genre ou une espèce végétale.

Fredlund et Tieszen (1994) ont étudié de nombreux échantillons modernes de sol (horizon humique) prélevés dans le Nord des Grandes Plaines américaines, répartis au sein de formations herbacées dominées par différentes sous-familles. Ces auteurs ont démontré qu'à l'aide d'assemblages phytolithiques, statistiquement représentatifs, plusieurs grands types de formations herbacées pouvaient être clairement caractérisés malgré les problèmes de multiplicité et de redondance évoqués précédemment. Un phytolithe ne permet donc pas de caractériser un taxon, mais un assemblage phytolithique permet de caractériser une formation végétale en traçant les sous-familles graminéennes qui y prédominent.

Un nombre important d'études paléo-environnementales a été mené à l'aide d'assemblages phytolithiques sur des matériels différents tels que des horizons humiques fossiles, des loess ou sédiments lacustres et marins. Ces études ont été menées essentiellement dans les Grandes Plaines américaines (Lewis, 1981; Fredlund et al., 1985; Kurmann, 1985; Fisher et al., 1995; Fredlund & Tieszen, 1997a; Fredlund & Tieszen, 1997b; Kelly et al., 1998; Baker et al., 2000; Stromberg, 2002), mais aussi en Amérique du Sud (Piperno & Becker, 1996; Alexandre et al., 1999; Blinnikov et al., 2002; Piperno & Jones, 2003), en Europe (Delhon et al., 2003), en Afrique (Alexandre et al., 1997b; Mworio-Maitima, 1997; Barboni et al., 1999; McLean & Scott, 1999; Runge & Fimbel, 1999; Albert et al., 2000; Mercader et al., 2001; Scott, 2002; Abrantes, 2003b; Ishida et al., 2003), en Océanie (Tsutsuki et al., 1993; Carter, 2000; Carter & Lian, 2000; Horrocks et al., 2000; Carter, 2002; Prebble et al., 2002), en Australie (Wallis, 2001), en Asie (Tsutsuki et al., 1993; Inoue & Sase, 1995; Jiang, 1995; Lu et al., 2002) et en Alaska (Thorn, 2001).

Par contre, le nombre d'études portant sur des assemblages phytolithiques modernes échantillonnés sous des végétations précisément décrites est faible comparé aux études d'assemblages fossiles. De plus, le nombre d'assemblages par type de végétation est aussi généralement très faible. L'étude la plus complète concerne les prairies du Nord des Grandes Plaines américaines (Fredlund & Tieszen, 1994) où 50 assemblages modernes ont été prélevés au sein de 16 prairies ayant des compositions graminéennes différentes. Quelques échantillons ont aussi été prélevés en Arizona sous une forêt de *Pinus Ponderosa* et dans des pelouses environnantes par Kerns et al. (2001). Au Panama, Piperno et Jones (2003) présentent 3 assemblages modernes prélevés sous forêt tropicale décidue et sous savane. En Europe, Delhon et al. (2003) proposent 5 assemblages modernes de pelouse, chênaie, pinède et ripisylve. En Afrique de l'Ouest, Alexandre et al. (1997b) présentent des assemblages modernes pris sous forêt tropicale et en savane. En Afrique centrale, Runge et al. (1999) ont étudié 30 assemblages sous forêts et savanes. En Afrique de l'Est, Barboni et al. (1999) présentent le comptage de 3 assemblages. En Nouvelle Zélande, Prebble et al. (2002) ont échantillonné 28 sites (110 assemblages) sous des végétations et microclimats différents. Ces assemblages sont interprétés grâce aux descriptions qualitatives des formations végétales. Mis à part l'étude de Fredlund et al. (1997b) et plus récemment celle de Prebble et al. (2002 I et II) aucune tentative de calibration quantitative entre les assemblages phytolithiques et la végétation ou le climat n'a encore été envisagée.

I. 2. 5. Représentation spatiale et temporelle des assemblages phytolithiques modernes

Il a souvent été avancé qu'un assemblage phytolithique issu de la partie superficielle d'un sol représente la végétation locale *via* sa dégradation *in situ* (Piperno, 1988; Mulholland, 1989). Des études ultérieures ont montré que la dispersion des phytolithes dépend de plusieurs contraintes qu'il est nécessaire d'investiguer avant toute interprétation des assemblages (Fredlund & Tieszen, 1994; Alexandre et al., 1997b; Barboni et al., 1999; Prebble et al., 2002). En effet, la structure de la végétation, le contexte géomorphologique et climatique vont influencer sur le caractère local ou extra-local du signal enregistré par l'assemblage, par le biais du processus de dispersion. Des études ont montré que plusieurs facteurs peuvent être responsables de la dispersion des phytolithes aux échelles extra-locale et régionale : le vent, l'action combinée des feux et du vent, les apports colluviaux ou alluviaux ainsi que le transport par les herbivores doivent être considérés (Piperno, 1988; Fredlund &

Tieszen, 1994; Alexandre et al., 1997b; Barboni et al., 1999; Kerns et al., 2001; Prebble et al., 2002). Finalement, un assemblage phytolithique issu d'un milieu fermé tel qu'une forêt où l'impact du vent et du ruissellement est faible sera plus indicatif de la végétation locale alors qu'un assemblage de milieu ouvert, soumis au vent, au ruissellement ou au pâturage sera plus influencé par la végétation régionale (Fredlund & Tieszen, 1994; Prebble et al., 2002). Ce phénomène de transport aérien ou fluvial peut-être très important puisque plusieurs carottes océaniques ont fait l'objet d'études phytolithiques, notamment en bordure des zones Sahariennes, Sahéliennes et Soudaniennes d'Afrique de l'Ouest (Diester-Haass et al., 1973; Bukry, 1979; Barcena et al., 2001; Abrantes, 2003) ou à l'embouchure de grands fleuves (Jansen & Van Imperen, 1991; Piperno, 1997).

Un assemblage de sol intègre l'apport de phytolithes pendant un laps de temps difficile à estimer. C'est le phénomène d'héritage. La durée d'enregistrement que représente un assemblage est très variable. Elle dépend en effet du taux de production de litière et de sa vitesse de dégradation (Alexandre et al., 1997a) mais aussi du temps de résidence des phytolithes dans le sol qui est lié à leur vitesse de translocation et de dissolution (Piperno, 1988; Fredlund & Tieszen, 1994; Alexandre et al., 1997a). Les variables qui vont contrôler la dissolution sont essentiellement la surface spécifique des phytolithes (positivement corrélée à leur solubilité) et le pH du sol (Bartoli & Wilding, 1980; Piperno, 1988; Prebble et al., 2002). Peu de travaux ont essayé de quantifier la distribution des phytolithes dans des profils de sols et de discuter l'âge moyen des assemblages phytolithiques. Ces études offrent des résultats qui diffèrent en fonction du type de sol. En effet, Alexandre et al. (1999) montrent sur un profil de sol ferrallitique, sous climat tropical (Salitre, Brésil) qu'à 30 cm de profondeur l'âge moyen des phytolithes est d'environ 1000 ans. Piperno et Becker (1996) établissent que les phytolithes extraits des 20 premiers centimètres d'un Oxisol argileux, sous climat tropical (Manaus, Brésil) ont un âge inférieurs à 45 ans (datations C^{14} sur phytolithes). En domaine tempéré, Bartoli (1981) montre que pour deux sols différents (sol brun et podzol) sous le même climat (Vosges, France), la dissolution et la translocation des phytolithes peuvent varier d'un facteur 10 entre ces deux types de sols.

I. 3. Objectif de cette thèse et choix des sites d'études

Le but de cette thèse est d'établir des fonctions de transfert entre assemblages phytolithiques modernes et caractéristiques de la structure des formations herbacées, elles-mêmes liées aux

contraintes climatiques, édaphiques et/ou anthropiques. Cette étude est menée dans le même esprit que celui initié par Fredlund et al (1994; 1997b), c'est à dire en utilisant des assemblages suffisamment nombreux pour être représentatifs, basés sur des comptages statistiquement corrects et établis sur des types de phytolithes ayant une valeur taxonomique démontrée. Les résultats sont analysés à l'aide d'indices phytolithiques proposés par Twiss (1987; 1992) et Alexandre et al. (1997b). Ces indices sont :

- indice 1 (**Iph**): proportion de phytolithes de graminées basses à cycle photosynthétique en C₄ (Chloridoideae), relativement à la somme de phytolithes de graminées hautes à cycle photosynthétique en C₄ (Panicoideae) (Twiss, 1987; Twiss, 1992). Cet indice indique l'adaptation de la formation végétale à l'aridité.
- indice 2 (**Ic**) : proportion de phytolithes de graminées à cycle photosynthétique en C₃ (Pooideae) relativement à la totalité des phytolithes de graminées (Twiss, 1987; Twiss, 1992). Cet indice indique l'adaptation de la formation végétale à une température minimale et/ou à des P_{CO2} fortes (zones d'altitudes).
- indice 3 (**D/P**) : proportion de phytolithes caractéristiques des éléments ligneux, relativement à la somme de phytolithes de graminées (Alexandre et al., 1997b). Ce dernier indice indique la densité du couvert arboré en milieu intertropical.
- indice 4 (**Fs**) : proportion des phytolithes de cellules bulliformes de l'épiderme des graminées par rapport au total des phytolithes caractéristiques, indique le degré de silicification de ces cellules, lié au stress hydrique (cette étude).

Afin d'établir les relations entre assemblages phytolithiques modernes et végétation, nous avons choisi des zones géographiques et climatiques distinctes qui présentent une ou plusieurs caractéristiques à priori traçables par les phytolithes et plus précisément par les indices phytolithiques.

Dans la perspective d'intégrer ces données phytolithiques aux méthodes de reconstitution des végétations qui utilisent des marqueurs, comme la méthode de biomisation pollinique (Jolly et al., 1998), les assemblages phytolithiques sont systématiquement confrontés aux données polliniques, lorsqu'elles sont disponibles. Des biomes herbacés, susceptibles d'être décrits par les phytolithes, sont définis et comparés aux biomes polliniques. L'intégration des données phytolithiques permettra d'améliorer les biomisations polliniques, notamment la caractérisation des biomes herbacés. Les végétations reconstruites pour certaines périodes clef

du passé pourront être confrontées à celles simulées par des modèles prédictifs de végétation et permettront ainsi de vérifier leur validité.

I. 4. Organisation du mémoire

Ce mémoire est présenté sous forme de publications, chacune présentant l'étude d'un indice phytolithique :

1. Les formations herbacées à graminées hautes et basses ainsi que les formations désertiques intertropicales seront abordées à l'aide de 62 échantillons prélevés au Sénégal et Mauritanie par A-M. Lézine (1987; 1988; 1991; 1995), à travers quatre des zones bioclimatiques définies par White (1983). Une fonction de transfert sera établie entre indices phytolithiques et stress hydrique exprimé par le rapport AET/PET (évapotranspiration réelle sur évapotranspiration potentielle). Plusieurs biomes phytolithiques seront proposés et confrontés aux biomes polliniques (1998). L'article, soumis à *Journal of Biogeography*, s'intitule "Grass water stress and grass-dominated biome definition estimated from phytoliths in West Africa".
2. Afin de tester la capacité des assemblages phytolithiques à tracer les formations herbacées dominées par les Pooideae (i.e. majoritairement en C₃) en zone intertropicale, l'indice phytolithique Ic proposé et développé en zone tempérée par Twiss (1987; 1992) sera appliqué à des échantillons prélevés en Afrique de l'Est (Kenya et Tanzanie) le long d'un gradient altitudinal. L'article, à soumettre s'intitule "Testing the Ic phytolith index as a proxy of C₃/C₄ grass dominance in tropical areas: application at two sites in East Africa (Mt Kenya and Mt Rungwe)".
3. L'indice phytolithique D/P, indicateur du couvert arboré, sera calibré sur un transect de 750m à travers une transition forêt-savane, échantillonné par A. Vincens et al. (2000) ; cet indice D/P reflétant la structure végétale sera également confronté aux mesures de LAI (indice de surface foliaire, en anglais *Leaf Area Index*) effectuées le long du transect tous les 10m (Cournac et al., 2002). L'article, soumis à *Global and Planetary Changes*, s'intitule "A phytolith index as a proxy of tree cover density in tropical areas: calibration with Leaf Area Index along a forest-savanna transect in southeastern Cameroon".
4. Les potentialités des assemblages phytolithiques à enregistrer les formations herbacées et forestières seront aussi testées en zone Méditerranéenne. L'étude concernera 30 échantillons prélevés sur le Massif du Luberon pour lesquels des relevés botaniques exhaustifs ont été

réalisés. L'article soumis à *Review of Paleobotany and Palynology* s'intitule "Advantages and disadvantages of phytolith analysis for the reconstruction of Mediterranean vegetation: an assessment based on modern phytolith, pollen and botanical data (Luberon, France)".

5. Finalement, un dernier chapitre présentera une biomisation appliquée à l'ensemble des sites étudiés à l'aide des assemblages phytolithiques.

CHAPITRE II. CALIBRATION DES RELATIONS ENTRE ASSEMBLAGES PHYTOLITHIQUES, DISPONIBILITE EN EAU (AET/PET) ET CARACTERISATION DES BIOMES HERBACES EN C₄ INTERTROPICAUX EN AFRIQUE DE L'OUEST.

II. 1. Résumé étendu de l'article: Grass water stress and grass-dominated biome definition estimated from phytoliths in West Africa.

Nous proposons dans ce chapitre d'établir les relations entre d'une part les assemblages phytolithiques modernes, et d'autre part la végétation et le climat des zones Soudaniennes à Sahariennes en Afrique de l'Ouest. Plus spécifiquement, le but est de calculer une fonction de transfert entre certains indices phytolithiques et la disponibilité en eau exprimée par le rapport AET/PET (rapport entre évapotranspiration réelle et évapotranspiration potentielle). Ce rapport est un paramètre couramment utilisé pour contraindre la distribution des végétations aux échelles continentales et globales (Prentice et al., 1992; Sykes et al., 1996). Des biomes déduits sur ces données phytolithiques et pouvant être confrontés aux biomes déduits des données polliniques sont aussi proposés. L'idée d'établir des biomes "phytolithiques" s'inscrit dans la perspective de compléter les biomes polliniques relativement imprécis pour les zones intertropicales sèches à forte composante graminéenne.

Matériel et Méthode

Soixante deux assemblages phytolithiques modernes sont étudiés le long d'un gradient d'aridité croissante sud-nord au Sénégal et Mauritanie, à travers quatre zones bioclimatiques définies par White (1983). La description du type de végétation potentielle auquel appartient chacun des échantillons (Figure II.1) est faite à l'aide de la classification de White (1983), la nomenclature des végétations selon Yangambi (CSA, 1956) et les termes "basse" et "haute" employés pour différencier les prairies de Grandes Plaines Américaines (Fredlund & Tieszen, 1994). Les 4 zones de végétation peuvent être décrites comme suit: (1) la zone Guinéenne est caractérisée par une mosaïque de forêts décidues et savanes boisées avec un couvert graminéen dominé par des Panicoideae pérennes ; (2) la zone Soudanienne est constituée de forêts sèches et de savanes à graminées hautes pérennes et annuelles (Panicoideae et Arundinoideae) ; (3) la zone Sahélienne se compose de savanes, boisées ou non, à graminées basses, essentiellement des Chloridoideae et Arundinoideae ; (4) la zone Saharienne est couverte de buissons et pelouses semi-désertiques et désertiques avec des graminées

essentiellement annuelles (Chloridoideae, Arundinoideae) et une Panicoideae pérenne très présente (*Panicum turgidum* selon Le Houérou (1993a)).

Les données météorologiques sont interpolées ((Leemans & Cramer, 1991; CSE, 2000) pour chaque site et le rapport AET/PET est calculé selon la méthode utilisée par Harrison et al. (1993). L'erreur standard d'interpolation de AET/PET est de l'ordre de 0.04, par contre celle sur l'estimation AET/PET par le modèle de Harrison et al. (1993) n'est pas connue.

L'extraction (Kelly, 1990), la classification (Twiss et al., 1969; Mulholland, 1989; Twiss, 1992; Fredlund & Tieszen, 1994; Kondo et al., 1994; Alexandre et al., 1999; Barboni et al., 1999) et le comptage des phytolithes ont permis d'identifier 10 types (Plate II.1) et d'estimer une erreur de comptage de l'ordre de $\pm 3.5\%$ (de l'écart type).

Les assemblages phytolithiques sont analysés et discutés à l'aide de trois indices: (1) D/P, la proportion de phytolithes caractéristiques des éléments ligneux, relativement à la somme de phytolithes de graminées, indiquant la densité du couvert arboré ; (2) Iph, la proportion de phytolithes de graminées basses à cycle photosynthétique en C_4 , relativement à la somme de phytolithes de graminées hautes à cycle photosynthétique en C_4 , indiquant l'adaptation de la formation végétale à l'aridité ; (3) Fs, la proportion de phytolithes de cellules bulliformes de l'épiderme des graminées par rapport au total des phytolithes comptés, indique le degré de silicification de ces cellules, lié au stress hydrique.

La méthode statistique de régression multiple en mode bootstrap (Efron, 1979; Guiot, 1990) est utilisée pour estimer le rapport AET/PET à partir des indices phytolithiques, et une analyse discriminante permet d'établir les biomes phytolithiques. Les biomes polliniques sont établis à partir de la méthode de biomisation développée pour l'Afrique par Jolly et al. (1998) et légèrement modifiée par Peyron et al. (2000).

Résultats

Les assemblages phytolithiques (figure II.2, table II.1) sont classés selon un gradient longitudinal et donc selon une aridité croissante. Ils montrent que les savanes à graminées basses peuvent être différenciées des savanes à graminées hautes à l'aide du Iph pour une valeur seuil fixée à $20 \pm 1.4\%$ et que l'indice Fs (proportion des cellules bulliformes silicifiées) augmente dans les échantillons depuis la zone Guinéenne jusqu'à ceux de la zone Saharienne. Les figures II.3 et II.4 confirment que les indices Fs et Iph sont négativement corrélés à AET/PET. Des régressions entre ces deux indices et ce paramètre climatique peuvent être alors estimées. Afin de prendre en compte la diminution du Iph observée en zone

saharienne le terme quadratique centré $(Iph-20)^2$ est ajouté (20 étant le Iph moyen). On trouve :

$$AET/PET (\%) = a_0 + a_1Fs + a_2Iph + a_3(Iph-20)$$

avec $a_0 = 42.5$, $a_1 = -0.538 \pm 0.075$, $a_2 = -0.326 \pm 0.087$ et $a_3 = 0.008 \pm 0.068$, avec les barres d'erreur correspondant à un écart type.

Le coefficient de corrélation (R) entre observations et estimations vaut 0.80 ± 0.04 . La vérification (indépendante) établie à l'aide de la méthode bootstrap montre que la relation est très significative ($R = 0.71 \pm 0.14$). Ces résultats correspondent à la figure II.5.

Cette relation est validée par application à des assemblages échantillonnés dans des zones bioclimatiques limites ou en dehors de celles qui ont servi à la calibration (voir Table II.2). Les résultats montrent que l'estimation du rapport AET/PET en zone désertique (désert de Sonora, Mexique) est correcte puisqu'elle se situe dans la limite de l'intervalle de confiance des mesures de AET/PET. Par contre, l'application en zone beaucoup plus humide (Tanzanie et Cameroun) montre que cette équation est incapable d'estimer AET/PET pour des valeurs du rapport supérieures à 0.45.

Le rapport AET/PET estimé par les phytolithes est ensuite comparé à celui estimé à partir des données polliniques pour la même zone et avec un nombre d'échantillons presque équivalent (figure II.6). Les résultats montrent que l'estimation de AET/PET produite par les phytolithes est comparable à celle des pollens ($R = 0.84 \pm 0.04$).

Finalement, 4 biomes herbacés sont définis "a priori" suivant les zones bioclimatiques de White (1983): 1) le biome "formation herbacée (en C_4) désertique" qui correspond à la zone Saharienne. 2) le biome "savane à graminées basses" correspondant à la zone Sahélienne. 3) le biome "savane à graminées hautes" qui est caractéristique de la zone Soudanienne et 4) le biome "forêt tropicale mésophyle" correspondant à la zone Guinéenne. L'objectif est ici de voir si les assemblages phytolithiques sont aptes à prédire l'appartenance à l'un de ces quatre groupes. Ce genre de problématique est typiquement abordé par une analyse discriminante qui consiste à calculer les probabilités d'appartenance à un groupe à partir de variables prédictives, en l'occurrence : (1) l'abondance des phytolithes "sphériques rugueux" produits par les arbres ; (2) l'abondance des cellules bulliformes silicifiées (type "éventail", Fs) ; (3) l'abondance du type "haltère" ; (4) l'abondance des cellules du type "croix" produites par les *Panicoideae* ; (5) l'abondance des cellules du type "selle" produites par les *Chloridoideae*. Les résultats montrent que les assemblages phytolithiques permettent d'assigner correctement le biome correspondant dans plus de 90% des sites échantillonnés (Table II.4). Cette biomisation a été appliquée à d'autres assemblages phytolithiques provenant de zones géographiques

différentes (Mexique, Tanzanie et Cameroun). Les résultats confirment que les fonctions discriminantes des biomes "formation herbacée (en C₄) désertique", "savane à graminées hautes" et "forêt tropicale sèche" établies en Afrique de l'Ouest sont extrapolables à d'autres régions très éloignées. Aucun échantillon issu de "savane à graminées basses" n'était disponible pour vérifier si ce biome est lui aussi bien prédit.

La dernière partie de cet article met en confrontation les biomes "phytolithiques", les biomes "polliniques" et les biomes définis d'après des images satellites (Olson et al., 1983; Olson, 1994b). Ceci permet d'estimer les correspondances qu'il y a entre chacun des types de biomes (figure II.7).

Discussion-conclusion

En zones inter-tropicales et particulièrement en zones arides, le degré d'ouverture de la végétation, la fréquence des feux et la force des vents favorisent certainement le transport éolien des phytolithes sur de grandes distances. Cette étude montre que les assemblages phytolithiques modernes sont capables de refléter les grands types de végétations ainsi que l'un des paramètres climatiques qui les conditionnent (AET/PET). Les savanes à graminées basses et à graminées hautes sont correctement différenciées à l'aide de l'indice phytolithique I_{ph}, dont l'acuité à tracer la physionomie des formations herbacées dominées par les graminées en C₄ et sa valeur en tant qu'indicateur du stress hydrique est discutée. Les résultats montrent aussi que la quantité de cellules bulliformes silicifiées dans les assemblages augmente proportionnellement au AET/PET local. Cette relation est aussi discutée, notamment concernant sa validité en zone humide où le stress hydrique subi par la plante peut ne plus être en relation directe avec le AET/PET local.

Pour la première fois en zone inter-tropicale, une fonction de transfert est calibrée entre des indices phytolithiques et climatiques. La relation établie n'est pour l'instant valable que pour des valeurs de AET/PET comprises entre 0.1 et 0.45. Elle a toutefois les mêmes qualités prédictives que les données polliniques pour cette zone. Il serait nécessaire d'augmenter le nombre d'assemblages modernes pour élargir son domaine d'application.

L'utilisation conjointe des phytolithes et des grains de pollens extraits d'enregistrements sédimentaires devrait permettre une meilleure fiabilité des estimations du rapport AET/PET.

Les 4 biomes établis offrent, contrairement aux pollens, une image de la physionomie des formations herbacées dominantes en Afrique de l'Ouest. Les biomes "formation herbacée (C₄) désertique", "savane à graminées basses" et "savane à graminées hautes" sont clairement définis sur la zone d'étude. Il est maintenant nécessaire d'élargir le domaine de calibration à

des zones plus forestières et plus froides, de façon à vérifier la validité du biome "forêt tropicale sèche" et d'établir un biome "formation herbacée en C₃".

II. 2. Données phytolithiques supplémentaires

L'article de ce chapitre fait référence à 42 assemblages phytolithiques additionnels qui ont été utilisés pour vérifier les relations établies en Afrique de l'Ouest. Un certain nombre d'entre eux, ne faisant pas l'objet de publication, sont brièvement présentés dans ce paragraphe. C'est le cas de 7 échantillons prélevés dans le désert de Sonora au Mexique (Ortiz et Gachet, communication personnelle). Ceux de Kandara (Cameroun) sont présentés dans le chapitre III et ceux de Masoko (Tanzanie) sont présentés dans le chapitre IV.

- *Echantillons du désert de Sonora (Mexique)*

Les échantillons du désert de Sonora ont été prélevés dans le sous-biome désertique appelé "lower Colorado river valley" (Turner & Brown, 1994) qui est caractérisé par une végétation de buissons (*Encelia farinosa*, *Ambrosia dumosa*, *Larrea tridentata* et *Cercidium microphyllum*), de cactus (*Carnegiea gigantea*) et de graminées en touffes, essentiellement *Hilaria rigida* (Chloridoideae).

Huit échantillons (dont un stérile) ont été prélevés en mars 2001 par M. Ortiz et S. Gachet entre les latitudes 31,6°N et 31,94°N et les longitudes -113,28°E et -113,48°E. C'est essentiellement la couche supérieure de sables fins ou grossiers qui a été prélevée. Seuls deux échantillons (SB2-3 et SB2-4) l'ont été sur des dunes où une mince couche humique avait pu se développer.

Les comptages sont présentés dans le tableau II.2.1. Afin de pouvoir les comparer avec les assemblages de l'Afrique de l'Ouest, les pourcentages sont calculés sans prendre en compte les phytolithes de type "cellule longue". De façon synthétique, les assemblages révèlent que la proportion de phytolithes produits par les arbres et arbustes (dicotylédones ligneuses) "sphériques rugueux" est très faible (0 à 7%), donnant un D/P compris entre 0 et 0.08, comparable aux D/P calculés en zones Saharienne et Sahélienne de l'Afrique de l'Ouest. Le pourcentage de phytolithes produit par les Panicoideae (de type "haltère") est lui aussi très faible, inférieur à 17%, et donc bien inférieur à la zone Sahélienne, sauf pour les deux échantillons SB2-3 et SB2-4 où ont été relevés respectivement 40 et 31% de ce type. La proportion des phytolithes produits par les Chloridoideae (type "selle") est importante (11 à 37%), comparable aux plus fortes valeurs enregistrées dans les échantillons de la zone

Sahélienne. Ces valeurs produisent des Iph très élevés, compris entre 52 et 79% (35 et 24% pour SB2-3 et SB2-4), et donc supérieures à celles calculées en zone Sahélienne.

La présence de phytolithes produits par des Pooideae (4 à 14%) différencie très largement les assemblages désertiques de Sonora de ceux d'Afrique de l'Ouest. Leur abondance est expliquée par la présence d'espèces de Pooideae envahissantes favorisées par l'agriculture et la proximité des végétations de type Méditerranéen. Les espèces relevées sont *Schismus arabicus*, *Schismus barbatus* (Arundinoideae) et *Bromus rubens* (Pooideae) (Turner & Brown, 1994). Comme il en a déjà été fait mention dans le premier paragraphe, ce fait souligne l'importance des perturbations que l'homme a pu provoquer sur les relations climat-végétation actuelle.

II. 3. Perspectives

II. 3. 1 Application à des échantillons fossiles

Suite à cette étude, la relation établie entre les index phytolithiques et le AET/PET ainsi que la biomisation sera appliquée aux échantillons fossiles d'une carotte sédimentaire prélevée dans la même zone d'étude. Nous disposons des assemblages phytolithiques du lac Guiers, publiés par Alexandre et al. (1997) et couvrant les derniers 6000 ans. Les spectres polliniques ont été publiés par Lézine (1987; 1989). Il faudra, avant d'appliquer ces fonctions de transfert, reprendre les comptages phytolithiques fossiles afin qu'ils soient comparables aux assemblages actuels. Par exemple le type nommé "corck cell like" par Alexandre et al. (1997b) n'a pas été observé dans les assemblages actuels ; or, il est très présent dans certains assemblages fossiles. Il est aussi nécessaire de reprendre les spectres polliniques afin d'estimer le rapport AET/PET et les biomes à l'aide de la méthode de biomisation (Jolly et al., 1998). Les biomes "polliniques" pourront alors être confrontés aux biomes "phytolithiques". Ces résultats permettront d'affiner les connaissances du climat dans cette région, notamment durant l'optimum climatique de l'Holocène à 6000 B.P. (Before Present) qui est l'objet de nombreuses études (e.g. Jolly et al., 1998; Prentice & Webb, 1998; Peyron, 1999; Peyron et al., 2000).

II. 3. 2 Application à d'autres domaines climatiques

Fredlund et Tieszen (1997b) ont montré que la distribution des sous-familles de graminées dans les grandes plaines américaines est liée notamment aux températures moyennes du mois

de juillet et qu'une fonction de transfert basée sur des assemblages phytolithiques était capable d'estimer ces températures. La méthode de calibration est proche de celle que nous avons utilisé dans cette étude. Les deux études sont complémentaires puisque menées dans deux domaines climatiques différents. Mais parce que la distribution des graminées dans ces deux domaines est contrainte par des paramètres climatiques différents, ces fonctions de transfert ne peuvent pas être appliquées indifféremment dans les deux domaines. Il est peut-être envisageable de regrouper les deux séries d'assemblages phytolithiques et d'essayer de contraindre températures et AET/PET conjointement.

Une collaboration est aussi en cours avec Lyu Houyan qui a établi de très nombreux assemblages modernes en Chine (Wang & Lyu, 1992), mais dont les écrits nécessitent d'être traduits et compilés de la même façon que nos assemblages pour être ensuite interprétés en termes climatiques.

II. 4. Grass water stress and grass-dominated biome definition estimated from phytoliths in West Africa.

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Abstract

The aim of this study is to calibrate the relationship between vegetation structure, phytolith indices and climate parameters, in order to define new phytolith-derived biomes and assess the reliability of phytolith data for testing vegetation models. 62 modern soil surface samples have been collected in West Africa, Mauritania and Senegal along a latitudinal transect across four bioclimatic zones defined by White (1983): Guinean, Sudanian, Sahelian and Saharan zones. The results are interpreted based on modern phytolith assemblages and compared with modern pollen data from the same region. Desert, tall and short grass associations are discriminated both by their phytolith index (Iph), which is defined as the proportion of saddle phytolith type to the total of cross, dumbbell and saddle ones, and by the proportion of fan-shaped phytolith type (Fs) among the characteristic phytoliths. Along this transect, the vegetation distribution is mainly constrained by water availability, which can be represented by the ratio between annual actual evapotranspiration and the annual equilibrium evapotranspiration (AET/PET). We show that this ratio can be accurately estimated by this phytolith index and the percentage of the silicified bulliform cells and phytolith-based estimates agree well with the reconstruction based on modern pollen data. In the second part, using 5 non-ambiguous phytolith types, 4 biomes can be characterized using a discriminant analysis: “desert C₄-grassland”, “tall grass savanna”, “short grass savanna” and “tropical mesophilous forest”. Phytolith-derived biomes are compared with pollen-derived biomes and actual vegetation biomes. Finally we show that phytoliths are very complementary to pollen data in reconstructing past vegetation and climates.

Keywords : phytoliths, pollen, West Africa, paleovegetation, paleoclimate, grassland biomes

Introduction

Global vegetation models provide a means of translating the outputs from climate model into maps of potential vegetation distribution for present, past and future climate scenarios (Prentice et al., 1992; Haxeltine & Prentice, 1996). One of the output of such models are biomes, which may be defined as the world's major plant and animal communities, classified according to the predominant vegetation and characterized by adaptations of organisms to that particular environment. Biomes are well determined by macroclimatic and soil characteristics. The simplest vegetation models are based on bioclimatic indicators developed from climatic variables reflecting specific processes of plant growth or survival. These indicators, when properly chosen, are able to predict locations and potential shifts of biome limits in response to past or future climate change (Cramer, 2002). Examples of such indicators are growing degree days, absolute cold tolerance limits or estimates of drought stress based on a simple water balance model, i.e. the ratio of annual actual evapotranspiration to the annual equilibrium evapotranspiration (AET/PET).

Such biome models can be coupled to climatic models to simulate past vegetation (Prentice et al., 1992; Claussen & Esch, 1994) and the validity of these simulations is assessed by comparison with vegetation reconstructed from proxy data. To this end, the biomization method (Prentice et al., 1996; Prentice & Webb, 1998; Prentice et al., 2000b) has been devised to reconstruct biomes from pollen data by assigning pollen taxa to one or more Plant Functional Types (PFTs) and by considering biomes as combinations of one or several PFTs (Jolly et al., 1998). This method has proven to be very efficient for forest biomes. However, grass-dominated biomes, which are today the most widespread continental biomes are not accurately characterized by pollen data because of the lack of precise pollen identification of species or subfamilies of Poaceae. For instance, except in Europe (Tarasov et al., 1999), the two PFTs “warm grasses/shrubs” and “cool grasses/shrubs” defined by Prentice et al (1992) cannot be distinguished using modern pollen data set (Jolly et al., 1998). Samples collected in the “steppe” biome (dry tropical grassland) are also often incorrectly assigned to either the “savanna” biome (wet tropical grassland), the “tropical xerophytic woods/scrub” biome or the “temperate xerophytic woods/scrub” biome by the biomization method (Jolly et al., 1998). This lack of precision is particularly worrying for reconstructing or modeling vegetation of the last glacial period, when grass dominated-biomes were more widespread than today.

Phytoliths are amorphous silica particles that precipitate in and/or between the cells of living plant tissues. Phytolith assemblages have recently been shown to be a promising tool to discriminate between the various grasslands (Fredlund & Tieszen, 1994; Alexandre et al.,

1997; Barboni et al., 1999). Fossil phytolith assemblages from soils, buried soils and lake sediments have been used to reconstruct paleovegetation changes. Because of redundancy and multiplicity (Rovner, 1971; Mulholland, 1989; Fredlund & Tieszen, 1994), one phytolith type cannot be uniquely related to one plant taxon and fossil assemblages are interpreted in term of vegetation type, by comparison with modern assemblages collected from soil humic horizons or erosion surfaces. However, although Fredlund and Tieszen (1997b) presented a calibration between phytolith assemblages and temperature for the American Great Plains, there is no advanced calibration between modern phytolith assemblages, bio-climatic data and vegetation biomes in the inter-tropical zone. The aim of this study is to fill this gap by first calibrating the relationship between phytolith indices, vegetation structure, and annual amount of growth-limiting drought stress on plants expressed by the ratio AET/PET for the West-African bio-climatic zones. The resulting climate proxy is tested on a few modern phytolith assemblages from other geographical areas (Cameroon, Tanzania and Mexico) and compared with AET/PET estimated by pollens for these areas. In a second step, phytolith-derived biomes are also proposed and the reliability and usefulness of these phytolith-derived biomes for testing vegetation models is assessed through a comparison with pollen-derived biomes for the studied area.

Environmental setting

The West-African area sampled for this study ranges between 12°N (South of Senegal) and 23°N (South of Mauritania) (fig. II. 1). This area is divided into four latitudinal bio-climatic zones: the Guinean zone, the Sudanian zone, the Sahelian zone and the Saharan zone (White, 1983). Climate and vegetation features of the four zones are synthesized on fig. II. 1.

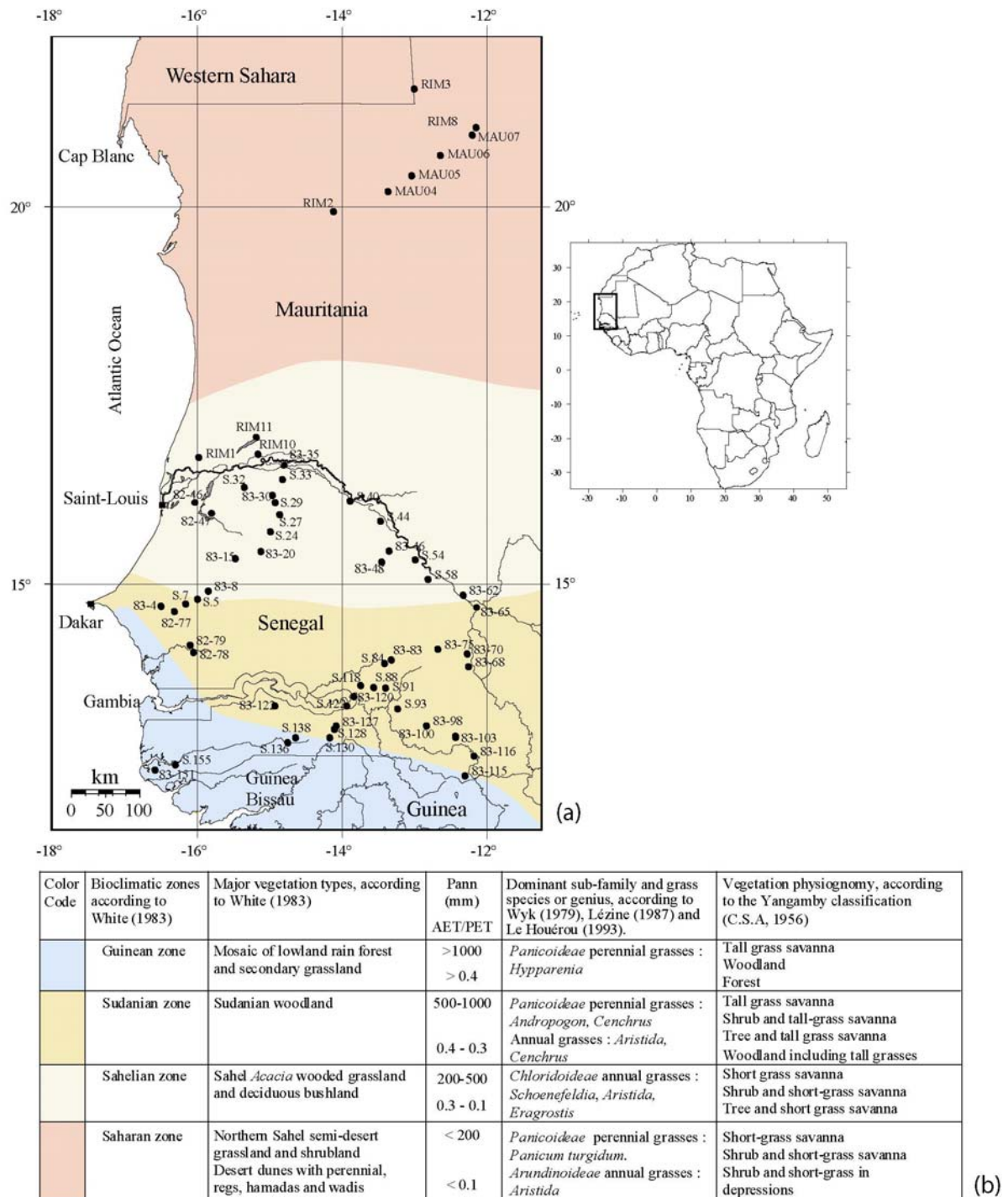


Figure II. 1. (a) Location of the samples in West Africa and main bioclimatic zones after White (1983); (b) Climatic patterns and dominant grass sub-family, major vegetation types and vegetation physiognomy of the 4 sampled bioclimatic zones.

Climate

Climatic zoning is characterized from South to North by a decrease in mean annual rainfall from 1500 to 100 mm and an increase in the length of the dry season from 5 to more than 9 months. The mean temperature of the coldest month is 25°C in the southern region and 19°C in the northern region. The mean temperature of the warmest month stabilizes between 30 and 31°C.

Rainfalls distribution over the area is connected to the seasonal migration of the Intertropical Convergence Zone . Three major wind systems dominate the area: the summer South-South-Westerly monsoonal winds; the winter North-Easterly trades winds (or Harmattan), and the summer African Easterly Jet (Ratmeyer et al., 1999b; Wyputta & Grieger, 1999; Huang et al., 2000).

Vegetation

The South-North rainfall gradient is reflected by the current latitudinal distribution of four major vegetation zones described by White (1983) based on woody elements. The only system which describes with accuracy the different tropical grasslands through continuity of the herbaceous cover, height of grasses and tree cover density is the Yangambi nomenclature (CSA, 1956). We will refer to both nomenclatures in this study. However, following the North American nomenclature which distinguishes between short grass and tall grass prairies (Fredlund & Tieszen, 1994), we propose to use the terms "tall grass savanna" and "short grass savanna" in place of "savanna" and "steppe", used in the Yangambi nomenclature. Finally, the four vegetation zones can be defined below: 1) The Guinean zone (mean annual rainfall of more than 1000 mm.yr⁻¹) is defined by White (1983) as a mosaic of lowland rain forest and secondary grasslands dominated by perennial grasses such as *Hypparenia* (Panicoideae subfamily) (Wyk, 1979). The same formations may be defined as forests, woodlands and tall grass savannas according to the Yangambi nomenclature. 2) The Sudanian zone (mean annual rainfall ranging from 1000 to 500 mm.yr⁻¹) is covered by dry forests, woodlands, and grasslands, according to White (1983). The same formations may be defined as woodlands, tree and tall grass savannas, shrub and tall grass savannas according to the Yangambi nomenclature. Grass cover is dominated by perennial grasses (Menaut, 1983) such as *Andropogon* (Panicoideae subfamily) in association with annual grasses such as *Cenchrus* (Panicoideae subfamily) and *Aristida* (Arundinoideae subfamily) (Wyk, 1979). In the Soudano-Sahelian transition zone (mean annual rainfall ranging from 400 to 600 mm.yr⁻¹)

grass cover is dominated by the annual *Cenchrus biflorus* (Panicoideae subfamily) and *Schoenefeldia gracilis* (Chloridoideae subfamily), with some vestigial perennial grasses (Le Hou  rou, 1993). 3) The Sahelian zone (mean annual rainfall ranging from 500 to 200 mm yr⁻¹) is covered by wooded grasslands and grasslands according to White (1983). According to the Yangambi nomenclature the same formations may be defined as tree and short grass savannas, shrub and short grass savannas and short grass savannas. The grass cover is dominated by annual grasses such as *Aristida* (Arundinoideae subfamily) (Wyk, 1979) and more precisely in Senegal by *Aristida mutabilis* and *Eragrostis tremula* (Chloridoideae subfamily) (Le Hou  rou, 1993a), *Aristida funiculata*, *Schoenefeldia gracilis* and *Cenchrus biflorus* (Arundinoideae and Chloridoideae subfamily) (Trochain, 1940). 4) The Saharan zone (mean annual rainfall lower than 200 mm yr⁻¹) is covered by semi-desert grasslands and shrublands growing between the dunes (White, 1983). According to the Yangambi classification (1956), these formations are shrubs and short grass savannas although they are restricted to small areas and are dominated both by annual grasses such as *Aristida* (Arundinoideae subfamily) and by the perennial grasses *Panicum turgidum*; (Panicoideae subfamily) (Wyk, 1979; Le Hou  rou, 1993a; Le Hou  rou, 1993b). The grass subfamilies that dominate in the Guinean, Sudanian and Saharan zones are considered to be similar to those that preceded human impact (Le Hou  rou, 1993a). However, the Sahelian zone is composed almost entirely of annual grass species and there is apparently no climatic reason why several species of perennial grasses could not thrive in this zone. The explanation for their absence apparently is the combined effect of fire and a long, severe dry season (Le Hou  rou, 1993a). Perennial grass species that preceded human impact probably belonged to same sub-family of some vestigial Panicoideae perennial grass species found in the Soudano-Sahelian subzone defined by Le Hou  rou (1993a).

Olson et al. (1983; 1994a; 1994b) presented a biome classification for global vegetation . This classification will be considered below, when discussing new grass-dominated biomes derived from phytolith data. The Olson's dataset has 1-km nominal spatial resolution with 94 land ecosystem classes considered. It was compiled from patterns of pre-agricultural vegetation, modern aerial surveys and intensive biomass data from research sites. It is generally used in works dealing with biomization of Africa (Jolly et al., 1998).

Sample names	Latitude °N	Longitude °E	Conc-shaped	Crenate spherical	Rough spherical	Smooth spherical	Point-shaped	Fans-shaped (Fs)	Dumbbell	Cross	Saddle	Sum	Non-classified	*Iph %	**Fs %	***DP	AEI/PET	Annual Rainfall (mm)
RIM 3	21.53	-13.00	0	2	4	5	36	52	18	0	6	123	143	25.00	42.28	0.04	0.05	91
RIM 8	21.03	-12.15	1	7	5	2	46	43	13	0	5	122	172	27.78	35.25	0.05	0.06	98
MAU 07	20.93	-12.20	0	2	9	11	53	56	61	1	11	180	202	22.45	31.11	0.06	0.06	99
MAU 06	20.63	-12.63	3	0	4	5	55	55	61	0	6	189	263	8.96	29.10	0.02	0.06	102
MAU 05	20.40	-13.03	1	1	1	2	44	44	26	3	5	127	262	14.71	34.65	0.01	0.06	103
MAU 04	20.23	-13.37	1	3	4	5	53	53	49	2	21	191	240	29.17	27.75	0.02	0.06	102
RIM 2	19.93	-14.08	1	3	5	6	54	62	8	0	2	141	242	20.00	43.97	0.04	0.06	101
RIM 11	16.93	-15.20	0	0	2	3	36	93	45	0	41	239	299	47.67	38.91	0.01	0.16	225
RIM 10	16.73	-15.17	0	0	6	2	36	90	22	1	16	173	349	41.03	52.02	0.04	0.17	227
RIM 1	16.68	-15.97	2	3	18	9	38	97	35	1	5	208	271	12.20	46.63	0.10	0.16	230
83-35	16.50	-14.60	2	0	4	1	67	78	5	5	27	189	128	72.97	41.27	0.02	0.16	226
S33	16.39	-14.82	4	0	12	4	29	27	114	5	46	241	163	27.88	11.20	0.05	0.17	234
S32	16.29	-15.35	0	1	1	4	36	37	48	5	22	154	191	29.33	24.03	0.01	0.18	256
83-30	16.17	-14.93	2	0	5	2	37	39	85	6	23	199	310	20.18	19.60	0.03	0.18	252
S40	16.10	-13.89	0	0	15	3	47	45	74	4	60	248	196	43.48	18.15	0.07	0.22	313
S29	16.08	-14.92	0	0	9	3	31	26	77	3	39	188	225	32.77	13.83	0.05	0.19	272
82-47	16.00	-14.95	3	3	12	3	37	46	148	7	31	290	303	23.17	16.87	0.02	0.21	289
82-46	16.00	-15.95	5	0	5	1	32	42	119	0	38	249	136	16.67	15.86	0.04	0.21	289
S27	15.92	-14.86	2	0	2	2	42	18	104	9	53	229	162	31.93	7.86	0.00	0.22	302
S44	15.83	-13.47	0	0	3	2	40	42	94	10	30	221	221	22.39	19.00	0.01	0.26	370
S24	15.69	-14.99	0	0	1	1	17	13	129	1	34	196	225	20.73	6.63	0.01	0.26	368
83-46	15.43	-13.35	1	1	6	2	26	17	125	22	67	263	162	31.31	6.46	0.02	0.27	386
83-20	15.42	-15.12	5	0	8	2	26	16	95	14	77	243	212	41.40	6.58	0.04	0.29	397
83-15	15.33	-15.47	0	1	4	2	27	22	28	8	11	103	164	23.40	21.36	0.04	0.29	400
S54	15.31	-12.99	0	0	2	3	52	32	96	3	24	212	209	19.51	15.09	0.01	0.29	447
83-48	15.28	-13.45	1	1	4	1	42	58	82	14	47	250	214	32.87	23.20	0.02	0.28	421
S12	15.21	-15.17	0	3	16	12	46	25	72	2	19	195	205	20.43	12.82	0.10	0.28	397
S58	15.06	-12.81	0	0	4	3	44	19	96	8	16	234	194	36.59	8.12	0.02	0.32	523
83-8	14.90	-15.85	2	9	15	4	28	28	47	10	53	260	168	33.54	17.87	0.06	0.30	482
83-62	14.85	-12.33	1	2	2	3	62	27	57	18	48	223	183	39.02	12.27	0.01	0.33	528
S7	14.79	-15.99	0	1	11	15	53	50	66	0	3	199	227	4.35	25.13	0.06	0.30	507
83-65	14.75	-12.25	1	0	5	1	12	6	139	14	49	227	275	24.26	2.64	0.02	0.33	539
S5	14.72	-16.16	0	0	19	4	29	57	51	0	13	173	167	20.31	32.95	0.13	0.30	505
83-4	14.70	-16.50	1	1	33	3	58	49	77	12	16	258	152	18.99	18.99	0.16	0.30	509
82-77	14.63	-16.32	1	1	12	3	30	41	104	16	29	237	88	19.46	17.30	0.05	0.30	505
82-79	14.17	-16.10	1	1	1	3	28	14	122	13	30	213	531	18.18	6.57	0.00	0.32	572
83-75	14.12	-12.67	0	0	11	1	29	25	131	22	22	241	213	12.57	10.37	0.05	0.36	664
82-78	14.08	-16.05	0	2	20	5	23	12	191	13	22	288	334	9.73	4.17	0.08	0.32	572
83-70	14.05	-12.27	0	0	1	0	21	5	180	17	13	237	126	6.19	2.11	0.00	0.36	667
83-83	13.97	-13.32	4	0	1	0	14	6	178	21	14	238	176	6.57	2.52	0.00	0.38	739
S84	13.93	-13.41	0	0	3	0	26	10	148	24	18	229	279	9.47	4.37	0.01	0.38	755
83-68	13.88	-12.25	2	1	10	2	39	13	152	15	12	246	213	6.70	5.28	0.04	0.37	716
S118	13.63	-13.74	1	0	7	1	2	24	128	7	11	181	252	7.53	13.26	0.04	0.39	779
S88	13.60	-13.56	0	1	5	4	19	17	155	5	29	235	207	15.34	7.23	0.02	0.39	780
S91	13.59	-13.40	0	19	70	12	32	23	82	16	4	258	255	3.92	8.91	0.49	0.40	887
83-120	13.48	-13.83	0	1	14	6	24	12	176	10	11	254	292	5.58	4.72	0.06	0.39	781
83-122	13.35	-14.93	2	0	4	2	19	17	178	11	21	254	366	10.00	6.69	0.02	0.42	812
S122	13.35	-13.94	1	0	0	0	17	20	93	10	13	154	341	11.21	12.99	0.00	0.40	825
S93	13.31	-13.23	3	6	6	2	23	13	154	13	11	231	154	6.18	5.63	0.03	0.40	863
83-98	13.08	-12.83	0	1	6	1	5	2	136	16	8	175	279	5.00	1.14	0.04	0.41	909
83-127	13.07	-14.08	0	2	81	10	49	32	75	4	5	258	163	5.95	12.40	0.49	0.40	887
S128	13.03	-14.10	0	1	7	18	45	38	118	0	9	236	288	7.09	16.10	0.03	0.40	886
83-100	13.03	-12.63	1	0	14	4	18	10	172	11	13	243	117	6.63	4.12	0.06	0.42	982
S130	12.92	-14.17	0	0	5	2	31	29	91	10	13	181	285	11.40	16.02	0.03	0.40	882
83-103	12.92	-12.43	3	1	9	2	17	13	145	19	9	218	349	5.20	5.96	0.04	0.44	1087
S138	12.88	-14.86	1	0	11	6	42	42	75	4	11	192	213	12.22	21.88	0.06	0.39	896
S136	12.85	-14.74	0	0	10	2	42	57	39	3	13	166	238	23.64	34.34	0.06	0.39	890
83-116	12.67	-12.18	2	1	1	0	8	2	148	8	6	174	432	2.50	1.15	0.01	0.46	1183
S155	12.55	-16.30	0	56	144	8	8	10	10	1	6	237	96	35.29	4.22	4.97	0.40	1283
83-151	12.48	-16.58	0	54	158	19	8	5	8	2	0	254	119	0.00	1.97	6.87	0.40	1267
83-115	12.40	-12.30	1	0	7	2	10	7	214	6	12	259	206	5.17	2.70	0.03	0.45	1175

Table II. 1. Detailed counts of modern phytolith assemblages from West Africa, phytolith indices and climate data.

Phytolith indices are expressed as follow:

* Iph = *Chloridoideae* phytoliths (saddle type) / (*Chloridoideae* + *Panicoideae* phytoliths (saddle + cross + dumbbell types)).

** Fs = % fan-shaped types (classified phytoliths - elongate phytolith types).

*** D/P = Ligneous dicotyledon phytoliths (rough spherical types) / Poaceae phytoliths (saddle + cross + dumbbell + point + fan-shaped types).

AET/PET = actual annual evapotranspiration / annual potential evapotranspiration, interpolated for the sampling sites (error = ± 0.04).

Materials and methods

Materials

Phytolith samples

Soil surface samples were collected by Anne-Marie Lézine between 1987 and 1995 during several field trips (1987; 1988; 1991; 1995). The sampling method consists in collecting individual sub-samples of the upper one cm of the soil (litter excluded), at random, over an area of about one hundred square meters. Sub-samples are mixed together.

Phytolith assemblages were extracted from 5 samples from the Guinean zone, 25 samples from the Sudanian zone, 24 samples from the Sahelian zone and 9 samples from the Saharan zone (fig. II. 1). 42 additional modern phytolith assemblages, from Mexico (Sonoran desert), Cameroon (Kandara) and Tanzania (Masoko) were extracted to test the calibration done using West African samples. Location and vegetation types of sampled sites and main characters of phytolith assemblages are summarized in Table 2.

Sample sites	Number of samples	Longitude	Latitude	Vegetation types	Averaged observed AET/PET	Iph	Fs	D/P	Averaged AET/PET estimated from phytoliths	Phytolith-derived biomes
Sonora (Mexico)	7	113°20 W	31°50 N	Desert	0.12 ±0.04	53.07	15.8	0.05	0.19 ±0.04	Desert C ₄ -grassland
Kandara (Cameroon)	26	13°43 E	4°20 N	Forest and tall grass savanna	0.94 ±0.04	0.02	6.29	2.02	0.40 ±0.02	Tropical dry forest Tall grass savanna
Masoko (Tanzania)	10	34°45 E	8°20 S	Woodland	0.62 ±0.04	8.35	15.29	0.68	0.32 ±0.01	Tall grass savanna

Table II. 2. Location vegetation types, averaged "observed" AET/PET (obtained by a water balance model and interpolated at the sites), phytolith indices, averaged phytolith-estimated AET/PET and phytolith derived biomes for samples from the Sonoran desert (Mexico), Kandara (Cameroon) and Masoko (Tanzania).

Climate data

Mean monthly precipitation and temperature averaged over 30 years from 12 meteorological stations are obtained from the database of Leemans & Cramer (1991) and from the "Office Météo du Senegal" (CSE, 2000). To evaluate the annual amount of growth-limiting drought stress on plants, we calculate the ratio between annual actual evapotranspiration over potential one AET/PET using a simple water balance model (Harrison et al., 1993). Required input data for calculating AET/PET are site latitude, soil water storage capacity, temperature, precipitation and sunshine. The potential evapotranspiration (function of net radiation and temperature) is the evaporative demand. It approximates actual evapotranspiration under conditions of adequate water supply (Stephenson, 1998). The parameter AET/PET, also called Priestley-Taylor coefficient, is commonly used as one of the main climatic control on the vegetation distribution at continental or global scales (Prentice et al., 1992; Sykes et al., 1996).

First, we calculate PET and AET at the meteorological stations using the water balance model. At this stage, the estimation error for AET and PET cannot be calculated because we do not have measurements of these variables at the meteorological stations. Second, AET and PET are interpolated separately at each sampling site, using a weighted average method according to the inverse distance and after reduction at sea level (Goery & Guiot, 1996). Third, the ratio AET/PET has been calculated. The error on AET/PET induced by the interpolation method has been calculated by comparison of the interpolations at the meteorological stations with the values obtained by the water balance model. This error standard deviation is approximately 0.04. From South to North of the studied zone, AET/PET regularly decreases from 0.45 ± 0.04 to 0.05 ± 0.04 . Interpolated AET/PET are presented for each sampling site (table 1).

Methods

Phytolith extraction, classification and counting

Phytoliths were extracted from 20g of dry soil sieved at 2mm, after: 1) dissolution of carbonates, using HCl (3 %); 2) oxidation of organic matter, using H₂O₂ (30 %) heated at 90°C until reaction subsides; 3) sieving at 60 µm; 4) removal of clays after sedimentation; 5) densimetric separation of phytoliths ($d < 2.3$) from the 2-60µm fraction in a heavy liquid of ZnBr₂ ($d = 2.3$) (Kelly, 1990).

The recovered fraction, including opal phytoliths and diatoms fragments, is mounted on microscope slides, in glycerin for 3D observation, and in Canada Balsam for counting. Microscopic observations are done at 600X magnification. More than 200 phytoliths with diameter of greater than 5 µm and with taxonomic significance (classified phytoliths) were counted. Phytoliths without taxonomic significance (non-classified phytoliths) because of original shape, dissolution or fragmentation are also counted. Assemblages are presented as percentages of the sum of classified phytoliths. Double counting of a same slide by a single person give a reproducibility (s.d.) of $\pm 3,5\%$.

Phytoliths are classified according to the classification of Twiss (1969; 1992), augmented by Mulholland (1989), Fredlund and Tieszen (1994), Kondo et al. (1994), Alexandre et al. (1997) and Barboni et al (1999). Ten phytolith types were identified. They are illustrated on Plate II.1.

Four phytolith types are produced by non-grasses taxa. The cone-shape type (1) is attributed to the Cyperaceae (sedge) (Le Cohu, 1973; Ollendorf, 1987; Kondo et al., 1994; Wallis, 2003). The crenate spherical phytolith type (2) is produced by Palmae (Kondo et al., 1994; Runge, 1999; Runge & Fimbel, 1999; Vrydaghs & Doutrelepon, 2000). The rough spherical phytolith type (3), is produced by the wood of tropical trees and shrubs (lignous dicotyledon) (Scurfield et al., 1974; Kondo et al., 1994; Alexandre et al., 1997). The smooth spherical type (4) appears to have several origins. According to Kondo et al. (1994), this type is produced in the epidermis of leaves and in the ray or parenchyma cells of dicot twigs and wood. They have been recovered in small proportions from several tropical herbaceous monocots and in greater quantities from a small number of tropical arboreal dicot leaves and seeds (Piperno, 1988). Recent investigation of tropical grasses show that the smooth spherical type is also produced in significant amounts by grass roots (Alexandre et al., 2000).

The following types are produced by grasses: The point-shaped type (5) originates from micro-hair or prickles of all grass epidermis (Palmer et al., 1985; Kaplan et al., 1992). The fan-shaped phytolith type (6) (Twiss et al., 1969; Kondo et al., 1994) are produced in

bulliform cells also called motor-cells, of all grass epidermis. Although bulliform cells may also occur in sedge, no silicified bulliform cells have been observed in sedges up to now. Silicified short cells from grass epidermis, the dumbbell (7) and cross (8) types occur dominantly in the Panicoideae subfamily (Twiss et al., 1969; Mulholland, 1989; Fredlund & Tieszen, 1994; Kondo et al., 1994), gathering essentially tall C₄ grasses adapted to warm climate and high available soil moisture (Teeri & Stowe, 1976; Tieszen et al., 1979; Cabido et al., 1997; Scott, 2002). The saddle type (9), is produced in high proportion by the Chloridoideae *subfamily* (Twiss et al., 1969; Mulholland, 1989; Fredlund & Tieszen, 1994; Kondo et al., 1994), a group of short C₄ grasses adapted to warm and dry climate or low available soil moisture (Tieszen et al., 1979; Livingstone & Clayton, 1980). The elongate type (10) originates from silicified long cells of all grass epidermis. Because it may be confused with weathered diatoms or sponge spicules, this type was included in the non-classified group.

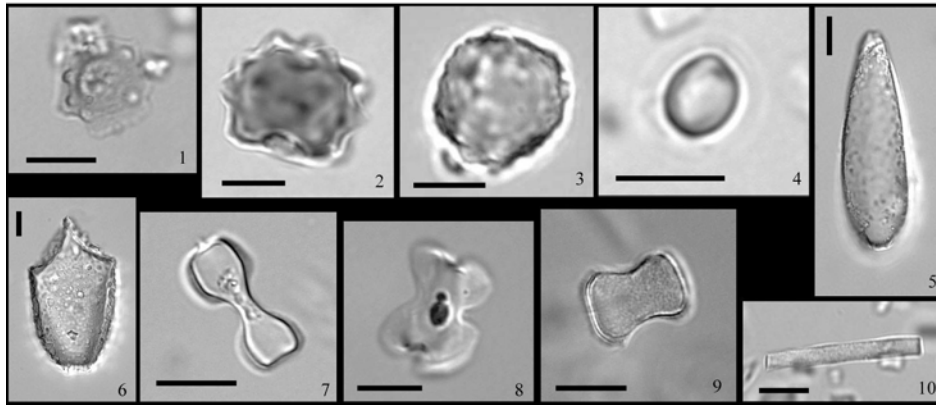


Plate II. 1. Microphotographs of representatives of the 10 types of classified phytoliths; Scale bar = 10 μm: (1) Cone shaped type; (2) Crenate spherical type; (3) Rough spherical type; (4) Smooth spherical type; (5) Point-shaped; (6) Fan-shaped type (also Fs); (7) Dumbbell type; (8) Cross type; (9) Saddle type, (10) Elongate type.

Calculation of phytolith indices

Phytolith data will be discussed through three phytolith indices. Two of them are commonly in use in phytolith studies: 1) The D/P index is the ratio of the rough spherical phytoliths, produce by tropical woody dicotyledon, to the sum of Poaceae phytoliths (dumbbell, cross, saddle, point-shaped and fan-shaped types). It was first used by Alexandre et al. (1997) in West and Central Africa in order to estimate the tree cover density. In modern samples, a value of D/P of 7 was found in a semi-evergreen forest in Congo, whereas values lower than 0.2 characterize savannas with various tree cover densities in Senegal. However, Alexandre et al (1997) did not distinguish elongated phytolith types from point-shaped and fan-shaped types. So, the D/P index without the elongated types in the sum of Poaceae phytoliths, as we used, should be higher. Barboni et al. (1999) calculated a D/P ratio of 0.1 for a shrub steppe and of 0.7 for the margin of a riparian forest in the West side of the Middle Awash valley (Ethiopia). Error assigned to this index is 7% (s.d. on rough spherical type plus max s.d. on Poaceae phytolith types).

2) The Iph index is the ratio of Chloridoideae type (saddle type) to the sum of Chloridoideae and Panicoideae types (saddle, cross and dumbbell types). This index was first defined by Diester-Haass et al. (1973) from assemblages from marine sediments off West Africa to identify humid-arid transitions in West Africa during Pleistocene and Holocene. It was later used for vegetation reconstructions from continental sediments, soils and buried soils from African, Brazilian and Mediterranean sites (Alexandre et al., 1997; Barboni et al., 1999; Delhon et al., 2003). High Iph values (>20-40%) record grasslands dominated by Chloridoideae, i.e. xerophytic short grass savannas, and hence prevalence of warm and dry climatic conditions. Conversely, low Iph values (<20-40%) indicate associations in which Panicoideae, i.e. mesophytic C₄-grasses dominate, suggesting warm and humid climate and/or high available soil moisture. However, local association of perennial Panicoideae grasses with annual Chloridoideae may occur in Saharan desert zones (Le Houérou, 1993a). Such vegetation will induce low Iph (<20-40%) connected to local conditions, despite the regional dryness. Geographical scale recorded by phytolith assemblages will be discussed later. Error assigned to this index is $\pm 7\%$ (s.d. on saddle type plus max s.d. of saddle, cross or dumbbell types).

3) We define the third phytolith index, Fs (fan-shaped index), as the percentage of fan-shaped phytolith type to the sum of grass phytoliths minus the elongate phytolith type. Hypotheses on its environmental significance are discussed later, considering statistical relations between

phytolith indices and AET/PET data. Error assigned to this index is $\pm 3.5\%$ (s.d. on fan-shaped type).

Statistical analysis and biomization methods

Simple correlation and bootstrapped regression methods are used for evaluating the strength of the relationship between phytolith indices and AET/PET. The bootstrapping regression method (Efron, 1979; Guiot, 1990) is a technique to estimate, by simulations, statistics for unknown population distributions. Original observations are re-sampled in a suitable way to construct pseudo data sets on which the estimates are performed. Each pseudo data set has the same size as the raw data set and is composed by random extraction with replacement. The suitable statistics (e.g. means, standard deviations, correlations, regression coefficients) are calculated for each pseudo data set and are averaged to provide the bootstrap estimate. Variability of the calculated quantity among the various pseudo data sets provides us with the needed confidence intervals. Only a portion of the samples is used in each pseudo-data set. The remaining data set is used for independent verification.

The biomization method using African pollen data was developed by Jolly et al. (1998) and slightly modified by Peyron et al. (2000). Pollen are assigned to plant functional types (PFTs), which are, for that purpose, broad classes of plants defined by stature, leaf form, phenology and bioclimatic factors. A combination of PFTs defines each biome (Prentice et al., 1992). For each modern spectrum, a score is calculated for each PFT, given as the sum of the square root of the percentage of taxa belonging to the PFT, and a biome is deduced. Using an artificial neural network technique, these PFT scores are then calibrated in terms of climate (e.g. annual rainfall, AET/PET, temperature) (Peyron et al., 2000).

Phytolith-derived biomes are defined using a linear discriminant analysis (Tomassone et al., 1988). Discriminant analysis is used to determine which variables discriminate between two or more naturally occurring groups. Four groups (biomes) are “a priori” defined from the samples membership of the vegetation types described before. Five variables (phytolith types) are used to predict to which groups the samples belong. Coefficients of the linear discriminant functions are calculated to relate each variable to each group. In order to verify the reliability of the calculated coefficients, a second run of discriminant function analysis is performed where we “forget” one over three samples. We re-calibrate the discriminant functions on the remaining observations, but with only three groups because the sample size of the forest group is too small. Then we assign the “forgotten” samples to one of the three groups and we check if the assignment corresponds to the true membership.

Results

Phytolith assemblages

Phytolith assemblages are presented on fig. II. 2 and table 1. In all assemblages, the Cyperaceae phytolith (cone-shape type) is weakly represented (less than $2\pm 0.07\%$), as expected because of its sensitivity to dissolution and fragmentation in litter and soil (Alexandre *et al.*, 1997). The Palmae phytolith (crenate type) accounts for less than $7\pm 0.25\%$ in most of the samples but reaches values higher than $20\pm 0.7\%$ in samples from forests of the Guinean zone (S.155 and 83-151). The rough spherical type produced by tropical woody dicotyledons presents an average values of $20\pm 0.7\%$ in the Guinean zone, $6\pm 0.2\%$ in tall-grass savannas of the Sudanian zone, $3\pm 0.1\%$ in short-grass savannas of the Sahelian zone and $3\pm 0.1\%$ in the Saharan zone. The D/P ratio is always lower than 1 except in rainforests (S.155 and 83-151) where it reaches 5 and 7. The smooth spherical type ranges from 0 to $8\pm 0.28\%$ and does not show any pattern specific to the vegetation. Within the group of phytoliths diagnostic of Poaceae, the point-shaped phytolith type accounts for 1 to $38\pm 1.33\%$. Percentage of this phytolith type increases from the Guinean to the Saharan zone. The Fs index generally increases from the southern to the northern samples (0 to $52\pm 1.82\%$). In the Guinean, Sudanian and Sahelian zones Fs accounts for less than $25\pm 0.88\%$ except for samples S.5 and S.136 (33 ± 1.16 and $34\pm 1.19\%$). The four Northern Sahelian samples, present very high Fs (39 ± 1.37 to $52\pm 1.82\%$), as well as samples from the Saharan zone (31 ± 1.09 to $441.54\pm\%$). An increasing trend of Fs with AET/PET clearly appears.

The dumbbell type reaches very high values in the Sudanian tall grass savanna zone (from 29 ± 1 to $85\pm 2.97\%$ with an average of $58\pm 2.03\%$) compared to the Sahelian zone (from 2 ± 0.07 to $65\pm 2.28\%$ with an average of $37\pm 1.3\%$). The cross phytolith type also reaches its maximum abundance (from 0 to $10\pm 0.35\%$) in the Sudanian zone. The saddle type accounts for 0 to $32\pm 1.12\%$, and is more abundant in the Sahelian short grass savanna zone (from $2\pm$ to $32\pm\%$ with an average of $17\pm 0.6\%$) than in the Sudanian zone (from 1 ± 0.04 to $14\pm 0.49\%$ with an average of $7\pm 0.25\%$). An increasing trend of Iph index from the Guinean to the Sudanian zone clearly appears. Most of the Sudanian and Guinean samples (23 versus 25 samples) present Iph index lower than $20\pm 1.4\%$, except two samples taken from the rain forest (S.155, $Iph=35\pm 2.45\%$) and on the Casamance grassy riverside (S.136= $24\pm 1.68\%$). Most of the Sahelian samples (21 out of 24) are characterized by Iph index higher than $20\pm 1.4\%$. Sample S.54, with a Iph of $19.5\pm 1.37\%$, is not far from the previous value. Two samples (RIM 1 and 82-47) present values of $12.2\pm 0.85\%$, and $16.7\pm 1.17\%$ respectively, clearly lower than $20\pm 1.4\%$. The first one (RIM 1) is located in a tree savanna (*Acacia* and

Balanites) while the second one (82-47) is taken along the shore of Lake Guiers. Saharan samples show variable Iph indices ranging from 9 ± 0.63 to $29 \pm 2.03\%$.

To summarize, an Iph boundary of $20 \pm 1.4\%$ differentiates tall from short grass savanna associations in West Africa.

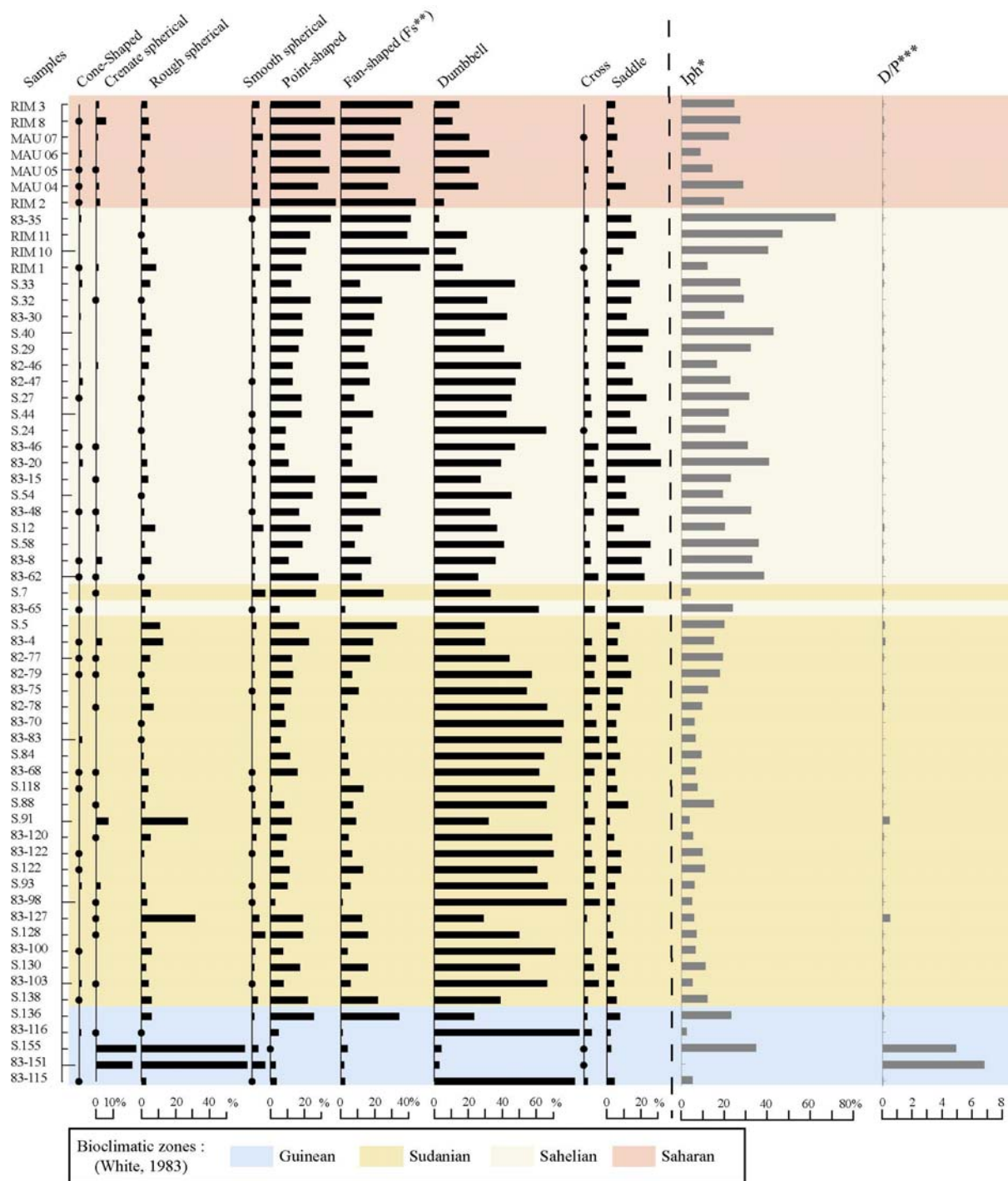
Figure II. 2. Phytolith assemblages: abundances of phytolith types are expressed as % of the characteristic phytolith sum. Abundance lower than 1% are identified by a dot.

Phytolith indices are expressed as follow:

* Iph = *Chloridoideae* phytoliths (saddle type) / (*Chloridoideae* + *Panicoideae* phytoliths (saddle + cross + dumbbell types)).

** Fs = % fan-shaped types (classified phytoliths - elongate phytolith types).

*** D/P = Ligneous woody dicotyledon phytoliths (rough spherical types) / Poaceae phytoliths (saddle + cross + dumbbell + point + fan-shaped types).



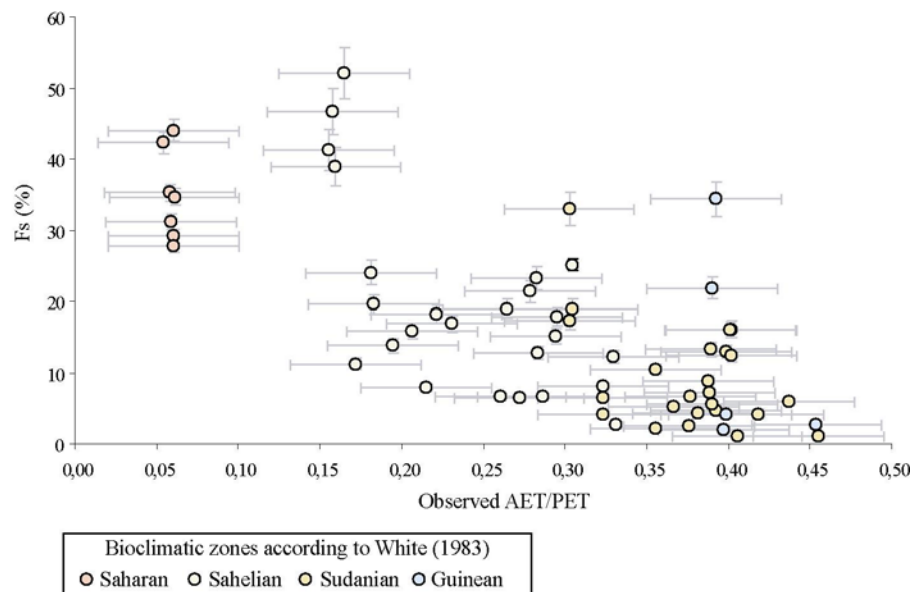


Figure II. 3. Fs index (% fan-shaped types (classified phytoliths - elongate phytolith types)) versus AET/PET for the West African samples. Error from the interpolation method for observed AET/PET has been estimated at 0.04. Error assigned to Fs index is 3.5% (s.d. on fan-shaped type).

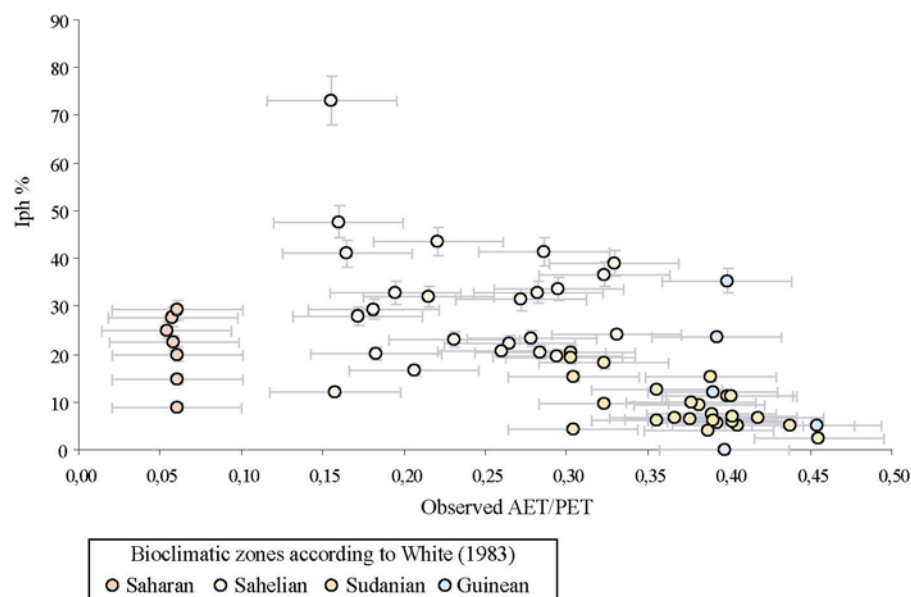


Figure II. 4. Iph index (*Chloridoideae* phytoliths (saddle type) / (*Chloridoideae* + *Panicoideae* phytoliths (saddle + cross + dumbbell types))) versus AET/PET for the West African samples. Error (standard deviation) from the interpolation method for observed AET/PET has been estimated at 0.04. Error (standard deviation) assigned to Iph index is 7% (s.d. on saddle type plus max s.d. of saddle, cross or dumbbell types).

Statistical relationships between AET/PET and phytolith indices

Figs II. 3 and II. 4 show that Fs and Iph indices are negatively correlated with AET/PET from the Guinean to the Sahelian zone. Calibration of the relationship between AET/PET and these two indices is made using the following bootstrapped quadratic regression:

$$\text{AET/PET (\%)} = a_0Fs + a_1\text{Iph} + a_2(\text{Iph}-20)^2$$

where the coefficients $a_0 = -0.605 \pm 0.075$, $a_1 = -0.387 \pm 0.087$ and $a_2 = 0.272 \pm 0.068$ are the regression coefficients. The two regressors Fs and Iph are the previously defined phytolith indices. The quadratic term $(\text{Iph}-20)^2$ is introduced in order to take into account the decreasing Iph index in the Saharan zone. The value of 20 is the Iph average calculated from our data set.

The multiple correlation coefficient between estimated and observed values of AET/PET is 0.80 ± 0.04 (s.d.). The (independent) verification correlation is 0.71 ± 0.14 (s.d.), which is highly significant. Estimated AET/PET versus observed AET/PET and summary statistics are presented on fig. II. 5.

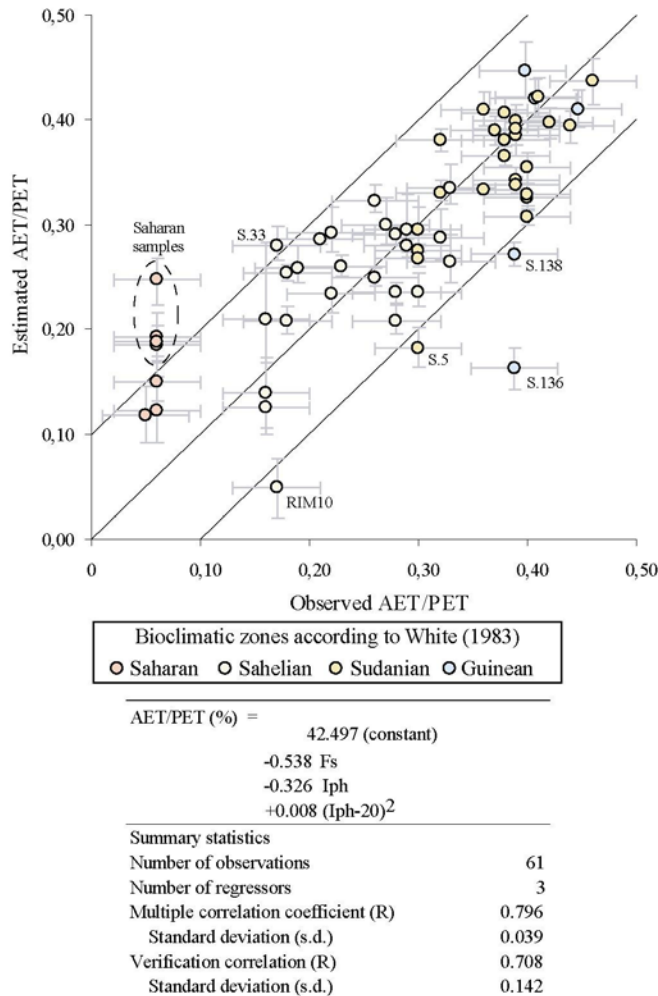


Figure II. 5. AET/PET estimated from phytolith indices versus "observed" AET/PET (obtained by a water balance model and interpolated at the sites), for the West African samples. Error (standard deviation) from the interpolation method for observed AET/PET has been estimated at 0.04. Error (standard deviation) of estimated AET/PET is calculated by orthogonal regression bootstrap.

The correlation coefficient ($R = 0.80$) with a standard deviation of 0.04 is fairly significant. However over- or under-estimations of AET/PET are significant (>0.1) for 9 sites :

AET/PET is overestimated by 0.13 to 0.19 for 4 Saharan samples. This is due to their low Iph index imperfectly simulated by the third regressor $(Iph - 20)^2$ and certainly to their proximity to the 4 samples from the northern Sahelian zone that present much higher values of Fs than samples from the desert zone. However, the regression is better when using the third regressor $(Iph - 20)^2$ than when using only two regressors ($R = 0.76 \pm 0.04$). An alternative approach could be to remove the Saharan samples to maintain the linearity of the relationship but this would make it applicable only in non-desert environments. When we do this, the regression is also worse with a R of 0.76 ± 0.04 . AET/PET is also overestimated by +0.11 for the Sahelian sample S.33, due to a low Fs. Under-estimation of AET/PET by -0.12 for RIM 10 (northern Sahelian zone), -0.12 for S.5 (Sudanian zone), -0.23 for S.136 and -0.12 for S.138 (Guinean zone), is linked to their high Fs indices ($34.3 \pm 1.2\%$ and $21.8 \pm 0.76\%$) instead of elevated values of observed AET/PET (0.39). Local water stress or high transpiration leading to the production of high amount of silicified bulliform cells may explain such high Fs (see discussion).

In order to check the reliability of the relationships for other geographic areas, while remaining at the boundary of the climatic conditions chosen for the calibration, three sets of modern phytolith assemblages are processed (Table 2). Error is calculated by orthogonal bootstrap regression. Samples from the Sonoran desert (Mexico) present low observed AET/PET (0.12 ± 0.04), while sample sites from Cameroon and Tanzania are much more humid (AET/PET is respectively 0.94 ± 0.04 and 0.62 ± 0.04) than the wettest site of our calibration set (0.46 ± 0.04). The results show that AET/PET is over-estimated for the Sonoran desert samples by 0.07, which is at the limit of the confidence interval. This is due to 2 samples out of 5 showing a low Iph, relative to the local occurrence of perennial *Panicoideae* grass as in the Saharan zone and a low Fs ($10 \pm 0.35\%$). It may also be due to the difficulty in calculating such a parameter from meteorological observations in desertic environments.

AET/PET calculated for Cameroon and Tanzania are under-estimated by 0.54 and 0.3 respectively, which is much more significant. The reason is that the regression equations have been established from West African samples, where low values of F_s and I_{ph} occur with values of AET/PET between 0.40 and 0.45. It is then impossible for the regression to produce values of AET/PET higher than 0.45 with null values of F_s and I_{ph} .

Finally these results show that AET/PET is estimated from phytolith indices, with a good accuracy, for the Sahelian, Sudanian zones and Guinean zones. It is over-estimated by 0.13 to 0.19 for the Saharan zone. The phytolith proxy presented here can be applied to other inter-tropical areas for estimating AET/PET ranging from 0.1 ± 0.04 to 0.45 ± 0.04 .

Comparison between phytolith and pollen-derived estimations of AET/PET

Fig. II. 6 gathers observed and estimated AET/PET from phytolith data presented in this study and pollen data presented in Peyron (1999), covering the same sampling zones. Difference between observation and estimation of AET/PET by pollen is usually lower than 0.1. Over- or under-estimations of AET/PET are significant (>0.1) for only 5 out of 74 sites. This figure shows that pollen estimation is slightly better than phytolith estimation, with correlation coefficients and standard deviation of 0.84 ± 0.04 (bootstrap verification set: $r = 0.76 \pm 0.08$) and 0.80 ± 0.04 respectively. In the Sudanian and Guinean zones, AET/PET is as well as estimated by phytoliths and by pollen (mean error = +0.03). AET/PET of Sahelian samples are very well estimated by phytoliths (mean error = +0.01) and by pollen (mean error = -0.02). In the Saharan zone AET/PET is overestimated by pollen (mean error = -0.02) and is overestimated by phytoliths (mean error = +0.11).

Finally, pollen and phytolith data are complementary for estimating AET/PET in the Guinean and Sudanian zones. Phytoliths provide improved estimation for the Sahelian zone. However, AET/PET of Saharan samples appear less well estimated by the phytoliths, although these discrepancies between observed and estimated values is related to the difficulty in taking into account the local occurrence of perennial *Panicoideae* grass as in the Saharan zone.

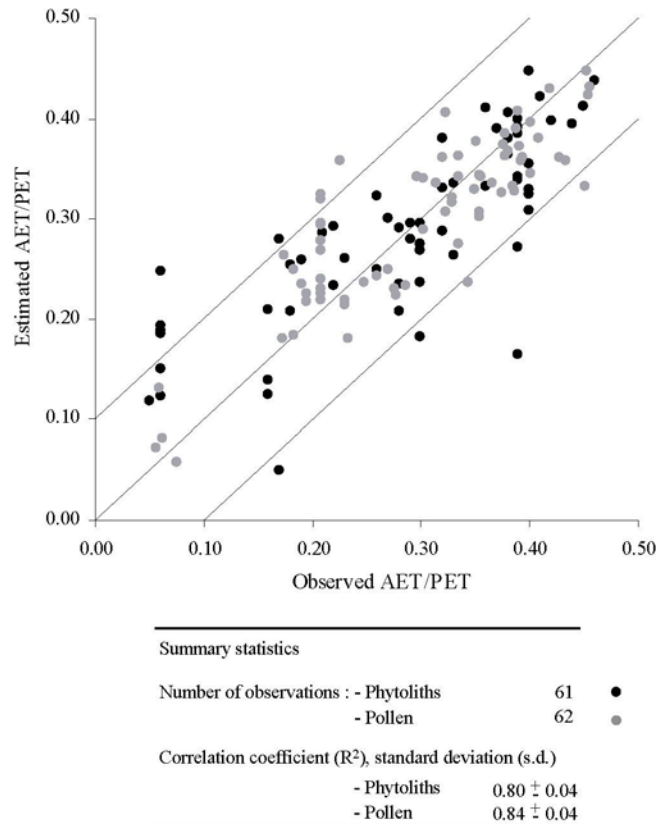


Figure II. 6. Observed and estimated AET/PET from phytolith (black points) and pollen data (grey points) for the West African samples. Error from the interpolation method for observed AET/PET has been estimated at 0.04. Error of phytolith and pollen estimated AET/PET is calculated by orthogonal regression bootstrap.

Definition of new phytolith-derived grassland biomes

Four grassland biomes were “a priori” defined according to the bioclimatic zones described by White (1983): 1) The “desert C₄-grassland” or “biome 1” (B1) is characteristic of the Saharan zone. It is dominated by shrub and short grass savannas with annual and perennial grasses. 2) The “short grass savanna” biome or “biome 2” (B2) is characteristic of the Sahelian zone. It is made of shrub and/or tree grass (annual) savannas. 3) The “tall grass savanna” biome or “biome3” (B3) is characteristic of the Sudanian and Guinean zones. It is made of woodlands, tree and tall grass savannas with perennial grasses. 4) The “tropical mesophilous forest” biome, or “biome 4” (B4) is dominant in the Guinean zone. It is constituted of dry tropical forests. Five phytolith variables are used to predict to which biome the samples belong: 1) abundance of rough spherical type; 2) abundance of silicified bulliform cells (or Fs); 3) abundance of dumbbell type; 4) abundance of cross type; 5) abundance of saddle type. These variables are chosen because of their clear taxonomic significance (see methods).

Calibration of the relationships between variables and biomes is made from the whole set of assemblages from Senegal and Mauritania. Table 3 presents the coefficients of the 5 variables for each of the four discriminant functions (one per biome). A correct assignment of assemblages to biomes is accomplished for 57 of the 62 samples. The 5 incorrect assignments are:

- (1) RIM 1 and 82-47 belong to the “short grass savanna” biome and are assigned to the relatively close “tall grass savanna” biome. For RIM, this is due to a low proportion of saddle type in the assemblage. For 82-47, this is due to the high proportion of dumbbell types in the assemblage, which may be related to the local predominance of Panicoideae grasses in contrast to the zonal dominance of Chloridoideae grasses.
- (2) S5 is assigned to the “short grass savanna” biome while it belongs to the “tall grass savanna” biome. This is explained by a low proportion of dumbbell types in the assemblage, in relation with the location of this sample at the limit of the Sudanian zone.
- (3) S7 is assigned to the “desert C₄-grassland” biome instead of the “tall grass savanna” biome. This incorrect assignment is explained by the high proportion of silicified bulliform cells phytolith type (Fs) in the assemblage, maybe in relation to local water stress or high transpiration (see discussion).
- (4) S-136 is assigned to the “short grass savanna” biome instead of the “tall grass savanna” biome, due to the abundance of silicified bulliform cells and to a related low

percentage of dumbbell type. This may also be explained by local water stress or high transpiration.

The independent verification is verified for 19 assemblages in a second step (Table 4). A new discriminant analysis is calibrated on 41 samples, without taking into account these 19 samples and after removing B4 which is represented only by two samples. Probabilities for the 19 independent samples to be assigned to B1, B2 or B3 are presented in table 5. The results are highly significant. Each sample has been assigned to the right biome except RIM 1, which is characterized by a low proportion of saddle type instead of the zonal dominance of Chloridoideae grasses.

In order to check the reliability of this biomization when applied to other inter-tropical areas than West Africa, phytolith-derived biomes were predicted for the 8 assemblages from the desert scrubs of the Sonoran Desert (Mexico) (Turner & Brown, 1994); for the 26 assemblages from "tall grass savanna" and "dry deciduous forest" of Cameroon (Guineo-Congolian phytogeographical region (Letouzey, 1968; White, 1983) and for the 10 assemblages from the "wetter Zambezian miombo woodlands" (White, 1983) of Tanzania. Assemblages from the Sonoran desert are correctly attributed to the "desert C₄-grassland" biome. Assemblages from Cameroon are correctly assigned to the "tropical mesophilous forest" biome and to the "tall grass savanna" biome. Assemblages from Tanzania originate from a woodland with a grass cover made of Panicoideae are correctly assigned to the "tall grass savanna" and "tropical mesophilous forest".

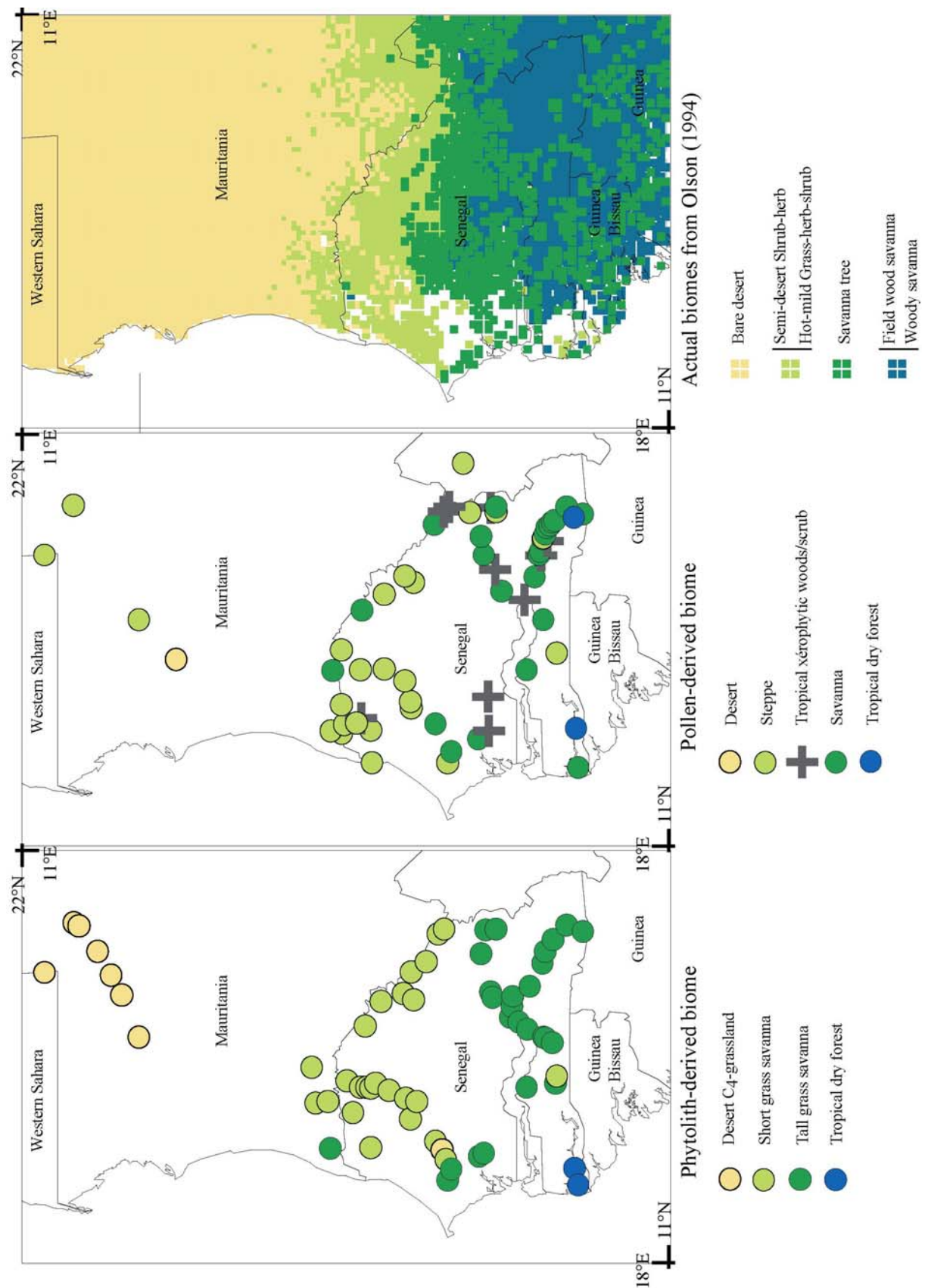
At this point, it is interesting to notice that there is no assemblage in the calibration set with a proportion of rough spherical type between the those found in the grasslands (i.e. 4.3 ± 5.3) and those found in the dense forest assemblages (i.e. 61.5 ± 1). Consequently, the regressor coefficient "rough spherical" is too roughly estimated to assign properly dry forests samples, which have intermediate proportions of this type. More samples from dry forest biomes with significant tree cover density are necessary to improve this calibration.

Finally, the calibration of grass dominated-biomes derived from phytolith data, successfully made for the West African C₄-grasslands, can also be applied with confidence to other geographic areas dominated by C₄-grasslands.

Comparison between phytolith-derived biomes, pollen-derived biomes and actual biomes

A visual comparison of 3 maps displaying phytolith-derived biomes, pollen-derived biomes, slightly modified from Jolly et al. (1998), and actual biomes defined by Olson et al. (1983; 1994a; 1994b) is presented in fig. II. 7. Six biomes defined by Olson occur in the studied zone: "Bare desert" is defined as clay or rock (with algae or lichens) only briefly and sparsely covered by ephemeral seedlings or flushes from a few rooted perennials, tuft plants or very sparse shrubs; "Semi-desert Shrub-herb" is defined as low open shrublands (<10% of woody cover), and some low shrublands (>10% of woody cover); "Hot-mild Grass-herb-shrub" is defined as other grasslands, from hot climates to mild (neither hot summers nor cold winters: i.e. maritime or tropical montane) with or without drought; "Savanna-tree"/shrub mosaics is defined as isolated trees above grass/shrub groundcover to patches of woodland or open forest (10-30% of woody cover). "Field wood savanna" is defined as dispersed woody cover (~20-40%) over most 1-km cells; "Woody savanna" with 30-50% tree crown cover overtops herb ground cover but may include woods patches as in "Field wood savanna".

The only two samples from the "tropical mesophilous forest", defined by phytoliths, are assigned to a "tropical mesophilous forest" biome and a "savanna" biome by pollens. They correspond to a "Seasonal tropical forest" biome (mostly evergreen to semideciduous) and to the "Mangrove" biome of Olson (not drawn on Fig. II. 7). Most of the "Savanna" biome and "Tropical xerophytic woods/scrub" defined by pollen (20 out of 26 and 8 out of 10 sites respectively) and of the "tall grass savanna" biome defined by phytoliths (22 of 27) are located in the "Woody savanna" and "Field wood savanna" biomes defined by Olson et al. (1994a; 1994b). Most of the "steppe biome" defined by pollen (27 of 34) and of the "short grass savanna" biome defined by phytoliths (24 of 25) are located in the "Hot-mild Grass-herb-shrub" and "Semi-desert Shrub-herb" of Olson. The "desert C₄-grassland" biome defined by phytoliths (7 of 8) correspond to the "Bare desert" biome from Olson. Only one sample from this zone is assigned in the "desert biome" defined by pollen, and the 3 other samples are assigned to the "steppe biome".



To summarize, the “tall grass savanna” biome defined by phytoliths corresponds to the “savanna” and “tropical xerophytic wood/scrub” biomes defined by pollen and they occur essentially in the “Woody savanna” biome defined by Olson et al. (Olson, 1994a; Olson, 1994b). The “short grass savanna” biome defined by phytoliths corresponds to the “steppe” biome defined by pollen and occurs in the “Hot-mild Grass-herb-shrub” and “Field wood savanna” defined by Olson et al. (1994a; 1994b). The “desert C₄-grassland” biome defined by phytoliths corresponds to the “Bare desert” biome of Olson (1994a; 1994b) and cannot really be compared to desert pollen biome which is too poorly characterized by pollen.

Figure II. 7. Modern phytolith-derived biomes (this study), pollen-derived biomes (Peyron, 1999) and actual biomes defined by Olson et al. (1994a; 1994b) for West Africa. In the Olson's map, white pixels correspond to infrequent biomes (Ex. Mangrove) and anthropized zones.

Discussion

Spatial scale recorded by the phytolith assemblages

In tropical areas and especially in arid areas, the extent of open vegetation, the high frequencies of fires and the strength of the trade winds would favor aeolian transportation of phytoliths. Aeolian transportation of Saharan dust in quantities and over long distances is well documented (Ruddiman, 1997; Grousset et al., 1998; Ratmeyer et al., 1999a; Ratmeyer et al., 1999b; Chiapello & Moulin, 2002). Phytolith studies of sediments from the Atlantic Ocean, off the West and North-West African coast show that phytoliths from West-Africa are also subject to long distance transportation (Diester-Haass et al., 1973; Flores et al., 2000; Abrantes, 2003b). The two major continental wind systems which are likely to transport West African particles are the low altitude northeasterly trade winds in winter, and the mid altitude African Easterly Jet in summer (Huang et al., 2000; Zhao et al., 2000; Abrantes, 2003b). At the latitude of the Saharan zone, northeasterly trade winds prevail as transport agent (Huang et al., 2000) which should not affect the sensitivity of phytolith assemblages to zonal vegetation. At the latitudes of the Sahelian, Sudanian and Guinean zones, the northeasterly trade winds and the African Easterly Jet alternate (Ratmeyer et al., 1999b; Huang et al., 2000). While the African Easterly Jet is parallel to the vegetation zones, the trade winds should transport phytoliths southward, reducing differences between Sahelian, Sudanian, and Guinean phytolith assemblages. This aeolian transport should also affect pollen records.

However, wind transportation does not prevent a clear distinction between Saharan, Sahelian, Sudanian and Guinean phytolith assemblages. In fact, the four bioclimatic zones are clearly distinguished through AET/PET estimation and biome designations made from phytolith analysis, although some discrepancies between observed and estimated data occur due to local vegetation features. We may conclude that phytolith assemblages from these areas are sensitive to the local vegetation but also connected to zonal vegetation dominance.

Significance of the Iph index in term of C₄-grassland physiognomy and water stress (AET/PET)

The Iph index is considered in this study as reflecting the dominance of short C₄-grasses (mainly Chloridoideae) versus tall-C₄-grasses (mainly Panicoideae) in a given vegetation zone. Because Chloridoideae species tolerate high temperature extremes and aridity better than other grasses (Jacobs, 1987), the Iph index is also dependent on humidity-aridity balance. Wyk (1979) established through field and bibliography study that the dominant Chloridoideae

genus of Africa (*Chloris* and *Eragrostis*) are characteristic of dry tall grass savannas from Sudanian areas with less than 700 mm/year of rainfall and of Sahelian short grass savannas. However, the relationships between high Iph index, short C₄-grasses dominance, and aridity may suffer some exceptions for the following reasons: 1) Some Panicoideae are annual short grasses adapted to local humid areas in arid zones. This is the case of *Panicum turgidum*, a Panicoideae perennial short-grass (Hutchinson & Dalziel, 1968 - 1972; Le Houerou, 1988) found in Sahara, and that produces assemblages with high Iph instead of reflecting the regional desert conditions. This example explains the several discrepancies between observed and estimated AET/PET using phytolith analysis, as pointed out earlier. 2) Grass communities may include large amount of grasses from the Arundinoideae subfamily which produces both phytolith types categorized as “Panicoideae” (e.g. *Aristida*, *Stipa*) and “Chloridoideae” (e.g. *Phragmites*) types and may influence the Iph index in one way or another. For example, Arundinoideae grasses in the Sahelian zone is mainly represented by *Aristida* (Trochain, 1940) which may lower the Iph index. However, Arundinoideae grasses are never dominant in the West-African grasslands (Trochain, 1980; Wyk, 1979) which limits their effect on the Iph index. .

This study confirms that the Iph index is a good indicator of short and tall grass savannas in West Africa. As tall and short grass dominance is also related to AET/PET (Parton et al., 1994; Stephenson, 1998) the Iph index may also be related to AET/PET ranges:

Iph values higher than $20 \pm 1.4\%$ characterize 22 of the 24 short grass savannas growing under AET/PET ranging from 0.15 ± 0.04 to $0.30-0.35 \pm 0.04$, while Iph values lower than $20 \pm 1.4\%$ characterize 23 of the 25 tall grass savannas growing under AET/PET ranging from $0.30-0.35 \pm 0.04$ to 0.45 ± 0.04 and 3 of the 7 desert C₄-grasslands growing under AET/PET of 0.05 ± 0.04 . This result reassess the Iph boundary of 30% previously suggested by Alexandre et al. (1997) after studying five samples from our 62 samples set. The Iph boundary of $20\% \pm 1.4$ is lower than the Iph boundary of about 40% calculated from Kurmann (1985) and Fredlund and Tieszen (1997b) data, which discriminates tall grass prairies from short grass prairies recorded by Pleistocene, Holocene and modern phytolith assemblages in North America. Disagreement between African and North-American Iph boundaries may result from different proportions of Chloridoideae, Arundinoideae and Panicoideae grasses in North-American and African short and tall grass savannas. This observation suggests that another calibration of the relationships between Iph, grassland physiognomy and AET/PET must be done specifically for the North-American grasslands.

Significance of the Fs index in term of water stress (AET/PET)

Bulliform cells are part of the epidermis of grasses and other monocots such as sedges (Andrejko & Cohen, 1984). They differ from other epidermal cells in being larger and more inflated (Ellis, 1976). This type of cells occurs most commonly, but not exclusively, at the basis of adaxial furrows (Shields, 1951). The outer epidermal walls of these cells have the ability to contract in width when the leaf is dehydrated, which promotes the grass leaf-rolling response to moisture loss (O'Toole & Cruz, 1980; Hsiao et al., 1984; Moulia, 1994; Hernandez et al., 1999). Decreasing turgor of the bulliform cells occurs when the leaf transpires before rolling. O'Toole and Cruz (1980) also showed that degrees of rice leaf rolling is linearly related to leaf water potential, depending on water deficit length. Thus, two factors are controlling the leaf rolling: high transpiration and water stress.

The process involved in silicification of bulliform cells is not well documented. Parry and Smithson (1958) suggested, with microscopic observations, that in developing leaves deposits of silica occur first in normal epidermal cells, and that bulliform cells accumulate silica in a later stage. According to the same authors, silica depositions in bulliform cells may completely upset their hygroscopic and water storage functions and might be an initial cause of the desiccation of the leaf. Sangster and Parry (1968) studied the formation of silicified bulliform cells in three cultivated grass species. These authors showed by counting under the microscope the number of silicified bulliform cells per leaf area that formation of silicified bulliform cells occur preferentially when species normally grown under dry conditions are cultivated under wet conditions. Andrejko and Cohen (1984) also suggested that the siliceous filling of bulliform cells is greatest in plants where transpiration is highest and where the root system has been submerged. According to these data, the hypothesis proposed here is that leaf rolling due to an increase of transpiration and/or an increase in duration of water stress would lead to silica saturation and precipitation. The more plants transpire and/or suffer water stress, the more silicified bulliform cells (Fs) they would produce. Our results confirm this hypothesis. Indeed, proportion of silicified bulliform cells in phytolith assemblages (Fs) increases when regional AET/PET decreases. Local wet areas in dry zones may also induce high transpiration rates and high production of silicified bulliform cells, as suggested previously from our data.

A phytolith proxy of AET/PET: the application domain

The relationship between Iph and Fs phytolith indices and AET/PET proposed in this study applies to C₄-grassland areas where AET/PET ranges from 0 to 0.45±0.04, and where rainfall

and evapotranspiration are the main environmental controls on vegetation distribution. Such C₄-grasslands are common in inter-tropical areas (e.g. West Africa, South America, India, Australia) and were even more widespread during the last glacial period.

However the proxy presented here should be used with caution when applied to phytolith assemblages with the following features:

- 1) When the Chloridoideae phytolith (saddle type) is absent from the assemblage, and when the Iph index reaches 0, the relationship presented here will underestimate AET/PET.
- 2) When the tropical woody dicotyledon phytolith (rough spherical type) show a higher abundance, another relationship should be done, using the D/P phytolith index (tropical woody dicot. phytoliths versus Poaceae phytoliths) as a fourth regressor.
- 3) When C₃-grasses phytoliths (circular, rectangle or crenate types, according to Twiss et al. (1969), Mulholland (1989) and Fredlund and Tieszen (1994)) are also well represented, another relationship should also be calculated, including the Ic index (C₃-grasses phytoliths versus C₃- plus C₄-grasses phytoliths) as a regressor.

In summary, the present proxy will be very useful for reconstructing past AET/PET when working on phytolith assemblages dominated by Panicoideae and Chloridoideae C₄-grass phytoliths, devoid of Pooideae C₃-grasses and with a few tropical woody dicotyledon phytoliths.

Archaeological evidence indicates that human activities have had a large impact on the Sahelian vegetation over the last 2000 years (Le Hou  rou, 1993a). Effect of overgrazing may have: (1) eliminated perennial grasses such as Panicoideae (*Andropogon*) and Arundinoideae (*Aristida*); (2) replaced mesic annual grasses of the Panicoideae subfamily by more xeromorphic grasses of the Arundinoideae and Chloridoideae subfamilies (Le Hou  rou, 1993a). Thus, both climate and human impact may be responsible for the current widespread of Chloridoideae grasses in the Sahelian zone and for the high Iph calculated from the related modern phytolith assemblages. Past AET/PET may thus be under-estimated when applying the present proxy to fossil phytolith assemblages with high Iph.

Complimentary phytolith- and pollen-derived biomizations

Both phytolith and pollen-derived biomizations appear accurate for distinguishing between tall and short grass savannas when probability of the spectra to be assigned to one or another biome is high. When probability decreases, chances of assigning an incorrect biome to the

data increase. This is when using both phytolith and pollen data in the same biomization would help to more accurately discriminate the reconstructed biome. One approach would be to use the phytolith-derived biomes to constrain pollen-derived biomes as done by Cheddadi et al. (1997) with climate estimated from pollen constrained by lake-level changes. But firstly, phytolith and pollen biomes have to be defined to describe the same vegetation types. Secondly, as developed by Cheddadi et al. (1997), the pollen-derived biome would be rejected if it is inconsistent with the phytolith-derived biome. This method would also be applied directly by adding a ratio, which is a function of the phytolith coefficients for the variables of the discriminant functions, to scores of PFTs used in the pollen biomization.

While pollen has difficulty simulating the desert biome, phytolith data appear more reliable. This is due to 1) the ability of phytolith assemblages to characterize grass covers when non-grass taxa are scarce, as this may be the case in some desert areas; 2) the ability of phytolith assemblages to trace the length or intensity of water stress suffered by grasses and 3) because of the high regional contribution of pollen in open area. The accuracy of phytoliths to simulate the desert biome is very interesting, especially as phytolith, contrary to pollen, are well preserved in such oxidized zones.

Conclusion

1) Calibration of the relationship between phytolith indices, vegetation structure, and AET/PET, is successfully made for the West-African bio-climatic zones:

- Characterization of the grass cover (dominated by short Chloridoideae grasses or tall Panicoideae grasses) is accurately made through the phytolith index Iph. A boundary of $20 \pm 1.4\%$ discriminates tall grass savannas from short grass savannas.
- Water stress and transpiration suffered by the grass cover can be estimated through a second phytolith index Fs.
- These two phytolith indices can be combined to get a new proxy of the annual amount of growth-limiting drought stress on grasses, expressed by the ratio AET/PET:

$$\text{AET/PET} = -0.605 \text{ Fs} - 0.387 \text{ Iph} + 0.272 (\text{Iph} - 20)^2$$

The above proxy is reliable for estimating AET/PET ranging from 0.1 ± 0.04 to 0.45 ± 0.04 , although very low AET/PET can be slightly over-estimated. It can be used from fossil phytolith assemblages dominated by Panicoideae and Chloridoideae C₄-grass phytoliths, devoid of Pooideae C₃-grasses and with a few tropical ligneous woody dicotyledon phytoliths. AET/PET is even more accurately estimated from pollen data ($r = 0.84$). This is partly related to the higher amount of pollen data. Special efforts should be made in the future, to sample various types of grasslands, and analyze the modern phytolith assemblages in term of phytolith indices.

We can suggest from these results that combining phytolith and pollen proxies of AET/PET for C₄-grasslands would help to better constrain this climate parameter. As AET/PET is a bioclimatic indicator commonly used in vegetation models, such a combination would help to make model/data comparisons more efficient.

2) Four phytolith-derived biomes are proposed: "Desert C₄-grassland", "Short grass savanna", "Tall grass savanna" and "Tropical mesophilous forest". Phytolith biomization accurately simulates inter-tropical C₄-grass dominated biomes and especially the desert C₄-grassland biome, in contrast to pollen biomization.

In this case, the use of both pollen and phytolith fossil data in biomization methods would improve the simulation of grass-dominated biome distributions in the past in West Africa and enhance the efficiency of model/data comparisons.

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CHAPITRE III. VALIDITE ET LIMITES DE L'INDICE PHYTOLITHIQUE IC EN TANT QUE TRACEUR DES SOUS-FAMILLES PANICOIDEAE (C₄ ET C₃) ET POOIDEAE (C₃) EN ZONE D'ALTITUDE INTERTROPICALE; APPLICATION A DEUX SITES EST-AFRICAIN : MT KENYA (KENYA) ET MT RUNGWE (TANZANIE).

III. 1. Résumé étendu de l'article : Testing the Ic phytolith index as a proxy of Panicoideae (C₄ and C₃) and Pooideae (C₃) grass subfamilies dominance on tropical mountains : application at two sites in East Africa (Mt Kenya and Mt Rungwe).

Ce chapitre permet de vérifier l'aptitude des assemblages phytolithiques à tracer l'étagement selon l'altitude des sous familles de graminées en zone inter-tropicale. Nous discutons également de la validité et des limites de l'indice phytolithique Ic, indice développé par Twiss (Twiss, 1987; Twiss, 1992) dans les Grandes Plaines Américaines en tant que traceur des formations herbacées en C₄ et C₃, essentiellement liées à la température en zone tempérée (Teeri et Stowe, 1976; Epstein et al., 1997).

En zone inter-tropicale, les graminées en C₃ sont inféodées, à quelques rares exceptions, aux zones d'altitudes. Plusieurs mécanismes tels que la température, la pression partielle de CO₂ et le degré d'humidité du sol (voir revue dans Ehleringer et al., 1997; Epstein et al., 1997) favorisent un type de photosynthèse par rapport à un autre. Ainsi, le rapport C₃/C₄ est fortement lié aux conditions climatiques. Il fait l'objet de très nombreuses études, notamment pour l'estimer à des périodes clefs du passé et mieux appréhender les mécanismes qui le gouvernent (e.g. Cerling et al., 1997; Ehleringer et al., 1997; Pagani et al., 1999; Boom et al., 2002; Winslow et al., 2003).

Nous avons étudié des assemblages phytolithiques échantillonnés le long d'un gradient altitudinal (Mont Kenya -Kenya- et Mont Rungwe -Tanzanie-), depuis les formations herbacées de basses altitudes dominées par les C₄ jusqu'à celles de hautes altitudes uniquement en C₃.

Matériel et méthode

Treize échantillons prélevés dans les 6 grandes zones de végétations du Mont Kenya (Figure III. 1) ont été analysés pour leur contenu phytolithique. Ils sont répartis depuis 2000m

d'altitude jusqu'à 4500m. Six échantillons ont été prélevés autour du lac Masoko (760m d'altitude) situé à 20 km au sud du Mont Rungwe où ont été prélevés quatre autres échantillons entre 2150 et 2960m d'altitude. Les relevés botaniques exhaustifs des Poaceae et Cyperaceae effectués, sur des cadrats, sur les flancs Nord-Ouest et Est du Mont Kenya sont présentés en figure III. 2.

Les assemblages phytolithiques sont analysés et discutés à l'aide de l'indice Ic (Twiss, 1987; Twiss, 1992) qui est le rapport des phytolithes essentiellement produit par les Pooideae (Poaceae à cycle photosynthétiques uniquement en C₃) sur la somme des phytolithes produit par les graminées en C₃ et C₄. L'indice D/P qui est un indicateur de la densité du couvert arboré et l'indice Iph qui permet de différencier les savanes à graminées basses des savanes à graminées hautes sont aussi présentés pour discuter de leur validité dans ces zones d'altitude. D'autre part, afin de comparer l'indice Ic avec les relevés botaniques, deux indices botaniques sont calculés pour les échantillons du Mont Kenya :

$$Ib_1 = \frac{\%Pooideae}{\%Pooideae + \%Panicoideae + \%Chloridoideae}$$

$$Ib_2 = \frac{\%Pooideae + \%Arundinoideae}{\%Pooideae + \%Arundinoideae + \%Panicoideae + \%Chloridoideae}$$

Résultats

Les assemblages phytolithiques montrent de très nettes différences entre les échantillons de basses altitudes, en zone de savanes arborées à graminées en C₄, et ceux de plus hautes altitudes où les graminées en C₄ et C₃ coexistent (figure III. 4). Les échantillons de la zone de forêts d'altitude (Montane Forest) sont caractérisés par des valeurs de Ic moyennes. La zone de bambous (Bamboo zone) et les pelouses d'altitudes sont bien différenciées par les assemblages phytolithiques, par contre les autres zones de végétations ne le sont pas.

Certains types de phytolithes montrent des variations d'abondance en fonction de l'altitude, mais c'est l'indice Ic qui semble être le mieux corrélé avec l'augmentation des Pooideae selon l'altitude (figure III. 4). La représentation de l'indice Ic et des indices botaniques Ib₁ et Ib₂ montre qu'ils évoluent parallèlement (figure III. 5a et 5b). La transition entre les formations herbacées dominées par les Panicoideae et puis par les Pooideae/Arundinoideae se situe autour de 2300 m d'altitude, aussi bien pour les indices botaniques que phytolithique. De façon à comparer la variabilité (moyenne et écart-type) de l'indice Ic et des indices botaniques nous les avons représentés en les regroupant en fonction des limites altitudinales des types de

végétation (méthode de représentation graphique appelée "box plot") (figure III.5c). Ceci montre que malgré une importante variabilité de l'indice I_c et des indices botaniques, ils co-évoluent ensemble suivant les zones de végétation. D'autre part, il semble que l'indice I_c reflète mieux l'indice I_{b2} que l'indice I_{b1} .

Discussion et conclusion

Les zones de végétations définies d'après les composantes arborées le long du gradient altitudinal (McKone, 1995; Wooller et al., 2000) ne sont pas bien caractérisées par l'indice D/P. Cet indice qui a été proposé par Alexandre et al. (1997; 1999) et calibré en zone inter-tropicale de basse altitude par Bremond et al. (soumis) semble donc ne pas être applicable pour des espèces tropicales d'altitude. Ceci permet de mieux définir les zones géographiques d'application de cet indice puisque d'autres études effectuées en domaine tempéré avaient déjà relevé qu'il n'était pas applicable partout de la même manière. La signification de l'indice I_{ph} , reconnu comme étant un bon traceur des savanes à graminées basses et savanes à graminées hautes et utilisé pour estimer le stress hydrique (AET/PET) subi par la formation herbacée, est aussi discutée.

Cette étude montre que le I_c est un bon traceur de la proportion des Pooideae et Arundinoideae par rapport aux Panicoideae mais qu'il n'est par contre pas sur cette zone d'étude un traceur de la proportion en C_3/C_4 des graminées. Ceci parce que les échantillons du Mont Kenya ont été prélevés dans une zone où les Panicoideae, habituellement à cycle photosynthétique en C_4 , sont ici en C_3 . La validité de cet indice en tant qu'indicateur paléo-environnemental est donc discutée. Le fait que ces Panicoideae en C_3 ne représentent que 20% des espèces de Panicoideae et qu'elles sont inféodées à certains milieux permet d'affirmer que cet indice estime correctement la proportion des sous-familles graminéennes Pooideae et Panicoideae en zone intertropicale soit, potentiellement, la domination des Poaceae en C_4 ou C_3 .

III. 2. Perspectives quantification et application à des échantillons fossiles

Cette étude montre que l'indice I_c est un bon traceur de la distribution des Pooideae + Arundinoideae relativement aux Panicoideae. Aucune calibration de l'indice n'a pu être faite faute de données botaniques exhaustives (tenant compte par exemple du recouvrement réel de chaque espèce au sein des quadrats et entre les quadrats) et compte-tenu du petit nombre d'échantillons dont nous disposions. La perspective à ce travail est d'augmenter le nombre

d'assemblages analysés (d'autres échantillons sont disponibles au sein de chaque zone), ce qui permettra de les comparer aux relevés botaniques plus précis puisque plus restreints.

Il sera aussi intéressant d'échantillonner un nouveau transect altitudinal où la transition C_3/C_4 est observée : par exemple en Argentine (Cabido et al., 1997), dans les Andes du Nord (Boom et al., 2001) ou bien encore à Hawaï (Rundel, 1980). Il sera ensuite nécessaire d'étudier les paramètres bio-climatiques qui contrôlent la distribution de *Panicoideae* en C_3 , afin de préciser quel type d'information bio-climatique l'indice I_c peut apporter.

L'analyse conjointe d'autres indicateurs tels que les données polliniques peut nous permettre d'utiliser tout de même cet indice en tant que traceur du rapport C_3/C_4 des graminées. En effet, les données polliniques permettent de caractériser le type de forêt et donc d'interpréter les assemblages phytolithiques, puisque les *Panicoideae* en C_3 sont inféodées aux sous-bois de forêt dense ou d'altitude.

Un test sur des données fossiles sera effectué sur les assemblages phytolithiques de 32 échantillons extrait de la carotte lacustre de Masoko (Alvarado, 2003). La carotte a été prélevée dans les sédiments du lac Masoko (Tanzanie) à basse altitude (760m) et couvre les derniers 50000 ans. On pourra alors confronter nos résultats avec les sorties du modèle GUESS-LPJ (voir chapitre V) dont un des paramètres simulé est justement le rapport C_3/C_4 des graminées.

III. 3. Testing the Ic phytolith index as a proxy of Panicoideae (C₄ and C₃) and Pooideae (C₃) grass subfamilies dominance on tropical mountains : application at two sites in East Africa (Mt Kenya and Mt Rungwe).

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Article à soumettre

Abstract

The aim of the study was to assess the reliability of phytolith assemblages and indices for tracing grass subfamilies dominance and tree cover density on East-African montane slopes and to discuss potentialities and limitations of the Ic index for tracing Pooideae, Panicoideae, C₃ and C₄ grass distributions. Modern samples were collected on the eastern and north-western slope of Mont Kenya, from 2000m to 4500 m a.s.l. and on the northern and southern slope of Mont Rungwe (Tanzania), from 800m to 3000 m a.s.l. This study permits to specify the geographical application domain of the D/P phytolith index as proxy of tree cover density and the Iph index as tracer of C₄-tall and C₄-short grasses or as proxy of AET/PET. We show that Ic phytolith index is a good proxy of Pooideae and Arundinoideae proportions among Panicoideae. If it is assumed that 80% of Panicoideae are C₄ plants, this index has a great potentiality to trace C₃/C₄ grasses variation.

Keywords : phytoliths, botanical survey, Mount Kenya, Mount Rungwe, C₃/C₄ grasses, Tanzania.

Introduction

The modern spatial patterns of C₄ and C₃ grasses show that C₄ grasses dominate at low elevation in tropical and subtropical regions, that the transition from C₄ to C₃ grasses takes place between about 30° and 45° in latitude, and that C₃ grasses dominate at higher latitudes (Cerling et al., 1997). The crossover point favouring C₃ over C₄ grasses depends on temperature during the growing season and partial pressure of CO₂ (pCO₂). Ecosystems dominated by C₄ grasses are favoured under low pCO₂ associated with high temperature (Cerling et al., 1997; Ehleringer et al., 1997; Collatz et al., 1998; Pagani et al., 1999; Boom et al., 2002; Winslow et al., 2003). Local distribution of C₃ versus C₄ grasses appear more complex: in tropical area, at given elevation, C₄ grasses abundance appears inversely correlated with soil moisture (Young & Young, 1983).

Global vegetation models provide C₃/C₄ grass distribution (e.g. Prentice et al., 1992; Haxeltine & Prentice, 1996; Sitch et al., 2003) that correctly describes actual vegetation at global scale, but becomes less reliable at local or regional scales, especially when they run for situations much different from the present one. One way to assess their efficiency is to confront their outputs to palaeodata. Some datasets have been compiled for that. For instance, the BIOME 6000 project aims at providing palaeodata from the mid-Holocene period as a benchmark to evaluate simulations with coupled climate-biosphere models, and thus to assess the extent of biogeophysical (vegetation-atmosphere) feedbacks in the global climate system (Prentice & Webb, 1998).

Several proxies can be used to infer past changes in the contribution of C₃ versus C₄ grasses to the vegetation composition. Fossil pollen assemblages are not suited to determine these contributions as all grasses (Poaceae) pollen grains are identical. The stable carbon isotopic composition ($\delta^{13}\text{C}$) of plant biomass is a tool allowing identification of C₃ versus C₄ photosynthetic pathways. However, the total organic carbon (TOC) of sediments represents a complex mixture of diverse sources hardly distinguished. For instance, both terrestrial arboreal, non-arboreal and fresh aquatic components may present the C₃-pathway, and cannot be discriminated using the $\delta^{13}\text{C}$ of TOC. Grass-cuticle analysis has also shown promising in palaeoecological studies. Recent research has developed additional methods for obtaining better past grassland information using the $\delta^{13}\text{C}$ analysis of selected organic matter, in grass epidermis (Beuning & Scott, 2002), in grass pollen grains (Descolas-Gros et al., 2001) or on occluded organic matter of phytoliths (Kelly et al., 1991; Kelly et al., 1998; McClaran & Umlauf, 2000), but remain scarce. When they are preserved, sub-fossil grass cuticles retain micro-morphological features that permit identification to subfamily, supertribe, tribe and, in

some instances, genus or species level (Mworia-Maitima, 1997; Wooller & Agnew, 2002; Wooller et al., 2003).

Phytoliths are amorphous silica particles that precipitate in and/or between the cells of living plant tissues. Phytoliths and phytolith assemblages are a good tool to discriminate among different grass subfamily-dominated biomes (Twiss, 1992; Fredlund & Tieszen, 1994; Alexandre et al., 1997; Barboni et al., 1999; Prebble et al., 2002; Scott, 2002; Bremond et al., submitted-b). Twiss (1992) proposed that the proportion of C₃ to C₄ grasses can be approximated by comparing the number of phytoliths produced by Pooideae to the sum of phytoliths produced by Chloridoideae and Panicoideae grass subfamily. This ratio is called Ic. It is based on the fact that all Pooideae are C₃ plants, all Chloridoideae are C₄ and 79% of Panicoideae are C₄ (Watson et al., 1985; Watson & Dallwitz, 1992). On this basis, fossil phytolith assemblages from soils, buried soils, lake sediments, and marine cores have been used to reconstruct C₃/C₄ grass dominance (Fredlund & Tieszen, 1997b; Barboni et al., 1999; Baker et al., 2000; Blinnikov et al., 2002; Scott, 2002; Stromberg, 2002; Abrantes, 2003a). However, currently, only Fredlund and Tieszen (1994) have demonstrated the relationship between modern phytolith assemblages and C₃/C₄ grass dominance. Their study was conducted in the North American Great Plains over fifteen sites from all of the major grassland compositional regions. In the inter-tropical zone, none advanced confrontation exists between modern phytolith assemblages and C₃/C₄ grass dominance.

The aim of the study is twofold: 1) to assess the reliability of phytolith assemblages and indices for tracing Pooideae, Panicoideae and Chloridoideae grass dominance, as well as tree cover density, on East-African montane slopes, and 2) to discuss potentialities and limitations of the Ic index for tracing Pooideae, Panicoideae, C₃ and C₄ grass distributions, in the same area. In this prospect, 13 modern soil samples were collected on the eastern and north-western slope of Mont Kenya, from 2000m to 4500m above sea level (a.s.l.), and 11 soil samples were collected on the northern and southern slope of Mont Rungwe (Tanzania), from 800m to 3000m a.s.l.

Material and methods

Mont Kenya

Mount Kenya is located on the equator (0°S; 37.1°E) in Kenya, East Africa (Fig. III. 1a). It is the second highest mountain in Africa (5199 m above sea level (a.s.l.)) and forms an isolated conical massif with a basal diameter of about 120 km. It was formed by volcanic activity

during Tertiary and Quaternary, mainly between 2.6 and 3.1 Myr BP although there have been more recent eruptions on the eastern side of the mountain until about 1 Myr BP (in Tattersfield et al., 2001). The climate is characteristic of the inter-tropical convergence zone (ITCZ), with large diurnal temperature oscillations and small monthly variations during the course of the year (in Wooller et al., 2000). Two rainfall seasons occur from March to June and from October to November (Coe, 1967). Dry seasons (July–September and December–February) have at least one month with less than 60 mm of rain, and a minimum mean monthly temperature of 18°C.

Vegetation fires at the end of the dry seasons reinforce the climatically induced vegetation zonation. The present-day vegetation shows marked altitudinal zonation (Fig. III. 1b reconstructed from Wooller et al. (2000), Ficken et al. (2002), Wooller and Agnew (2002) and Wooller et al. (2003)) the basal plateau zone (disturbed tall grass savanna) is dominated by *Themeda triandra* (Panicoideae; C₄) and other Panicoideae grasses (mainly C₄) that frequently burn. This grassland grades up into the Montane forest belt (**a** ; ~1960-2500 m a.s.l.), occupying the wettest areas. and which contains sparse Panicoideae (essentially C₃ under the forest), Arundinoideae (mainly C₃), and Bambusoideae (C₃) grasses and sedges. The Bamboo zone (**b** ; ~2450-2900 m a.s.l.) is dominated by Bambusoideae grasses (*Arundinaria alpina*). The *Hagenia–Hypericum* zone (**c** ; ~2900-3000 m a.s.l.) is dominated by woody trees, shrubs, and some grasses (Panicoideae and Pooideae grasses (C₃ and C₄)). The Ericaceous zone (**d** ; ~3000-3400 m a.s.l.) is dominated by woody shrubs and Pooideae grasses (C₃). Some patches of Panicoideae grasses are located in the lower part of this zone. Afroalpine zone (**e** ; ~3400-4200 m a.s.l.) is dominated by Pooideae tussock grasses (C₃) with some sedges. The Nival zone (**f** ; ~4200-5199 m a.s.l.) presents isolated Pooideae grasses (C₃) in very sheltered areas. There is a gap in the forest on the northern flank of Mount Kenya, which corresponds with relatively low rainfall values. This forest gap is believed to have originated as a result of human disturbance (in Wooller et al., 2000).

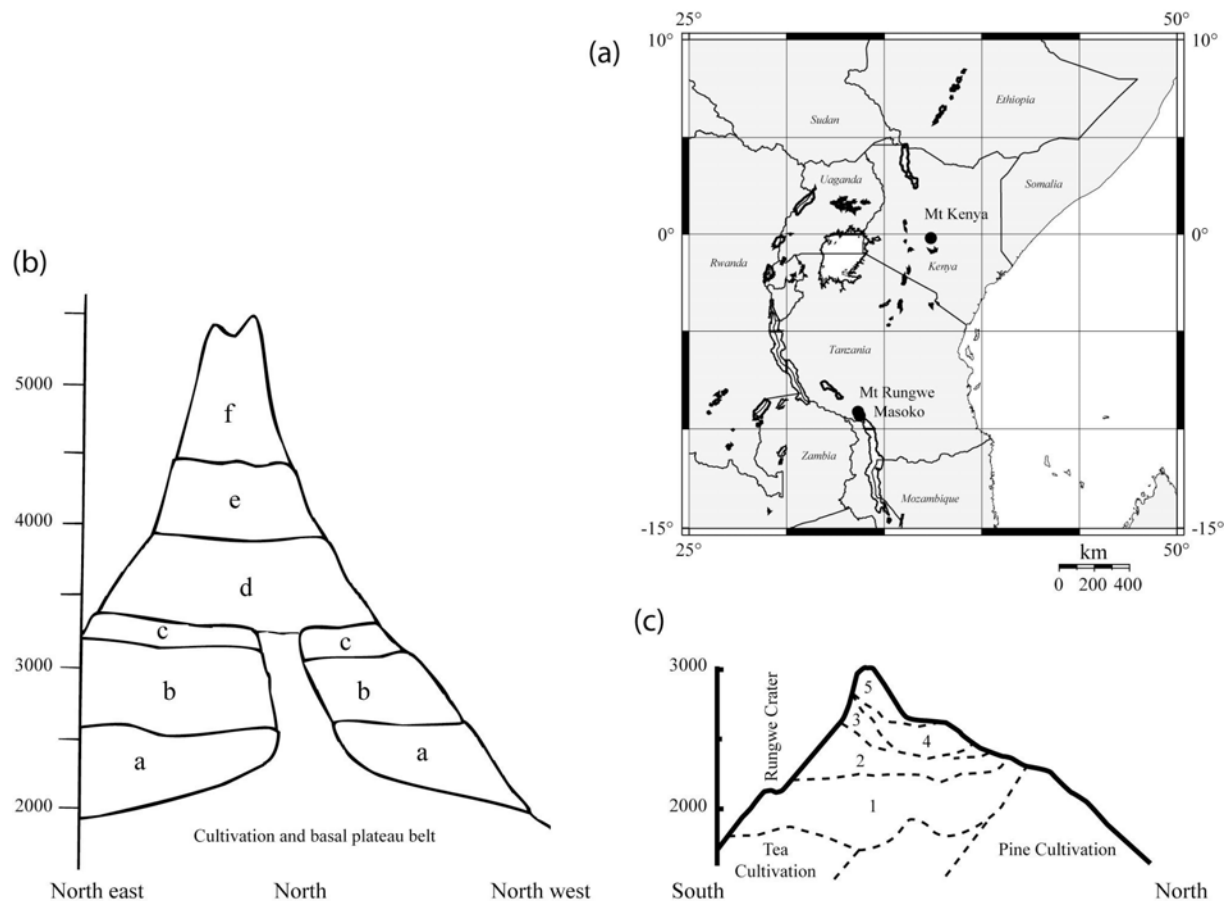


Figure III. 1. (a) Location and vegetation zones (see text for explanation) of (b) Mount Kenya and (c) Mount Rungwe in East Africa.

Three studies on the distribution of C_3 and C_4 grass species along altitudinal gradients were previously conducted on Mount Kenya: 1) Tieszen et al. (1979) attempted to sample intensively the grass communities along a northeast-southwest altitudinal gradient (from 2000 to 3900 m a.s.l.) almost devoid of forest cover. Botanical statements are not available but the general pattern suggests clearly that the low altitudes contain mainly C_4 grasses and the high altitudes mainly or only C_3 grasses. The few C_3 species (10% of the total), which do grow at low altitudes, occupy special habitats, usually the understoreys of closed canopy forests. 2) on the same slope but following a different track also almost devoid of forest (Timau track) between 2800 and 3200 m a.s.l., Young and Young (1983) studied the distribution of grass species, with the percentage of C_4 species decreasing steadily with increasing elevation. This was due mainly to a decreasing number of C_4 species, the absolute number of C_3 species remaining constant. 3) Wooller et al. (2001) published an altitudinal survey of grasses and sedges conducted on the Sirimon (north-western flank), and the Chogoria (eastern flank)

tracks, covered by forest. Conversely to Tieszen et al. (1979), Wooller et al. (2001) have not found the crossover between the abundance of C₄ and C₃ grasses in the grass species distribution, but show that (i) C₃-Panicoideae grasses mainly settle at low elevations, under forest canopy, (ii) high elevations are only covered by C₃-Pooideae and few C₃-Arundinoideae, and (iii) the zone around the tree line is characterized by C₄-Panicoideae grasses. Botanical statements are presented in Fig. III. 2. Phytolith samples were collected along the Sirimon and Chogoria tracks.

Mount Rungwe

Mount Rungwe is located at 9°S, 33°E in Tanzania, East Africa (Fig. III. 1b), from 1400 to 2960 m a.s.l. It is a dormant volcano built up mainly of phonolitic trachyte lavas and tuffs, overlying a foundation of phonolites and basalts. Soils are well drained with low bulk density sandy loams, and particularly thin and rocky in the high grasslands. Soils are classified as Vitric andosols and other Andosols with areas of Lithosols (F.A.O., 1998). Estimated rainfall ranges from 1550 mm to 1850 mm.yr⁻¹ on the northern and southern slopes, respectively. There is only one dry season occurring from June to October, with maximum estimated temperatures (at middle elevations) of 20°C in October and a minimum of 9°C in June and July (McKone, 1994; McKone, 1995).

The vegetation distribution on Mount Rungwe is, according to McKone (1994; 1995) and botanical statements conducted during phytolith samples collection, as follow : **1)** the Montane forest is found at low elevations (1500m a.s.l.) on southern and western slopes. *Pseudobromus sylvaticus* (Pooideae ; C₃) and *Cyperus* sp. have been observed on the southern flank under dense forest canopy. On the northern flank, in open areas enclosed within the Montane forest, tussock Panicoideae grass (*Schizachyrium brevifolium* ; C₄) is dominant. **2)** The Upper Montane forest (100m a.s.l.) shows typical fairly thick undergrowth and numerous lianas. Large stands of regenerating bamboo are prominent in the southern and southwestern slopes. Short to medium grasses occur in small patches throughout the Upper Montane forest. Dominant species from this zone is *Arundinaria alpina* (Arundinoideae ; C₃), *Pennisetum* sp., and *Andropogoneae* sp. (Panicoideae; C₄) are also present. **3)** the Ericaceous belt is mostly developed at upper southern and southeastern elevations, between 2600 and 2800m a.s.l., generally representative of a transitional zone between forest and upper grasslands. This zone is dominated by *Erica arborea* with fewer *Protea* sp., and low stature *Hagenia abyssinica*.

Altitudinal distribution of C₃ and C₄ grass and sedge species on the Chogoria track, Mount Kenya (from Wooller et . 2001)

Sub-family	Species	1900	1980	2000	2100	2150	2450	2500	2600	2750	2800	2850	3100	3150	3200	3250	3400	3550	3600	3750	4000	4150
C4	Panicoideae	<i>Setaria megaphylla</i>	1																			
C4	Panicoideae	<i>Miscanthus violaceus</i>			0.5																	
C4	Panicoideae	<i>Digitaria abyssinica</i>				0.5																
C4	Panicoideae	<i>Panicum subalbidum</i>					0.5															
C4	Panicoideae	<i>Pennisetum clandestinum</i>											0.5									
C4	Chloridoideae	<i>Eleusine jaegeri</i>											1									
C4	Panicoideae	<i>Cymbopogon nardus</i>										0.5			0.5							
C4	Cyperaceae	<i>Cyperus kerstenii</i>											1	1								
C4	Cyperaceae	<i>Bulbostylis atrosanguinea</i>										1	1	1	1	1						
C4	Panicoideae	<i>Andropogon lima</i>													0.5							
C4	Panicoideae	<i>Exotheca abyssinica</i>													1	1	1					
C3	Cyperaceae	<i>Cyperus ajax</i>	1																			
C3	Panicoideae	<i>Oplismenus compositus</i>	1	1	1																	
C3	Panicoideae	<i>Isachne mauritiana</i>	1	1	1	1																
C3	Panicoideae	<i>Acrachne volkensii</i>			1	1																
C3	Pooideae	<i>Stipa dregeana</i>			1	1																
C3	Cyperaceae	<i>Carex chlorosaccus</i>				1	1															
C3	Arundinoideae	<i>Arundinaria alpina</i>					1	1	1	1	1											
C3	Cyperaceae	<i>Cyperus fischerianus</i>						1	1													
C3	Cyperaceae	<i>Carex johnstonii</i>						1	1	1												
C3	Pooideae	<i>Phalaris arundinacea</i>					0.5					1	1		1							
C3	Panicoideae	<i>Andropogon schirensis</i>					1					1	1		1	1						
C3	Cyperaceae	<i>Carex petitiata</i>										1										
C3	Pooideae	<i>Festuca africana</i>										1										
C3	Pooideae	<i>Brachypodium flexum</i>							1	1	1	1	1		1							
C3	Cyperaceae	<i>Carex conferta</i>							1	1	1	1	1		1							
C3	Pooideae	<i>Agrostis quinqueseta</i>													1	1						
C3	Pooideae	<i>Bromus leptoclados</i>														0.5						
C3	Pooideae	<i>Agrostis volkensii</i>														1	1					
C3	Pooideae	<i>Festuca costata</i>														1	1					
C3	Pooideae	<i>Koeleria capensis</i>														0.5	0.5	1	1	1		
C3	Arundinoideae	<i>Pentstemon borussica</i>														1	1	1	1	1	1	
C3	Pooideae	<i>Festuca pilgeri</i>														1	1	1	1	1	1	
C3	Pooideae	<i>Poa leptoclada</i>														0.5						1
C3	Pooideae	<i>Anthoxanthum nivale</i>																1	1	1	1	1
C3	Pooideae	<i>Agrostis trachyphylla</i>																	1	1	1	1
C3	Arundinoideae	<i>Pentstemon minor</i>																			0.5	0.5
lb1			0	0	25	28.6	x	50	0	100	100	100	57.1	44.4	x	66.7	83.3	100	100	100	100	100
lb2			0	25	28.6	x	62.5	100	100	100	100	100	57.1	44.4	x	72.7	85.7	100	100	100	100	100

Altitudinal distribution of C₃ and C₄ grass and sedge species on the Sirimon track, Mount Kenya (from Wooller et . 2001)

Sub-family	Species	2800	2830	2840	2850	2905	3100	3200	3240	3250	3400	3550	3600	3650	3750	4000	4150	4200
C4	Cyperaceae	<i>Cyperus sesquiflorus</i>			1													
C4	Cyperaceae	<i>Cyperus niger</i>								1								
C4	Panicoideae	<i>Andropogon amethystinus</i>									1							
C4	Cyperaceae	<i>Bulbostylis atrosanguinea</i>									1	1	1					
C3	Cyperaceae	<i>Carex peregrina</i>	1															
C3	Pooideae	<i>Stipa dregeana</i>	1															
C3	Bambusoideae	<i>Ehrharta erecta</i>	1	1		1		1	1	1								
C3	Pooideae	<i>Streblochaete longiarista</i>			1	1	1											
C3	Cyperaceae	<i>Cyperus derelilema</i>					1											
C3	Arundinoideae	<i>Arundinaria alpina</i>			1	1	1											
C3	Cyperaceae	<i>Carex petitiata</i>						1										
C3	Pooideae	<i>Festuca africana</i>						1										
C3	Cyperaceae	<i>Cyperus sp.</i>						1										
C3	Arundinoideae	<i>Pentstemon minor</i>						1										
C3	Pooideae	<i>Brachypodium flexum</i>							1	1								
C3	Pooideae	<i>Bromus leptoclados</i>							1									
C3	Pooideae	<i>Poa annua</i>							1									
C3	Pooideae	<i>Poa schimperiana</i>							1									
C3	Cyperaceae	<i>Isolepis fluitans</i>								1								
C3	Pooideae	<i>Poa leptoclada</i>				1		1	1						1			
C3	Cyperaceae	<i>Carex conferta</i>							1						1			
C3	Arundinoideae	<i>Pentstemon borussica</i>								1				1	1			
C3	Cyperaceae	<i>Carex monostachya</i>								1						1		
C3	Pooideae	<i>Calamagrostis hedbergii</i>									1	1	1					
C3	Pooideae	<i>Agrostis trachyphylla</i>									1	1	1	1	1	1	1	1
C3	Pooideae	<i>Festuca pilgeri</i>									1	1	1	1	1	1	1	1
C3	Pooideae	<i>Anthoxanthum nivale</i>									1	1	1					
C3	Pooideae	<i>Koeleria capensis</i>													1			
lb1		100	x	100	100	100	100	100	100	x	66.7	100	100	100	100	100	100	100
lb2		100	x	100	100	100	100	100	100	x	75	100	100	100	100	100	100	100

NB: 0.5 = not located within a quadrat but present in the locality; 1 = located in at least one quadrat in a set of three; --- treeline

Altitudinal zones concerning by phytolith sampling

Figure III. 2. (a) Altitudinal distribution of C₃ and C₄ grass and sedge species on the Chogoria track, Mount Kenya (from Wooller et . 2001). **(b)** Altitudinal distribution of C₃ and C₄ grass and sedge species on the Sirimon track, Mount Kenya (from Wooller et . 2001).

4) The Bushed Grasslands occur up to the forest, with lesser bushlands and heaths at upper elevations. Dominant grasses are *Andropogoneae* sp. and *Brachypodium flexum* (Pooideae; C₃). 5) The mountain top grasses are short and generally occur above 2500m, though the tree-line influenced by fire varies from 2000m in the southwest to 2800m near Rungwe Peak. Observed dominant grass species are *Poa leptochlada* and *Deschampsia flexuosa* (Pooideae ; C₃), plus *Pentaschistis chrysurus* (Arundinoideae ; C₃).

Samples were collected on Mont Rungwe and at lower altitude (760 m a.s.l.) around Masoko lake, located at 20 km South to Mount Rungwe. The vegetation is a miombo woodland (open tropical forest), also qualified as Wooded tall grass savanna by the Yangambi vegetation classification (CSA, 1956), dominated by *Brachystegia* and *Uapaca* trees. The grass cover is made of *Panicum* sp., *Imperata cylindrica*, *Hyparrhenia* sp. (Panicoideae ; C₄) and *Eragrostis congesta* (Chloridoideae; C₄).

Phytolith samples

Samples from Mount Kenya were collected in 1997 (January and February) by Mat Wooller along Chogoria and Sirimon tracks, from 1900 to 4200 m a.s.l. (Wooller, 1999). The sampling method consisted in collecting individual sub-samples of the upper soil layer (1cm in depth after litter removal). Thirteen soil surface samples have been treated for phytolith extraction with 3 samples from the lower and upper parts of the Montane forest, 2 samples from the Bamboo zone, 2 from the *Hagenia–Hypericum* zone, 2 from the Ericaceous zone and 4 samples from the lower and upper part of the Afroalpine zone.

Samples from Mount Rungwe (from 2150 to 2966 m a.s.l.) and Masoko lake (780 m a.s.l.) were collected for the present study in November 2001. The same sampling method used on Mont Kenya has been applied over homogeneous areas of about 50 m² to collect a total of 10 samples with 1 sample collected at the edge of one small volcanic crater in the southern bank of Rungwe Montane forest, 3 samples on the northern slope (one in a tussock grassland under the Montane forest, one at the edge of the Ericaceous belt in the bushed grassland, and one at the top in short and burnt grasses), and 6 samples around the Masoko lake (3 under *Uapaca* wooded savanna and, 3 under *Brachystegia* wooded savanna).

Phytolith extraction, classification and counting

Phytoliths are extracted from 20g of dry soil, slightly crushed and sieved at 2mm, after 1) grinding ; 2) dissolution of carbonates, using HCl (3 %) ; 3) iron oxides removal using sodium citrate (C₆H₅Na₃O₇) and sodium dithionite (Na₂O₄S₂, H₂O₂) ; 4) organic matter

oxidation, using H_2O_2 (30 %) heated at 90°C until reaction subsides; 5) sieving at $60\ \mu\text{m}$; 6) clays removal ; and 7) densimetric separation of phytoliths in a ZnBr_2 heavy liquid ($d=2.3$) (Kelly, 1990).

The recovered fraction, including opal phytoliths and a few diatoms is mounted on microscope slides in glycerin for 3D observation and in Canada Balsam for counting at 600X magnification. Phytolith conservation is good in all the samples analyzed. More than 300 phytoliths with diameter greater than $5\ \mu\text{m}$ and with taxonomic significance are counted. Numerical counting values are reported in appendix 1. Phytolith assemblages are presented as a percentage of the sum of classified phytoliths. Double counting has been done for several slides; and gives an error of 3% (s.d.). Phytoliths are classified according to the classification of Twiss (1969; 1992), improved and completed by phytolith shape descriptions of Mulholland (1989) Fredlund and Tieszen (1994), Kondo et al. (1994), Alexandre et al. (Alexandre et al., 1997) and Barboni et al. (Barboni et al., 1999). The different phytolith types identified and counted are illustrated in Fig. III. 3. Amorphous silica particles without specific form have not been counted.

Counting of silicified short cells from grass epidermis allows distinguishing 3 among 5 grass subfamilies. The cross (1) and dumbbell (2) phytolith types occur dominantly in the Panicoideae grass subfamily (Twiss et al., 1969; Mulholland, 1989; Fredlund & Tieszen, 1994; Kondo et al., 1994). The saddle (3) type is produced in high proportion by the Chloridoideae grass subfamily (Twiss et al., 1969; Mulholland, 1989; Fredlund & Tieszen, 1994; Kondo et al., 1994). The uni-lobate (4) type corresponds to the pooid type proposed by Twiss (1969). It associated the rondel type described by Mulholland (1989) also named conical and pyramidal by Fredlund and Tieszen (1994), plus the keeled type also described by Fredlund and Tieszen (1994). Both the uni-lobate and the poly-lobate (5) types, also named crenate by Fredlund and Tieszen (1994), are mainly produced by the Pooideae subfamily (Twiss et al., 1969). The rectangle type (6) is produced by Pooideae grasses (Twiss et al., 1969; Mulholland, 1989; Kondo et al., 1994). The point-shaped (7) type originates from micro-hair or prickles of all grass epidermis (Palmer et al., 1985; Kaplan et al., 1992). The fan-shaped (8) phytolith type (Twiss et al., 1969; Kondo et al., 1994) is produced inside the bulliform-cells of all grass epidermis. The elongate (9) type (smooth and sinuous elongate types are merged in this same group) are phytoliths from long-cells of all grass epidermis. Among the other grass subfamilies, Bambusoideae and Arundinoideae produce the same general types as discussed previously; no types are really distinctive to the subfamily level

(Brown, 1984; Watson et al., 1985; Ollendorf, 1987; Mulholland, 1989) Even though the Poaceae classification of Watson and Dalwitz (1992) could not be used as an evidence due to the multiplicity and redundancy of many grass phytolith types preventing the attribution of phytoliths to species or genus (Rovner, 1971; Brown, 1984; Mulholland, 1989), the abaxial leaf blade epidermis descriptions of the grass classification of Watson et al (Watson et al., 1985) and Watson and Dallwitz (1992) have been taken into account. All C₃-Arundinoideae grasses genus reported by Wooller et al. (2001) from our sampled sites, mainly produce the poly-lobate phytolith type except *Pentaschistis*, which mainly produces the dumbbell type.

Four characteristic phytolith types produced by non-Poaceae taxa are counted : the cone-shaped type (10) is produced by Cyperaceae (sedge) (Le Cohu, 1973; Ollendorf, 1987; Kondo et al., 1994; Wallis, 2003), the crenate spherical (11) phytolith type is produced by Palmae (Kondo et al., 1994; Runge, 1999; Runge & Fimbel, 1999; Vrydaghs & Doutrelepon, 2000), the rough spherical (12) phytolith type is produced in the wood of tropical trees and shrubs (ligneous dicotyledon) (Scurfield et al., 1974; Kondo et al., 1994), and the smooth spherical (13) type, which may have several origins according to Kondo et al. (1994). This type is produced in the epidermis of leaves and in parenchyma cells of dicotyledons twigs and wood. It has been recovered in small proportions from several tropical herbaceous monocots and in greater quantities from a small number of tropical arboreal dicotyledon leaves and seeds (Piperno, 1988). Recent investigation of tropical grasses shows that the smooth spherical type is also produced in significant amounts in grass roots (Alexandre et al., 2000).

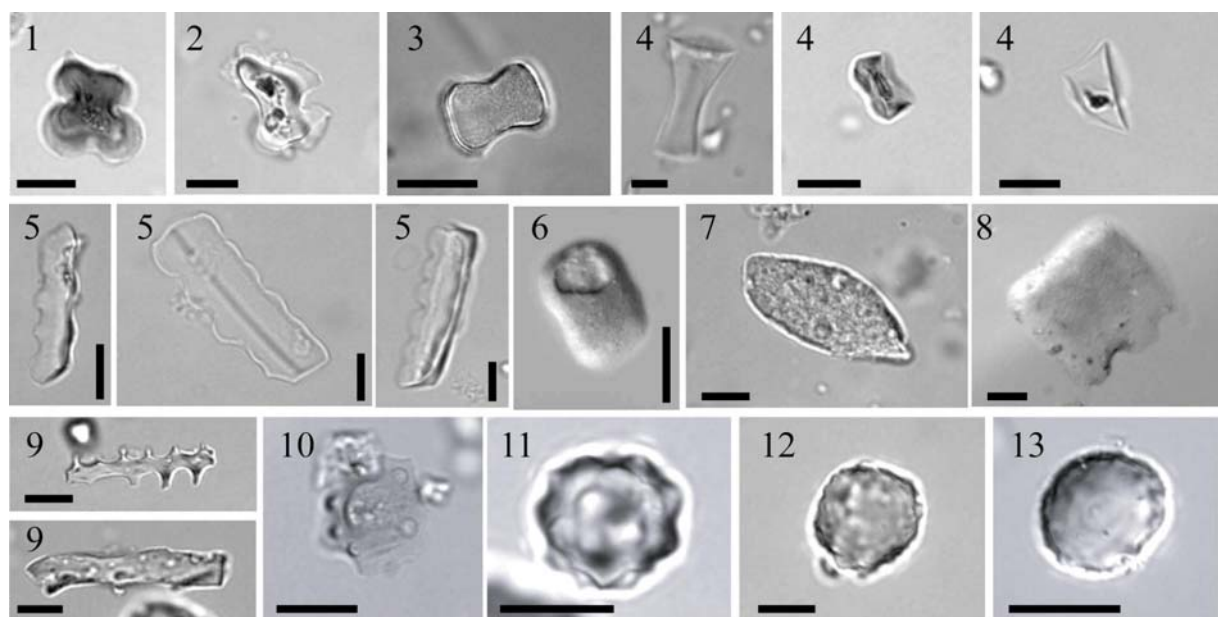


Figure III. 3. Microphotographs representatives of the 11 types of classified phytoliths counted in this study; Scale bar = 10 μm : (1) cross, (2) dumbbell, (3) saddle, (4) uni-lobate, (5) poly-lobate, (6) rectangle, (7) point-shaped, (8) fan-shaped, (9) elongate (smooth and sinuous elongate types are merged in this same group), (10) cone-shaped type, (11) crenate spherical, (12) rough spherical, (13) smooth spherical.

Phytolith indices

Phytolith data are discussed through the Ic index defined by Twiss (1987; 1992) to estimate the relative proportion of C₃ grasses (Pooideae) present in the American Great Plains as compared to the total C₃+C₄ grasses (see equation [1]).

$$Ic = \frac{\%Pooideae.phytoliths}{\%Pooideae + \%Panicoideae + \%Chloridoideae.phytoliths} \quad [1]$$

Ic is the ratio of Pooideae phytolith types (uni-lobate, poly-lobate and rectangle) versus the sum of Pooideae, Chloridoideae (saddle), and Panicoideae phytolith types (cross and dumbbell). High Ic values suggest an abundance of Pooideae, and hence an abundance of C₃ grasses. Counting error assigned to this index is $\pm 6\%$ (max s.d. on Pooideae phytolith types plus max s.d. on Panicoideae and Chloridoideae phytolith types). However, two cautions have to be made about this index : 1) C₃ Panicoideae grass species exist (21% of all Panicoideae) and may produce cross and dumbbell phytolith types, which can be confused with C₄ Panicoideae phytoliths. 2) As discussed before Arundinoideae and Bambusoideae grasses may produce all grass phytolith types, which can limit the Ic index as proxy of C₃ grasses abundance. These two points will be discussed later.

Two additional phytolith indices defined and calibrated in previous studies (Bremond et al., submitted-a; Bremond et al., submitted-b) are used for discussing the phytolith data :

1) The Iph index, which is the ratio of Chloridoideae type (saddle type) to the sum of Chloridoideae and Panicoideae types (saddle, cross and dumbbell types). This index was defined by Diester-Haass et al. (1973) and used for vegetation reconstructions from continental sediments, soil and buried soils from African and Brazilian sites (Alexandre et al., 1997; Barboni et al., 1999). High Iph values (>20-40%) record grasslands dominated by Chloridoideae, low Iph values (<20-40%) indicate associations in which Panicoideae dominated. It has also been calibrated as proxy of AET/PET (annual actual evapotranspiration over potential one) in West Africa by Bremond et al. (submitted-b). Iph values less than 20%

are observed in moist regions where AET/PET is higher than 0.30, whereas values of Iph higher than 20% are observed in drier zones (AET/PET < 0.30).

2) The D/P index is the ratio of the rough spherical phytolith, produced by tropical woody dicotyledon, versus the sum of Poaceae phytoliths (dumbbell, cross, saddle, point-shaped, and fan-shaped types). It was first used by Alexandre et al. (1997) and Barboni et al. (1999) in West and Central Africa in order to estimate the tree cover density. This index has been also calibrated in terms of LAI proxy in a forest-savanna transition in Cameroon (Bremond et al., submitted-a).

Common grass subfamilies distribution and botanical indices

Panicoideae grasses are adapted to warm and wet climate or high available soil moisture (Hartley, 1958; Teeri & Stowe, 1976; Tieszen et al., 1979; Cabido et al., 1997; Scott, 2002). Panicoideae grasses are mainly represented by C₄ grasses (79% of taxa according to Watson et al. (1985)). C₃ grasses of the Panicoideae subfamily, grow in more shaded and humid areas, such as under tropical forest canopy Tieszen et al.; (1979). Tieszen et al. (1979) reported less than 12% of C₃-Panicoideae species among total Panicoideae species on Mount Kenya. The Chloridoideae are exclusively all C₄ grasses (Livingstone & Clayton, 1980). They are adapted to warm and dry climate or dry soil conditions (Tieszen et al., 1979; Livingstone & Clayton, 1980). The Pooideae subfamily is exclusively composed of C₃ grasses (Watson et al., 1985) abundant in temperate and cold zones but also found in the inter-tropical zone at high elevations (Tieszen et al., 1979; Livingstone & Clayton, 1980; Tieszen et al., 1997; Scott, 2002; Winslow et al., 2003). The Arundinoideae subfamily is mainly made of C₃ grasses (92% of taxa according to Watson et al. (1985)) and Bambusoideae are all C₃ grasses. Cabido et al. (1997), surveying an altitudinal transect in Central Argentina, reported that Pooideae and Panicoideae grasses distributions are respectively negatively and positively correlated to the mean maximum temperature of the warmest month, decreasing with elevation; while the other grass subfamilies do not show such a relation.

In order to compare the Ic index with botanical data, the proportion of sub-family grasses, according to the mean altitudinal distribution of species, has been calculated for the Mont Kenya samples. Two botanical indices, coherent with the Ic index, are also calculated.

Percentage are calculated from the presence (1) absence (0) and presence but not in the quadrat (0.5) by summing these coefficients for each species from an altitude level.

The first botanical index, strictly comparable with I_c , is I_{b1} (equation [2]) :

$$I_{b1} = \frac{\%Pooideae}{\%Pooideae + \%Panicoideae + \%Chloridoideae} \quad [2]$$

As it has been noticed that Arundinoideae produced mainly poly-lobate phytolith types, a second index I_{b2} has been calculated (equation [3]) :

$$I_{b2} = \frac{\%Pooideae + \%Arundinoideae}{\%Pooideae + \%Arundinoideae + \%Panicoideae + \%Chloridoideae} \quad [3]$$

As botanical statements were not systematically done on Mount Rungwe and around Masoko Lake, botanical indices cannot be calculated for those sampled sites.

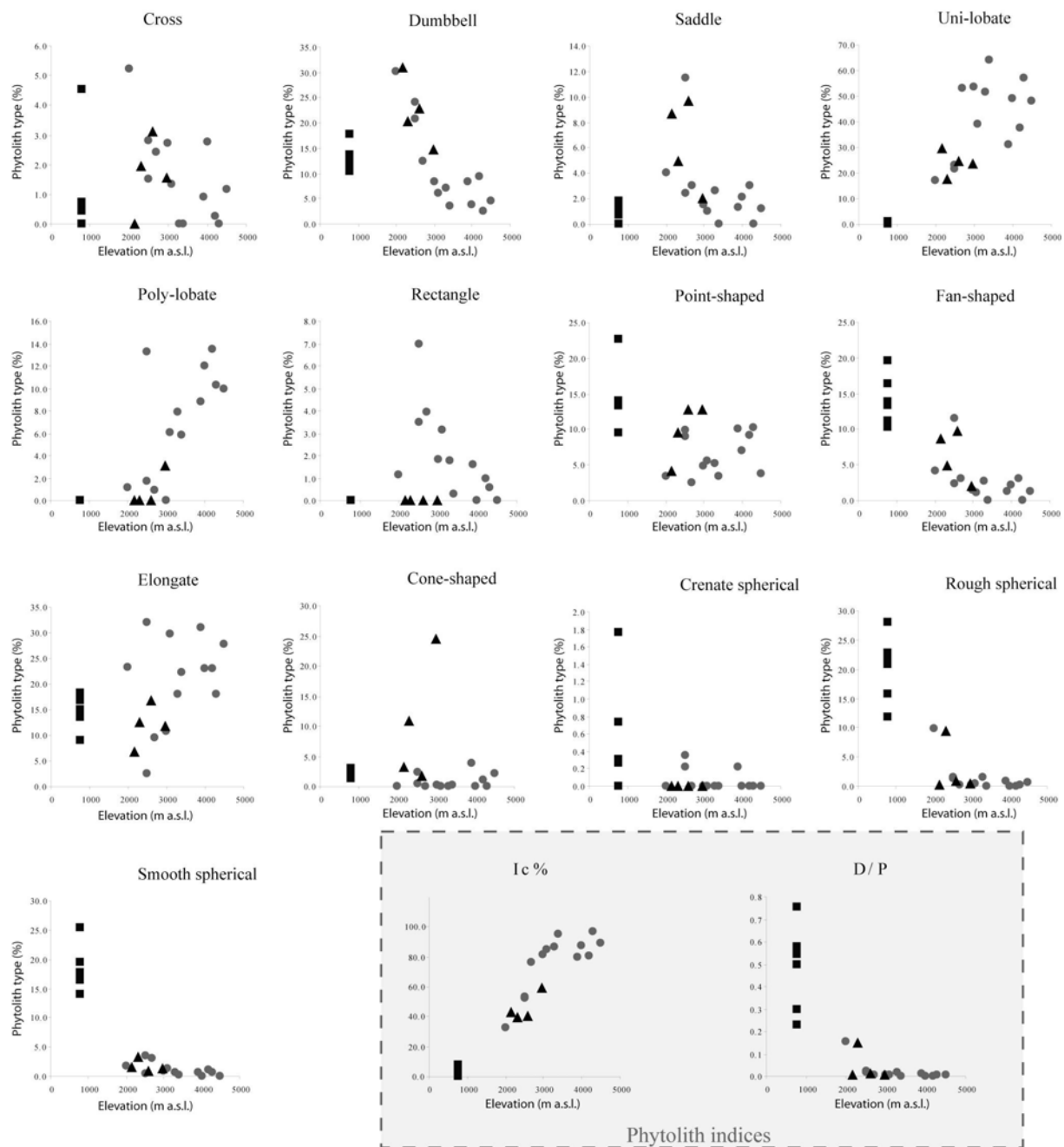


Figure III. 4. Abundances of the 13 phytolith types counted and phytolith indices Ic^* and D/P^{**} calculated within the 3 studied sites (Mont Kenya, Mount Rungwe, and Masoko Lake) in relation to the site elevation.

* Ic = Pooideae phytoliths (Poly-lobate, uni-lobate and rectangle type) / (Pooideae + Chloridoideae + Panicoideae phytoliths (saddle + cross + dumbbell types)).

** D/P = Ligneous dicotyledon phytoliths (rough spherical types) / Poaceae phytoliths (saddle, cross, dumbbell, point- and fan-shaped).

Results

Relation between phytolith assemblages, phytolith indices (D/P, Iph and Ic) and vegetation zones

Abundances of the 13 phytolith types and phytolith indices Ic and D/P within the 3 sites (Mont Kenya, Mount Rungwe, and Masoko Lake) in relation to the site elevation are presented on Fig. III. 4 (detailed counts are presented in appendix 1). Phytolith assemblages from Masoko samples are clearly differentiated from those collected above 1000 m in altitude, with high abundance of rough spherical, smooth spherical, dumbbell, point- and fan-shaped types, low Ic index (from 0 to 8.1%) and high D/P index (from 0.2 to 0.8), in agreement with the above miombo or tree and tall grass savanna, rich in ligneous dicotyledon, Panicoideae and Chloridoideae grasses. The montane forest (1950-2300 m a.s.l.) on Mont Rungwe and Mont Kenya, is clearly characterized by medium Ic (from 33 to 53%) and D/P (0.15 for LM 1-2 and RGW 23). The Bamboo zone (2670 ; 2920 m. a.s.l.), only sampled in Mount Kenya, is characterized by highest amount of "fan-shaped" type (9% and 15%). The highest grasslands (up to 3500 m a.s.l.) are characterized by the highest Ic index (80 to 96%) and D/P index equals to zero. The Iph index ranges from 0 to 11% around Masoko Lake, from 11 to 27% on Mont Rungwe and from 0 to 30% on Mont Kenya. It seems to increase with the occurrence of Arundinoideae grasses.

The *Hagenia-Hypericum*, Ericaceous, and Afro-alpine zones cannot be discriminated from phytolith assemblages and phytolith indices.

Relation between phytolith Ic index, botanical indices and elevation

From low to high altitudes, in the studied areas, Ic increases inversely to the Panicoideae grass dominance and directly with Pooideae grasses, as temperature decreases. Around Masoko Lake, where Pooideae grasses are absent, the mean Ic values is very low (3%). In Rungwe samples, the Ic index increases from 40 to 60% in relation with the raising of Pooideae grasses. Variations of phytolith and botanical indices with elevation, for Mont Kenya, are presented in figure III. 5a and 5b. Parallel trends are clearly displayed, although the botanical statements show that 100% of the grass cover is made of Pooideae and Arundinoideae at about 3300 m a.s.l. while the phytolith index Ic stay between 80 and 98% above this elevation.

The cross-over between Panicoideae and Pooideae/Arundinoideae dominance appears both from botanical and phytolith indices (Ib and Ic = 50%) at around 2300m a.s.l. This is the elevation where the C₄/C₃ grass cross-over is displayed by Tieszen et al. (1979) on a gradient

devoid of forest cover. In order to evaluate and to compare the dispersion of botanical and phytolith data set, indices have been reported using box plots (Fig. III. 5c). For the Montane forest zone (1900 to 2500m.a.s.l), mean Ic (46%) is slightly over Ib₂ (36%) and over Ib₁ (14%). For the Bamboo zone (2500 to 2925m.a.s.l), mean Ic (79%) is slightly under mean Ib₁ and Ib₂ (89%). There is no botanical data existing for the *Hagenia-Hypericum* zone (2925-3000m.a.s.l) where mean Ic is 86%. In the Ericaceous zone (3000-3530m.a.s.l), the mean Ic is slightly over Ib₁ (60%) and Ib₂ (63%) and from the Alpine zone (>3530m.a.s.l), mean Ic (88%) is under the 100% of Ib₁ and Ib₂. The Ic index seems to be more correlated with Ib₂, particularly for the Montane forest zone where Ib₁ and Ib₂ are singularly different, reflecting the general increase of both Pooideae and Arundinoideae grasses with elevation.

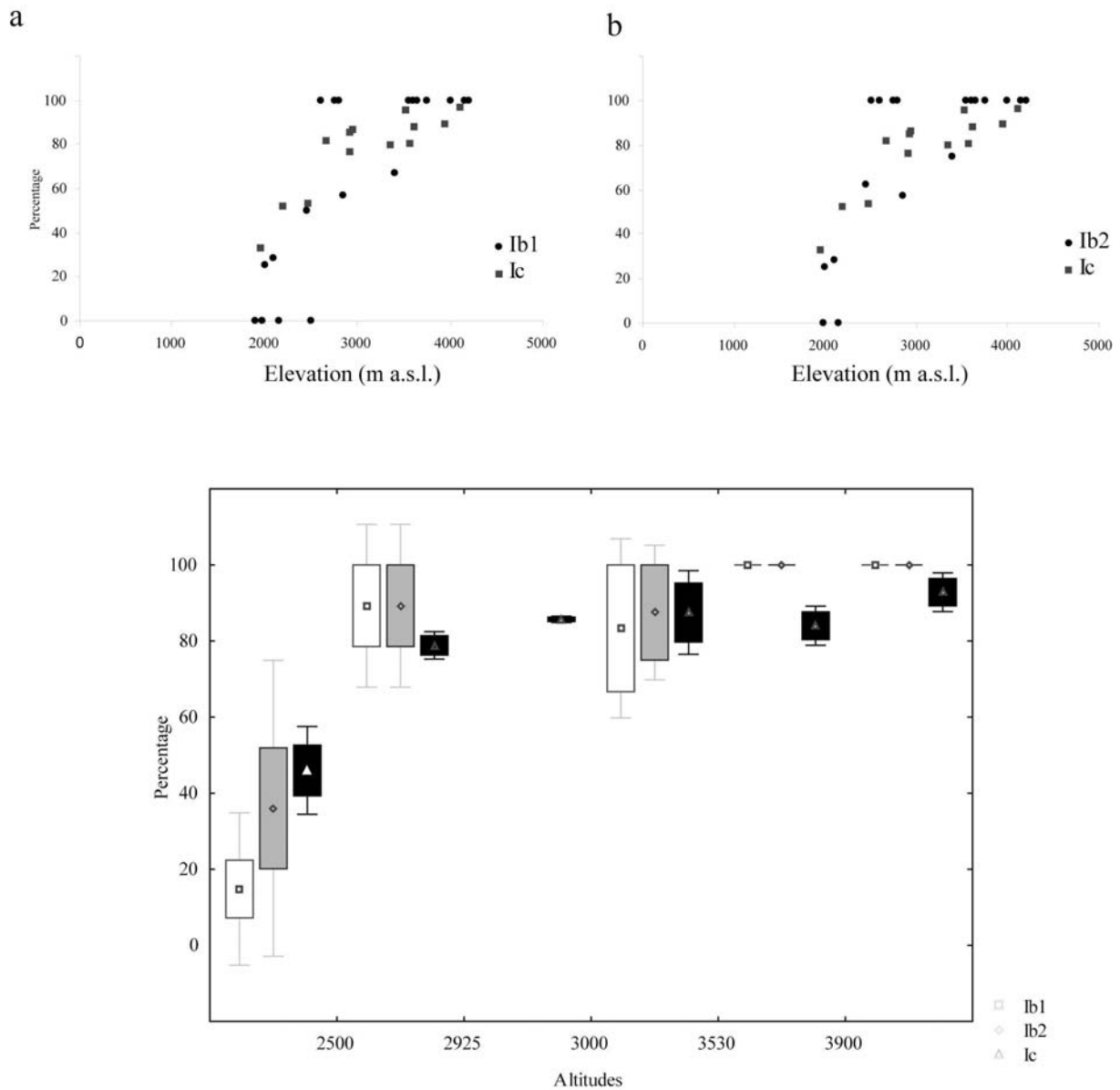


Figure III. 5. Variations of Ic* index and botanical indices (Ib₁** and Ib₂***) with elevation for Mont Kenya. (a-b) xy-plots (c) box-plots where the elevation range is distributed into classes related to the boundaries of the vegetation types (Wooller et al., 2000; Wooller and Agnew, 2002; Wooller et al., 2003). The standard error on the average is represented by the box height and the standard deviation by whiskers.

* Ic= Pooideae phytoliths (Poly-lobate, uni-lobate and rectangle type) / (Pooideae + Chloridoideae + Panicoideae phytoliths (saddle +cross + dumbbell types)).

$$** Ib_1 = \frac{\%Pooideae}{\%Pooideae + \%Panicoideae + \%Chloridoideae}$$

$$*** Ib_2 = \frac{\%Pooideae + \%Arundinoideae}{\%Pooideae + \%Arundinoideae + \%Panicoideae + \%Chloridoideae}$$

Discussion

Limitation of D/P for tracing the wooded vegetations on East-African mountains

The discrete zones of wooded vegetation distributed over the altitudinal gradient (McKone, 1995; Wooller et al., 2000) are not all clearly distinguished by modern phytolith assemblages. Except the "miombo" and montane forest zones, which settle below 2500m a.s.l., higher vegetation zones dominated by woody dicotyledons (such as *Hagenia*, *Hypericum* and *Erica arborea*) show a D/P index equals to zero. The D/P index was defined (Alexandre et al., 1997; Alexandre et al., 1999) and calibrated (Bremond et al., submitted-a) as a proxy of tree cover density for African inter-tropical vegetations adapted to tropical low elevation conditions. The rough spherical phytolith was also used as indicator of ligneous dicotyledons in tropical low elevation areas. While phytolith studies conducted on non-tropical ligneous vegetations (temperate and Mediterranean) evidenced that the rough spherical phytolith type is not systematically produced by non-tropical trees (Stromberg, 2002; Delhon et al., 2003; Bremond et al., submitted-c). Similarly, ligneous dicotyledon (trees and shrubs) such as *Macaranga*, *Cassipourea*, *Tabernaemontana*, *Canthium* and *Vitex*, which dominate the canopy in Mount Kenya, at high elevation in the montane forest, may not produce the rough spherical phytolith type used for calculation of the D/P index. This result specifies the geographical application domain of the D/P phytolith index. Physiological mechanisms, and environmental constraints controlling the production of the rough spherical phytolith remain unknown.

Limitation of Iph for tracing C₄-tall and C₄-short grass dominance on East-African mountains

The whole set of samples presents an Iph index ranging from 0 to 27% although Chloridoideae grasses are nearly absent from the above grass covers. Indeed, except for one quadrat at 3000 m a.s.l. on Mount Kenya, where a Chloridoideae grass species (*Eleusine jaegeri*) has been observed (Wooller et al., 2001), this subfamily is not present.

Therefore, the saddle phytolith type is produced in small amount by other grass subfamilies than the Chloridoideae, here the Arundinoideae and Pooideae subfamilies, as already observed in previous studies (Watson et al., 1985; Mulholland, 1989; Watson & Dallwitz, 1992; Kondo et al., 1994). Consequently, the Iph index must be used carefully when Pooideae/Arundinoideae grasses may be present in the source vegetation. In such a case, the Iph index is not a tracer of C₄-tall and C₄-short grasses or a proxy of AET/PET as it is in areas poorer in Arundinoideae grasses (Alexandre et al., 1997; Barboni et al., 1999; Bremond et al., submitted-b).

Reliability of Ic for tracing Panicoideae, Pooideae and Arundinoideae grass dominance on East-African mountains

We have not calculated any quantitative correlation coefficient between *Ic* and botanical indices of grass species for Mont Kenya samples because the presence/absence score is not representative of species biomass as demonstrated by Young and Young (1983), while phytolith abundances and thus, phytolith productions, are related to the biomass of grass subfamilies (Johnston et al., 1967; Mulholland, 1989). However, general trends clearly show that *Ic* steadily increases with botanical indices and especially with *Ib*₂ on Mont Kenya (fig. III. 5c), and with elevation on Mont Rungwe and Mont Kenya (fig. III. 4). This results evidences that the phytolith index *Ic* is a reliable tracer of *Ib*₂ (% of Pooideae + Arundinoideae species / % of Pooideae + Arundinoideae + Panicoideae + Chloridoideae species), with values close to zero when Pooideae and Arundinoideae grasses are absent, such as in tropical low elevation areas (e.g. around Masoko Lake), a value close to 50% when Panicoideae and Pooideae/Chloridoideae are equally represented, and values up to 80-100% when the grass cover is only made of Pooideae and Arundinoideae grasses such as in tropical high elevation areas (this study) but also in temperate, Mediterranean and cold bioclimatic zones (Fredlund & Tieszen, 1994; Kondo et al., 1994; Prebble et al., 2002; Bremond et al., submitted-c).

Ic never reaches 100% when the grass cover is made of 100% of Panicoideae and Chloridoideae grasses (fig. III. 5) because Arundinoideae grasses produce in high amount the Pooideae phytolith types, in addition to small amount of Panicoideae and Chloridoideae types (Brown, 1984; Watson et al., 1985; Ollendorf, 1987; Mulholland, 1989). Such a multiple phytolith production is also called multiplicity by Fredlund and Tieszen (Fredlund & Tieszen, 1994; Fredlund & Tieszen, 1997b).

The *Ic* index was first proposed by Twiss (1992) as a “Climatic Index” predicting the C₃ and C₄ grass composition of the American Great Plains, based on the evidence that all Pooideae are C₃ grasses, all Chloridoideae are C₄ and 79% of Panicoideae are C₄ grasses (Watson et al., 1985). Contrary to previous surveys of grasses distribution on Mount Kenya, which have focused on grasslands of the northern flank (Tieszen et al., 1979; Young & Young, 1983), the survey of Wooller et al. (2001) passed through the montane forest covering most of the slopes of Mount Kenya. This survey did not find any crossover between the abundance of C₄ and C₃ grasses as evidenced by Tieszen et al. (1979) and Young and Young (1983). Our study, based on the Wooller (1999) samples, shows that a crossover between Panicoideae and

Pooideae/Arundinoideae grasses occurs at the same elevation, around 2300m a.s.l. because the zone close the tree line, where C₄-Panicoideae have been noticed, have not been sampled. The botanical crossover is well mirrored by the phytolith Ic index. However, the Panicoideae grasses show a C₃ photosynthetic pathway adapted to the montane forest conditions. A lack of microclimatic data does not permit to further discuss the different settlements of C₃- and C₄-Panicoideae grasses on Mont Kenya.

Finally, Ic is a good indicator of the relative distribution of the Panicoideae (may be C₄ or C₃ grasses) and Pooideae (C₃ grasses) + Arundinoideae (C₃ grasses) following a clear trend with elevation on East-African mountains. Although this phytolith index is often discussed as a tracer of C₃ and C₄ grasses distribution, because Panicoideae grasses are mostly C₄ grasses, such a conclusion should be drawn with caution.

Conclusion

Firstly, because at high elevation, in the montane forest, the rough spherical phytolith type is absent from the assemblages, this study permit to specify the geographical application domain of the D/P phytolith index as proxy of tree cover density.

Secondly, we show that Iph can be non-null when Pooideae/Arundinoideae grasses are present in the source vegetation even if non Chloridoideae occur. In such a case, the Iph index is not a tracer of C₄-tall and C₄-short grasses or a proxy of AET/PET as it is in areas poorer in Arundinoideae grasses.

Thirdly, this study highlights two important remarks: 1) if the survey of C₃ and C₄ graminoids of Mount Kenya published by Wooller et al. (2001) is not an exception from the general accepted altitudinal distribution of C₃ and C₄-grasses (Livingstone & Clayton, 1980), the presence of C₄-grasses at high altitude has important implications for reconstruction of past vegetation. 2) the present results show that Ic index is a good proxy of Pooideae and Arundinoideae proportions among Panicoideae. If it is assumed that 80% of Panicoideae are C₄ plants, this index has a great potentiality to trace C₃/C₄ grasses variation. Moreover, C₃-Panicoideae being constrained to tropical forest understoreys (Tieszen et al., 1979; Rundel, 1980; Schwartz, 1991; Wooller et al., 2001), a better trace of the forest could provide a good tool to differentiate the C₃ signal from Panicoideae.

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CHAPITRE IV. RELATION ENTRE ASSEMBLAGES PHYTOLITHIQUES ET DENSITE DU COUVERT ARBORE EN DICOTYLEDONES LIGNEUSES.

IV. 1. Calibration de l'indice phytolithique D/P avec le LAI (Leaf Area Index) en domaine intertropical.

Résumé étendu de l'article : A phytolith index as a proxy of tree cover density in tropical areas : calibration with Leaf Area Index along a forest-savanna transect in south-eastern Cameroon.

En zones inter-tropicales plusieurs études ont montré que les dicotylédones ligneuses, soit l'essentiel des arbres et des arbustes, produisent un type caractéristique de phytolithes : le "sphérique rugueux" (Scurfield et al., 1974; Welle, 1976; Kondo et al., 1994; Runge, 1999). Alexandre et al. (1997) ont proposé un indice phytolithique, nommé D/P, qui est le rapport de ce type de phytolithe sur des types caractéristiques produits par les Poaceae. Ceci dans l'idée de donner une indication sur la densité du couvert arboré en dicotylédones ligneuses. Cet indice a été par la suite plusieurs fois utilisé (Barboni et al., 1999; Stromberg, 2002; Delhon et al., 2003) mais sans que l'on sache réellement bien l'interpréter. Cet article propose une calibration de l'indice D/P avec des mesures précises de la densité du couvert arboré données par le LAI (Leaf Area Index). Pour cela, des échantillons modernes ont été collectés le long d'un transect de 750 m, à travers une transition forêt-savane où ont également été effectuées des mesures de LAI (Cournac et al., 2002).

Le choix de calibrer l'indice D/P avec le LAI réside dans le fait que le LAI est un indice reconnu comme étant un paramètre clé du fonctionnement des peuplements forestiers (Bréda et al., 2002). Il est ainsi une variable de sortie de très nombreux modèles de végétation (e.g. Woodward et al., 1995; Smith et al., 2001; Sitch et al., 2003). Cette calibration entre le D/P et le LAI permettra par la suite d'intégrer cet indice phytolithique aux modèles qui utilisent des marqueurs pour reconstruire les végétations passées (e.g. Prentice et al., 1996; Jolly et al., 1998; Marchant et al., 2001).

Matériel et Méthode

Le site de Kandara est situé au Sud-Est du Cameroun à 640m d'altitude (Figure IV.1a). La végétation appartient à la région phytogéographique Guinéo-Congolaise selon Letouzey (1968) et White (1983). C'est une mosaïque de forêts semi-décidues et de savanes à graminées

hautes (Figure IV.1b). Le transect traverse 5 types de végétations (Youta Happi, 1998; Achoundong et al., 2000) le long duquel 26 échantillons de sol prélevés sous la litière ont été collectés en 1997 par A. Vincens et al. (2000). Chaque échantillon correspond à 20-30 prélèvements (1 cm^3) au sein de parcelles contiguës d'une surface de $10 \times 30 \text{ m}^2$ le long du transect m (exceptées deux parcelles d'une surface de 10×10 et $15 \times 10 \text{ m}^2$).

L'extraction (Kelly, 1990), la classification (Twiss et al., 1969; Mulholland, 1989; Twiss, 1992; Fredlund & Tieszen, 1994; Kondo et al., 1994; Alexandre et al., 1999; Barboni et al., 1999) et le comptage des phytolithes ont permis d'identifier 11 types (Figure IV.2) et d'estimer une erreur de comptage de l'ordre $\pm 3\%$ (de l'écart type).

L'indice D/P représente la proportion de phytolithes caractéristiques des éléments ligneux (sphérique rugueux), relativement à la somme de phytolithes de graminées (sauf le type "allongé"). L'erreur attribuée à cet indice est estimée à $\pm 6\%$.

Les mesures de LAI ont été faites à 2 m du sol tout les 10 m (Cournac et al., 2002). Deux séries ont été effectuées, elles ont été moyennées entre elles et estimées, par moyenne mobile, pour chaque parcelle échantillonnée (Figure IV.3a).

Enfin, les assemblages phytolithiques sont confrontés aux spectres polliniques (pourcentage des pollen d'arbres (AP)) des même échantillons (Vincens et al., 2000), (Figure IV.3b).

Résultats

Les assemblages phytolithiques permettent de différencier 5 zones de végétation (Figure IV.4) à l'aide essentiellement de la proportion du type "haltère" et de la valeur de l'indice D/P : 1) la savane à graminées hautes ; (2) la zone de transition entre la savane et la forêt ; (3) la forêt jeune à *Albizia* ; (4) la forêt mature à *Rinorea* et (5) la zone marécageuse à *Raphia* (Palmier).

L'indice D/P confronté aux mesures de LAI (Figure IV.3a) montre que les valeurs les plus faibles sont enregistrées, pour les deux, en zone de savane et les plus fortes sous forêt, avec des valeurs intermédiaires à la lisière de la forêt. Plus en détails on remarque que dans la zone de savane le LAI n'augmente que pour 3 parcelles sous un bosquet d'*Albizia* alors que l'indice D/P reste élevé sur 6 parcelles. De plus, le D/P n'enregistre aucune variation sur les parcelles 13 et 14 qui ont récemment subi une coupe alors que le LAI marque une forte diminution. D'autre part, le D/P est plus élevé dans la forêt mature à *Rinorea* que dans la forêt à *Albizia* alors que le LAI n'enregistre pas de différence notable entre ces deux forêts. De ce fait, la relation entre le LAI et le D/P apparaît clairement non-linéaire (Figure IV.5). Trois fonctions sont proposées pour estimer la meilleure relation entre le LAI et le D/P. La première fonction (c1) reflète au mieux la distribution des points. La deuxième fonction (c2) est contrainte de

passer par l'origine pour ne pas être influencée par les échantillons de savane qui présentent un LAI nul mais un D/P non nul en raison de la faible distance entre les parcelles et du fait que le LAI ne prend pas en compte les arbustes en dessous de 2m. La première fonction a nécessairement un meilleur r^2 mais sous-estime le LAI pour les faibles valeurs de D/P. Ces deux premières fonctions ont une asymptote à 3.5 alors que le LAI peut atteindre 7 en forêt tropicale dense (Bréda et al., 2002). La troisième fonction (c3) y remédie, avec pour conséquence un r^2 plus faible que pour les autres fonctions (Figure IV.5).

Discussion et conclusions

La confrontation des mesures de LAI avec les assemblages phytolithiques et les spectres polliniques a montré que chacun d'eux n'enregistre pas la végétation à la même échelle spatiale. Le LAI mesure les variations du couvert arboré de façon ponctuelle tandis que les phytolithes semblent être plus représentatifs du couvert arboré moyen. On suppose que la non-similarité des enregistrements dans la savane est essentiellement due à des jeunes repousses d'*Albizia* qui ne sont pas mesurées par le LAI mais qui par contre produisent des quantités importantes de phytolithes. Ce phénomène serait amplifié par l'accumulation de phytolithes après le passage du feu qui brûle chaque année tous les jeunes plants d'*Albizia*. Contrairement aux phytolithes, le pourcentage de pollen d'arbres reste aussi bien faible dans la savane que sous le bouquet d'*Albizia*. Le fait que les jeunes pousses d'*Albizia* n'aient pas le temps de produire de pollens avant de brûler explique certainement pourquoi on n'en retrouve pas dans les spectres de savane. Leur mode de dissémination entomophile explique par ailleurs le fait qu'on ne perçoive pas le bosquet dans les données polliniques.

Cette étude a aussi montré que les assemblages phytolithiques et polliniques n'enregistrent pas la végétation avec la même échelle de temps que le LAI. En effet, les assemblages représentent une végétation moyenne sur plusieurs années alors que le LAI donne une image instantanée de la végétation. Cette distorsion entraîne nécessairement une imprécision dans la calibration des relations entre ce qui est appelé "échantillons modernes" et des mesures réellement instantanées. Une équation prédictive du LAI d'après l'indice D/P a pu cependant être établie. La troisième fonction, malgré le fait qu'elle ait le plus faible r^2 , a été privilégiée parce qu'elle permet de s'affranchir des distorsions qui viennent d'être d'exposées.

Plusieurs précautions sont à prendre pour appliquer cette relation : (1) du fait que le D/P ne prenne pas en compte la production de phytolithes par les palmiers, le LAI peut être sous-estimé lorsqu'ils sont présents en grande quantité dans les assemblages ; (2) la proportion des cellules bulliformes silicifiées étant liée au stress hydrique subi par la plante, on peut observer

que leur quantité peut augmenter de façon non proportionnelle avec les autres phytolithes produits par les graminées, ce qui peut induire une sous-estimation du LAI ; (3) la relation qui a été établie entre phytolithes de dicotylédones ligneuses et phytolithes de Poaceae doit être vérifiée et calibrée pour les zones inter-tropicales qui présentent un couvert herbacé à cycle photosynthétique en C_3 , du fait de la différence de productivité en phytolithes entre les graminées C_4 et C_3 .

IV. 2. Perspectives d'application à des échantillons fossiles

La relation établie sera appliquée aux assemblages de la carotte lacustre de Masoko (voir III. 2.) et confrontée aux assemblages polliniques, qui reflètent eux aussi le couvert arboré. Les valeurs estimées de LAI seront alors confrontées à celles simulées par le modèle de végétation LPJ-GUESS, en collaboration avec C. Hély.

Ces résultats seront aussi utilisés pour interpréter 30 assemblages phytolithiques fossiles collectés dans des niveaux sédimentologiques du Middle Awash (Ethiopie) où ont été retrouvés les ossements d'Aramis ("Sagantole Formation", - 4.39 ± 0.03 Ma). L'étude, en cours, se fait en collaboration avec D. Barboni et R. Bonnefille.

IV. 3. A phytolith index as a proxy of tree cover density in tropical areas : calibration with Leaf Area Index along a forest-savanna transect in southeastern Cameroon.

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Abstract

The aim of the study is to calibrate the phytolith index of tree cover density, D/P (the ratio of ligneous dicotyledons phytoliths (D) over Poaceae phytoliths (P)) with Leaf Area Index (LAI) measurements. Modern soil samples from southeastern Cameroon, collected along a continuous forest-savanna transect have been analyzed for phytoliths. Phytolith assemblages and D/P index, clearly record the physiognomy of the forest and the savanna communities and of the transition between the two. A highly significant relationship was obtained between D/P and LAI. The relationship between phytolith data and the vegetation transect is also discussed and compared with existing palynological results obtained along the same transect.

Keywords: phytoliths, LAI, pollen, tropical forest-savanna transition, calibration, Cameroon.

Introduction

Past fluctuations of tropical forest-savanna boundaries are linked to climatic changes (e.g. Servant et al., 1993; Zogning et al., 1997; Maley & Brenac, 1998; Vincens et al., 1998; Vincens et al., 1999), natural or anthropic fires (e.g. King et al., 1997; Salgado-Labouriau, 1997; Cochrane et al., 1999; Lykke, 2000) and recent human deforestation (Achard et al., 2002). Records of these fluctuations are fundamental to discriminate between natural and human constraints on vegetation changes and to further understand the impact of vegetation changes on the global carbon cycle (Schimel et al., 2001; Schimel & Baker, 2002) and vice versa (Harrison & Prentice, 2003; Nemani et al., 2003).

Pollen and $\delta^{13}\text{C}$ measurements from peat, sediments and soil organic matter are commonly used as tracers of forest-savanna boundaries changes (e.g. Schwartz et al., 1986; Guillet et al., 1988; Aucour et al., 1994; Olago et al., 1999; Dupont et al., 2000; Schwartz et al., 2000; de Freitas et al., 2001; Behling, 2002; Lamb et al., 2003; Wille et al., 2003). However, pollen-based reconstructions may be limited by the destruction of pollen in oxidizing deposits and by variation in pollen production and dispersal among plant species (Jolly et al., 1996; Vincens et al., 1997; Vincens et al., 2000). ^{13}C values of total organic matter record variation of C_3 versus C_4 plants. As C_3 plants include numerous taxa other than ligneous dicotyledons, $\delta^{13}\text{C}$ values of total organic matter do not exactly represent the tree cover density (Alexandre et al., 1999; Schwartz et al., 2000).

Phytoliths originating from wood of tropical ligneous dicotyledons can be clearly differentiated from phytoliths originating from Poaceae. Consequently, phytolith assemblages from tropical forests are easily distinguished from those produced by savannas (Alexandre et al., 1997; Barboni et al., 1999; Runge, 1999; Runge & Fimbel, 1999). Phytolith assemblages are well preserved in modern soils (e.g. Piperno & Becker, 1996; Alexandre et al., 1999; Kerns, 2001; Kerns et al., 2001; Prebble et al., 2002; Bremond et al., submitted-b; Bremond et al., submitted-c), fossil humic horizons (e.g. Fredlund & Tieszen, 1997b; Delhon et al., 2003), loess (e.g. Fredlund & Tieszen, 1994; Piperno & Becker, 1996; Carter, 2000) and sediments (e.g. Alexandre et al., 1997; Fredlund & Tieszen, 1997b; Barboni et al., 1999; Baker et al., 2000; Carter & Lian, 2000; Wallis, 2001; Carter, 2002; Prebble & Shulmeister, 2002). The phytolith index D/P (phytoliths characteristic of tropical ligneous dicotyledons versus sum of phytoliths characteristic of Poaceae), was proposed by Alexandre et al. (1997) as a proxy of tree cover density, and has been calculated by several authors for tropical and non-tropical phytolith assemblages. These studies confirmed the reliability of the D/P index for tracing the tree cover density in the inter-tropical zone. However, the comparison has only been made

between modern phytolith assemblages and qualitative description of the vegetation physiognomy (Alexandre et al., 1997; 1999; Barboni et al., 1999). The D/P index has never been confronted with quantitative vegetation data. In non-tropical zones, some ligneous dicotyledons produce a very low amount of distinctive phytoliths, which limits the use of D/P to restricted areas (Stromberg, 2002; Delhon et al., 2003; Bremond et al.).

The aim of this study is to calibrate the relationship between the D/P index calculated from modern phytolith assemblages and the Leaf Area Index (LAI) measured along a 750m forest-savanna transect in a tropical area, the Kandara region, Cameroon (Cournac et al., 2002). Phytolith data are also compared with pollen spectra taken from the same samples (Vincens et al., 2000).

The Leaf Area Index (LAI) is the cumulative leaf area above ground per unit of soil surface expressed in square meter of leaves per square meter of ground. LAI is an important property of plant communities because it is strongly correlated to the photosynthetic and water exchange characteristics of the canopy. As a result, LAI is an output of numerous vegetation models (Woodward et al., 1995; Smith et al., 2001; Sitch et al., 2003).

Such a calibration between D/P and LAI is the key stone for a later use of the D/P index in models using proxy to reconstruct vegetation (e. g. Prentice et al., 1996; Jolly et al., 1998; Marchant et al., 2001).

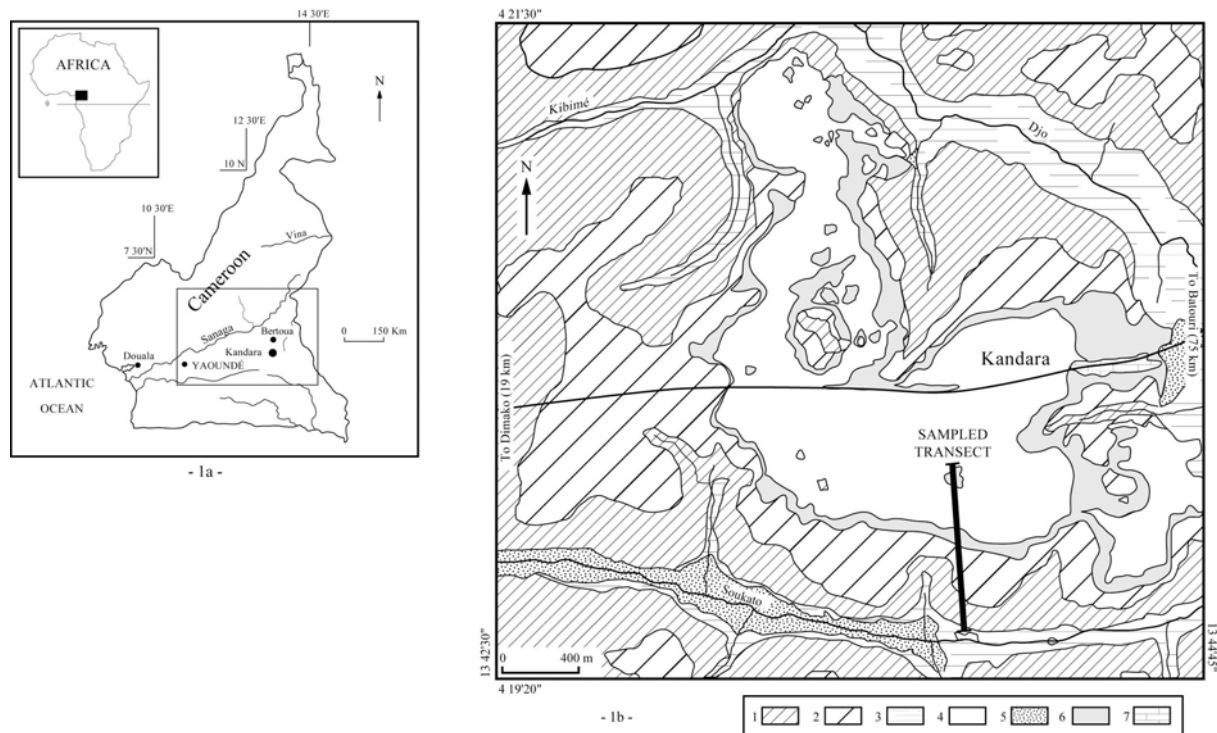
Environmental setting

Figure IV. 1. (a) Location map of the Kandara site in south-eastern Cameroon, (b) location of the studied transect in the Kandara area and main vegetational communities [1: *Rinorea* forest; 2: *Albizia* forest; 3: *Raphia* swamp; 4: shrub and tall grass savanna; 5: herbaceous swamp; 6: recent transgressive forest (1951–1993); 7: village]; from Youta Happi (1998).

The Kandara site is located in the southeastern part of Cameroon ($4^{\circ}20'N$, $13^{\circ}43'E$), at 640 m above sea level (Fig. IV. 1a). Soils are ferralsols on the interfluves, and gelysols in the valley (Beyala et al., 2000). The wet tropical climate is characterized by a mean annual rainfall of about 1600 mm, a dry season (precipitation less than 50mm/month) from December to January, and a mean annual temperature of $23.8^{\circ}C$ (Bertoua, meteorological station).

The area, covered by a mosaic of semi deciduous forests and savannas, belongs to the Guineo-Congolian phytogeographical region (Letouzey, 1968; White, 1983). The site is characterized by a shrub and tall grass savanna enclosed by a semi-deciduous forest (Fig. IV. 1b). The 750m sampled transect crosses five vegetation communities which are, from the north to the south: (1) a shrub and tall grass savanna dominated by *Imperata cylindrica* and *Pennisetum purpureum* (Panicoideae sub-family) with young *Albizia* and some *Albizia* cluster; (2) a savanna-forest transition divided in two parts: a *Pteridium* (monocot) ecotone; (2a) and a *Margaritaria* (ligneous dicotyledon) ecotone with undetermined Poaceae species (2b); (3) a

young *Albizia* forest with a grass cover dominated by *Leptaspis* sp., (4) a mature *Rinorea* forest with a grass cover still dominated by *Leptaspis* sp.; and (5) swampy formations dominated by the palm *Raphia mombutorum*, with an herbaceous cover made of Cyperaceae and undetermined Poaceae species (Youta Happi, 1998; Achoundong et al., 2000; Beyala et al., 2000).

Youta Happi (1998) and Achoundong et al. (2000) have demonstrated through botanical studies and aerial photographs that the forest has been recently spreading into the savanna.

Material and methods

Samples

Modern samples were collected in 1997 by Vincens (2000) for pollen analysis. The samples were collected from south to north, on 26 contiguous plots located along a 750 m transect. Each plot measured $30 \times 10 \text{ m}^2$, except samples 2 ($10 \times 10 \text{ m}^2$ at the *Raphia* swamp-mature forest boundary) and 18 ($15 \times 10 \text{ m}^2$ at the young forest-savanna boundary). Each sample consists on 20-30 sub-samples (1 cm^3) of soil or litter collected randomly within each plot and then mixed together. The understory vegetation of Plots 10, 13-14 and 16 located in the young *Albizia* forest were cleared 1 or 2 years before sampling (Vincens, personal com.). An *Albizia* cluster occurs in plots 23 to 25, located in the shrub and tall grass savanna.

Phytolith extraction, classification and counting

Phytoliths were extracted from 20g of dry soil, slightly crushed and sieved at 2mm, after 1) grinding; 2) dissolution of carbonates using HCl (3 %); 3) removal of iron oxides using sodium citrate ($\text{C}_6\text{H}_5\text{Na}_3\text{O}_7$) and dithionite ($\text{Na}_2\text{O}_4\text{S}_2$, H_2O_2); 4) organic matter oxidation using H_2O_2 (30 %) and heated at 90°C until reaction subsides; 5) sieving at $60 \mu\text{m}$; 6) clays removal; and 7) densimetric separation of phytoliths in a Zn Br_2 heavy liquid ($d=2.3$) (Kelly, 1990).

The recovered fraction, including opal phytoliths and a few diatoms was mounted on microscope slides in glycerin for 3D observation and in Canada Balsam for counting at 600X magnification. More than 300 phytoliths with taxonomic significance and diameter greater than $5 \mu\text{m}$ (minimum size for determination) were counted. Phytolith assemblages were calculated as a percentage of the sum of classified phytoliths. Repeat counts have been made of several slides and gave a counting error of 3% (s.d.). Phytoliths were classified according to the classification of Twiss et al. (1969) and Twiss (1992), improved and completed by

phytolith shape descriptions of Mulholland (1989) Fredlund and Tieszen (1994), Kondo et al. (1994), Alexandre et al. (1997), Barboni et al. (1999) and (Runge, 1999).

The different phytolith types identified and counted are illustrated in figure IV. 2. Counting silicified short cells from grass epidermis allowed 3 among 5 grass subfamilies to be distinguished. The cross (1) and dumbbell (2) phytolith types occur predominantly in the Panicoideae grass subfamily (Twiss et al., 1969; Mulholland, 1989; Fredlund & Tieszen, 1994; Kondo et al., 1994) and mainly represent C₄ grasses adapted to warm and wet climate or high available soil moisture (Teeri & Stowe, 1976; Tieszen et al., 1979; Cabido et al., 1997; Scott, 2002). Some C₃ grasses of the Panicoideae subfamily also grow in shaded areas, under tropical forest canopy (Schwartz, 1991 and Schwartz, unpublished). The saddle (3) type is produced in high proportion by the Chloridoideae grass subfamily (Twiss et al., 1969; Mulholland, 1989; Fredlund & Tieszen, 1994; Kondo et al., 1994), representative of C₄ grasses adapted to warm and dry climate or dry soil conditions (Tieszen et al., 1979; Livingstone & Clayton, 1980). The uni-lobate (4) phytolith type, also named rondel by Mulholland (1989), as well as the poly-lobate (5) type are mainly produced by the Pooideae subfamily (Twiss et al., 1969) which is comprised of C₃ grasses abundant in temperate and cold zones but also found in the inter-tropical zone at high elevations (Tieszen et al., 1979; Livingstone & Clayton, 1980; Tieszen et al., 1997; Scott, 2002; Winslow et al., 2003). The point-shaped (6) type originates from micro-hair or prickles of all grass epidermis (Palmer et al., 1985; Kaplan et al., 1992). The fan-shaped (7) type (Twiss et al., 1969; Kondo et al., 1994) are produced inside the bulliform-cells of all grass epidermis. The elongate (8) type (smooth and sinuous elongate types are merged in the same group) are phytoliths from long-cells of all grass epidermis. Three characteristic phytolith types produced by non-Poaceae taxa were counted as well: the crenate spherical (9) phytolith type produced by Palmae (Kondo et al., 1994; Runge, 1999; Runge & Fimbel, 1999; Vrydaghs & Doutrelepon, 2000), the rough spherical (10) type produced in the wood of tropical trees and shrubs (lignous dicotyledon) (Scurfield et al., 1974; Kondo et al., 1994), and the smooth spherical (11) type, which may have several origins according to Kondo et al. (1994). This type is produced in the epidermis of leaves and in parenchyma cells of dicotyledons twigs and wood. It has been found in small proportions in several tropical herbaceous monocots and in greater quantities from a small number of tropical arboreal dicotyledon leaves and seeds (Piperno, 1988). Recent investigation of tropical grasses show that the smooth spherical type is also produced in significant amounts in grass roots (Alexandre et al., 2000). Amorphous silica particles without specific form have not been counted.

The D/P index discussed in this study is the ratio of dicotyledon phytolith type (rough spherical) over the sum of Poaceae phytolith types (dumbbell, cross, saddle, uni-lobate, poly-lobate, fan-shaped and point-shaped). Elongate types were not included in the sum of Poaceae types because they are usually multiply broken and may be confused with weathered diatoms or sponge spicules. This index has a 6% error (s.d. on rough spherical type plus s.d. on Poaceae phytolith types).

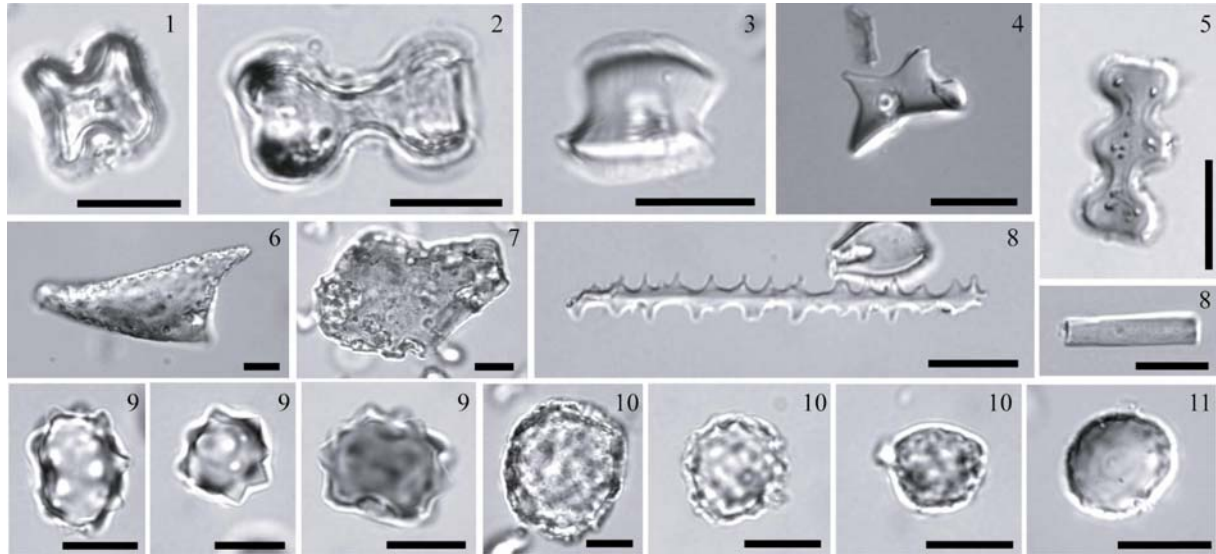


Figure IV. 2. Microphotographs representatives of the 11 types of classified phytoliths counted in this study; Scale bar = 10 μm : (1) Cross, (2) Dumbbell, (3) Saddle, (4) Uni-lobate, (5) Poly-lobate (6) Point-shaped, (7), Fan-shaped (8) Elongate types (smooth and sinuous elongate types are merged in the same group), (9) Crenate spherical, (10) Rough spherical, (11) Smooth spherical.

LAI data

We have used values of LAI measured along the studied transect by Cournac et al. (2002). These authors performed LAI measurements at 2m above ground every 15 m, using a photo-resistor with fish-eyes optics. The measurement error related to the type of captor is ± 0.3 . These LAI measurements do not take into account the density of shrub and grass covers, unlike LAI estimates from satellite data. Two series of LAI measured on different days and by two operators are presented by Cournac et al. (2002), and are very close. In order to obtain LAI values, we averaged the two series together, then took an average value of the three measurements found in each plot (figure IV. 3a). The LAI is lower than 1.20 in the tall-grass savanna (null in the plots 20 and 21 (*Pteridium* ecotone) and medium (1.20) under the *Albizia* cluster). It increases in the *Margaritaria* ecotone then stays relatively constant in the young

Albizia and mature *Rinorea* forests (2.68 to 3.81). No clear distinction can be made between these two types of forest. At 370 m (corresponding to plots 13 and 14), the drop in LAI value is due to the recent clearing of the plot. The highest values of LAI measured in the denser part of the forest are relatively low compared to the value of 7 usually reached under tropical species (Bréda et al., 2002).

Pollen data

We have used pollen data collected and published by Vincens et al (2000), and particularly the percentage of arboreal pollen (AP) (figure IV. 3b). The highest values of AP (>50%) are found in forest samples, the lowest ones (<10%) in savanna samples and *Pteridium* ecotone, with intermediate values (mean of 30%) at the savanna–forest transition (plots 17 and 18). Seven main pollen zones, established on the basis of significant changes in the proportion of the major taxa, have been distinguished by the authors (Figure IV. 4). Compared with the pollen data, the LAI measurements along the same transect show very similar trends. The highest values of LAI were always obtained from plots inside the forest, the lowest ones in savanna. The main differences are observed under the *Albizia* cluster occurring in the savanna (plots 23, 24, 25) where the LAI is about 1.2, though AP is very scarce, particularly *Albizia* pollen.

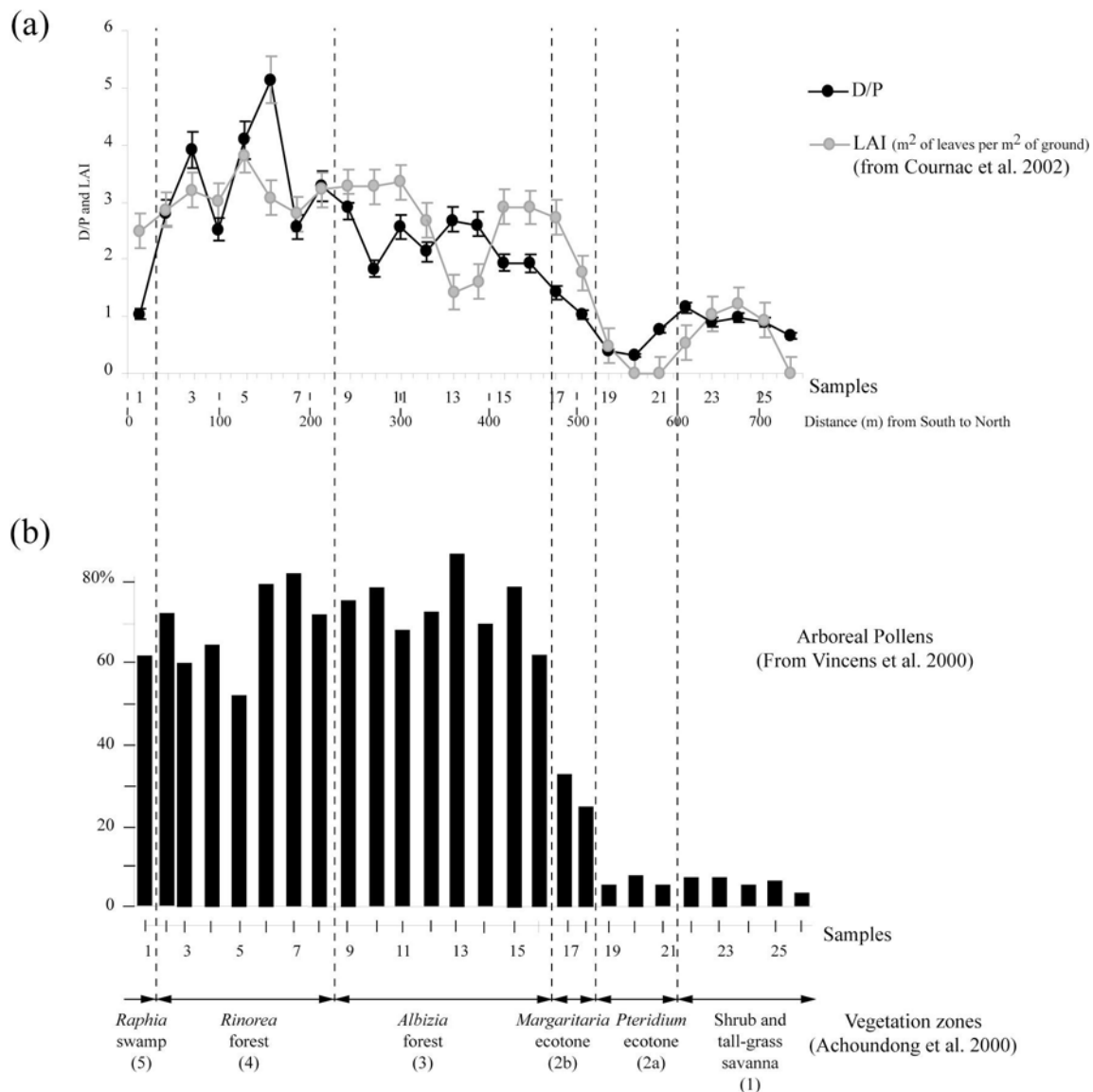


Figure IV. 3. (a) Distribution of D/P phytolith index (Ligneous dicotyledon phytoliths (rough spherical types) / Poaceae phytoliths (saddle, cross, dumbbell, point and silicified bulliform cells), LAI (Cournac et al. 2002), (b) Arboreal Pollen (AP) (Vincens et al. 2000) along the studied transect in Kandara, south-eastern Cameroon. Vegetation zones from Achoundong et al. (2000) are figured in dotted lines.

Error (standard deviation) assigned to D/P index is 6% (s.d. on rough spherical type plus max s.d. on Poaceae phytolith types).

Measurement imprecision related to the type of the LAI captor is ± 0.3 (Cournac et al. 2002).

Results

Phytolith assemblages

Phytolith conservation was good in all the samples analyzed. Abundances of the 11 phytolith types and the D/P index are presented in figure IV. 4, and numerical values in appendix 1. Among Poaceae phytoliths, the cross type, uni-lobate type, poly-lobate type and saddle type are poorly represented. The smooth spherical phytolith type never accounts for more than 2.5%. Five phytolith zones have been established, on the basis of significant changes in the proportions of the rough spherical type, crenate type, dumbbell type and of the D/P index. Phytolith zone 1 (samples 26 to 19) is characterized by the highest abundances of the dumbbell type, which always accounts for more than 25% (except sample 22 with 21.8%) and by relatively low abundances of the rough spherical type that accounts for less than 45%. The D/P index ranges from 0.33 to 1.16. This phytolith zone encompasses the pollen zones 1 and 2a and includes the samples collected in the shrub and tall grass savanna, and in the northern part of the transition zone (*Pteridium* ecotone). Phytolith zone 2 (samples 18 and 17), corresponds to the *Margaritaria* ecotone, and shows a significant increase of D/P from 1.03 to 1.42. These values are intermediate between the D/P values of zone 1 and 3. This phytolith zone includes pollen zone 2b and one sample of the pollen zone 2a. Phytolith zone 3 (samples 16 to 10) is characterized by abundances of the rough spherical type ranging from 51.5% to 65.4%, and by decreasing proportions of the dumbbell type. The D/P index varies between 1.82 and 2.68. This phytolith zone exactly matches the pollen zones 3 and 4 and includes the samples collected under the young *Albizia* forest, with the exception of the most southern one. Phytolith zone 4 (samples 9 to 2) is characterized by abundances of the rough spherical type ranging from 57.7 to 70.4%, and by the lowest proportions of dumbbell type. The D/P index ranges from 2.4 to 11.5%. This phytolith zone exactly matches the pollen zones 5 and 6 and includes the samples collected under the mature *Rinorea* forest and the southern sample of the young *Albizia* forest. Phytolith zone 5 (sample 1), in the *Raphia* swamp is easily distinguished from the previous ones by lower abundance of rough spherical type (14.6%), and domination of the crenate type from *Palmae* (64.8%). The D/P index is equal to 1.

Comparison between D/P index, LAI and AP

D/P Index, LAI and AP distributions along the transect show roughly similar trends (Fig. IV. 3 and 4). The lowest values (D/P<1.16; LAI<1.20; AP<10%) are obtained from the savanna and the *Pteridium* ecotone samples, while the highest ones (D/P>1.82; LAI>2.68;

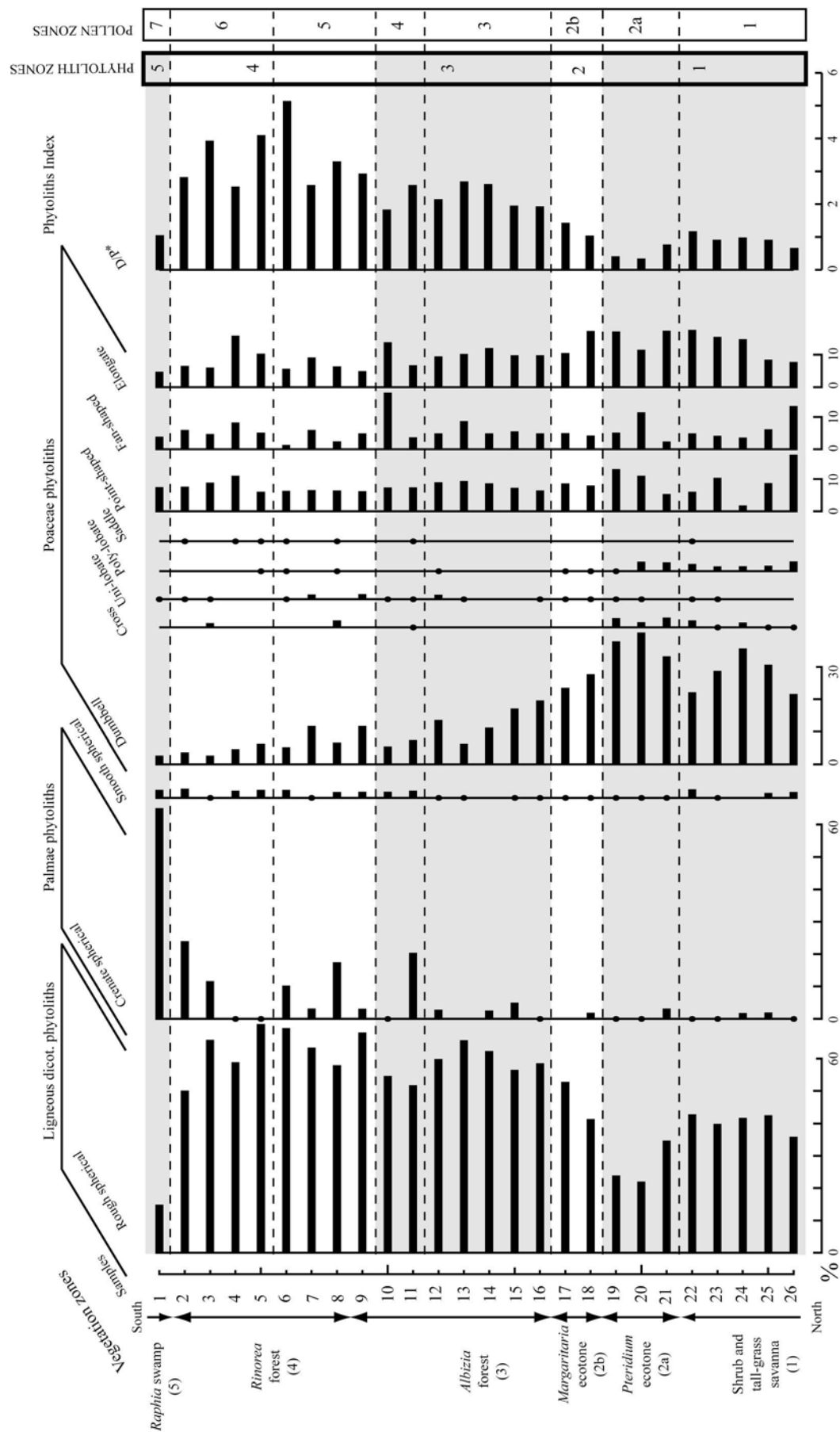
AP>50%) are found in the young *Albizia* and mature *Rinorea* forests. D/P, LAI and AP present intermediate values in the *Margaritaria* ecotone. However, when examined in detail, the three indicators show several differences. In the savanna, under the *Albizia* cluster, the LAI values of plot 23 to 25 are mid-range (1.04, 1.20 and 0.93), whereas medium D/P values are obtained for plots 21 to 26 (from 0.65 to 0.76). The AP values remain under 10%.

In the *Margaritaria* ecotone, LAI and AP increase rapidly (1.77 to 2.74 and 25 to 34%) to the young *Albizia* forest where they reach respectively 2.91 and 62% at sample 16, while D/P increases more slowly up to sample 14 where it reaches 2.60.

In the young *Albizia* forest, LAI measured in plots 13 and 14 are from 1.5 to 2 units lower than in the other plots of this forest, certainly linked to recent clearing on these two plots. D/P and AP still record the pre-clearing state and are high (D/P average of 1.93) across this vegetation zone. LAI reaches a plateau in the young *Albizia* forest and stays constant (around 3, with the exception of plot 5 with 3.81) in the mature *Rinorea* forest, while D/P shows higher values and higher variations in the mature *Rinorea* forest (from 2.52 to 5.13) than in the young *Albizia* forest (from 1.82 to 2.68). AP values for samples taken from these two forests fluctuate between 54 to 90% with no significant difference between the two forest types. In the mature *Rinorea* forest sample 6 presents the highest value of D/P (5.1) whereas LAI and AP do not show any noticeable increase. Lastly, in the *Raphia* swamp, rich in palm trees (monocotyledons), LAI and AP stay high while D/P, which is proportional to ligneous dicotyledon abundances, significantly decreases down to 1.04.

Figure IV. 4. Abundances of phytolith types (% of the characteristic phytolith sum minus the elongate type). Abundance lower than 1% are figured by a dot. Vegetation zones according to Achoundong et al. (2000) and pollen zones established by Vincens et al. (2000) are figured against phytolith zones.

* D/P = Ligneous dicotyledon phytoliths (rough spherical types) / Poaceae phytoliths (saddle, cross, dumbbell, point- and fan-shaped).



Statistical relationships between D/P and LAI

D/P versus LAI data are plotted on figure IV. 5. Sample 1 from the *Raphia* swamp, and samples 13 and 14 from the cleared plots were excluded as they are dominated by local conditions. The relationship is clearly not linear. Three different functions were used to try and quantify the relationship between LAI and D/P, using the Simplex algorithm (Nedler & Mead, 1965; Caceci & Cacheris, 1984). This algorithm minimizes the residuals between observations and estimates, using the least squares criterion. The percentage of variance explained (r^2) and summary statistics for each function are presented in figure IV. 5.

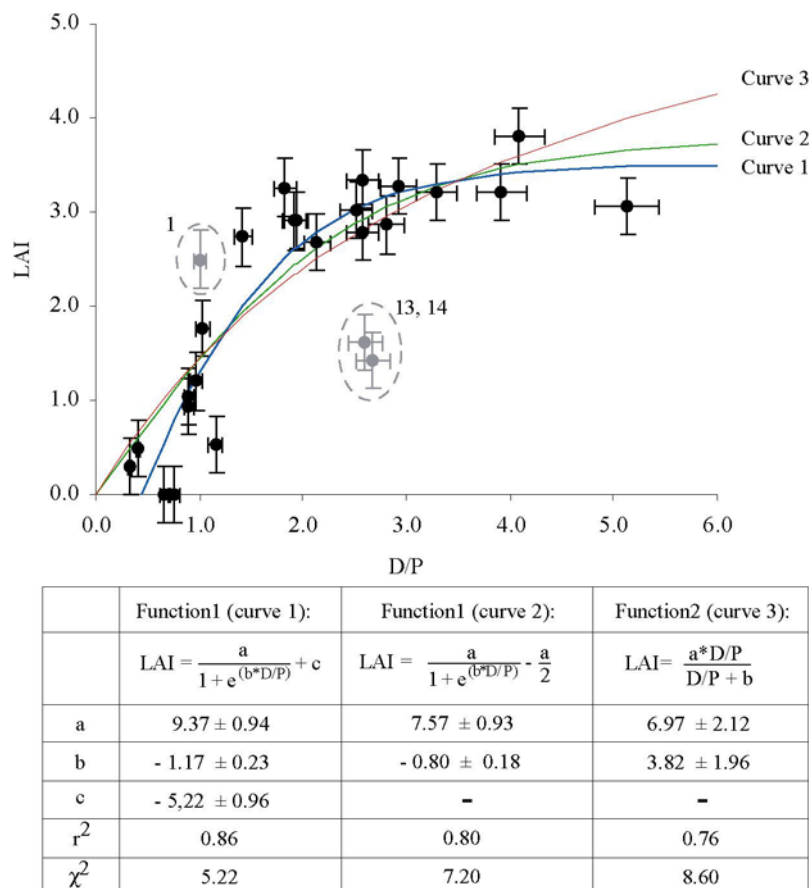


Figure IV. 5. D/P phytolith index versus LAI. Sample 1, 13 and 14 have been excluded to estimate best fitting curves. Function 1 is used with the constrain that the curve cross the origin (curve 1) and without constrain (curve 2); The parameters of the curves are a, b, c (see equations), r^2 is the proportion of the variance explained, χ^2 is the chi-square, d. f. is the number of degree of freedom and p is the probability associated with χ^2 .

As described above, samples from savanna have measured LAI equal to zero but present a low but not null D/P. The very short distance between two plots (30m) may induce an artifact because phytolith assemblages from open sites represent vegetation from a wider surrounding area than in forest. The second reason is the LAI measurement, which does not take into account shrubs smaller than 2m, which would produce dicotyledon phytolith types. Therefore, we have estimated two sets of close function: one with no constraint (function 1) and a second with the constraint that the curve crosses the origin (function 2). The latter has necessarily a lower r^2 . Both functions present an asymptote at, respectively, 3.5 and 3.78. As the function 1 does not cross the y axis at the origin, LAI will be under-predicted for low values of D/P with negative predicted value for $D/P < 0.4$. With an asymptote lower than 4, these two functions will systematically under-estimate LAI from any forest denser than that of Kandara.

The third function from which LAI is null when there is no tree cover has been used to fit our points. The r^2 is lower than the other functions but has an asymptote at 7. This characteristic is important as the highest value of LAI measured from tropical forest is 7 (Bréda et al., 2002).

Discussion

Space-scale recorded by LAI-phytoliths-pollens

LAI values were averaged for each phytolith and pollen samples, so short and rapid fluctuations have been smoothed. This method of LAI measurement is very sensitive to changes over short distance (less than a meter) in the tree cover density. In the tall-grass savanna, under the *Albizia* cluster, the D/P index records a wider signal of trees than LAI does. The reason for this discrepancy is not clear. It may be due to a production of dicotyledon phytoliths from shrubs and small trees not considered by LAI measurements made 2m above ground. It may also be due to transport of phytoliths by wind, especially after fires. In this case, and especially in open vegetation, phytolith assemblages would be representative of a larger spatial scale than LAI. In contrast to the phytoliths, the AP frequencies remain low under the *Albizia* cluster. As soil pollen samples are representative of a vegetation averaged over a minimum area of about 300 m² (Vincens et al., 2000), dispersal of *Albizia* pollen may also explain this difference.

Time-scale recorded by LAI-phytoliths-pollens

In the *Albizia* forest, the difference between the abrupt drop registered by the LAI, corresponding to the recent clearing of the plots, and the relative stability of the D/P index and the AP frequencies, is mainly related to the different time scales recorded by the 3 methods.

LAI measurements are instantaneous, whereas phytolith and pollen assemblages are representative of a vegetation averaged over several years. This problem of varying time scales is very important in the perspective of calibration between phytolith assemblages from called "modern samples" and instantaneous vegetation measurements.

The edge of the forest is not as well recorded by phytolith as LAI. The difference may be due to movement of the forest colonization front. As the D/P index is a ratio between trees and grasses, it is possible that in the youngest part of the forest, grasses are still present in important quantity in the forest understory and would gradually decrease with the maturity of the forest. As the botanical statements made along this transect are not exhaustive and concern only trees, there is no evidence to confirm this hypothesis. The fact that Poaceae pollen frequencies decrease more quickly in the forest than Poaceae phytoliths may be due to a difference in their productivity. Another reason could be an under-representation of Poaceae pollen, which is quickly masked by the numerous arboreal pollen taxa when coming into the forest communities (Vincens, personal. com).

Reliability of phytolith assemblages and D/P for tracing savanna and forest

It is possible to differentiate between savanna and forest communities along the transect path using phytolith assemblages and D/P index. The lowest values of D/P are registered in the tall grass savanna and the highest values of D/P are measured in the forest. The transition zone between savanna and forest, corresponding to the *Margaritaria* ecotone, shows intermediate D/P values.

As a slight difference appeared in the D/P index from the *Rinorea* and *Albizia* forests, we proposed two forest zones. However, there is no clear threshold to discriminate between the two phytolith zones. A higher quantity of phytolith produced by tree may be explained by the degree of maturity of the forest. Indeed, in the *Albizia* forest, which is younger than the *Rinorea* forest (Youta Happi, 1998; Achoundong et al., 2000), the D/P index has a lower averaged value.

At Kandara, the phytolith assemblages from the tall grass savanna have a higher D/P index than in previously published data. Alexandre et al. (1997) and Bremond et al. (Bremond et al., submitted-b), studying modern samples from West Africa, showed that the D/P index of tall grass savanna samples is always lower than 0.5 and usually lower than 0.1. Alexandre et al. (1997) included the "elongate type" with the Poaceae types which may explain the lower D/P index values. However, this does not explain the difference with the Bremond et al. (Bremond et al., submitted-b) study, in which these types were excluded, as in the present study. The

higher values obtained here are most likely as a result of the nature of the site, which is described as an enclosed savanna inside a forest, (and it is likely that the savanna samples have been influenced by the proximity of the forest). Further, in the Kandara tall grass savanna, 3 samples were taken under an *Albizia* cluster, which may increase the proportion of phytolith produced by trees as compared to Poaceae than elsewhere in the tall grass savanna. Another reason for the relatively high D/P in the present study tall grass savanna, which contrasts with the very low AP frequencies registered by Vincens et al. (2000), is the prominent presence of young growth *Albizia* trees, which burn every year. The young *Albizia* trees are certainly not mature enough to produce pollen but it has been observed that rough spherical phytoliths are produced in very young *Albizia* (Alexandre, personal observations) and the accumulation of phytoliths in the soil after many years with fires might be significant. The *Raphia* swamp is clearly differentiated from the vegetational communities by the proportion of crenate type, a phytolith exclusively produced by palm trees. The production of phytoliths by Palmae is known to be important; however no study has yet clearly demonstrated the productivity with quantifiable measurements. It therefore remains difficult to estimate the real proportion of palm trees present in the swamp with phytolith assemblages.

The D/P index: a proxy of LAI

Three regression equations between D/P and LAI are proposed here. All three demonstrate advantages and disadvantages for the estimate of LAI from the D/P index. The function 1 has the best fit but crosses the abscissa at 0.4. For a null LAI, measured in pure grassland the D/P ratio is also null (Bremond, personal observation). Therefore, this equation will underestimate LAI for low values of D/P. The second function, which crosses the origin, allows low values of D/P to be predicted. The third equation is based on a function with a lower slope than the two other, and has a lower r^2 . However, there are several theoretical reasons why these function should be chosen over the others: first, the lower slope, whilst in disagreement with plots, may still be more realistic. As discussed above, this studied transect crosses a transition between savanna and forest that is not only very abrupt but also has a fast expansion of forest, which is recorded with a slight lag in the phytolith assemblages. The D/P index increases from savanna to forest more slowly than LAI, and there is no average value that allows this lag to be calibrated correctly. The second reason is that the curve crosses the origin, permitting to avoid the problem of the positive D/P values in the tall grass savanna where LAI is null. The third reason is the asymptote of LAI at 7. This function is therefore

coherent with the range of LAI values because the value 7 is usually the highest value measured in tropical forest (Bréda et al., 2002).

Application limits of D/P as proxy of LAI

1- All relationships between D/P and LAI are significant but not ideal for several reasons. Whilst LAI measurements do not show differences between the two forest types, the D/P index is higher in the *Rinorea* forest than in the *Albizia* forest. The reason is that D/P is more likely to be related to the biomass of ligneous dicotyledons than LAI. Measurements of basal area from Youta Happi (1998) show that there is an important difference of above ground biomass between the *Rinorea* and the *Albizia* forests and suggest such a hypothesis. Another source of discrepancies between LAI and D/P comes from the instantaneous nature of the LAI measurements along the Kandara transect, which may under-estimate LAI values. Indeed, in a deciduous or semi-deciduous forest, as in Kandara, LAI is dependent on dry and wet seasons through the quantity of leaves in trees. Therefore, such error could be estimated and corrected using several measurements of LAI throughout the year or by comparison with monthly LAI values estimated from satellites, available globally at high resolution (8 km²) and for at least 2 decades (Myneni et al., 1997). This would reduce the variability between LAI and pollens or phytoliths measurements discussed above in the time-scale section.

2- The D/P index is calculated without phytoliths produced by Palmae. Therefore, this index is not representative of the real LAI but it is based on the assumption that the production of phytolith from Palmae is stronger than dicot trees and, to our knowledge, no study has compared phytolith productivity between dicot and Palmae. The LAI would be overestimated if phytoliths from Palmae were included. As the occurrence of Palmae in forest ecosystem is constrained to specific edaphic conditions (Kahn & de Granville, 1992; de Granville, 2002), it was preferable to exclude them from the D/P index, but to be aware that LAI may be under-evaluated when Palmae phytolith are counted in the assemblages. It should also be noted that several samples (2, 3, 6, 8, 11) presenting a significant percentage of Palmae phytoliths were kept in the calibration process. Even though Palmae trees are physically outside the transect on which LAI was measured, these trees have a very high productivity of phytoliths, and therefore generate a form of pollution of the modern samples. As the presence of palm tree has no bearing on the LAI measurements, the D/P index should correctly reflect the real LAI.

3- In altitudinal tropical forest, where C₃ grasses are dominant (Pooideae and Arundinoideae), the relationship between D/P and LAI could differ because C₃ grasses usually produce less phytoliths than C₄ grasses (Johnston et al., 1967; Mulholland, 1989). In these regions, another

correlation function should be calibrated. Further, the productivity of phytoliths from altitudinal tropical tree species may differ from tropical species.

4- The D/P index was developed by Alexandre et al. (1997) in West Africa in order to estimate the tree cover density. This ratio was established on the assumption of the exclusive competitive relationship between grasses and trees, so as the non-Poaceae herbaceous components are not taken into account, it is possible that an error is introduced. If non-Poaceae herbaceous components increase, the D/P would stay constant, whilst the real tree cover density decreases. Further, the fan-shaped phytolith type is included with the sum of short cells produced by Poaceae. As the production of this phytolith type is related to the water stress and the evapotranspiration rate (Bremond et al., submitted-b), the tree cover density can be under-evaluated. However, over short distance, as on the Kandara transect, this should have little effect. In contrast to Alexandre et al. (1997), we have not included the "elongate type" in the sum of short cells produced by Poaceae because they are usually multi-broken and may be confused with weathered diatoms or sponge spicules and would result in over-estimation of the proportion of Poaceae.

Summary and conclusion

Phytolith assemblages and the D/P ratio measured at Kandara accurately show the modern succession of ecosystems crossed by the study transect from a tall grass savanna to a mature semi-deciduous forest. For the first time and in contrast to other studies, this work provides the reader with a numerical analysis of the tree cover density phytolith index. A function is proposed to estimate LAI from the D/P index ($LAI = \frac{6.97 \times D/P}{D/P + 3.82}$). This relationship may be applied to reconstruct vegetation from fossil phytolith assemblages. However, there are several factors which may limit the application of the LAI estimation:

- LAI can be underestimated if Palmae phytoliths are locally present in significant amount;
- LAI can also be under-predicted if the proportion of bulliform type does not increase proportionally with Poaceae short cell phytoliths. This problem may affect sites with special soil texture such as swamps, where soil water stress may be very important;
- the relationship between ligneous dicotyledons and Poaceae phytoliths should be checked and calibrated under tropical forest with C₃ grass cover due to the productivity differences between phytoliths from C₄ and C₃ grasses.

Finally, this phytolith index is the first proxy calibrated in terms of quantitative estimation of the tree cover density, which can be directly compared with vegetation model output. However, much more LAI measurement and modern D/P index from denser forest are required to confirm our present relationship.

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Samples	Rough spherical	Crenate spherical	Smooth spherical	Dumbbell	Cross	Uni-lobate	Poly-lobate	Saddle	Point-shapped	Fan-shaped	Elongate	Sum	D/P
26	147	4	6	88	1	0	11	0	71	54	31	413	0.65
25	186	7	5	134	4	0	6	0	37	26	36	441	0.90
24	137	5	0	117	4	0	4	0	5	11	48	331	0.97
23	142	2	2	102	1	1	4	0	36	14	55	359	0.90
22	185	4	10	95	8	2	8	2	25	20	76	435	1.16
21	144	12	2	138	11	0	10	0	21	9	72	419	0.76
20	100	2	1	185	6	2	12	0	49	51	52	460	0.33
19	111	2	3	177	12	2	1	0	60	23	80	471	0.40
18	156	6	2	104	0	1	2	0	29	15	65	380	1.03
17	190	0	1	84	0	1	2	0	30	17	37	362	1.42
16	190	3	3	63	0	1	0	0	20	15	31	326	1.92
15	194	16	2	58	0	0	0	0	24	18	33	345	1.94
14	216	8	0	38	0	0	0	0	29	16	41	348	2.60
13	217	0	1	20	0	3	0	0	30	28	33	332	2.68
12	233	10	3	52	0	4	1	0	34	18	36	391	2.14
11	167	65	6	23	3	2	0	3	23	11	21	324	2.57
10	208	3	6	20	0	1	0	0	27	66	52	383	1.82
9	219	9	5	37	0	4	0	0	19	15	15	323	2.92
8	161	48	4	18	5	0	1	2	17	6	17	279	3.29
7	221	10	2	40	0	4	0	0	22	20	31	350	2.57
6	195	28	6	14	0	1	2	1	17	3	15	282	5.13
5	233	1	7	20	0	0	1	1	19	16	33	331	4.09
4	214	2	7	16	0	0	0	1	39	29	57	365	2.52
3	192	33	2	7	3	1	0	0	25	13	17	293	3.92
2	177	84	9	12	0	3	0	2	26	20	22	355	2.81
1	49	217	7	8	0	3	0	0	24	12	15	335	1.04

Appendix IV. 1. Detailed counts of phytolith types, recovered from modern soil samples from southeastern Cameroon, collected along a continuous forest-savanna transect.

IV. 4. Relation entre assemblages phytolithiques et densité du couvert arboré en domaine méditerranéen: limites de la méthode.

Résumé étendu de l'article: Advantages and disadvantages of phytolith analysis for the reconstruction of Mediterranean vegetation : an assessment based on modern phytolith, pollen and botanical data (Luberon, France).

Il n'y a que très peu d'assemblages phytolithiques actuels ou fossiles en zone Méditerranéenne (Albert et al., 1999; Albert et al., 2000; Delhon et al., 2003) qui aient été étudiés. La seule étude mettant en relation des assemblages actuels et certains types de végétation ne concerne que 4 échantillons prélevés sous une ripisylve, une chênaie, une pinède et une pelouse (Delhon et al., 2003).

Cette présente étude essaie ainsi de répondre à plusieurs questions :

- 1- Une grande partie des sols méditerranéens s'établissent sur un substrat calcaire très pauvre en silice disponible pour les plantes. Est-ce que la végétation qui s'y développe produit des phytolithes en assez grande quantité pour qu'en les extrayant des sols on puisse effectuer des comptages significatifs ?
- 2- A la différence du pollen, les assemblages phytolithiques permettent de renseigner les sous-familles des graminées dominantes. Est-ce que cette précision taxonomique est suffisante pour décrire les formations herbacées Nord Méditerranéennes ?
- 3- Est-ce que l'indice phytolithique D/P, traceur de la densité du couvert arboré en domaine tropical (Alexandre et al., 1997 et voir chapitre II) est applicable au domaine Méditerranéen ?
- 4- Les Pinaceae, très présentes dans le domaine Méditerranéen, peuvent-elles être tracées par un type de phytolithes comme le suggèrent plusieurs études ?
- 5- La physionomie de la végétation Méditerranéenne, pouvant varier sur de courtes distances, peut-elle être tracée par les assemblages phytolithiques ?

Les assemblages phytolithiques seront confrontés aux spectres polliniques pour certains échantillons.

Matériel et Méthode

Trente et un échantillons de surfaces ont été prélevés sur le Mont Luberon (43°49N, 5°30W) , sous quatre types de végétations (des pinèdes, des chênaies, des garrigues et des pelouses), dans des parcelles de 20×20m². Des relevés botaniques exhaustifs sont disponibles pour chacune des parcelles. Les graminées dominantes sont des Pooideae (*Bromus erectus*, *Festuca*

gracilor, *Brachypodium retusum*, *Stipa pennata*, *Poa bulbosa* et *Koeleria valesiana*), les dicotylédones ligneuses sont essentiellement des chênes (*Quercus coccifera*, *Q. pubescens* et *Q. ilex*), les pins étant représentées par *Pinus halepensis* et *P. sylvestris*.

L'extraction (Kelly, 1990), la classification (Twiss et al., 1969; Mulholland, 1989; Twiss, 1992; Fredlund & Tieszen, 1994; Kerns, 2001; Blinnikov et al., 2002; Delhon et al., 2003) et le comptage des phytolithes ont permis d'identifier 8 types (Figure IV. 5. 3).

Le comptage des pollens est fait selon la méthode standard de Reille (1990). Les pollens étant bien conservés dans tous les échantillons, 88 taxons sont identifiés.

Résultats

Une quantité suffisante de phytolithes a pu être extraite (à peu près 0.03% du poids sec) et les types comptés sont produits pour tous les assemblages à plus de 90% par les graminées (Figure IV. 5. 2). Le type "uni-lobé" est dominant dans tous les assemblages (53% à 89%) et réparti de façon homogène quel que soit le type de végétation. Le type rectangle, peu présent (0% à 5%), ne semble pas non plus varier avec la végétation ; par contre le type "poly-lobé" (0% à 20%) est plus abondant dans les échantillons de pelouses. Ces trois types sont produits spécifiquement par les Pooideae (Twiss et al., 1969; Mulholland, 1989; Twiss, 1992). Les types "pointe" et "allongé" produits par l'ensemble des graminées sont relativement bien représentés (respectivement 3% à 22% et 1% à 18%) avec une abondance plus forte du type "pointe" dans les échantillons hors pelouses. La somme des phytolithes de graminées confrontée au pourcentage d'espèces de Poaceae dans chaque parcelle (Figure IV. 5. 4) ne montre aucune tendance significative ; par contre le type "poly-lobé" semble être plus significativement lié au pourcentage d'espèces (Figure IV. 5. 5). Les garrigues, naturellement pauvres en espèces de Poaceae (8% à 32%), offrent des assemblages phytolithiques avec peu de type "poly-lobé" (moins de 8%). Parallèlement, les pelouses qui sont constituées par plus de 25% d'espèces de Poaceae ont pour la majorité d'entre elles (10 sur 14) plus de 25% de "poly-lobé" dans leurs assemblages.

Les types "sphériques rugueux" produits par les dicotylédones ligneuses et "sphérique irrégulier avec des pointes" produits par les Pinaceae, sont très peu abondants dans tous les assemblages (inférieur à 4%) et leurs proportions ne peuvent être mises en relation avec la végétation.

Les spectres polliniques sont dominés par *Pinus*, *Cedrus*, *Quercus ilex*, *Quercus cocifera*, *Quercus* type décidue, *Buxus sempervirens*, et Poaceae (Figure IV. 5. 2). Les quatre types de

végétations ne peuvent pas être distingués par ces spectres. Pour interpréter de façon synthétique les assemblages, des biomes polliniques sont calculés selon la méthode développée par Prentice et al. (1996) et Peyron et al. (1998). La majorité des spectres sont assignés au biome Forêt mixte chaude, caractéristique de la zone Méditerranéenne. Deux spectres sont assignés au biome Forêt tempérée décidue du fait de la forte proportion de pollens arborés *Pinus* et *Cedrus* associés aux pollens de décidus.

Discussion

Cette étude apporte des réponses aux questions méthodologiques présentées en introduction, à savoir que (1) l'analyse phytolithique est utilisable sur les sols calcaires très pauvres en silice ; (2) les assemblages phytolithiques ne semblent pas discriminer les deux formations herbacées dominantes en zone nord Méditerranéenne que sont les garrigues et les pelouses pâturées ; (3) l'index D/P n'est pas applicable à ce site d'étude. Ce résultat, en désaccord avec l'étude de Delhon et al. (2003), peut être dû au fait que les chênaies et garrigues qui ont été étudiées sont trop jeunes pour être tracées par leur production phytolithique ; (4) l'efficacité des phytolithes en tant que traceur des Pinaceae en zone Nord Méditerranéenne est remise en question ; (5) du fait de l'absence de production par les dicotylédones ligneuses de phytolithes caractéristiques, la physionomie de la végétation Méditerranéenne sera difficilement tracée par des assemblages phytolithiques.

Finalement, cette étude montre non seulement les limites de l'utilisation des phytolithes en domaine Méditerranéen mais aussi la nécessité d'obtenir d'autres assemblages actuels dans cette zone puisque plusieurs pistes et suggestions sont avancées.

IV. 5. Advantages and disadvantages of phytolith analysis for the reconstruction of Mediterranean vegetation : an assessment based on modern phytolith, pollen and botanical data (Luberon, France).

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Abstract

We present here the results of a first study comparing modern soil phytolith assemblages with pollen and botanical data at a north Mediterranean site. This work has shown the following limitations and advantages of phytolith analysis for the reconstruction of Mediterranean vegetation :

1) Phytoliths are produced in sufficient quantities for analysis and are well preserved in limestone environments, widespread in the Mediterranean area. 2) Young stands of *Quercus ilex* and *Quercus coccifera*, widely distributed in the Mediterranean area do not produce characteristic phytolith types in sufficient quantities to allow the calculation of a reliable index of tree cover density. 3) Pine forests, dominated by *Pinus halepensis* and *Pinus sylvestris*, are not recorded in the studied phytolith assemblages. 4) Grassland and shrubland assemblages can be distinguished through their associated phytolith assemblages, in particular by the proportion of crenate phytoliths produced in the short cells of the grass epidermis. 5) The different vegetation groups on the massif cannot be distinguished by pollen analysis. Further studies, comparing modern phytolith assemblages and quantitative vegetation data, should be carried out on forest plots that have been established for several centuries to further assess the role of phytolith analysis in vegetation reconstructions in the Mediterranean region.

Keywords : Phytolith, Mediterranean, paleovegetation, pollen

Introduction

Previous reconstructions of the past vegetation in the continental Mediterranean zone have been mainly based on pollen (Prentice et al., 1996; Cheddadi et al., 1997; Peyron et al., 1998; Fauquette et al., 1999; Guiot et al., 1999; Jalut et al., 2000; Cheddadi et al., 2001), charcoal (Thinon, 1979; Thinon, 1992; Thiébault, 1997; Heinz & Thiébault, 1998) and plant macrofossil (Vernet, 1986; Digerfeldt et al., 1997) data. However, non-oxidizing areas such as peat bogs or lacustrine sediments in which where pollen are preserved are scarce in the Mediterranean zone. Continental records from coastal (Rose et al., 1999; Jalut et al., 2000) and marine (Combourieu-Nebout et al., 1998) sediments record a signal from a larger spatial scale as they receive an influx of pollen from various sources. Further, none of those proxies are able to trace grassland dynamics and forest-grassland shifts over time with any accuracy.

Phytoliths are amorphous silica particles that precipitate in and/or between the cells of living plant tissues. As phytoliths are well preserved in oxidizing environments such as soils or buried soils, they may therefore help to compensate for the current lack of continental paleovegetation reconstructions in the Mediterranean area. Previous phytolith investigations have mostly concentrated on inter-tropical and temperate paleoenvironmental records. There are only a few existing studies from the Mediterranean region (Albert et al., 1999; Albert et al., 2000; Delhon et al., 2003) and even fewer studies of the calibration of modern soil surface phytolith assemblages with defined vegetations (Delhon et al., 2003). We present here an assessment of the advantages and limitations of phytolith analysis for the reconstruction of the past vegetation in the North Mediterranean area, based on the study of modern soil phytolith assemblages. Thirty-one modern soil phytolith assemblages and ten modern soil pollen assemblages are compared with mesological and exhaustive botanical surveys (Véla, 2002) in order to answer the following methodological questions:

1-Soils developed from limestone parent-rocks, such as leptosols (World Reference Base for Soil Resources; 1998), are widespread in the Mediterranean area. These soils do not contain a large amount of silica available for plant uptake. Does the vegetation occurring in these regions produce phytoliths, and do the soils contain sufficient phytoliths for reliable counting and analysis ?

2-In contrast to pollen data, phytolith morphological types help to discriminate grass subfamilies (Twiss, 1987; Twiss, 1992; Fredlund & Tieszen, 1994; Fredlund & Tieszen, 1997b). To what extent is this information important for the reconstruction of northern Mediterranean vegetation ?

3-In inter-tropical areas, the tree cover density is mirrored through the phytolith index d/p (the ratio of dicotyledon phytolith type to the sum of Poaceae phytoliths) (Alexandre et al., 1997). Does the same phytolith index reflect the tree cover density in the North Mediterranean zone indicated, as suggested by Delhon et al. (2003) ?

4-Pine species are currently widespread in the Mediterranean area. Several phytolith studies have suggested that pine populations produce characteristic phytolith types (Klein & Geis, 1977; Sangster et al., 1997; Kerns, 2001; Kerns et al., 2001; Blinnikov et al., 2002; Delhon et al., 2003). Are the pine phytolith proportions found in phytolith assemblages indicative of the above pine cover density ?

5-The Mediterranean vegetation physiognomy may be highly heterogeneous over short distances (Di Castri et al., 1981; Blondel & Aronson, 1999). What spatial and time scales are recorded in soil phytolith assemblages ?

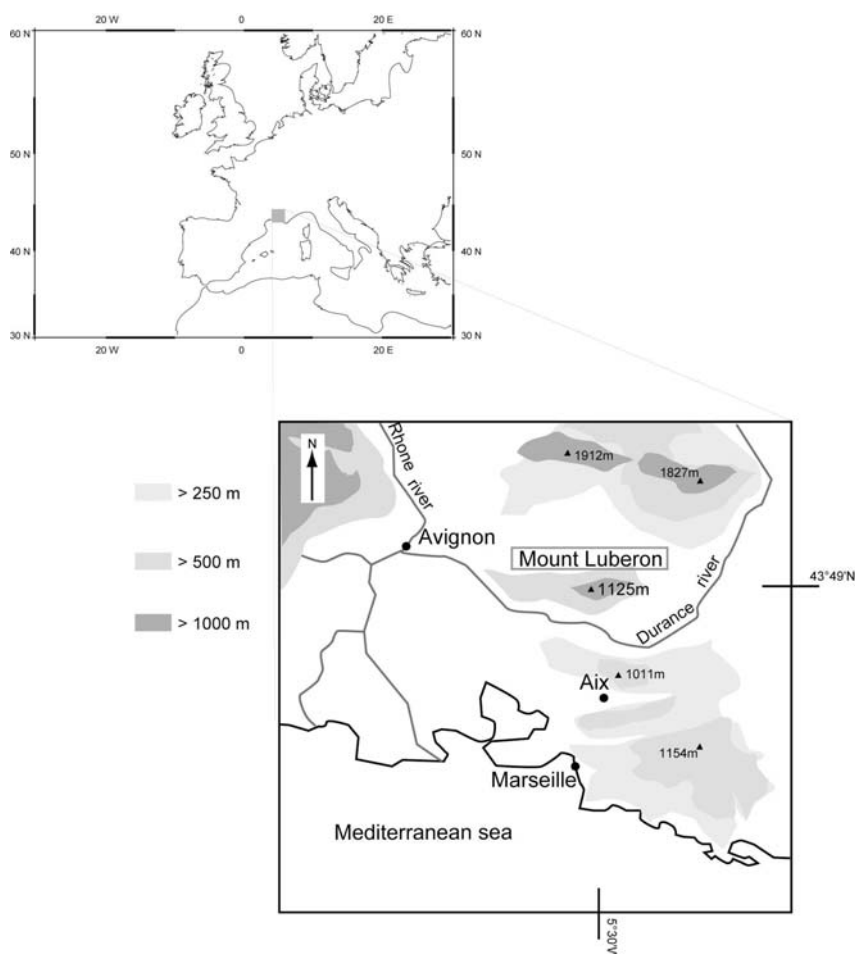


Figure IV. 5. 1. Location of the sampled site ; Mont Luberon, South-east of France.

Location of study sites

The Luberon mountain range (43°49'N, 5°30'W) is situated in the southeastern Mediterranean part of France, to the north of Marseille (Figure 1). The range is oriented east-west and lies between 300 m and 1124 m above sea level (a.s.l.). The substratum is made of Cretaceous and Oligocene limestone containing less than 8% of SiO₂. The sampled soils are Leptosols (World Reference Base for Soil Resources, 1998), a few centimetres thick, with a thin humic layer.

The massif is located in the Mediterranean sub-humid climate zone defined by cold winters. Annual rainfall is 700 mm. The vegetation of the western Luberon is organized in three zones linked to topo-climatic conditions (Tatoni et al., 1998; Véla et al., 1998): 1) mixed evergreen and summergreen oak grove found on the northern slopes; 2) the southern slopes are covered by grasslands and shrublands with patches of pinewood (*Pinus halepensis*); 3) the summit is covered with grasslands with small bushes. These high altitude grasslands have been influenced by grazing over a number of centuries (Véla et al., 1998).

The site was chosen because exhaustive botanical surveys have been done by one of the co-authors (Véla, 2002). As elsewhere in the Mediterranean region, human impact through fires, grazing and cultivation has been important in the Luberon range. Vegetation changes in the last century have been considered for every plot (Table IV. 5. 1). Where grazing has ceased in the last 50 years, the grasslands have been progressively replaced by shrublands.

Material and methods

Sampling

In order to have a relevant representation of the different vegetation types found on the massif, sample sites were chosen from 155 plots according to their botanical content (Véla, 2002), representative of pinewood, oak grove, shrubland or grassland. The first cm of humic horizon of thirty-one plots of 20 X 20 m² were sampled (Table 1). Phytolith and pollen samples of 50 g consisted of 5 sub-samples collected at the center of the plot and at the 4-middle points of the diagonals.

As the sampled soils are all leptosols, impact of soil environment is not taken into account when discussing selective preservation of phytolith assemblages from one plot to another.

Vegetation survey

Botanical surveys were carried out following Godron (1983). More than 300 species were classified.

Vegetation types	Plot Name	Dynamics of the vegetation	Estimated ages
Grassland/ <i>Cedrus atlantica</i>	CPL04	Grassland to non native cedrus forest	younger than 50 years
Grassland	CPL06		Stable (> 100 years)
Grassland	CPL11		Stable (> 100 years)
Grassland	GLC08		Stable (> 100 years)
Grassland	GLC15		Stable (> 100 years)
Grassland	GLC20		Stable (> 100 years)
Grassland	GLE15		Stable (> 100 years)
Grassland	GLE21		Stable (> 100 years)
Grassland	GLW03		Stable (> 100 years)
Grassland	GLW04		Stable (> 100 years)
Grassland	HP02	Grassland to shrubland	Stable (> 100 years)
Grassland	HP05		Stable (> 100 years)
Grassland with oak shrub	TR12		Stable (> 100 years)
Grassland/Oak grove	GLE04		younger than 50 years
Oak and beech forest	GLC05		Stable (> 100 years)
Oak grove	GLC13		Stable (> 100 years)
Oak grove	HP04		Stable (> 100 years)
Shrubland	CM17		Stable (> 100 years)
Shrubland	CPL01		Stable (> 100 years)
Shrubland	CPL12		Stable (> 100 years)
Shrubland	GLW07	Grassland to shrubland Grassland to grassed glade Grassland to <i>Buxus sempervirens</i> shrubland	younger than 100 years
Shrubland	HP08		younger than 50 years
Shrubland	TR19		younger than 50 years
Shrubland	TR21		younger than 50 years
Shrubland/Grassland	GLC14		younger than 50 years
Shrubland/Grassland	TR14		younger than 50 years
Pinewood with Poaceae	CM05		Stable (> 100 years)
Pinewood with Poaceae	GLC07		younger than 100 years
Pinewood with Poaceae	TR06		younger than 50 years
Pinewood with Poaceae	GLC19		younger than 50 years
Pinewood with Poaceae	CM06	Shrubland to pinewood Grassland to pinewood	younger than 100 years

Table IV. 5. 1. Definition and history of the current vegetation types covering the sampled plots.

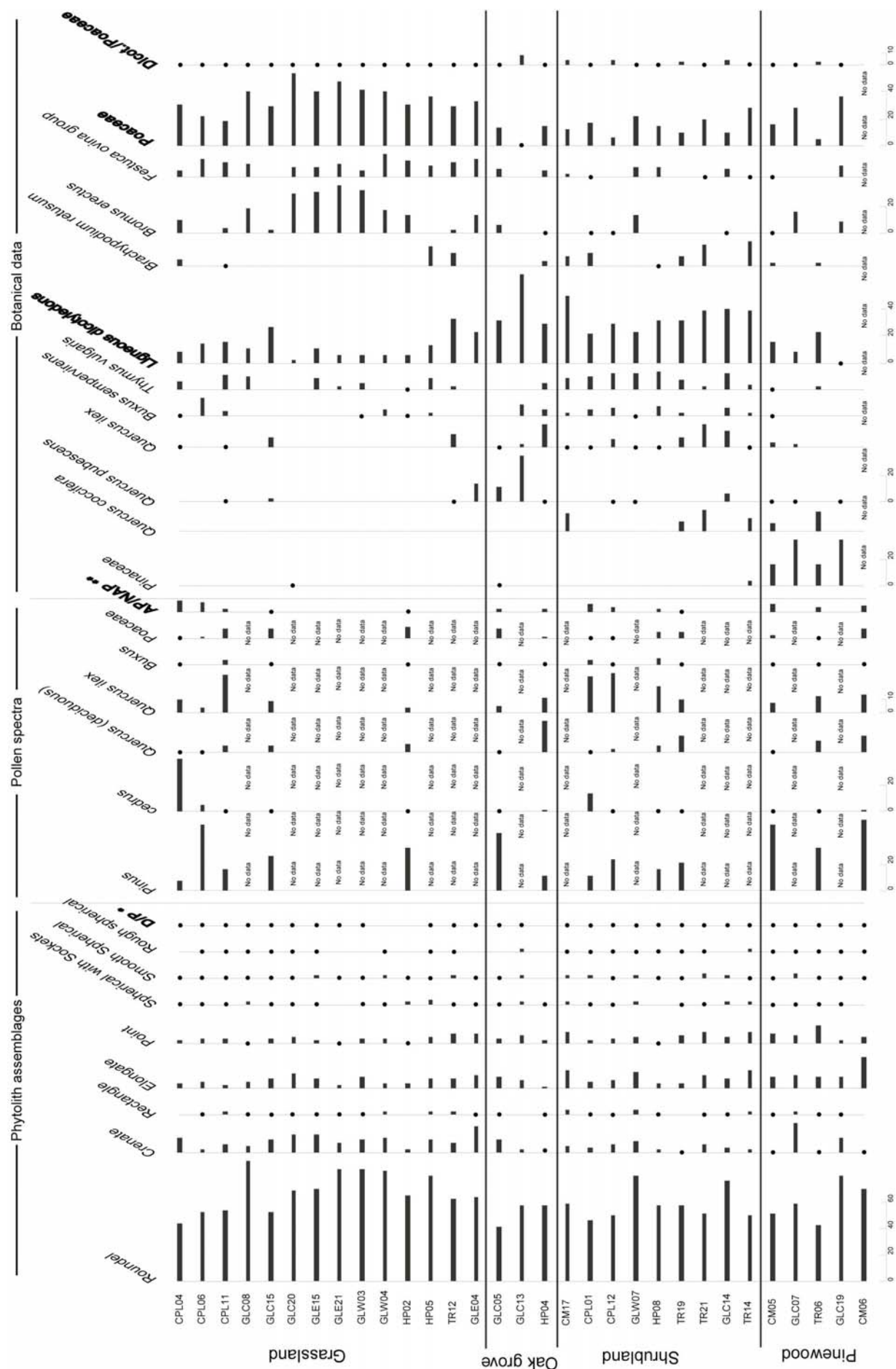
Every individual of the same species was counted and then classified into one of six classes based on the abundance of that species (calculated as a proportion of the sum of all counted individuals): scarce (class 0.5), less than 10% (class 1), from 10 to 25% (class 2), from 25 to 50% (class 3), from 50 to 75% (class 4) and higher than 75% (class 5). The data are presented here as fixed percentages equal to the middle value of the class and adjusted to 100%. This transformation from the class counting method into percentage data, necessary for statistical treatments, may induce an error of up to 30 %.

The dominant Poaceae species found are *Bromus erectus*, *Festuca ovina* group (*F. marginata* and *F. gracilior*), *Brachypodium retusum*, *Stipa pennata*, *Poa bulbosa* and *Koeleria valesiana*. These species belong to the Pooideae subfamily. The dominant ligneous dicotyledons are oaks (*Quercus coccifera*, *Quercus pubescens* and *Quercus ilex*) and, to a lesser extent, thyme (*Thymus vulgaris*), a little shrub. Pinaceae species are dominated by *Pinus halepensis* and *Pinus sylvestris* (*Pinus nigra* planted on GLC07 plot). The proportion of dominant ligneous dicotyledon, Poaceae and Pinaceae species per plot are shown in figure IV. 5. 2, with the plots grouped into four vegetation groups: grassland, shrubland, oak grove and pinewood.

The change in the vegetation for each plot (Table 1) has been estimated by considering information on past pastoral habits, the estimated age of dominant trees, the vegetation structure and the species composition of communities (pioneers species) (Véla 2002).

Phytolith extraction and counting

Phytoliths were extracted from 20g of dry soil, following dissolution of carbonates, using HCl (3 %), and oxidation of organic matter, using 30 % hydrogen peroxide heated at 90°C until reaction subsides. The samples were passed through a 60 µm sieve and clays were removed according to the Stock law. Densimetric separation of phytoliths was carried out using zinc bromide heavy liquid ($d=2.3$) (Kelly, 1990). The recovered fraction, including opal phytoliths and diatoms was weighed and mounted on microscope slides using glycerine for observation of the 3D shape, and Canada Balsam for counting. Microscopic observations were performed at 600X magnification. More than 200 characteristic phytoliths were counted from each sample. Only phytoliths with a diameter greater than 5 µm and which could be taxonomically identified were counted. These were then classified using the classification of Twiss (1969; 1992), improved and completed by the phytolith shape descriptions of Fredlund and Tieszen (1994), Kondo et al. (1994), Alexandre et al. (1997) and Barboni et al (1999).



Identified phytolith types are illustrated in figure IV. 5. 3. Roundel, crenate and rectangle types are mainly produced in short cells of epidermis of the Pooideae grass subfamily (Twiss et al., 1969; Mulholland, 1989; Twiss, 1992), gathering C₃-grasses abundant in temperate and North Mediterranean areas. The elongate type (smooth and sinuous are merged in the same group) are phytoliths from long-cells of all grass epidermis. The point-shaped type originate from micro-hair or prickles of all grass epidermis (Palmer et al., 1985; Kaplan et al., 1992).

Non-Poaceae taxa also produce characteristic phytolith types. The spherical rough phytolith type, is produced by the wood of trees and shrubs (ligneous dicotyledon) in tropical areas (Scurfield et al., 1974; Kondo et al., 1994; Alexandre et al., 1997; Barboni et al., 1999). The "medium to large multifaceted polyhedrals" phytolith type produce by oaks (Kondo et al., 1994) have not been observed in the assemblages.

The smooth spherical type appears to have several origins. According to Kondo et al. (1994), this type is produced in the epidermis of leaves and in the ray or parenchyma cells of dicot twigs and wood. They have been recovered in small proportions from several tropical herbaceous monocots and in greater quantities from a small number of tropical arboreal dicot leaves and seeds (Piperno, 1988). Recent investigation of tropical grasses show that the smooth spherical type is also produced in significant amounts by grass roots (Alexandre et al., 2000). The spherical-with-sockets type was also counted. This type has been described by Delhon et al. (2003) and has also been named the *spiked type* by Blinnikov et al. (2002) and the *spiny body* by Kerns (2001). These authors suggest that this type is produced by Pinaceae species.

Identification was possible for more than 60% of the counted phytoliths. Phytolith assemblages are presented in figure IV. 5. 2 as a percentage of the sum of classified phytoliths. A 5% counting error was estimated by counting the phytoliths on a slide two times.

Figure IV. 5. 2. Abundances of phytolith types (% of the characteristic phytolith sum), pollen (%percentage of the counted pollen sum) and botanical species (% estimated after botanic statements following Godron, 1983) for the studied plots. Abundance lower than 1% are figured by a dot.

* D/P = Ligneous dicotyledon phytoliths (smooth and rough spherical types) / Poaceae phytoliths (roundel, crenate and rectangle types).

** AP/NAP = Arboreal pollens / Non arboreal pollens.

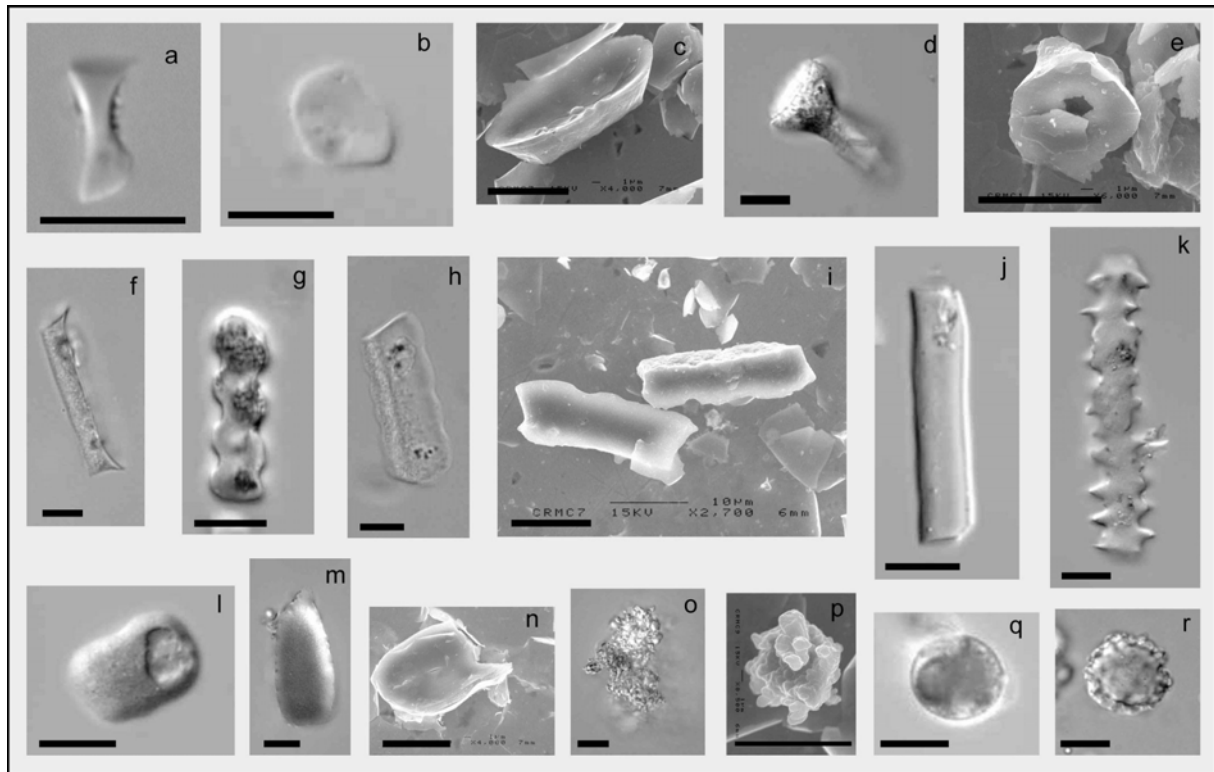


Figure IV. 5. 3. Photographs of representatives of the eight classes of phytolith types counted in this study (see text for explanation); Scale bar = 10 μm :

(a) microphotograph of a roundel type (Mulholland, 1989), side view; (b) microphotograph of a roundel type, top view; (c) SEM-photograph of this roundel type, top view; (d) microphotograph of a second roundel type, side view; (e) SEM-photograph of this roundel type, top view; (f) microphotograph of crenate type (Fredlund and Tieszen, 1994), side view; (g) microphotograph of crenate type, top view; (h) microphotograph of crenate type, under view; (i) SEM-photograph of crenate type; (j, k) microphotograph of elongate type (Twiss, 1969); (l) microphotograph of rectangle type (Twiss, 1969); (m) microphotograph of point type (Twiss, 1969); (n) SEM-photograph of point type; (o) microphotograph of spherical with sockets type; (p) SEM-photograph of spherical with sockets type; (q) microphotograph of smooth spherical type; (r) microphotograph of rough spherical type.

Pollen counting and identification

Pollen counting was carried out following the standard method of Reille (1990). At least 550 pollen grains were identified and counted at $\times 250$ and $\times 1000$ magnifications. Pollen conservation was high in all samples. Whilst a total of 88 taxa were identified, only those taxa present in significant quantities are shown on figure IV. 5. 2.

Results

Phytoliths

A sufficient amount of phytoliths was found in all soil samples (about 0.03% of the dry weight). Grass phytoliths, which include five types, made up between 86% to 99% of the classified types for all assemblages (Figure IV. 5. 2). The roundel type is largely dominant in the assemblages, ranging from 53% to 89% and is homogeneously distributed between assemblages from the four vegetation groups. The crenate type accounts for 0% to 20% with high abundances occurring most frequently in the grassland group assemblages. The rectangle type accounts for 0 % to 5% and does not show any pattern specific to the vegetation groups. These three phytolith types are characteristic of the Pooideae grass subfamily, which is the only grass subfamily represented on the plots. Elongate and point type phytoliths, which originate in the long-cells and micro-hairs of grass epidermis were present in quantities ranging between 3% to 22% and 1% to 18% respectively, with the highest abundance of the point-shaped phytoliths occurring in the non-grassland assemblages. The sum of all grass phytolith abundance has been plotted against the sum of Poaceae species recorded by botanical survey (figure IV. 5. 4). No obvious relation can be seen from this figure. After running numerous correlation analysis between the majority of the phytolith types and the botanical data (species or group of species), the best relationship found is between the crenate phytolith type abundance and the sum of Poaceae species (Figure IV. 5. 5). As shown in figure IV. 5. 2, the shrubland plots with fewer Poaceae species (8 to 32% of all botanical species) produce phytolith assemblages with lower proportions of the crenate type (less than 8% of the characteristic phytoliths). In comparison, most of the grassland plots produce phytolith assemblages with high proportion of the crenate type; although 4 of the 14 plots studied have a low abundance of this type.

The abundance of Poaceae species found in oak grove and pinewood plots varies widely (7 to 35%), their phytolith assemblages also show a wide range of crenate type abundances (0,3 to 32%). However, correlation was found between the two variables.

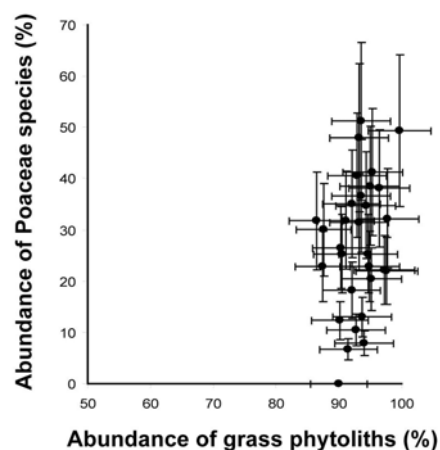


Figure IV. 5. 4. Abundance of grass phytoliths versus abundance of Poaceae species recorded by botanical statement.

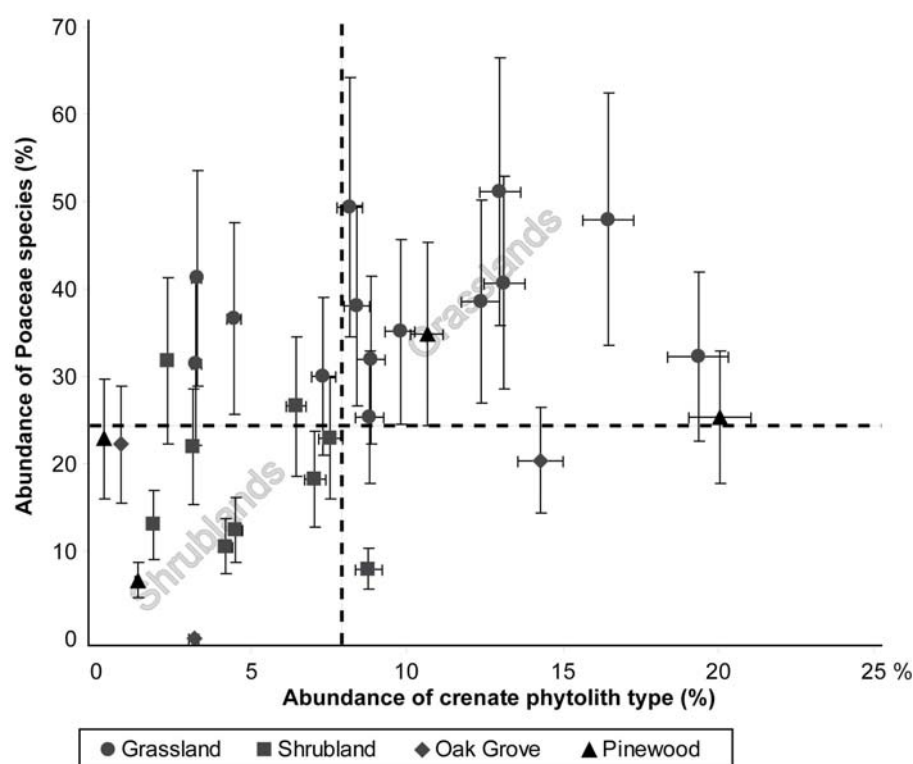


Figure IV. 5. 5. Sum of the crenate phytolith type plotted versus the sum of Poaceae species recorded by botanical statement.

The abundance of the rough spherical phytolith type is very low in all assemblages, ranging from 0% to 3%, with no difference between the assemblages taken from shrubland and grassland plots. The rough spherical type was found at values greater than 1 % in 5 of the 9 shrubland assemblages and in 2 of the 14 grassland assemblages.

Abundances of the smooth spherical type range between 0 and 5 % in both grassland and forest assemblages.

The spherical-with-sockets phytolith type, varies between 0% and 4% in all assemblages, and is not found at greater proportions in the samples taken from pinewoods.

Pollen

The pollen spectra are dominated by *Pinus*, *Cedrus*, *Quercus ilex*, *Quercus coccifera*, deciduous *Quercus*, *Buxus sempervirens* and *Poaceae* (figure IV. 5. 2). The four vegetation groups cannot be distinguished on the basis of their pollen spectra. *Quercus ilex* and *Quercus coccifera* pollen were abundant in both shrubland and grassland spectra. For example, in CPL11, a grassland plot covered by less than 1 % of *Quercus ilex*, pollen abundance of *Quercus ilex* and *Quercus coccifera* account for 39 % of the total pollen sum. *Pinus* pollen was found at high proportions in all spectra. In order to better interpret the composition of pollen spectra in relation to the vegetation groups, we have applied the biomization method to the pollen samples. This method assigns pollen spectra to the biome with which it has the highest affinity (Prentice et al., 1996; Peyron et al., 1998). Once calculated, the chosen biomes were then compared with the vegetation groups. The majority of the spectra are assigned to the Warm Xerophytic biome, a biome commonly used for describing Mediterranean vegetation. Two plots were assigned to a Temperate Deciduous biome (CPL04 and CPL06), due to the high abundance of arboreal pollen taxa such as *Pinus* and *Cedrus*.

Discussion

The methodological questions raised in introduction can now be assessed, in the light of the main results of this study:

1- The studied soil phytolith assemblages show for the first time that whilst the amount of soil phytoliths recovered is low, they occur in sufficient quantities to allow statistical counting, despite the low levels of SiO₂ in the parent rock. This result confirms that phytolith analysis can be used as a record of the vegetation developed on carbonaceous soils, and provides

support for the hypothesis of active uptake of silica by plants (Lauwers & Heinen, 1974; Kaufman et al., 1981; Raven, 1983).

2- Pooideae phytoliths are dominant in all modern assemblages. The variations of the proportion of these types in samples taken from grassland to forest and shrubland assemblages are not sufficient enough to allow differentiation between the three vegetation types. However, the abundance of the crenate type appears more dependent on the percentage of Poaceae species occurring on a given plot. Shrubland and grassland assemblages show respectively low and high proportion of this type. This relation was not found between the other short cell phytolith types, and may be explained by differences in phytolith production between sub-families. This hypothesis would suggest that grass species settled in open areas would produce the crenate type in higher quantities than grass species growing in closed areas. However, statistical analysis of the relationships between grass phytolith type and grass species abundance did not show any correlation between the variables and does not provide any support for this hypothesis. A second hypothesis is that phytolith type production varies within a same species in indirect relation to the tree and shrub cover density.

Non-Pooideae grass subfamilies that may occur in the Mediterranean area (e.g. *Arundinoideae* grass subfamily) were not found in any of the studied plots. As phytolith analysis is unable to discriminate further than grass subfamilies, the studied assemblages show a homogeneous grass-cover. The same limitation will occur anywhere where the study site is located in a mono-subfamily grass cover.

3- One aim of this study was to examine if the phytolith index of tree cover density, commonly used in tropical studies (Alexandre et al., 1997; Alexandre et al., 1999; Barboni et al., 1999), may be used for Mediterranean vegetation reconstructions. Our results show that the rough spherical type, produce by ligneous dicotyledon, occurs at very low quantities in the oak forest and shrubland assemblages. When the smooth spherical types are added to the rough spherical types in the d/p index, as proposed by Delhon et al. (2003) the new index remains low and shows no relation to the tree cover density. This result suggests that oaks, whilst dominating the tree cover of the studied plots, do not produce the rough spherical phytolith type in sufficient quantities to be used as an indicator. This applies equally to the other dicot species observed on the plots. A review of phytolith studies from temperate and cool areas (Twiss, 1983; Tsutsuki et al., 1993; Fredlund & Tieszen, 1994; Fredlund & Tieszen, 1997b) shows that this type is absent from the reported phytolith assemblages, which strengthens the hypothesis of a low production of the rough spherical phytolith type by non-tropical dicot species. Albert et al. (1999; 2000) found a small proportion of spheroid scabrate

or verrucated phytoliths, similar to the rough spherical type, from samples taken both inside and outside of a cave in Israel (Mediterranean zone). However, the source of this phytolith type was not identified. As the studied oak groves were recently established (mainly within the last 50 years), the proportions of the rough spherical types may have been further reduced in the soil samples, as these would contain a record of phytolith deposition over a greater period of time.

Although most tropical woody dicotyledon species appear to produce the rough spherical type, this is not true of the North Mediterranean woody species. Therefore, care must be taken when using the d/p ratio for estimating tree cover density in the North-Mediterranean area. Further investigation of temperate and Mediterranean woody dicotyledon species producing this type is required to reach a better understanding of the meaning of the d/p phytolith ratio in non-tropical areas.

4- Our results show that the abundances of the spherical-with-sockets phytolith type cannot be used to identify the pinewood studied here, dominated by *Pinus halepensis*, *Pinus nigra* and *Pinus sylvestris*. A number of different pine phytolith types have been identified (Klein & Geis, 1977; Kondo et al., 1994; Kerns, 2001; Kerns et al., 2001; Blinnikov et al., 2002), some of which are morphologically similar to the spherical-with-sockets identified by Delhon et al. (2003) as a pine tracer. However, these were only observed in tissue and they may not be preserved in soil assemblages, due to selective dissolution and fragmentation in the litter. Further, as the spherical-with-sockets type does not have a distinct morphology and may be confused with other weathered phytolith types, comparisons must be made with care.

Kerns et al. (2001) studied soil phytolith assemblages under a pine forest dominated by *Pinus ponderosa*. The authors found high proportion of a “spiny body” phytolith type. S.E.M. photographs of this type show it to be similar to the “spherical-with-sockets” type. However the relation between the abundance of this type and pine cover is not clear. Further examination of modern assemblages collected under pinewoods of different age and dominant species is required before the reliability of the spherical-with-sockets phytolith type as a pine tracer can be assessed.

5- The heterogeneity of the vegetation physiognomy of the studied plots is mainly due to changes in the height and density of tree and shrub cover height instead of the composition of tree species. Such short distance changes in plant physiognomy are not reflected in the soil phytolith assemblages. This is mainly due to the absence of characteristic phytoliths produced by oaks, which dominate the studied site and are widespread in the Mediterranean area.

In addition, modern phytolith assemblages are representative of the vegetation composition over a period of many years. Examination of the vegetation dynamics over the last 100 years shows a change from an open to a closed vegetation. We assumed that modern phytolith assemblage from the first centimeter of soil humic horizons represent the vegetation dynamic during between a few years and a few hundred years. If soil samples record more than one hundred years of phytolith deposition, then the recent establishment of shrublands and pinewoods in this area may not be mirrored by phytolith assemblages. This may explain the lack of forest signal noted above. However, three oak groves are older than 100 years and should be recorded by phytolith assemblages. As they are not, we assume that these forests do not produce characteristic phytolith signal.

The different vegetation groups on the massif could not be distinguished using pollen analysis. The pollen spectra studied here record a regional vegetation signal, resulting from transportation of pollen by the strong and frequent winds which are characteristic of the area.

Conclusion

This first attempt at calibrating of modern soil phytolith assemblages with pollen and botanical data at a north Mediterranean site, has shown the following benefits and limitations of phytolith analysis for the reconstruction of Mediterranean vegetation:

Phytoliths are produced in sufficient quantities for analysis and are well preserved in limestone environments, widespread in the Mediterranean area. Examination of the phytolith record from soils and buried soils as well as from carbonaceous sediments may help to compensate for the current lack of continental paleoenvironmental records in this area. However, the phytolith index commonly used for tracing the tree cover density in tropical areas cannot be used in the Mediterranean domain without further confirmation of its reliability. Our study shows that young *Quercus ilex*, *Quercus coccifera* and *Quercus pubescens* which are widespread both today and during the Holocene in the North Mediterranean area, do not produce characteristic phytolith types in sufficient amounts to allow a reliable index to be calculated. Variations in the pine cover, dominated by *Pinus halepensis* and *Pinus sylvestris*, are also not recorded in the studied phytolith assemblages.

The phytolith assemblages are mainly composed of grass phytoliths and this provides some useful information on the grass cover. The proportion of Pooideae grasses relative to the non-grass species appears to be shown in the grass phytolith assemblages: grassland and shrubland assemblages can be distinguished by their proportion of crenate phytoliths. This relation needs

to be confirmed and explain by further studies on similar vegetation characterized by grass cover exclusively composed of Pooideae.

Finally, whilst phytolith analysis has been shown to be reliable for recording changes in the subfamilies form the grass cover in temperate, cold and inter-tropical areas, this technique appears to be of limited use for recording Mediterranean vegetation changes, which usually do not induce a sufficient change in grass cover. Further testing is required on modern assemblages originating from forests which have been in place for several centuries to further assess the ability of phytolith analysis to record the tree cover density in temperate and Mediterranean areas.

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CHAPITRE V. VERS L'INTEGRATION DE LA DYNAMIQUE DES BIOMES HERBACES DANS LES MODELES DE VEGETATION

V. 1. Définition des biomes "phytolithiques"

V. 1. 1 Matériels et Méthodes

Les quatre premiers chapitres ont permis de caractériser de façon ponctuelle des assemblages et des indices phytolithiques en relation avec une végétation donnée bien définie. Le but de ce chapitre est d'essayer de définir quels biomes herbacés et arborés sont correctement décrits en utilisant la totalité des assemblages phytolithiques modernes obtenus au cours de cette thèse.

Nous avons établi 6 biomes capables de décrire les grands types de végétation qui ont été échantillonnés, à savoir : 1) les pelouses dominées par des graminées en C₃ de la zone Méditerranéenne (Luberon) ainsi que celles d'altitude en Afrique de l'Est (monts Rungwe et Kenya), l'ensemble étant nommé "formation herbacée en C₃" ; 2) les savanes à graminées basses de la zone Sahélienne sont attribuées au biome "savane à graminées basses" ; 3) le biome "désert" inclut les formations herbacées désertiques de la zone Saharienne en Afrique de l'Ouest ainsi que celles du désert de Sonora au Mexique ; 4) les savanes à graminées hautes de la zone Soudanienne de l'Afrique de l'Ouest et celles des flancs du mont Rungwe sont attribuées au biome "savane à graminées hautes" ; 5) les savanes à graminées hautes plus fortement arborées que celles de la zone Soudanienne correspondant à la forêt claire autour du lac Masoko (Tanzanie) ainsi qu'à la savane incluse à Kandara (Cameroun) sont attribuées au biome "savane arborée à graminées hautes" ; 6) les forêts tropicales, essentiellement échantillonnées à Kandara appartiennent au biome "forêt tropicale". Ces types de végétation potentielle, ou biomes, ont été définis à l'aide de leur appartenance aux zones bioclimatiques définies par White (1983), ainsi qu'à l'aide de la classification des végétations africaines de Yangambi (CSA, 1956), et de la connaissance précise des végétations que nous pouvions avoir pour certains échantillons. Le tableau V.1. présente la correspondance des 6 biomes avec les zones bioclimatiques de White (1983) et la physionomie des végétations selon Yangambi (CSA, 1956) pour l'Afrique.

La méthode employée pour attribuer un biome d'après un assemblage phytolithique est la même que celle utilisée dans le chapitre II. L'analyse discriminante (Tomassone et al., 1988) a été utilisée pour estimer les meilleures variables prédictives (types ou groupes de types de phytolithes) capables d'assigner les relevés à un ou l'autre des biomes précédemment décrits. Plusieurs séries de tests ont été faites avec différentes variables. Par exemple, l'ensemble des 14 types phytolithiques comptés (voir annexe V.1), ou bien uniquement les phytolithes ayant

une valeur taxonomique évidente (voir classification retenue en chapitre I), ou encore les indices phytolithiques Iph, Fs, Ic et D/P.

Finalement, cinq variables ont été retenues : 1) le type "sphérique rugueux" produit par les dicotylédones ligneux, (Variable *arbres*) ; 2) la somme des types produits par les Panicoideae ("haltère" et "croix") (Variable *Panicoid*) ; 3) le type "selle" qui est produit par les Chloridoideae (Variable *Chloridoid*) ; 4) la somme des types produits essentiellement par les Pooideae ("uni-lobé", "poly-lobé" et "rectangle") (Variable *Pooid*) ; 5) les cellules bulliformes silicifiées (type "éventail") (Variable *Bulliforme*). Le choix de ces variables s'est fait d'une part parce qu'elles avaient les meilleurs résultats en terme de pourcentage de relevés correctement prédits et d'autre part parce que ce sont des types phytolithiques ayant une valeur taxonomique reconnue (voir chapitre I). Le pourcentage initial, c'est à dire établi sur les 14 types de phytolithes comptés, n'est pas recalculé ; la somme des variables utilisées ne fait donc pas 100%.

La première étape, celle de calibration, consiste à attribuer un biome "à priori" à chacun des échantillons en fonction de leur appartenance aux types de végétation précédemment décrits. L'analyse discriminante permet alors de calculer, pour chaque biome, une fonction discriminante qui est une combinaison linéaire des cinq variables prédictives. Cette calibration est faite sur les 156 échantillons qui ont été présentés dans les 4 chapitres précédents (43 appartiennent au biome "formation herbacée en C₃" ; 24 au biome "savane à graminées basses" ; 14 au biome "désert" ; 41 au biome "savane à graminées hautes" ; 15 au biome "savane arborée à graminées hautes" et 19 au biome "forêt tropicale"). Un seul échantillon, prélevé à Kandara dans une zone marécageuse recouverte de palmiers, a été exclu de l'analyse parce qu'un unique exemplaire pris sous ce type de végétation.

La deuxième étape consiste à valider ces coefficients. Pour cela on effectue une nouvelle analyse discriminante sur 75% des échantillons. Un échantillon sur 4 est exclu pour chacun des biomes. Les 25% restants ne sont assignés à aucun des biomes "a priori". Ils n'ont donc pas d'influence sur le calcul des fonctions discriminantes, mais ces dernières leur sont appliquées ce qui permet de calculer le biome le plus probable et chacune des probabilités d'appartenir à chacun des 6 biomes.

L'annexe V. 2 présente les pourcentages des 5 variables pour l'ensemble des échantillons ainsi que le biome qui leur est attribué.

Biomes "Phytolithiques"	Zones bio-climatiques (white, 1983)	Principaux type de végétation selon White (1983)	Physionomie de la végétation selon Yangamby (CSA, 1956)
Formation herbacée en C ₃	-	Formation herbeuse, végétation altimontaine en Afrique tropicale	Prairie altimontaine
Désert	Saharienne	Dunes désertiques à végétation pérenne; Reg, hamadas et wadis; Formation herbeuse et arbustive semi-désertique	Steppe buissonnante; Steppe herbacée et/ou graminéenne
Savane à graminées basses	Sahélienne	Formation herbeuse boisée et buissonnante	Savane herbeuse, savane arbustive, savane arborée
Savane à graminées hautes	Soudanienne	Forêt claire soudanienne	Savane arbustive, savane arborée, savane boisée
Savane arborée à graminées hautes	Zambésienne	Forêt claire zambézienne de type Miombo	Forêt claire
Forêt tropicale	Guinéo-Congolaise	Forêt ombrophile planitiaire	Forêt dense humide semi-décidue

Tableau V. 1. Correspondance des biomes "phytolithiques" avec les zones bioclimatiques de White (1983) et la physionomie des végétations selon Yangambi (CSA, 1956) pour l'Afrique.

V. 1. 2 Résultats et discussion

Les tests ont rapidement montré que le biome "désert" qui est attribué aux formations herbacées de la zone Saharienne et du désert de Sonora n'était au mieux défini que pour 64% des échantillons. Alors que nous montrons au chapitre II que ce biome est bien défini lorsqu'il est calibré sur les seuls échantillons west-africains, nous pouvons invoquer deux raisons pour expliquer la difficulté à le définir à partir d'un échantillonnage plus large : (1) Si les échantillons issus de la zone désertique africaine sont caractérisés par une très forte proportion de cellule bulliformes silicifiées, parce que l'abondance de ce type de phytolithe est fortement liée au stress hydrique exprimé par le AET/PET, nous supposons aussi qu'en zone très humide et chaude (par exemple en Tanzanie, à Masoko), l'évapotranspiration élevée des plantes va également en favoriser la production. Ainsi, lorsque l'ensemble des échantillons est utilisé pour le calcul des coefficients des fonctions discriminantes, il devient difficile de séparer ces deux sources et la fonction discriminante du désert devient moins prédictive. (2) Les assemblages phytolithiques du désert de Sonora, seuls autres échantillons désertiques que nous possédons, sont singuliers car ils ont des Pooideae dans les graminées dominantes (Turner & Brown, 1994). Cette sous-famille semble produire pas ou peu de cellules bulliformes silicifiées d'après ce que nous observons dans les assemblages du Luberon (chapitre III), ainsi que dans les assemblages modernes de Nouvelles Zélande (Kondo et al., 1994; Prebble et al., 2002). Ceci expliquerait pourquoi les assemblages du désert de Sonora ont des proportions de cellules bulliformes silicifiées plus faibles que ceux de la zone Saharienne ouest-africaine et sont parfois assignés au biome "savane à graminées basses".

Par ailleurs cette analyse discriminante fournit de bons résultats pour les autres biomes, à savoir la "savane à graminées hautes", la "savane arborée à graminées hautes" et la "forêt tropicale".

Avant de passer à la deuxième étape, nous avons exclu la variable "cellules bulliformes silicifiées" (type "éventail") ainsi que le biome "désert". Les échantillons qui étaient assignés à priori au biome "désert" ont été attribués au biome "savane à graminées basses" puisque la zone Saharienne et le Désert de Sonora sont également caractérisés par des formations herbacées basses. Par contre cette dénomination ne tient pas compte des différences de composante arborée qui existe avec la zone Sahélienne.

Le tableau V. 2. présente l'étape de calibration sur la totalité des échantillons, Les cinq fonctions discriminantes sont représentées par les coefficients des quatre variables. La qualité de la calibration est donnée par le pourcentage des échantillons correctement assignés.

CALIBRATION

(a) Fonction

		FtHerbC ₃	SavGramBas	SavGramHau	SavArbGramHau	ForTrop
	%	0.29	0.24	0.24	0.1	0.12
Arbres		0.37	0.28	0.39	1.19	2.16
Panicoideae		0.30	0.15	0.31	0.26	0.26
Chloridoideae		0.13	0.66	0.18	0.14	0.33
Pooideae		0.72	0.16	0.26	0.25	0.30
Constant		-30.74	-9.55	-11.98	-26.97	-75.57

(b) Probabilités

		FtHerbC ₃	SavGramBas	SavGramHau	SavArbGramHau	ForTrop
	%	0.29	0.24	0.24	0.1	0.12
FtHerbC ₃	89	41	0	5	0	0
SavGramBas	92	0	35	3	0	0
SavGramHau	84	1	3	32	2	0
SavArbGramHau	87	0	0	1	13	1
ForTrop	100	0	0	0	0	19
Total	90	42	38	41	15	20

Formation herbacée en C₃ : FtHerbC₃

Savane à graminées basses : SavGramBas

Savane à graminées hautes : SavGramHau

Savane arborée à graminées hautes : SavArbGramHau

Forêt tropicale : ForTrop

Signification des variables

Arbres: sphérique rugueux

Panicoid: croix et haltère

Chloridoid: selle

Pooid: uni-lobé, poly-lobé et rectangle

Tableau V. 2. (a) coefficient des 4 variables (colonne) pour les 5 fonctions discriminantes, une par biome (ligne); **(b)** % : nombre d'échantillons par biome et % d'échantillons correctement assignés.

L'étape de validation résumée au tableau V. 3. présente pour les cinq fonctions discriminantes calibrées sur 75% des échantillons, le pourcentage des échantillons de calibration correctement assignés, et la probabilité pour les 25% restants d'être assignés à un des 5 biomes. Cette seconde étape correspond à la validation de la fonction discriminante.

VERIFICATION

(a) Fonction

		FtHerbC3	SavGramBas	SavGramHau	SavArbGramHau	ForTrop
	%	0.29	0.24	0.24	0.09	0.13
Arbres		0.41	0.30	0.39	1.19	2.22
Panicoideae		0.32	0.15	0.30	0.26	0.25
Chloridoideae		0.10	0.72	0.21	0.17	0.37
Pooideae		0.76	0.16	0.27	0.26	0.33
Constant		-33.05	-10.53	-11.84	-26.44	-77.90

(b)

		FtHerbC3	SavGramBas	SavGramHau	SavArbGramHau	ForTrop
	%	0.29	0.24	0.24	0.09	0.13
FtHerbC3	91	32	0	3	0	0
SavGramBas	89	0	25	3	0	0
SavGramHau	86	1	2	25	1	0
SavArbGramHau	82	0	0	1	9	1
ForTrop	100	0	0	0	0	15
Total	90	33	27	32	10	16

(c)

		FtHerbC3	SavGramBas	SavGramHau	SavArbGramHau	ForTrop
	%					
FtHerbC3	82	9	0	2	0	0
SavGramBas	70	0	7	3	0	0
SavGramHau	89	0	0	8	1	0
SavArbGramHau	100	0	0	0	4	0
ForTrop	100	0	0	0	0	4
Total	88	9	7	13	5	4

Formation herbacée en C₃ : FtHerbC₃
 Savane à graminées basses : SavGramBas
 Savane à graminées hautes : SavGramHau
 Savane arborée à graminées hautes : SavArbGramHau
 Forêt tropicale : ForTrop

Signification des variables
 Arbres: sphérique rugueux
 Panicoid: croix et haltère
 Chloridoid: selle
 Pooïd: uni-lobé, poly-lobé et rectangle

Tableau V.3. (a) et (b) calibration sur les 75% de 156 échantillons. **(a)** coefficient des 4 variables pour les 5 fonctions discriminantes ; % : nombre d'échantillons par biome; **(b)** matrice d'assignation pour tout les biomes et (%) d'assignations correctes. **(c)** résultats d'assignation pour les 25% d'échantillons qui n' étaient assignés à aucun des biomes "a priori".

Le biome "formation herbacée en C₃" est correctement prédit par les assemblages phytolithiques puisque 89% des échantillons sont correctement assignés lors de la calibration et 82% lors de la vérification. Les échantillons mal décrits proviennent du sommet du Mont Rungwe (RGW 24 et RGW 27) et du Mont Kenya (LM 1-2, UM 1-2 et UM 3-1). Ils sont en effet attribués au biome "savane à graminées hautes" du fait de la grande quantité de phytolithes de type "haltère", produits par les Panicoideae. Le fait que les 31 assemblages phytolithiques du Luberon en zone tempérée ne présentent aucun type de phytolithe produit par les Panicoideae entraîne une sous-estimation du coefficient de la variable "Panicoid" dans la fonction discriminante "formation herbacée en C₃". La création d'un biome intermédiaire entre C₃ et C₄ est par conséquent à envisager.

Le biome "savane à graminées basses" est correctement décrit par les assemblages phytolithiques puisque 92% des échantillons sont bien assignés lors de la calibration et 70% lors de la vérification. Les échantillons mal assignés (83-65 ; S.88 ; S.122) proviennent essentiellement de la zone Saharienne de l'Afrique de l'Ouest. Ils sont attribués au biome "savane à graminées hautes" du fait d'une proportion plus importante de phytolithes produits par des Panicoideae que dans les autres échantillons de la même zone. La présence de *Panicum turgidum* (Panicoideae pérenne, (Le Houérou, 1993a)) en domaine Saharien peut expliquer ce problème que l'on ne rencontre d'ailleurs pas pour les échantillons du désert de Sonora au Mexique.

Le biome "savane à graminées hautes" est bien prédit par les assemblages phytolithiques pour 84% des échantillons (89% pour le jeu de vérification). Il est envisageable que les deux échantillons assignés au biome "savane arborée à graminées hautes" (S 91 et 83-127) ne soient pas mal assignés par les assemblages phytolithiques mais plutôt mal qualifiés "a priori". En effet, l'attribution "a priori" de ces biomes est faite pour l'ensemble des échantillons de l'Afrique de l'Ouest à l'aide de leur appartenance aux zones bioclimatiques de White (1983), ce qui ne permet pas de bien différencier certains échantillons qui auraient pu être prélevés sous un couvert arboré plus important. C'est le cas par exemple de l'échantillon 83-127 qui provient de la forêt claire Soudanienne et présente un AP (Arboreal Pollen) proche de 35%, le plus élevé de cette zone (Lezine, 1987).

Le biome "savane arborée à graminées hautes" est bien prédit puisque que 87% et 100% des échantillons sont correctement assignés lors de la calibration et de la vérification. Les deux

échantillons mal prédits lors de la calibration sont assignés à un biome plus ou moins boisé (i.e. "savane à graminées hautes" ou "forêt tropicale").

Le biome "forêt tropicale" est parfaitement prédit puisque l'ensemble des échantillons sont bien assignés. Toutefois, l'excellence de ce résultat par rapport aux autres biomes est certainement due au fait que l'attribution des biomes "a priori" a pu se faire de façon plus précise puisqu'à Kandara et à Masoko la végétation actuelle où ont été prélevés les échantillons était parfaitement connue (voir chapitre II et III).

Nous avons montré dans ce chapitre que les assemblages phytolithiques modernes étudiés dans cette thèse ont non seulement la capacité de renseigner le biome local auquel ils appartiennent mais qu'ils permettent aussi d'appliquer les relations définies à des échelles locales sur d'autres sites géographiquement très éloignés. Nous avons proposé 5 biomes phytolithiques: "formation herbacée en C₃", "savane à graminées basses", "savane à graminées hautes", "savane arborée à graminées hautes" et "forêt tropicale" qui caractérisent correctement plus de 95% des 156 échantillons étudiés. Il est cependant nécessaire d'échantillonner d'autres sites désertiques pour permettre une meilleure différenciation entre les savanes à graminées basses, les pelouses et les steppes désertiques comme l'avons suggéré au chapitre I.

V. 2. Intégration des données phytolithiques aux méthodes de biomisation polliniques : perspectives

Les 5 biomes phytolithiques qui sont proposés dans cette étude apportent une information complémentaire à ceux définis par les données polliniques : la composante graminéenne. D'après les nombreux assemblages phytolithiques modernes confrontés aux données polliniques présentés dans cette étude, nous pouvons attribuer des correspondances entre les biomes phytolithiques et polliniques. Le tableau V. 4. met en correspondance les deux types de biomes qui ont été observés pour les mêmes sites d'échantillonnage. Les dénominations des biomes polliniques sont établies d'après Peyron et al. (1998) et Prentice et al. (2000b). Un biome phytolithique correspond à un ou deux biomes polliniques. La précision est plus faible pour les biomes phytolithiques simplement parce que à l'exception des formations herbacées dominantes, la précision taxonomique de la végétation est plus restreinte que celle des pollens. De la même façon qu'est proposée l'analyse discriminante sur les assemblages

phytolithiques, il serait envisageable de faire une analyse discriminante en intégrant les pollens. Il faudrait, pour cela redéfinir une nouvelle biomisation où le type fonctionnel de plante (Pft) correspondant à "grass" dans les spectres polliniques serait subdivisé en graminées en C₃, graminées hautes en C₄ et graminées basses en C₄ selon les proportions des types phytolithiques correspondants. Une méthode plus probabiliste, telle que celle introduite par Gachet et al. (2003) pour la végétation tempérée, permettra certainement une approche plus rigoureuse, mais rien n'a encore été envisagé pour son application à la végétation tropicale.

Biome Phytolithique	Biomes Polliniques
Formation herbacée en C ₃	Forêt tempérée décidue + Forêt mixte chaude
Savane à graminées basses (+Désert)	Steppe + Désert
Savane à graminées hautes	Formation tropicale xérophytique + Savane
Savane arborée à graminées hautes	Savane
Forêt tropicale	Forêt tropicale décidue

Tableau V. 4. Correspondance entre biomes phytolithiques et polliniques observés sur l'ensemble des sites d'études. Les dénominations des biomes polliniques sont établies d'après Peyron et al. (1998) et Prentice et al. (2000).

V. 3. Perspectives pour l'amélioration des modèles prédictifs de végétation

Cette étude montre que l'analyse phytolithique permet d'estimer des paramètres descriptifs des végétations et particulièrement concernant les formations herbacées intertropicales : Graminées en C₄ hautes et en C₄ basses, couvert arboré (LAI) et rapport des graminées en C₃/C₄, ainsi qu'un paramètre climatique : AET/PET en zone inter-tropicale sèche. Ces paramètres sont couramment simulés par les modèles de végétation. C'est le cas notamment du modèle LPJ-GUESS (Sitch et al., 2003) qui simule LAI, AET et PET (voir figure V. 1 Poster présenté au "NCCR Climate's summer school 2003"). Nous avons entrepris (étude en cours) d'utiliser ce modèle pour simuler la composition de la végétation en Afrique durant l'Holocène moyen (6000 ans BP) et de confronter les sorties du modèles avec des marqueurs paléo-environnementaux. L'utilisation de ce genre de modèle dynamique peut permettre de mieux comprendre la sensibilité des écosystèmes aux changements climatiques tels que des

variations de précipitations, la durée de la saison sèche ainsi que des perturbations telle que la fréquence des feux. La première étape a été de calibrer le modèle sur des données de végétations actuelles. Pour cela, quatre sites, depuis l'équateur jusqu'à 15°N ont été étudiés (un en forêt tropicale dense, un en forêt semi-décidue, un en forêt décidue et un en savane à graminées basses). Pour chacun des sites, des Pfts polliniques modernes ont été estimés suivant la méthode de biomisation de Jolly et al. (1998) et Peyron (2000) (voir aussi chapitre II) et confrontés aux Pfts estimés par GUESS pour les conditions climatiques actuelles. Le LAI total du site estimé par GUESS a également été confronté aux mesures satellitales moyennes de LAI des 20 dernières années (Myneni et al., 1997). La deuxième étape, celle de validation a été d'estimer la composition des Pfts sur 10 autres sites et de les confronter aux Pfts polliniques. Les estimations du modèle et les caractéristiques de la végétation traduites par les pollens sont en accord sur la majorité des sites. La dernière étape a été d'appliquer les conditions climatiques à 6000BP estimées par PMIP (Joussaume et al., 1999) au modèle GUESS et de confronter les sorties avec les données polliniques. Les premiers résultats montrent que le modèle simule des végétations plus arides que celles enregistrées avec les pollens confirment ce qui a été mis en évidence par Joussaume et al. (1999) et bien d'autres études, à savoir que les modèles climatiques ne sont pas capables de rendre suffisamment compte de l'intensification de la mousson dans cette région d'étude. Le modèle, comme les pollens, montre que les formations herbacées étaient certainement beaucoup plus étendues qu'à l'actuel.

Les données phytolithiques n'ont pour l'instant pas été prises en compte puisque nous ne disposons que d'un seul site avec des assemblages modernes, mais la prochaine étape sera de simuler la végétation du bassin de Masoko (voir chapitre IV) et de confronter les simulations de GUESS avec les assemblages phytolithiques (Alvarado, 2003) et polliniques fossiles (Vincens, en cours). Le LAI estimé par les phytolithes pourra être directement confronté au LAI des Pfts forestiers estimés par GUESS. D'autre part, la proportion des herbacées en C₃ et C₄ simulée par GUESS pourra alors être confrontée à celle estimée par les phytolithes, ce qui n'est pas envisageable avec les pollens.

Relationships between climate change and African ecosystems using vegetation model GUESS

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INTRODUCTION

To estimate the likely current effect of climate change, we need to refer to changes that have occurred in the past and that would be close to those expected in the future. Among past periods, Holocene (ca 6000 yr BP) has been the most comparable period to now. Ecosystem functioning crosses all time scales from hourly to annual processes but the result known as the ecosystem dynamics behaves at the century time scale. Therefore, vegetation dynamics modeling is a very useful tool in analyzing long-term processes and their impacts.

The aim of this study is to use the LPJ-GUESS (General Ecosystem Simulator) model to simulate the natural ecosystem composition that has occurred in Africa at 6000 yr BP and to understand the sensitivity of ecosystem structure to climate change.

Global Plant Functional Types are first calibrated and validated to better assess the current vegetation composition variability.

Holocene climate scenarios are then tested.

MATERIAL & METHODS

1. Model Presentation

LPJ-GUESS combines individual-level detailed modeling of population dynamics with generalized representations of photosynthesis, respiration, allocation of assimilated carbon, and water and carbon exchange between soil, plant and atmosphere compartments (Fig. 1).

2. Data Inputs & outputs

- Vegetation: described as PFT with associated parameters.
- Climatic data: monthly precipitation, mean air temperature, and cloudiness for the 1901-1998 period from the CRU database.
- Soil: described in the LPJ database from the FAO classification.

3. Strategy

- Calibration on 4 sites from the Equator to 15°N to be representative of evergreen forest, deciduous forest, savanna, and arid grassland, respectively (White 1983).
- Ecosystem functioning described with the simulated Leaf Area Index (LAI) is compared to remotely sensed LAI available for the region over the last two decades (Myneni et al., 1997).
- Vegetation composition is compared to surface pollen records.

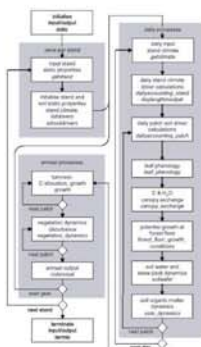


Figure 1. LPJ-GUESS structure from Smith et al. (2001)

Validation computed using 10 independent sites from the calibration step, and from which current pollen records provide a good proxy of the vegetation. Vegetation composition is compared to surface pollen records.

Holocene scenario extracted from the PMIP project (Jousseume et al. 1999) and applied to all sites in order to analyze shifts in vegetation composition, and to 10 new sites from which Holocene pollen records are available. This tested PMIP Holocene scenario uses [CO₂]=280 ppmv.

RESULTS

Calibration of LPJ-GUESS

Shade and drought tolerances: main sets of variables calibrated through the sapwood turnover, the root distribution, and the maximum evapotranspiration rate. The fire module has been implemented and the susceptibility to burn has been increased to allow fire to spread in African ecosystems. Calibrated values differ significantly from the original global PFT values.

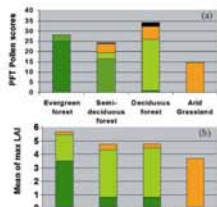
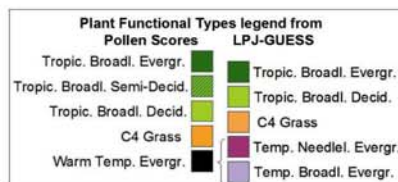


Figure 2. Comparison between the relative proportion of PFT pollen scores from surface sediment cores (a) and LAI outputs from GUESS (b)

In terms of vegetation composition, scores of pollen PFT and predicted LAI by GUESS show similar relative proportion of PFT excepted for the Semi-deciduous forest (Fig. 2).



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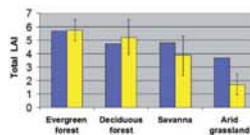


Figure 3. Comparison between total LAI predicted from GUESS (blue) and total LAI observed from remote sensing over the two last decades (yellow)

Predicted and Observed LAI present decreasing trends from the evergreen forest to the grassland with no significant difference within paired sites excepted for grasslands, which present significantly higher predicted values from LPJ-GUESS than observed from remote sensing (Fig. 3).

Validation of LPJ-GUESS

Comparisons between surface field pollen records and simulated LAI show good agreement in the functioning and the composition of the vegetation over the African tropics (Fig. 4a,b) with:

- 2 evergreen forests: GA2B and G10M
- 3 deciduous forests: BAMB, NYOS and NAWF
- 1 arid grassland site: TTDJ

4 sites present slight differences between both approaches. CO01 and EJAG are semi-deciduous forests for pollen records and deciduous forest for GUESS, while OHEE and OPII are deciduous forests for pollens and woody savannas for GUESS.

Only 3 sites present significant differences between predicted total LAI and remote sensed total LAI (Fig. 4c). In these cases, Total LAI predicted by GUESS is overestimated as compared to the remote sensed observation.

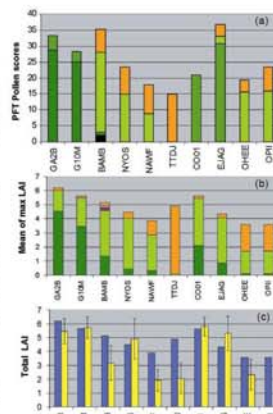


Figure 4. Comparison between the relative proportion of (a) current PFT pollen scores from surface sediment cores and (b) current LAI outputs from GUESS. (c) compares total LAI predicted from GUESS (blue) with total LAI observed from remote sensing over the two last decades (yellow).

Holocene climate and vegetation changes.

Through pollen records (Fig. 5a), Holocene vegetation between the Equator and 5°N was Semi-deciduous forest as compared to the current evergreen forest in place (White 1983). In the same way, current grasslands and woody savannas between 12°N and 14°N were already in place at 6000 yrs BP, whereas current desert sites northern to 15°N were more vegetated (from grassland to woody savannas).

Excepted for the true grassland sites (TJER, ARIK, ACHE, TIBE, TINT), all other predicted ecosystem compositions from GUESS (Fig. 5b) using the PMIP scenario #1 are significantly drier than expected from the pollen records with a woody savanna and a deciduous forest instead of semi-deciduous forests, and grasslands everywhere else.

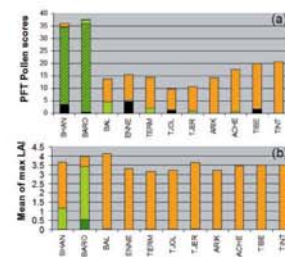


Figure 5. Comparison between the relative proportion of PFT pollen scores from Holocene sediment cores (a) and LAI outputs from GUESS using the PMIP project climate scenario (b)

DISCUSSION – CONCLUSION

Different Holocene climate scenarios (change in precipitation amount or seasonality), first selected to favor ecosystem dryness (to fit the shift from current evergreen to Holocene semi-deciduous forest), were rejected due to predicted composition even drier than the tested PMIP scenario. A likely explanation of this overestimated dryness is the northwards shift of monsoon towards Sahara desert at 6000 years BP to predict the Green Sahara (Jousseume et al. (1999) and seen in this study with grassland sites). However, this northward shift decreases southern precipitation which become deficient near the Equator. To fit the semi-deciduous forest composition from pollen record, precipitation in the current version of PMIP needs to be multiplied by 2 rather than decreased by 10 to 20% as suggested in the current version of PMIP. For drier regions where at least one extra dry month exists during Holocene as compared to current climate, the change in the PMIP would need to remove all dry months and at least multiply precipitation by a factor 3.

The good agreement between surface pollen compositions and predicted compositions from GUESS is a good starting point to deeper explore the changes in past vegetation composition due to climate changes, and there is a need to better assess the past climate.

CONCLUSIONS ET PERSPECTIVES

Les phytolithes sont un outil de reconstruction paléo-environnementale couramment utilisé puisque leur qualité de conservation et leurs potentialités à tracer les formations herbacées sont reconnues. Cependant, il semble que les étapes initiales qui consistent à établir une base de référence actuelle et à contraindre correctement l'enregistrement phytolithique avec des caractéristiques végétales ou climatiques n'aient pas été réellement faites. L'objectif de cette thèse était de commencer à combler cette lacune en établissant des fonctions de transfert entre des assemblages phytolithiques modernes et des paramètres descriptifs de la végétation, ceci pour des régions géographiques et climatiques distinctes, situées en zone intertropicale et en zone méditerranéenne, et présentant une ou plusieurs caractéristiques physiognomiques *a priori* traçables par les phytolithes. Nous avons également choisi d'orienter chacune des parties de cette thèse sur la calibration d'indices phytolithiques.

Afin d'envisager l'intégration des données phytolithiques aux méthodes de reconstitution des végétations, qui utilisent des marqueurs comme la méthode de biomisation pollinique (Jolly et al., 1998), des biomes herbacés, décrits par les phytolithes, ont été définis et confrontés aux biomes polliniques.

L'étude de soixante-deux assemblages phytolithiques modernes prélevés le long d'un gradient d'aridité croissante sud-nord au Sénégal et Mauritanie, à travers quatre zones bioclimatiques définies par White (1983) (Guinéenne, Soudanienne, Sahélienne et Saharienne) a démontré que les savanes à graminées basses (dominées par la sous-famille des Chloridoideae) et les savanes à graminées hautes (sous-famille Panicoideae) peuvent être différenciées à l'aide de l'indice **Iph** pour une valeur seuil fixée à $20 \pm 1.4\%$. Utilisé conjointement avec la proportion de cellules bulliformes silicifiées (indice **Fs**), cet indice est un bon indicateur du stress hydrique subit par la formation herbacée. Ceci nous permet de proposer une fonction de transfert pour estimer le rapport AET/PET. La fiabilité de cette fonction de transfert est très satisfaisante, comparable à la fiabilité des estimations fournies par les pollens pour la même zone.

Cette fonction de transfert ne reste pour l'instant applicable qu'aux zones Guinéenne, Soudanienne, Sahélienne et Saharienne c'est à dire pour des valeurs de AET/PET comprises entre 0.1 et 0.45. En perspective, une nouvelle fonction de transfert sera mise en place pour le domaine intertropical plus humide, en tenant compte par exemple de la couverture arborée qui augmente avec l'humidité.

En domaine tempéré, où la température joue un plus grand rôle sur la distribution des graminées que le AET/PET, c'est la fonction de transfert proposée par Fredlund et Tieszen (1997b) qui devra être appliquée et vérifiée sur d'autres aires géographiques telle que la Chine où de nombreux assemblages modernes pourront être utilisés (Wang & Lyu, 1992).

Pour la première fois en zone inter-tropicale, une fonction de transfert est calibrée entre des indices phytolithiques et le AET/PET. Ce rapport est un paramètre couramment utilisé pour contraindre la distribution des végétations aux échelles continentales et globales (Prentice et al., 1992; Sykes et al., 1996). L'estimation du AET/PET dans des enregistrements fossiles offrira une meilleure connaissance du climat passé, ce qui pourra être directement utilisé comme paramètre d'entrée de certains modèles de végétation.

L'indice **Ic**, qui permet de tracer les formations herbacées C₃ et C₄ dans les Grandes Plaines Américaines (Twiss, 1992), a été étudié à l'aide d'échantillons inter-tropicaux pris le long d'un transect altitudinal en Afrique. Le site d'étude avait été choisi *a priori* parce que des études botaniques y montraient une transition C₄/C₃ des graminées avec l'élévation de l'altitude. Cette étude montre que le **Ic** est un bon traceur de la proportion des Pooideae et Arundinoideae (uniquement C₃) par rapport aux Panicoideae (C₃ et C₄) mais qu'il n'est par contre pas sur cette zone d'étude un traceur de la proportion en C₃/C₄ des graminées. Ceci parce que les échantillons du Mont Kenya ont été prélevés dans une zone où les Panicoideae, habituellement à cycle photosynthétique en C₄, sont ici en C₃.

Si l'on considère que 80% des Panicoideae sont en C₄ et que les 20% en C₃ sont inféodées à des milieux précis pouvant être identifiés, alors nous pouvons affirmer que cet indice est potentiellement un bon traceur de la domination des Poaceae en C₄ ou C₃. Des échantillons supplémentaires issus de la même zone d'étude permettront d'établir une relation précise entre cet indice et les proportions des différentes sous-familles. D'autres échantillons issus d'une zone où la transition graminéenne C₄/C₃ est effectivement observée permettront quant à eux de vérifier la précision de l'indice **Ic** en tant que traceur potentiel du rapport graminéen C₃/C₄.

Lorsque le domaine d'application de cet indice sera plus précisément connu, nous pourrons alors confronter cet indice avec les sorties du modèle de végétation LPJ-GUESS par exemple, dont les variables de sortie distinguent la réponse des graminées en C₃ et C₄ (Sitch et al., 2003), permettant ainsi le calcul du rapport C₃/C₄ des graminées.

L'étude menée à Kandara au Cameroun montre que les assemblages phytolithiques et l'indice **D/P** permettent d'enregistrer précisément les successions de végétation depuis une savane à graminées hautes jusqu'au cœur d'une forêt semi-décidue mature. Nous montrons que l'indice **D/P** est un bon traceur de la densité du couvert arboré en dicotylédones ligneuses de la zone inter-tropicale. Pour la première fois, et contrairement aux autres études, ce travail permet d'établir une fonction de transfert pour estimer quantitativement l'indice foliaire ou LAI, paramètre clé du fonctionnement des peuplements forestiers.

Cette fonction de transfert doit être vérifiée pour des forêts tropicales plus denses. D'autre part, ses limites d'applications doivent être déterminées, notamment en forêt tropicale d'altitude.

L'estimation du LAI par les phytolithes est un paramètre du peuplement forestier très intéressant à simuler puisque c'est une sortie de très nombreux modèles de végétation. La relation établie sera appliquée aux assemblages d'une carotte lacustre de la zone intertropicale. Les valeurs estimées de LAI seront confrontées à celles simulées par le modèle de végétation LPJ-GUESS.

D'après notre étude conduite en domaine méditerranéen (Luberon) et les études menées par d'autres auteurs sur des assemblages phytolithiques en domaine tempéré, il semble que cet indice **D/P** ne soit pas utilisable pour caractériser les formations arborées tempérées. Cependant, cette hypothèse invalidant cet indice n'est issue que d'une seule étude. Les zones arborées que nous avons étudiées sont essentiellement buissonnantes, la perspective de ce travail sera d'échantillonner des forêts matures, en place depuis plusieurs décennies pour essayer de vérifier si cet indice peut tout de même tracer certains types de forêts méditerranéennes, et plus généralement tempérées.

L'analyse des assemblages phytolithiques en terme de biomes permet de se rapprocher des méthodes "polliniques". Plusieurs biomes définis par leur composante herbacée sont proposés, à savoir les biomes : "formation herbacée en C₃", "savane à graminées basses", "désert", "savane à graminées hautes", "savane arborée à graminées hautes" et "forêt tropicale". Tous les biomes sont correctement prédits sur les zones d'études où ils sont définis. Les pourcentages de bonnes attributions sont équivalents à ceux obtenus par les données polliniques seules, tout en permettant une plus grande résolution dans la définition des biomes herbacés là où l'approche pollinique atteint ses limites. Ces assemblages phytolithiques

offrent donc une information complémentaire à celle fournie par les pollens. Les phytolithes présentent également l'avantage de se disperser par le vent sur une moins grande distance en zones ouvertes comparativement aux pollens. De plus notre méthode a un réel potentiel dans les zones oxydantes où les pollens ne sont pas conservés.

Cependant, le nombre d'assemblages modernes à notre disposition par biome est insuffisant pour que chaque biome soit défini de manière définitive et extrapolable de façon systématique. A titre indicatif, les échantillons polliniques actuels, utilisés en référence par Prentice et al. (2000b) pour établir une carte mondiale des végétations (biomes) durant l'Holocène moyen (6000 ¹⁴C ans BP) et le dernier maximum glaciaire (18000 ¹⁴C ans BP) à l'exception de l'Amérique du Sud et de l'Australie, sont répertoriés sur la figure Ca. L'ensemble des échantillons phytolithiques actuels utilisés dans cette thèse sont quant à eux reportés dans la figure Cb. Sont également reportés tous les sites d'études publiés qui proposent des assemblages phytolithiques actuels établis de la même façon que celle proposée par Fredlund et Tieszen. (1994). Toutefois, l'inexistence d'une base de données phytolithiques internationale, telles que celles accessibles pour les pollens, peut nous avoir conduit à oublier certains des assemblages actuels.

Les cartes des figures Ca. et Cb. illustrent l'état des références phytolithiques actuelles disponibles, et de fait, la grande difficulté à extrapoler les résultats obtenus d'une région à une autre. Cependant, ces cartes suggèrent aussi les formidables perspectives d'étude des différentes formations herbacées restant à caractériser à l'aide des phytolithes. C'est le cas notamment des steppes froides et des zones désertiques qui représentent de très grandes superficies et qui n'ont pas ou pas bien pu être abordées au cours de cette étude.

Le faible nombre d'études d'assemblages modernes est aussi imputable à la lourdeur des manipulations d'extraction. Les 2-3 mois nécessaires à l'extraction d'un petit nombre d'échantillons sont un frein à l'utilisation de cet outil. De nouvelles techniques, notamment l'utilisation de fours à micro-ondes pour accélérer la destruction de la matière organique (Parr, 2002), doivent être explorées plus avant pour réduire les temps de manipulations et augmenter les potentialités des phytolithes en tant que marqueur paléo-environnemental.

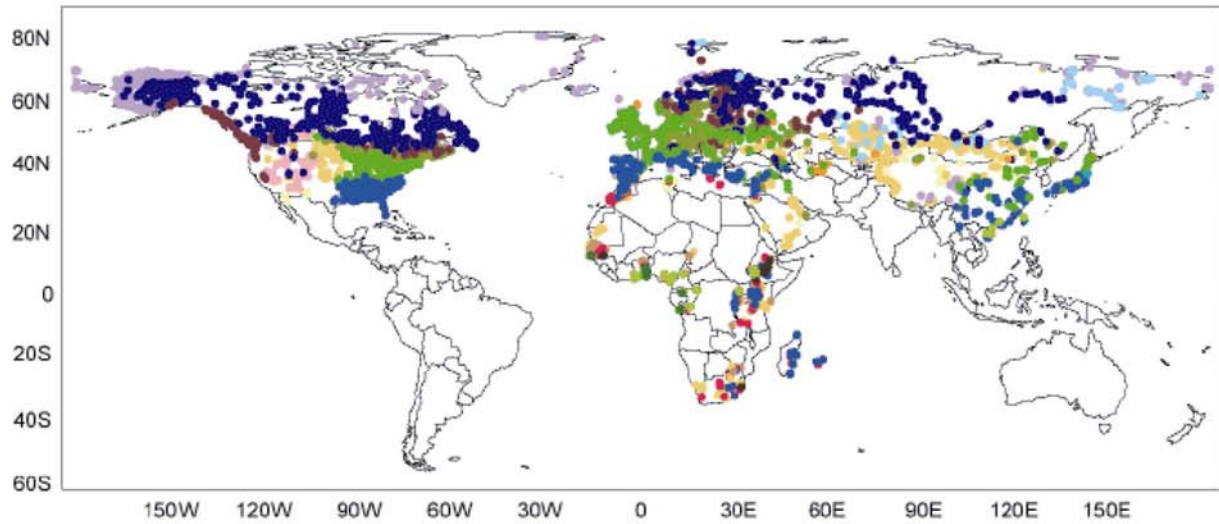


Figure C.a Echantillons polliniques actuels de la plus grande partie du globe à l'exception de l'Amérique du Sud et de l'Australie, modifié de Prentice et al. (2000). Légende des biomes :

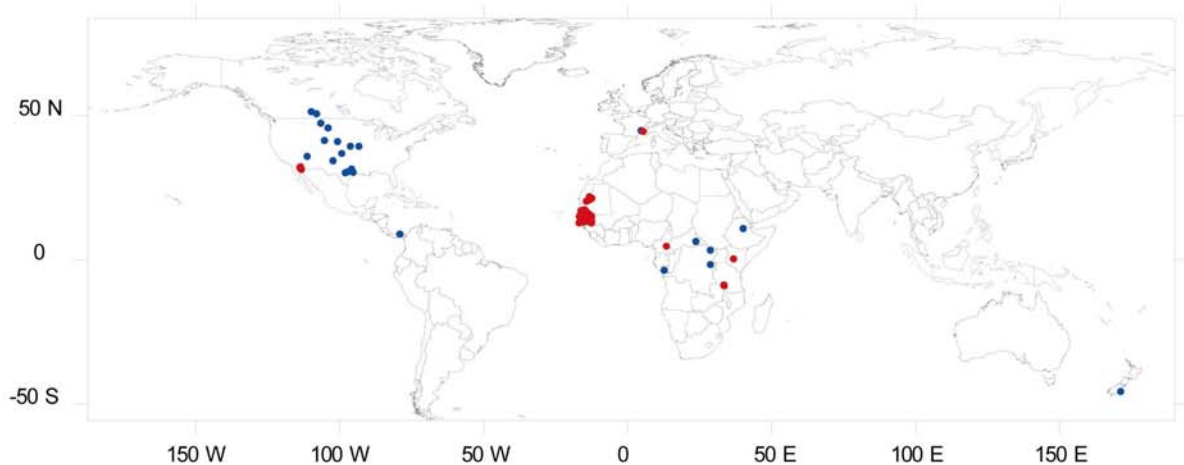


Figure C. b. Assemblages phytolithiques actuels :

- cette étude
- Publications :
[Fredlund et Tieszen (1994 et 1997) ; Alexandre et al. (1997); Barboni et al. (1998); Runge et al. (1999); Kerns et al. (2001); Prebble et al. (2002); Delhon et al. (2003); Piperno et al. (2003)].

Figure C. (a) Assemblages polliniques et **(b)** phytolithiques actuels.

A travers les quatre chapitres de cette thèse nous montrons donc que les phytolithes ont de réelles potentialités en tant que traceurs des formations herbacées mais nous remarquons aussi combien la méthode adoptée est encore peu répandue. Cette méthode, initiée par Fredlund et al. (1994; 1997b), basée sur l'étude d'assemblages nombreux renforcée de comptages statistiquement corrects, est primordiale si l'on veut que les phytolithes puissent apporter une information aussi fiable et reconnue que celle fournie par l'approche pollinique. Mais pour cela, il est nécessaire que la communauté de chercheurs qui utilise l'outil phytolithique s'accorde sur les termes d'une taxonomie précise et universelle. Ce problème devrait être réglé dans les années à venir puisqu'une classification est actuellement en préparation ('ICPN, International Code For Phytolith Nomenclature ; en cours). Mais le plus difficile sera de s'accorder sur la valeur prédictive de chacun de ces types. Pour cela, il faudra que les phénomènes de redondances et de multiplicités soient suffisamment connus.

La prochaine étape, faisant suite à cette thèse, sera d'intégrer l'information fournie par les phytolithes aux données polliniques pour améliorer les reconstructions paléo-environnementales et mieux contraindre les modèles prédictifs de végétation. Une étude de calibration et de confrontation du modèle LPJ-GUESS (Sitch et al., 2003) avec des données uniquement polliniques, parce que facilement utilisables, a été commencée. A court terme, les résultats obtenus au cours de cette thèse seront appliqués à l'étude de sédiments fossiles, conjointement aux données polliniques, et comparés aux végétations reconstruites par ce modèle.

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Région étudiée	Nom échant.	Long. N°	Lat. E°	Alt., m	Crenate Spherical	Rough Spherical	Smooth Spherical	Dumbbell	Cross	Saddle	Fan-shaped	Point-shaped	Long cells	Rectangle	Uni-lobate	Poly-lobate	Cone-shaped	Spherical with Sockets						
Kenya (Mont Kenya)	LM 1-2	37.05	-0.02	2000	0	17	10	52	9	7	5	6	40	2	29	2	2	179	139	13	10.3	3.6	32.7	0.152
	UM 1-2	37.05	-0.02	2500	1	7	2	96	7	11	12	46	148	16	106	8	2	462	314	22	9.6	3.8	53.3	0.023
	UM 3-1	37.05	-0.02	2500	1	4	11	69	8	33	3	26	7	20	61	38	7	288	281	26	30.0	1.1	52.0	0.016
	B 1-2	37.05	-0.02	2700		1	11	41	8	10	30	8	31	13	174	3		330	299	12	16.9	10.0	76.3	0.003
	B 2-3	37.05	-0.02	3000		1	3	28	9	5	50	16	36	6	178		1	333	297	12	11.9	16.8	81.4	0.003
	H 1-2	37.05	-0.02	3100		2	5	23	5	4	23	21	113	12	148	23		379	266	21	12.5	8.6	85.1	0.008
	H 3-1	37.05	-0.02	3300		5	2	24		9	13	18	61	6	175	27		340	279	10	27.3	4.7	86.3	0.018
	ES 1-2	37.05	-0.02	3400			1	12			1	12	77	1	221	20	1	346	269	10	0.0	0.4	95.3	0.000
	ES 2-3	37.05	-0.02	3900	1	4	34	37	4	6	5	45	138	7	139	39	17	476	338	2	12.8	1.5	79.7	0.014
	LAS 2-1	37.05	-0.02	4000			15	12	9	7	1	23	75	0	160	39		341	266	8	25.0	0.4	87.7	0.000
Tanzanie (Lac_Masoko)	LAS 3-2	37.05	-0.02	4200			4	38	1	12	4	37	92	4	151	54	4	401	309	5	23.5	1.3	80.4	0.000
	UAS 1-1	37.05	-0.02	4300		1	21	9			2	37	64	2	204	37		377	313	7	0.0	0.6	96.4	0.003
	UAS 3-3	37.05	-0.02	4500		2	0	16	4	4	2	13	95	0	165	34	7	342	247	18	16.7	0.8	89.2	0.008
	MAS 1	33.80	-9.36	780	0	52	47	25	1	0	47	23	40	0	0		5	240	200	18	0.0	23.5	0.0	0.542
	MAS 2	33.80	-9.36	780	0	82	45	95	2	9	47	51	68	0	0		13	412	344	21	8.5	13.7	0.0	0.402
	MAS 3	33.80	-9.36	780	0	61	46	30	0	2	37	37	49	0	0		6	268	219	64	6.3	16.9	0.0	0.575
	MAS 4	33.80	-9.36	780	0	97	58	78	6	13	42	64	65	0	0		8	431	366	46	13.4	11.5	0.0	0.478
	MAS 7	33.80	-9.36	780	8	94	75	62	3	8	51	64	79	0	1		9	454	375	45	11.0	13.6	1.4	0.497
	MAS 8	33.80	-9.36	780	1	61	54	49	0	4	63	87	58	3	3		5	388	330	57	7.5	19.1	10.2	0.292
	MAS 9	33.80	-9.36	780	2	76	48	29	2	3	28	36	37	3	3		8	275	238	27	8.8	11.8	15.0	0.731
Tanzanie (Mt_Rungwe)	MAS 12	33.80	-9.36	780	1	50	28	71	16	9	61	65	70	5	0		12	388	318	29	9.4	19.2	5.0	0.220
	MAS 14	33.80	-9.36	780	1	39	84	59	15	6	44	44	30	0	2		6	330	300	40	7.5	14.7	2.4	0.229
	GAZON	33.80	-9.36	780	15	56	63	40	0	5	100	66	22	2	5		10	384	362	37	11.1	27.6	13.5	0.257
	RGW 4	33.73	-9.17	2150		7	16	143	8	26	8	46	71	0	55		4	384	313		14.7	2.6	23.7	0.024
	RGW 7A	33.73	-9.17	2150		5	23	59	9	15	16	48	52	0	106	13	11	357	305		18.1	5.2	58.9	0.019
	RGW 9	33.73	-9.17	2150		5	4	138		39	46	33	55	0	19		31	370	315		22.0	14.6	9.7	0.018
	RGW 17	33.73	-9.17	2150		3	0	57	9	8	26	40	56	0	128		42	369	313		10.8	8.3	63.4	0.011
	RGW 19	33.73	-9.17	2150		1	5	104		29	49	14	23	0	99		11	335	312		21.8	15.7	42.7	0.003
	RGW 20	33.73	-9.17	2150		1	4	62		39	33	26	32	0	210		1	408	376		38.6	8.8	67.5	0.003
	RGW 23	33.73	-9.15	2300		29	10	62	6	15	30	29	38	0	54		33	306	268		18.1	11.2	39.4	0.148
Tanzanie (Mt_Rungwe)	RGW 24	33.70	-9.12	2600		3	3	81	11	34	25	45	59	0	86		6	353	294		27.0	8.5	40.6	0.011
	RGW 27	33.68	-9.17	2966		2	5	57	6	8	17	50	46	0	79	12	95	377	331		11.3	5.1	56.2	0.009

Annexe 1 : Comptage brut des 14 types phytolithiques ayant une valeur taxonomique démontrée et indices phytolithiques utilisés dans cette thèse. La catégorie "Inclassable" représente les phytolithes ayant des formes repérables mais sans valeur taxonomique connue.

Région étudiée	Nom échant.	Long. No	Latit. Eo	Altit, m	Crenate Spherical	Rough Spherical	Smooth Spherical	Dumbbell	Cross	Saddle	Fan-shaped	Point-shaped	Long cells	Rectangle	Uni-lobate	Poly-lobate	Cone-shaped	Spherical with Sockets					Somme	Somme (- long cells)	Inclassable	Iph (%)	Fs (%)*	Ic (%)	D/P
Mauritanie (Z.Saharienne)	RIM 3	-13.00	21.53	232	2	4	5	18	0	6	52	36					0		123	123	14		123	123	14	25.0	42.3	0	0.036
	RIM 8	-12.15	21.03	298	7	5	2	13	0	5	43	46					1		122	122	19		122	122	19	27.8	35.2	0	0.047
	MAU 07	-12.20	20.93	260	2	9	11	37	1	11	56	53					0		180	180	21		180	180	21	22.4	31.1	0	0.057
	MAU 06	-12.63	20.63	350	0	4	5	61	0	6	55	55					3		189	189	27		189	189	27	9.0	29.1	0	0.023
	MAU 05	-13.03	20.40	230	1	1	2	26	3	5	44	44					1		127	127	26		127	127	26	14.7	34.6	0	0.008
	MAU 04	-13.37	20.23	350	3	4	5	49	2	21	53	53					1		191	191	20		191	191	20	29.2	27.7	0	0.022
	RIM 2	-14.08	19.93	132	3	5	6	8	0	2	62	54					1		141	141	11		141	141	11	20.0	44.0	0	0.040
	83-35	-14.60	17.00	25	0	4	1	5	5	27	78	67					2		189	189	18		189	189	18	73.0	41.3	0	0.022
	RIM 11	-15.20	16.93	25	0	2	3	45	0	41	93	55					0		239	239	14		239	239	14	47.7	38.9	0	0.009
	RIM 10	-15.17	16.73	25	0	6	2	22	1	16	90	36					0		173	173	28		173	173	28	41.0	52.0	0	0.036
Sénégal (Z.Sahélienne)	RIM 1	-15.97	16.68	24	3	18	9	35	1	5	97	38					2		208	208	17		208	208	17	12.2	46.6	0	0.102
	S.33	-14.82	16.39	15	0	12	4	114	5	46	27	29					4		241	241	28		241	241	28	27.9	11.2	0	0.054
	S.32	-15.35	16.29	25	1	1	4	48	5	22	37	36					0		154	154	18		154	154	18	29.3	24.0	0	0.007
	83-30	-14.93	16.17	61	0	5	2	85	6	23	39	37					2		199	199	27		199	199	27	20.2	19.6	0	0.026
	S.40	-13.89	16.10	10	0	15	3	74	4	60	45	47					0		248	248	14		248	248	14	43.5	18.1	0	0.065
	S.29	-14.92	16.08	45	0	9	3	77	3	39	26	31					0		188	188	13		188	188	13	32.8	13.8	0	0.051
	82-47	-14.95	16.00	30	3	12	3	148	7	31	46	37					3		290	290	25		290	290	25	16.7	15.9	0	0.045
	82-46	-15.95	16.00	30	0	5	1	119	7	38	42	32					5		249	249	25		249	249	25	23.2	16.9	0	0.021
	S.27	-14.86	15.92	45	0	1	0	104	9	53	18	42					2		229	229	17		229	229	17	31.9	7.9	0	0.004
	S.44	-13.47	15.83	92	0	3	2	94	10	30	42	40					0		221	221	18		221	221	18	22.4	19.0	0	0.014
Sénégal (Z.Soudanienne)	S.24	-14.99	15.69	46	0	1	1	129	1	34	13	17					0		196	196	20		196	196	20	20.7	6.6	0	0.005
	83-46	-13.35	15.43	61	1	6	2	125	22	67	17	22					1		263	263	7		263	263	7	31.3	6.5	0	0.024
	83-20	-15.12	15.42	61	0	8	2	95	14	77	16	26					5		243	243	17		243	243	17	41.4	6.6	0	0.035
	83-15	-15.47	15.33	61	1	4	2	28	8	11	22	27					0		103	103	26		103	103	26	23.4	21.4	0	0.042
	S.54	-12.99	15.31	27	0	2	3	96	3	24	32	52					0		212	212	26		212	212	26	19.5	15.1	0	0.010
	83-48	-13.45	15.28	61	1	4	1	82	14	47	58	42					1		250	250	16		250	250	16	32.9	23.2	0	0.016
	S.12	-15.17	15.21	29	3	16	12	72	2	19	25	46					0		195	195	18		195	195	18	20.4	12.8	0	0.098
	S.58	-12.81	15.06	31	0	4	3	96	8	60	19	44					0		234	234	26		234	234	26	36.6	8.1	0	0.018
	83-8	-15.85	14.90	54	9	15	4	95	10	53	47	28					2		263	263	6		263	263	6	33.5	17.9	0	0.064
	83-62	-12.33	14.85	64	2	2	3	57	18	48	27	62					1		220	220	17		220	220	17	39.0	12.3	0	0.009
Sénégal (Z.Soudanienne)	S.7	-15.99	14.79	38	1	11	15	66	0	3	50	53					0		199	199	10		199	199	10	4.3	25.1	0	0.064
	83-65	-12.25	14.75	38	0	5	1	139	14	49	6	12					1		227	227	1		227	227	1	24.3	2.6	0	0.023
	S.5	-16.16	14.72	7	0	19	4	51	0	13	57	29					0		173	173	17		173	173	17	20.3	32.9	0	0.127

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Région étudiée	Nom échant.	Long. N°	Latit. E°	Altit. m	Crenate Spherical	Rough Spherical	Smooth Spherical	Dumbbell	Cross	Saddle	Fan-shaped	Point-shaped	Long cells	Rectangle	Unit-lobate	Poly-lobate	Cone-shaped	Spherical with Sockets							D/P	
Sénégal (Z.Soudanienne)	83-4	-16.50	14.70	61	9	33	3	77	12	16	49	58					1		Somme	Somme (- long cells)	Inclassable	Iph (%)	Fs (%)*	Ic (%)	0	0.156
	82-77	-16.32	14.63	54	1	12	3	104	16	29	41	30					1		258	258	17	15.2	19.0	0	0.055	
	82-79	-16.10	14.17	30	1	1	3	122	13	30	14	28					1		237	237	21	19.5	17.3	0	0.005	
	83-75	-12.67	14.12	61	0	11	1	131	22	22	25	29					0		213	213	24	18.2	6.6	0	0.048	
	82-78	-16.05	14.08	30	2	20	5	191	13	22	12	23					0		241	241	5	12.6	10.4	0	0.077	
	83-70	-12.27	14.05	61	0	1	0	180	17	13	5	21					0		288	288	3	9.7	4.2	0	0.004	
	83-83	-13.32	13.97	78	0	1	0	178	21	14	6	14					4		237	237	11	6.2	2.1	0	0.004	
	S.84	-13.41	13.93	61	0	3	0	148	24	18	10	26					0		238	238	12	6.6	2.5	0	0.013	
	83-68	-12.25	13.88	61	1	10	2	152	15	12	13	39					2		229	229	10	9.5	4.4	0	0.043	
	S.118	-13.74	13.63	40	0	7	1	128	7	11	24	2					1		246	246	21	6.7	5.3	0	0.041	
	S.88	-13.56	13.60	49	1	5	4	155	5	29	17	19					0		181	181	27	7.5	13.3	0	0.022	
	S.91	-13.40	13.59	62	19	70	12	82	16	4	23	32					0		235	235	17	15.3	7.2	0	0.446	
	83-120	-13.83	13.48	61	1	14	6	176	10	11	12	24					0		258	258	21	3.9	8.9	0	0.060	
	83-122	-14.93	13.35	30	0	4	2	178	11	21	17	19					2		254	254	8	5.6	4.7	0	0.016	
	S.122	-13.94	13.35	65	0	0	0	93	10	13	20	17					1		254	254	34	10.0	6.7	0	0.000	
	S.93	-13.23	13.31	58	6	6	2	154	13	11	13	23					3		154	154	43	11.2	13.0	0	0.028	
	83-98	-12.83	13.08	88	1	6	1	136	16	8	2	5					0		231	231	15	6.2	5.6	0	0.036	
	83-127	-14.08	13.07	38	2	81	10	75	4	5	32	49					0		175	175	27	5.0	1.1	0	0.491	
	S.128	-14.10	13.03	18	1	7	18	118	0	9	38	45					0		258	258	13	6.0	12.4	0	0.033	
Sénégal (Z.Guinéenne)	83-100	-12.63	13.03	110	0	14	4	172	11	13	10	18					1		236	236	16	7.1	16.1	0	0.063	
	S.130	-14.17	12.92	25	0	5	2	91	10	13	29	31					0		243	243	39	6.6	4.1	0	0.029	
	83-103	-12.43	12.92	198	1	9	2	145	19	9	13	17					3		181	181	16	11.4	16.0	0	0.044	
	S.138	-14.86	12.88	34	0	11	6	75	4	11	42	42					1		218	218	14	5.2	6.0	0	0.063	
	S.136	-14.74	12.85	7	0	10	2	39	3	13	57	42					0		192	192	29	12.2	21.9	0	0.065	
	83-116	-12.18	12.67	145	1	1	0	148	8	4	2	8					2		166	166	29	23.6	34.3	0	0.006	
	S.155	-16.30	12.55	33	56	144	8	10	1	6	10	2					0		174	174	27	2.5	1.1	0	4.966	
	83-151	-16.58	12.48	0	54	158	19	8	2	0	5	8					0		237	237	2	35.3	4.2	0	6.870	
	83-115	-12.30	12.40	297	0	7	2	214	6	12	7	10					1		254	254	0	0.0	2.0	0	0.028	

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Région étudiée	Nom échant.	Long. No	Lat. Eo	Alt., m	Crenate Spherical	Rough Spherical	Smooth Spherical	Dumbbell	Cross	Saddle	Fan-shaped	Point-shaped	Long cells	Rectangle	Uni-lobate	Poly-lobate	Cone-shaped	Spherical with Sockets	Somme	Somme (- long cells)	Inclassable	Iph (%)	Fs (%)*	Ic (%)	D/P
Cameroun (Savanne incluse)	1	13.72	4.33	640	217	49	7	8	0	0	12	24	15	0	3	0	0	0	335	320	1	0.0	3.8	27.3	1.043
	2	13.72	4.33	640	84	177	9	12	0	2	20	26	22	0	3	0	0	0	355	333	9	14.3	6.0	17.6	2.810
	3	13.72	4.33	640	33	192	2	7	3	0	13	25	17	0	1	0	0	0	293	276	1	0.0	4.7	9.1	3.918
	4	13.72	4.33	640	2	214	7	16	0	1	8	39	78	0	0	0	0	0	365	287	19	5.9	2.8	0.0	3.344
	5	13.72	4.33	640	1	233	7	20	0	1	2	19	47	0	0	1	0	0	331	284	11	4.8	0.7	4.5	5.419
	6	13.72	4.33	640	28	195	6	14	0	1	3	17	15	0	1	2	0	0	282	267	3	6.7	1.1	16.7	5.132
	7	13.72	4.33	640	10	221	2	40	0	0	2	22	49	0	4	0	0	0	350	301	15	0.0	0.7	9.1	3.250
	8	13.72	4.33	640	48	161	4	18	5	2	6	17	17	0	0	1	0	0	279	262	20	8.0	2.3	3.8	3.286
	9	13.72	4.33	640	9	219	5	37	0	0	7	19	23	0	4	0	0	0	323	300	2	0.0	2.3	9.8	3.269
	10	13.72	4.33	640	3	208	6	20	0	0	34	27	84	0	1	0	0	0	383	299	7	0.0	11.4	4.8	2.537
	11	13.72	4.33	640	65	167	6	23	3	3	11	23	21	0	2	0	0	0	324	303	15	10.3	3.6	6.5	2.569
	12	13.72	4.33	640	10	233	3	52	0	0	8	34	46	0	4	1	0	0	391	345	22	0.0	2.3	8.8	2.354
	13	13.72	4.33	640	0	217	1	20	0	0	14	30	47	0	3	0	0	0	332	285	8	0.0	4.9	13.0	3.239
	14	13.72	4.33	640	8	216	0	38	0	0	11	29	46	0	0	0	0	0	348	302	16	0.0	3.6	0.0	2.769
	15	13.72	4.33	640	16	194	2	58	0	0	5	24	46	0	0	0	0	0	345	299	19	0.0	1.7	0.0	2.230
	16	13.72	4.33	640	3	190	3	63	0	0	6	20	40	0	1	0	0	0	326	286	19	0.0	2.1	1.6	2.111
	17	13.72	4.33	640	0	190	1	84	0	0	9	30	45	0	1	2	0	0	362	317	7	0.0	2.8	3.4	1.508
	18	13.72	4.33	640	6	156	2	104	0	0	5	29	75	0	1	2	0	0	380	305	4	0.0	1.6	2.8	1.106
	19	13.72	4.33	640	2	111	3	177	12	0	13	60	90	0	2	1	0	0	471	381	17	0.0	3.4	1.6	0.419
	20	13.72	4.33	640	2	100	1	185	6	0	17	49	86	0	2	12	0	0	460	374	9	0.0	4.5	6.8	0.369
	21	13.72	4.33	640	12	144	2	138	11	0	7	21	74	0	0	10	0	0	419	345	20	0.0	2.0	6.3	0.770
	22	13.72	4.33	640	4	185	10	95	8	2	9	25	87	0	2	8	0	0	435	348	19	1.9	2.6	8.7	1.242
	23	13.72	4.33	640	2	142	2	102	1	0	8	36	61	0	1	4	0	0	359	298	26	0.0	2.7	4.6	0.934
	24	13.72	4.33	640	5	137	0	117	4	0	7	5	52	0	0	4	0	0	331	279	27	0.0	2.5	3.2	1.000
	25	13.72	4.33	640	7	186	5	134	4	0	6	37	56	0	0	6	0	0	441	385	11	0.0	1.6	4.2	0.995
	26	13.72	4.33	640	4	147	6	88	1	0	17	71	68	0	0	11	0	0	413	345	64	0.0	4.9	11.0	0.782
Mexique	Mex1	-113.28	31.70	200	1	10	3	42	3	91	24	64	67		9	0	0	0	314	247	1	66.9	9.7	6.2	0.043
(Désert Sonora)	Mex2	-113.00	31.00	254	0	21	0	32	2	40	78	71	87		41	0	0	0	372	285	121	54.1	27.4	35.7	0.080
	Mex3	-113.46	31.60	117	1	3	2	106	5	60	29	34	66		15	7	0	0	328	262	6	35.1	11.1	11.4	0.012
	Mex4	-113.48	31.58	95	1	17	3	71	9	25	29	57	52		11	6	0	0	281	229	3	23.8	12.7	13.9	0.082
	Mex5	-113.00	31.00	119	0	9	2	45	0	49	71	76	57		23	3	7	0	342	285	7	52.1	24.9	21.7	0.034
	Mex6	-113.31	31.94	215	4	15	5	18	0	28	80	83	62		11	1	3	0	310	248	6	60.9	32.3	20.7	0.068
	Mex7	-113.32	31.87	201	1	0	7	18	7	92	59	57	80		33	4	3	0	361	281	0	78.6	21.0	24.0	0.000

Annexe 1 : Comptage brut des 14 types phytolithiques ayant une valeur taxonomique démontrée et indices phytolithiques utilisés dans cette thèse. La catégorie "Inclassable" représente les phytolithes ayant des formes repérables mais sans valeur taxonomique connue.

Région étudiée	Nom échant.	Long. N°	Lat. E°	Alt., m	Crenate Spherical	Rough Spherical	Smooth Spherical	Dumbbell	Cross	Saddle	Fan-shaped	Point-shaped	Long cells	Rectangle	Uni-lobate	Poly-lobate	Cone-shaped	Spherical with Sockets	Somme	Somme (- long cells)	Inclassable	Iph (%)	Fs (%)*	Ic (%)	D/P
Luberon (Fr.)	CPL04	5.50	43.82	660	0	4	4					14	15	10	111	27		2	183	168	5		0	100	0.000
Luberon (Fr.)	CPL06	5.50	43.82	665	3	2	2					7	17	5	235	10		4	283	266	3		0	100	0.012
Luberon (Fr.)	CPL11	5.50	43.82	695	1	8	8					20	46	11	239	28		7	360	314			0	100	0.003
Luberon (Fr.)	GLC08	5.50	43.82	1035	1	4	4					9	40	8	203	11		5	281	241			0	100	0.004
Luberon (Fr.)	GLC15	5.50	43.82	1030	3	7	7					17	31	4	202	37		2	303	272	6		0	100	0.012
Luberon (Fr.)	GLC20	5.50	43.82	1025	1	2	2					6	37	1	201	40		4	292	255	4		0	100	0.004
Luberon (Fr.)	GLE15	5.50	43.82	935	2	8	8					6	32	2	205	39		5	299	267	2		0	100	0.008
Luberon (Fr.)	GLE21	5.50	43.82	1040	0	6	6					31	54	1	252	24		0	368	314			0	100	0.000
Luberon (Fr.)	GLW03	5.50	43.82	895	0	2	2					13	35	4	219	24		4	301	266			0	100	0.000
Luberon (Fr.)	GLW04	5.50	43.82	870	1	3	3					20	37	4	201	27		3	296	259	11		0	100	0.004
Luberon (Fr.)	GLW07	5.50	43.82	875	2	5	5					12	28	0	152	16		4	219	191	8		0	100	0.011
Luberon (Fr.)	HP02	5.50	43.82	695	0	1	1					3	17	0	182	7		7	217	200			0	100	0.000
Luberon (Fr.)	HP05	5.50	43.82	650	3	3	3					20	27	0	124	16		7	200	173			0	100	0.019
Luberon (Fr.)	TR12	5.50	43.82	398	4	5	5					16	49	7	198	23		5	307	258	11		0	100	0.016
Luberon (Fr.)	GLE04	5.50	43.82	835	0	5	5					12	50	2	192	61		1	323	273			0	100	0.000
Luberon (Fr.)	GLC05	5.50	43.82	1025	0	6	6					11	30	3	192	45		3	290	260			0	100	0.000
Luberon (Fr.)	GLC13	5.50	43.82	1025	6	5	5					6	15	0	137	6		5	180	165			0	100	0.040
Luberon (Fr.)	HP04	5.50	43.82	690	0	13	13					12	32	7	222	2		2	290	258	18		0	100	0.000
Luberon (Fr.)	CM17	5.50	43.82	325	4	2	2					23	65	10	143	11		8	266	201	9		0	100	0.021
Luberon (Fr.)	CPL01	5.50	43.82	667	5	12	12					25	46	2	219	20		4	333	287	7		0	100	0.019
Luberon (Fr.)	CPL12	5.50	43.82	685	2	5	5					21	43	12	200	25		5	313	270	3		0	100	0.008
Luberon (Fr.)	HP08	5.50	43.82	680	1	3	3					3	19	3	214	8		0	251	232	10		0	100	0.004
Luberon (Fr.)	TR19	5.50	43.82	360	3	11	11					14	43	8	211	5		4	299	256	1		0	100	0.013
Luberon (Fr.)	TR21	5.50	43.82	345	6	8	8					54	46	4	163	21		3	305	259	4		0	100	0.025
Luberon (Fr.)	GLC14	5.50	43.82	1030	0	4	4					13	36	3	200	11		6	273	237	17		0	100	0.000
Luberon (Fr.)	TR14	5.50	43.82	370	7	2	2					14	92	0	142	6		7	270	178	8		0	100	0.043
Luberon (Fr.)	CM05	5.50	43.82	355	4	2	2					7	27	4	256	1		3	304	277	6		0	100	0.015
Luberon (Fr.)	GLC07	5.50	43.82	1040	3	1	1					7	20	4	157	59		2	253	233	9		0	100	0.013
Luberon (Fr.)	TR06	5.50	43.82	385	6	1	1					6	9	2	173	4		2	203	194	4		0	100	0.032
Luberon (Fr.)	GLC19	5.50	43.82	1035	3	0	0					9	16	2	191	28		3	252	236	4		0	100	0.013
Luberon (Fr.)	CM06	5.50	43.82	375	4	7	7					9	21	7	201	3		0	252	231	3		0	100	0.018

Annexe 1 : Comptage brut des 14 types phytolithiques ayant une valeur taxonomique démontrée et indices phytolithiques utilisés dans cette thèse. La catégorie "Inclassable" représente les phytolithes ayant des formes repérables mais sans valeur taxonomique connue.

Echantillon	Région	Long	Lati	Alti	Biome a priori	Tree	Panicoid	Chloridoid	Pooid	Bulliform
LM 1-2	Kenya (Mont Kenya)	37.05	-0.02	2000	SavGramHau	12.23	43.88	5.04	23.74	3.60
UM 1-2		37.05	-0.02	2500	SavGramHau	2.23	32.80	3.50	41.40	3.82
UM 3-1		37.05	-0.02	2500	SavGramHau	1.42	27.40	11.74	42.35	1.07
B 1-2		37.05	-0.02	2700	PelouseC3	0.33	16.39	3.34	63.55	10.03
B 2-3		37.05	-0.02	3000	PelouseC3	0.34	12.46	1.68	61.95	16.84
H 1-2		37.05	-0.02	3100	PelouseC3	0.75	10.53	1.50	68.80	8.65
H 3-1		37.05	-0.02	3300	PelouseC3	1.79	8.60	3.23	74.55	4.66
ES 1-2		37.05	-0.02	3400	PelouseC3	0.00	4.46	0.00	89.96	0.37
ES 2-3		37.05	-0.02	3900	PelouseC3	1.18	12.13	1.78	54.73	1.48
LAS 2-1		37.05	-0.02	4000	PelouseC3	0.00	7.89	2.63	74.81	0.38
LAS 3-2		37.05	-0.02	4200	PelouseC3	0.00	12.62	3.88	67.64	1.29
UAS 1-1		37.05	-0.02	4300	PelouseC3	0.32	2.88	0.00	77.64	0.64
UAS 3-3		37.05	-0.02	4500	PelouseC3	0.81	8.10	1.62	80.57	0.81
MAS 1	Tanzanie (Lac_Masoko)	33.80	-9.36	780	SavArbGramHau	26.00	13.00	0.00	0.00	23.50
MAS 2		33.80	-9.36	780	SavGramHau	23.84	28.20	2.62	0.00	13.66
MAS 3		33.80	-9.36	780	SavArbGramHau	27.85	13.70	0.91	0.00	16.89
MAS 4		33.80	-9.36	780	SavGramHau	26.50	22.95	3.55	0.00	11.48
MAS 7		33.80	-9.36	780	SavArbGramHau	25.07	17.33	2.13	0.27	13.60
MAS 8		33.80	-9.36	780	SavArbGramHau	18.48	14.85	1.21	1.82	19.09
MAS 9		33.80	-9.36	780	SavArbGramHau	31.93	13.03	1.26	2.52	11.76
MAS 12		33.80	-9.36	780	SavGramHau	15.72	27.36	2.83	1.57	19.18
MAS 14		33.80	-9.36	780	SavGramHau	13.00	24.67	2.00	0.67	14.67
GAZON		33.80	-9.36	780	SavGramHau	15.47	11.05	1.38	1.93	27.62
RGW 4	Tanzanie (Mt_Rungwe)	33.73	-9.17	2150	SavGramHau	2.24	48.24	8.31	17.57	2.56
RGW 7A		33.73	-9.17	2150	SavGramHau	1.64	22.30	4.92	39.02	5.25
RGW 9		33.73	-9.17	2150	SavGramHau	1.59	43.81	12.38	6.03	14.60
RGW 17		33.73	-9.17	2150	PelouseC3	0.96	21.09	2.56	40.89	8.31
RGW 19		33.73	-9.17	2150	PelouseC3	0.32	33.33	9.29	31.73	15.71
RGW 20		33.73	-9.17	2150	PelouseC3	0.27	16.49	10.37	55.85	8.78
RGW 23		33.73	-9.15	2300	SavGramHau	10.82	25.37	5.60	20.15	11.19
RGW 24		33.70	-9.12	2600	PelouseC3	1.02	31.29	11.56	29.25	8.50
RGW 27		33.68	-9.17	2966	PelouseC3	0.60	19.03	2.42	27.49	5.14
RIM 3	Mauritanie (Z.Saharienne)	-13.00	21.53	232	Desert	3.25	14.63	4.88	0.00	42.28
RIM 8		-12.15	21.03	298	Desert	4.10	10.66	4.10	0.00	35.25
MAU 07		-12.20	20.93	260	Desert	5.00	21.11	6.11	0.00	31.11
MAU 06		-12.63	20.63	350	Desert	2.12	32.28	3.17	0.00	29.10
MAU 05		-13.03	20.40	230	Desert	0.79	22.83	3.94	0.00	34.65
MAU 04		-13.37	20.23	350	Desert	2.09	26.70	10.99	0.00	27.75
RIM 2		-14.08	19.93	132	Desert	3.55	5.67	1.42	0.00	43.97
83-35		-14.60	17.00	25	SavGramBas	2.12	5.29	14.29	0.00	41.27
RIM 11	Sénégal (Z.Sahélienne)	-15.20	16.93	25	SavGramBas	0.84	18.83	17.15	0.00	38.91
RIM 10		-15.17	16.73	25	SavGramBas	3.47	13.29	9.25	0.00	52.02
RIM 1		-15.97	16.68	24	SavGramBas	8.65	17.31	2.40	0.00	46.63
S.33		-14.82	16.39	15	SavGramBas	4.98	49.38	19.09	0.00	11.20
S.32		-15.35	16.29	25	SavGramBas	0.65	34.42	14.29	0.00	24.03
83-30		-14.93	16.17	61	SavGramBas	2.51	45.73	11.56	0.00	19.60
S.40		-13.89	16.10	10	SavGramBas	6.05	31.45	24.19	0.00	18.15
S.29		-14.92	16.08	45	SavGramBas	4.79	42.55	20.74	0.00	13.83
82-47		-14.95	16.00	30	SavGramBas	4.14	53.45	10.69	0.00	15.86
82-46		-15.95	16.00	30	SavGramBas	2.01	50.60	15.26	0.00	16.87
S.27		-14.86	15.92	45	SavGramBas	0.44	49.34	23.14	0.00	7.86
S.44		-13.47	15.83	92	SavGramBas	1.36	47.06	13.57	0.00	19.00
S.24		-14.99	15.69	46	SavGramBas	0.51	66.33	17.35	0.00	6.63
83-46		-13.35	15.43	61	SavGramBas	2.28	55.89	25.48	0.00	6.46
83-20		-15.12	15.42	61	SavGramBas	3.29	44.86	31.69	0.00	6.58
83-15		-15.47	15.33	61	SavGramBas	3.88	34.95	10.68	0.00	21.36
S.54		-12.99	15.31	27	SavGramBas	0.94	46.70	11.32	0.00	15.09
83-48		-13.45	15.28	61	SavGramBas	1.60	38.40	18.80	0.00	23.20
S.12	Sénégal (Z.Soudanienne)	-15.17	15.21	29	SavGramBas	8.21	37.95	9.74	0.00	12.82
S.58		-12.81	15.06	31	SavGramBas	1.71	44.44	25.64	0.00	8.12
83-8		-15.85	14.90	54	SavGramBas	5.70	39.92	20.15	0.00	17.87
83-62		-12.33	14.85	64	SavGramBas	0.91	34.09	21.82	0.00	12.27
S.7		-15.99	14.79	38	SavGramHau	5.53	33.17	1.51	0.00	25.13
83-65		-12.25	14.75	38	SavGramBas	2.20	67.40	21.59	0.00	2.64
S.5		-16.16	14.72	7	SavGramHau	10.98	29.48	7.51	0.00	32.95
83-4		-16.50	14.70	61	SavGramHau	12.79	34.50	6.20	0.00	18.99
82-77		-16.32	14.63	54	SavGramHau	5.06	50.63	12.24	0.00	17.30
82-79		-16.10	14.17	30	SavGramHau	0.47	63.38	14.08	0.00	6.57
83-75		-12.67	14.12	61	SavGramHau	4.56	63.49	9.13	0.00	10.37
82-78		-16.05	14.08	30	SavGramHau	6.94	70.83	7.64	0.00	4.17
83-70		-12.27	14.05	61	SavGramHau	0.42	83.12	5.49	0.00	2.11
83-83		-13.32	13.97	78	SavGramHau	0.42	83.61	5.88	0.00	2.52
S.84		-13.41	13.93	61	SavGramHau	1.31	75.11	7.86	0.00	4.37
83-68		-12.25	13.88	61	SavGramHau	4.07	67.89	4.88	0.00	5.28
S.118		-13.74	13.63	40	SavGramHau	3.87	74.59	6.08	0.00	13.26
S.88		-13.56	13.60	49	SavGramHau	2.13	68.09	12.34	0.00	7.23
S.91		-13.40	13.59	62	SavGramHau	27.13	37.98	1.55	0.00	8.91
83-120		-13.83	13.48	61	SavGramHau	5.51	73.23	4.33	0.00	4.72
83-122		-14.93	13.35	30	SavGramHau	1.57	74.41	8.27	0.00	6.69
S.122		-13.94	13.35	65	SavGramHau	0.00	66.88	8.44	0.00	12.99
S.93		-13.23	13.31	58	SavGramHau	2.60	72.29	4.76	0.00	5.63
83-98		-12.83	13.08	88	SavGramHau	3.43	86.86	4.57	0.00	1.14

Annexe 2. Pourcentage des 5 variables utilisées dans l'analyse discriminante pour l'ensemble des échantillons ainsi que le biome qui leur est attribué.

Echantillon	Région	Long	Lati	Alti	Biome a priori	Tree	Panicoid	Chloridoid	Pooid	Bulliform
83-127	Sénégal	-14.08	13.07	38	SavGramHau	31.40	30.62	1.94	0.00	12.40
S.128	(Z.Soudanienne)	-14.10	13.03	18	SavGramHau	2.97	50.00	3.81	0.00	16.10
83-100		-12.63	13.03	110	SavGramHau	5.76	75.31	5.35	0.00	4.12
S.130		-14.17	12.92	25	SavGramHau	2.76	55.80	7.18	0.00	16.02
83-103		-12.43	12.92	198	SavGramHau	4.13	75.23	4.13	0.00	5.96
S.138		-14.86	12.88	34	SavGramHau	5.73	41.15	5.73	0.00	21.88
S.136	(Z.Guinéenne)	-14.74	12.85	7	SavGramHau	6.02	25.30	7.83	0.00	34.34
83-116		-12.18	12.67	145	SavGramHau	0.57	89.66	2.30	0.00	1.15
S.155		-16.30	12.55	33	ForTrop	60.76	4.64	2.53	0.00	4.22
83-151		-16.58	12.48	0	ForTrop	62.20	3.94	0.00	0.00	1.97
83-115		-12.30	12.40	297	SavGramHau	2.70	84.94	4.63	0.00	2.70
Cam1	Cameroun	13.72	4.33	640	ForTrop	53.15	3.60	0.60	0.90	6.01
Cam2	(Savanne incluse)	13.72	4.33	640	ForTrop	69.57	3.62	0.00	0.36	4.71
Cam3		13.72	4.33	640	ForTrop	74.56	5.57	0.35	0.00	2.79
Cam4		13.72	4.33	640	ForTrop	82.04	7.04	0.35	0.35	0.70
Cam5		13.72	4.33	640	ForTrop	73.03	5.24	0.37	1.12	1.12
Cam6		13.72	4.33	640	ForTrop	73.42	13.29	0.00	1.33	0.66
Cam7		13.72	4.33	640	ForTrop	61.45	8.78	0.76	0.38	2.29
Cam8		13.72	4.33	640	ForTrop	73.00	12.33	0.00	1.33	2.33
Cam9		13.72	4.33	640	ForTrop	69.57	6.69	0.00	0.33	11.37
Cam10		13.72	4.33	640	ForTrop	55.12	8.58	0.99	0.66	3.63
Cam11		13.72	4.33	640	ForTrop	67.54	15.07	0.00	1.45	2.32
Cam12		13.72	4.33	640	ForTrop	76.14	7.02	0.00	1.05	4.91
Cam13		13.72	4.33	640	ForTrop	71.52	12.58	0.00	0.00	3.64
Cam14		13.72	4.33	640	ForTrop	64.88	19.40	0.00	0.00	1.67
Cam15		13.72	4.33	640	ForTrop	66.43	22.03	0.00	0.35	2.10
Cam16		13.72	4.33	640	ForTrop	59.94	26.50	0.00	0.95	2.84
Cam17		13.72	4.33	640	ForTrop	51.15	34.10	0.00	0.98	1.64
Cam18		13.72	4.33	640	SavArbGramHau	29.13	49.61	0.00	0.79	3.41
Cam19		13.72	4.33	640	SavArbGramHau	26.74	51.07	0.00	3.74	4.55
Cam20		13.72	4.33	640	SavArbGramHau	41.74	43.19	0.00	2.90	2.03
Cam21		13.72	4.33	640	SavArbGramHau	53.16	29.60	0.57	2.87	2.59
Cam22		13.72	4.33	640	SavArbGramHau	47.65	34.56	0.00	1.68	2.68
Cam23		13.72	4.33	640	SavArbGramHau	49.10	43.37	0.00	1.43	2.51
Cam24		13.72	4.33	640	SavArbGramHau	48.31	35.84	0.00	1.56	1.56
Cam25		13.72	4.33	640	SavArbGramHau	42.61	25.80	0.00	3.19	4.93
CPL04	Luberon (Fr.)	5.50	43.82	660	FtHerbC3	0.00	0.00	0.00	88.10	0.00
CPL06		5.50	43.82	665	FtHerbC3	1.13	0.00	0.00	93.98	0.00
CPL11		5.50	43.82	695	FtHerbC3	0.32	0.00	0.00	88.54	0.00
GLC08		5.50	43.82	1035	FtHerbC3	0.41	0.00	0.00	92.12	0.00
GLC15		5.50	43.82	1030	FtHerbC3	1.10	0.00	0.00	89.34	0.00
GLC20		5.50	43.82	1025	FtHerbC3	0.39	0.00	0.00	94.90	0.00
GLE15		5.50	43.82	935	FtHerbC3	0.75	0.00	0.00	92.13	0.00
GLE21		5.50	43.82	1040	FtHerbC3	0.00	0.00	0.00	88.22	0.00
GLW03		5.50	43.82	895	FtHerbC3	0.00	0.00	0.00	92.86	0.00
GLW04		5.50	43.82	870	FtHerbC3	0.39	0.00	0.00	89.58	0.00
GLW07		5.50	43.82	875	FtHerbC3	1.05	0.00	0.00	87.96	0.00
HP02		5.50	43.82	695	FtHerbC3	0.00	0.00	0.00	94.50	0.00
HP05		5.50	43.82	650	FtHerbC3	1.73	0.00	0.00	80.92	0.00
TR12		5.50	43.82	398	FtHerbC3	1.55	0.00	0.00	88.37	0.00
GLE04		5.50	43.82	835	FtHerbC3	0.00	0.00	0.00	93.41	0.00
GLC05		5.50	43.82	1025	FtHerbC3	0.00	0.00	0.00	92.31	0.00
GLC13		5.50	43.82	1025	FtHerbC3	3.64	0.00	0.00	86.67	0.00
HP04		5.50	43.82	690	FtHerbC3	0.00	0.00	0.00	89.53	0.00
CM17		5.50	43.82	325	FtHerbC3	1.99	0.00	0.00	81.59	0.00
CPL01		5.50	43.82	667	FtHerbC3	1.74	0.00	0.00	83.97	0.00
CPL12		5.50	43.82	685	FtHerbC3	0.74	0.00	0.00	87.78	0.00
HP08		5.50	43.82	680	FtHerbC3	0.43	0.00	0.00	96.98	0.00
TR19		5.50	43.82	360	FtHerbC3	1.17	0.00	0.00	87.50	0.00
TR21		5.50	43.82	345	FtHerbC3	2.32	0.00	0.00	72.59	0.00
GLC14		5.50	43.82	1030	FtHerbC3	0.00	0.00	0.00	90.30	0.00
TR14		5.50	43.82	370	FtHerbC3	3.93	0.00	0.00	83.15	0.00
CM05		5.50	43.82	355	FtHerbC3	1.44	0.00	0.00	94.22	0.00
GLC07		5.50	43.82	1040	FtHerbC3	1.29	0.00	0.00	94.42	0.00
TR06		5.50	43.82	385	FtHerbC3	3.09	0.00	0.00	92.27	0.00
GLC19		5.50	43.82	1035	FtHerbC3	1.27	0.00	0.00	93.64	0.00
CM06		5.50	43.82	375	FtHerbC3	1.73	0.00	0.00	91.34	0.00
Mex1	Mexique	-113.28	31.70	200	Desert	4.05	18.22	36.84	3.64	9.72
Mex2	(Désert Sonora)	-113.00	31.00	254	Desert	7.37	11.93	14.04	14.39	27.37
Mex3		-113.46	31.60	117	Desert	1.15	42.37	22.90	8.40	11.07
Mex4		-113.48	31.58	95	Desert	7.42	34.93	10.92	7.42	12.66
Mex5		-113.00	31.00	119	Desert	3.16	15.79	17.19	9.12	24.91
Mex6		-113.31	31.94	215	Desert	6.05	7.26	11.29	4.84	32.26
Mex7		-113.32	31.87	201	Desert	0.00	8.90	32.74	13.17	21.00

Pelouse en C3 : PelouseC3

Désert : Desert

Savane à graminées basses : SavGramBas

Savane à graminées hautes : SavGramHau

Savane arborée à graminées hautes : SavArbGramHau

Forêt tropicale : ForTrop

Tanza: Tanzanie

AfrW: Mauritanie, Sénégal

Cam: Cameroun

Lub: Luberon

Mex: Mexique

Annexe 2. Pourcentage des 5 variables utilisées dans l'analyse discriminante pour l'ensemble des échantillons ainsi que le biome qui leur est attribué.

Région étudiée	Longitude	Latitude	Altitude (m)	Précipitations (mm/an)	Espèces ou genres dominants	Sous-famille dominante	Référence Bibliographique
Mexique (DésertSonora)	19°28'N	98°55'W	2200	700	<i>Distichlis spicata</i>	Chloridoideae	Long et al. 1989
Mexique (DésertSonora)				<200	<i>Hilaria rigida</i> <i>Schismus arbiscus</i> <i>Schismus barbatus</i> <i>Bromus rubens</i>	Chloridoideae Arundinoideae Arundinoideae Pooideae	Turner et Brown, 1994
Cameroun (Savane incluse)	4°20'N	13°43'E	640	1600	<i>Imperata cylindrica</i> <i>Afromomum latifolia</i>	Panicoideae Panicoideae	Youta Happi, 1998
Sénégal (Z. Guinéenne)				>1000	<i>Hypparenia</i>	Panicoideae	Wyk, 1979
Sénégal (Z. Soudanienne)				1000-500	<i>Andropogon</i> <i>Cenchrus</i> <i>Aristida</i>	Panicoideae Panicoideae Arundinoideae	Menaut, 1983 Wyk, 1979
Sénégal (Transition Soudano-Sahélienne)				600-400	<i>Cenchrus biflorus</i> <i>Shoenefeldia gracilis</i>	Panicoideae Chloridoideae	Le Houéroux, 1983
Sénégal (Z. Sahélienne)				500-200	<i>Aristida</i> <i>Aristida mutabilis</i> <i>Eragrostis tremula</i> <i>Aristida feniculata</i> <i>Shoenefeldia gracilis</i> <i>Cenchrus biflorus</i>	Arundinoideae Arundinoideae Chloridoideae Arundinoideae Chloridoideae Panicoideae	Wyk, 1979 Le Houéroux, 1983 Trochain, 1940
Sénégal (Z. Sahélienne)	16°20'99"N	15°24'40"W		282	<i>Aristida mutabilis</i> <i>Eragrostis tremula</i> <i>Leptothrium senegalense</i> <i>Tragus berteronianus</i>	Arundinoideae Chloridoideae Chloridoideae Chloridoideae	Grouzis et Akpo, 1997
Mauritanie (Z. Saharienne)				<200	<i>Aristida</i> <i>Panicum turgidum</i>	Arundinoideae Panicoideae	Le Houéroux, 1983
Tanzanie (Lac_Masoko)	9°20'	33°45'	780		<i>Imperata cylindrica</i> <i>Hyparrhenia sp.</i> <i>Panicum sp.</i> <i>Eragrostis congesta</i>	Panicoideae Panicoideae Panicoideae Chloridoideae	Bremond et al. en prep.(cf. _page 75)
Tanzanie (Mont_Rungwe)	9°	33°	1400-2200 1400-2200 1400-2200 2200-2600 >2500 >2500 >2500 >2500	1850-1550	<i>Pseudobromus sylvaticus</i> <i>Schizachirium brevifolium</i> <i>Arundinaria alpina</i> <i>Pennisetum</i> <i>Andropogoneae</i> <i>Brachypodium flexum</i> <i>Poa leptochloa</i> <i>Deschampsia flexuosa</i>	Pooideae Panicoideae Arundinoideae Panicoideae Panicoideae Pooideae Pooideae Pooideae	Mc Kone 1995 et Bremond et al. en prep.(cf. page 75)

Kenya (Mont_Kenya) Voir relevés botaniques exhaustifs des herbacées des sites du Mont Kenya (Wooler et al. 2001) page 82.

Annexe 3a. Liste des taxons graminéens dominants (espèces ou genres) relevés dans la littérature pour l'ensemble des régions étudiées. Les longitude, latitude et altitude ne sont pas fournies lorsque les auteurs ne décrivent pas une végétation locale mais régionale. La liste détaillée des échantillons relatifs à chaque région est présentée en annexe 1.

Espèces	Echantillon	CPL04	CPL06	CPL11	GLC08	GLC15	GLC20	GLE15	GLE21	GLW03	GLW04	HP02	HP05	TR12	GLE04	GLE05	GLC13	HP04	CM17	CPL01	CPL12	GLW07	HP08
Ame ova	dicot	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.3	3.0	0.0	0.3	0.3	0.2	0.0	0.0	0.3	1.6	10.3
Bux sem	dicot	2.4	19.7	4.5	0.0	0.0	0.0	0.0	0.0	0.4	4.4	2.6	2.0	2.0	0.0	0.0	11.3	7.1	2.2	8.0	9.3	1.6	10.3
Cer an sif	dicot	0.0	0.0	0.0	0.0	0.0	2.1	2.2	2.7	0.0	0.0	0.3	2.0	3.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	1.6	2.9
Cis alb	dicot	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.2	14.6	8.0	0.0	0.0	0.0
Cor ave	dicot	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.3	0.0	0.0	0.0	0.0	0.0	0.0
Cor min	dicot	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	10.4	1.9	0.0	0.0	2.0	0.0	0.0	2.7	0.2	2.9
Cor mon	dicot	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cra mon	dicot	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	1.6	0.0
Cyt ses	dicot	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fag syl	dicot	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phi lat	dicot	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.2	2.2	0.0	0.0	0.0	0.0
Pru spi	dicot	0.0	0.0	0.0	0.0	2.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.3	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Que coc	dicot	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.6	0.0	0.0	0.0	0.0
Que hum	dicot	0.0	0.0	0.5	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	12.6	16.4	43.7	0.2	0.0	0.0	2.7	0.2	0.0
Que ile	dicot	2.4	0.0	0.5	0.0	9.6	0.0	0.0	0.0	0.0	0.0	2.6	0.0	10.4	0.0	0.3	3.2	27.2	0.2	2.3	9.3	0.2	0.3
Rha ala	dicot	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0
Ros agr s.l.	dicot	0.0	0.0	0.0	0.0	2.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.3	3.2	0.0	0.0	0.0	0.0	0.0	0.0
Ros can s.l.	dicot	0.0	0.0	0.0	0.0	2.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	3.2	0.0	0.0	0.0	0.0	0.0	0.0
Ros off	dicot	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.9	0.0	0.0	0.0	0.0
Ros rub mic	dicot	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sor an	dicot	0.0	0.0	0.0	0.0	9.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	8.8	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Thy vul	dicot	8.4	0.0	15.8	8.8	0.0	0.0	7.9	2.7	4.5	0.0	2.6	7.2	3.0	0.0	1.9	0.3	3.2	0.0	7.9	14.9	10.7	19.1
Vib lan	dicot	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ace mon	Poaceae	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	3.2	0.2	0.0	0.2	0.0	1.6	0.3
Ace opa	Poaceae	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bra pho	Poaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bra pin	Poaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bra ret	Poaceae	8.4	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.3	10.4	0.0	0.0	0.0	7.1	7.9	14.9	0.0	0.0	2.9
Bro ere	Poaceae	15.5	0.0	4.5	16.4	2.8	28.7	30.3	36.8	29.1	15.4	16.8	0.0	3.0	12.6	8.8	0.0	2.0	0.0	2.3	2.7	10.7	0.0
Bro hor	Poaceae	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bro squ	Poaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bro site	Poaceae	0.0	0.0	0.0	0.0	9.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dac glo	Poaceae	2.4	5.6	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	2.2	2.3	0.0	0.0	0.0
Fes gr. OVI	Poaceae	8.4	19.7	15.8	8.8	0.0	7.4	7.9	9.5	4.5	15.4	16.8	7.2	10.4	12.6	8.8	0.0	7.1	2.2	0.0	0.0	5.7	10.3
Fes rub	Poaceae	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hor mur (s.l.)	Poaceae	0.0	0.0	0.0	0.0	17.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hor mur lep	Poaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Koe val	Poaceae	0.0	0.0	0.0	8.8	0.0	0.0	0.0	2.7	4.5	4.4	2.6	0.0	0.0	0.0	0.0	0.0	2.0	0.0	2.3	2.7	0.0	2.9
Mel cil cil	Poaceae	8.4	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	0.2	0.3	0.0	0.0	0.0	2.0	0.0	2.3	0.0	0.0	2.9
Phi pra ser	Poaceae	0.0	0.0	0.0	0.0	0.0	7.4	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Poa bul	Poaceae	2.4	0.0	0.0	2.5	0.0	7.4	2.2	0.0	0.0	0.0	2.6	0.0	3.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Poa nem	Poaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poa pra	Poaceae	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sti pen s.l.	Poaceae	0.2	5.6	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.2	3.0	0.0	0.0	0.0	2.0	0.0	2.3	2.7	0.0	2.9
Ced atl	Pinaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ced atl	Pinaceae	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jun com	Pinaceae	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.3	3.2	0.0	0.0	0.0	0.0	1.6	0.0
Pin hal	Pinaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pin nig	Pinaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pin syl	Pinaceae	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other		35.8	46.1	52.5	53.8	25.1	42.7	46.7	44.1	56.1	58.8	48.5	52.6	33.9	41.7	31.5	11.3	32.3	34.6	38.7	48.4	60.1	31.4

Annexe 3b. Relevés botaniques exhaustifs en % des espèces (excepté les espèces très rares, i.e. <1%) pour chaque assemblage phytolithique du Luberon (France), d'après Véla (2002).

Titre : Calibration des fonctions de transfert entre assemblages phytolithiques, structure des végétations et variables bioclimatiques actuelles, pour l'intégration de la dynamique des biomes herbacés dans les modèles de végétation.

Les formations herbacées actuellement dominantes en zone intertropicale sont mal discriminées par les marqueurs de végétation courants. Ainsi, la modélisation de la végétation et les reconstitutions des climats passés dans ces zones sont limitées. Les phytolithes sont des particules d'opale formées par précipitation de silice amorphe entre et/ou dans les cellules de nombreuses plantes vivantes, couramment utilisés pour tracer la dynamique des formations herbacées. Cependant, les calibrations entre assemblages phytolithiques, végétation et climat sont rares.

Cette thèse établit des fonctions de transfert entre indices phytolithiques, caractéristiques des formations herbacées intertropicales actuelles, et contraintes bio-climatiques, en vue de pouvoir intégrer les données phytolithiques à la méthode de biomisation pollinique permettant des reconstitutions de végétation. Ceci permettra d'améliorer et de valider certains modèles prédictifs de végétation.

En Afrique de l'Ouest, l'indice **I_{ph}** permet de différencier les savanes à graminées basses des savanes à graminées hautes. Une fonction de transfert, établie pour estimer l'évapotranspiration (AET/PET), offre de bons résultats, comparables et complémentaires aux estimations fournies par la biomisation pollinique.

L'indice **I_c** étudié sur un gradient altitudinal en Afrique de l'Est estime correctement la proportion des sous-familles graminéennes Pooideae et Panicoideae en zone intertropicale soit, potentiellement, la domination des Poaceae en C₄/C₃, jusqu'alors difficilement enregistrée.

Pour la première fois un marqueur de végétation, l'indice **D/P**, est calibré de façon quantitative en terme de LAI le long d'un transect forêt-savane.

Finalement, une analyse discriminante utilisant la totalité des assemblages permet de définir six biomes phytolithiques. Ces biomes intégrés à la méthode de biomisation pollinique, offriront des reconstructions paléo-environnementales plus précises, notamment les transitions désert/savane/forêt.

Mots clés : phytolithes, formations herbacées, Poaceae, zone intertropicale, biomes, pollens, modèle de végétation, paléoclimatologie.

Title : Calibration of transfer functions between modern phytolith assemblages, vegetation physiognomy, and climate parameters for integration of grassland dynamics in vegetation models.

Grassland biomes are currently dominating the inter-tropical zone, but main proxies used do not reflect properly their range. Therefore, modeling activities and paleo-reconstructions in these zones are not convincing. Phytoliths are amorphous silica that precipitate in and/or between living plant cells. They are commonly used to trace grass dynamics. However, calibration between phytolith assemblages, vegetation, and climate parameters are scarce.

This thesis introduces transfer functions between phytolith indices, modern inter-tropical grassland physiognomies, and bio-climatic constraining variables. In a near future, we would like to (1) integrate phytolith data in the biomization method that allows reconstructing vegetation biomes, (2) improve and validate some vegetation models.

In West Africa, the **I_{ph}** phytolith index allows discriminating tall from short grass savannas. A transfer function is proposed to estimate the evapotranspiration (AET/PET). Results are good, similar and complementary to the pollen biomization estimates.

The **I_c** index, studied on an altitudinal gradient in East Africa, permits to accurately estimate the proportion of Pooideae and Panicoideae grass sub-families, and so potentially the C₄/C₃ grass dominance.

For the first time, a vegetation marker, the **D/P** index, has been quantitatively calibrated as proxy of Leaf Area Index, along a forest-savanna transition.

Finally, a discriminant analysis using all the modern assemblages presents six phytolith biomes. These biomes, when integrated into the pollen biomization method, will improve the definition of vegetation transition such as desert/savanna/forest.

Key words : phytoliths, grasslands, Poaceae, inter-tropical zone, biomes, pollen, vegetation models, paleoclimatology.

Discipline : Géosciences

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